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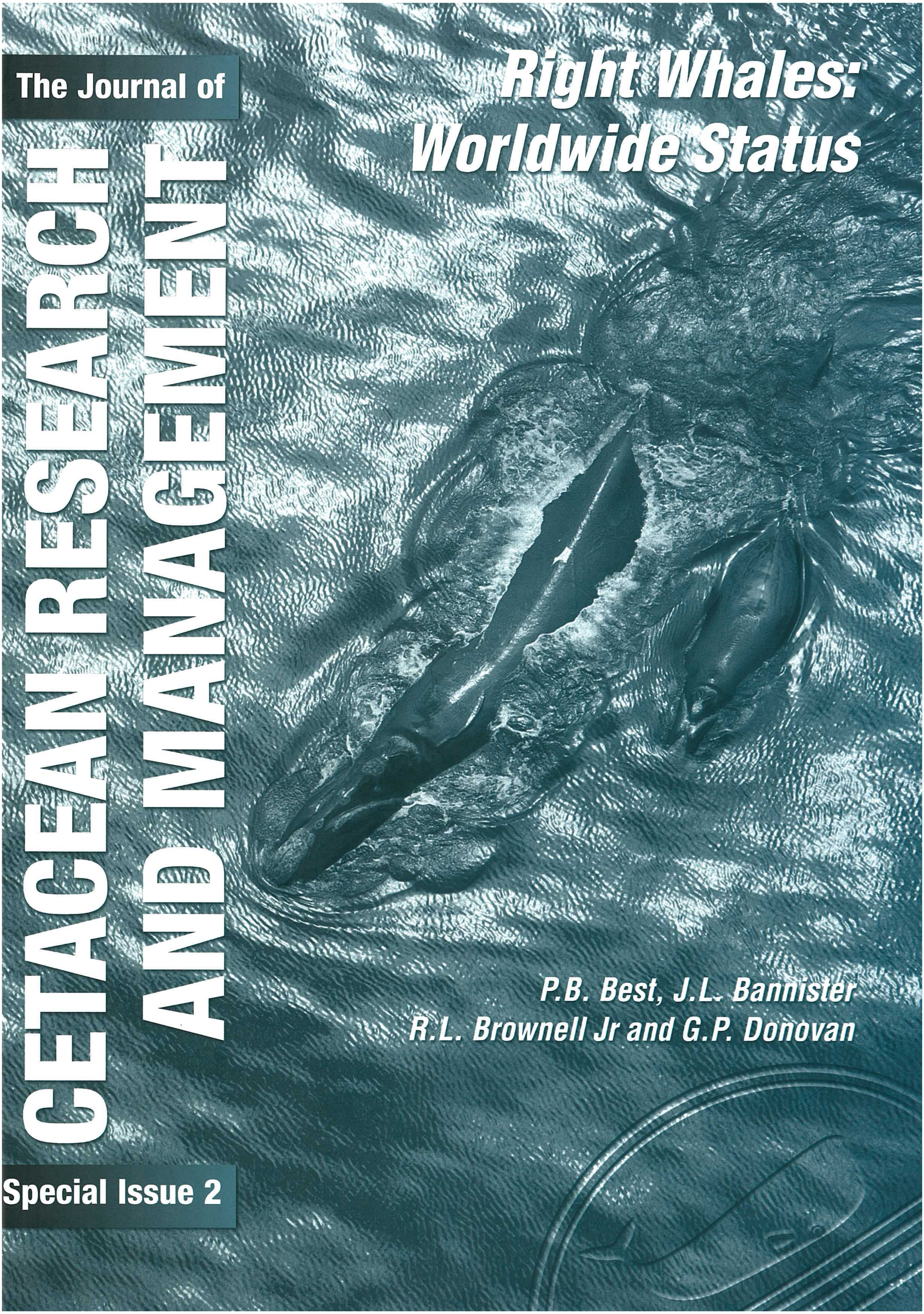
Right Whales: Worldwide Status

P.B. Best, J.L. Bannister
R.L. Brownell Jr and G.P. Donovan



Right Whales: Worldwide Status

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Editorial

Welcome to this, the second Special Issue of the *Journal of Cetacean Research and Management*. From time to time the *Journal* publishes special issues on particular topics (the first was on Chemical Pollutants and Cetaceans). Although these follow the same editorial standards and procedures, they often involve guest editors and will be hardbound. They are additional to the standard *Journal* subscription and charged for separately; they also have a different ISSN number (ISSN 1561-073X).

G. P. Donovan
Editor

Introduction

Right whales, genus *Eubalaena*, were once highly important commercially. They were the 'right' whales to catch because they were slow swimming, floated when dead and yielded great quantities of valuable oil and baleen. By the time 'modern' whaling began (*ca* 1865), right whales were rare in all oceans and they figure little in modern catches, apart from recently revealed illegal catches by the USSR (e.g. Tormosov *et al.*, 1998; Brownell *et al.*, 2001). Right whales (including bowheads, Greenland right and pygmy right) were the first whales to be protected internationally (in 1935) and their protected status has been continued by the International Whaling Commission since its founding in 1946 (Donovan, 1992). However, until recently there has been generally less interest in their status than in that of other, commercially more significant species, at least in the Commission's deliberations. Until 1982, when it adopted a moratorium on all commercial whaling (to take effect from the 1985/86 pelagic season), the Commission largely concerned itself with currently exploited species.

By 1981, two other species, humpbacks and blue whales, had been afforded official protection from commercial whaling throughout the world for 15 years (from 1966), whilst the gray whale had been protected from 1937. In 1981, the Commission (IWC, 1982) asked its Scientific Committee to assess the extent to which Commission actions in protecting species had led to their intended recovery (at that time, only two stocks, eastern North Pacific gray whales and South African right whales, had shown demonstrable recovery). The Scientific Committee decided that right whales were an appropriate choice for initial analysis for a number of reasons:

- data were available from several stocks worldwide;
- they are closely related to the bowhead (*Balaena mysticetus*) - a species depleted but subject to aboriginal whaling;
- the North Atlantic right whale was the first to be regularly caught commercially (by the Basques in the 12th century);
- although they were among the first to be protected internationally right whales were still among the rarest of large whales - they appeared to represent an extreme example of the inability of whale stocks to recover from excessive depletion.

That was the background to an international Symposium and Workshop held under the Commission's auspices in Boston, Massachusetts, in 1983 (IWC, 1986). Its major conclusion was that while there were signs of increase in at least two Southern Hemisphere populations (Argentina and South Africa), data were inadequate to demonstrate anything similar for Northern Hemisphere stocks. That was, however, a time of increasing research activity on a number of right whale stocks worldwide; high priority for the future was therefore given, *inter alia*, to ongoing and long-term photo-identification studies (then a relatively new research technique for right whales), and to systematic long-term standardised surveys.

By 1997, given considerable new information accrued in the 14 years since the Boston meeting, the Committee agreed it was time to undertake a Comprehensive Assessment of right whales worldwide (IWC, 1998). A striking aspect of the understanding of right whales then, as foreshadowed in Boston, was a recent documented increase in Southern Hemisphere stocks and a corresponding lack of any detectable increase in Northern Hemisphere stocks. Plans were drawn up for a Workshop to undertake the assessment. Two important aims, given the almost inevitably iterative nature of such work, were to identify gaps in knowledge and recommend ways they could be addressed. A major focus was to attempt to explain the contrast between Northern and Southern Hemisphere populations

The Workshop took place in Cape Town, South Africa, over six days, March 19-25, 1998. As before, it was preceded by a two-day public Symposium, at which 24 papers were presented on the results of recent work. Convened and organised locally by Best and colleagues from the Mammal Research Institute, University of Pretoria, and chaired by Bannister, the Workshop attracted 38 participants, from ten countries. Given the concerns over the situation in the western North Atlantic (e.g. Kraus, 1990), the United States was well-represented (16 participants). Local South African interest was also strong (ten participants). The organisers were specially pleased to welcome a Russian representative, in view of the recent disclosure of major illegal catches by Soviet fleets up to the early 1970s, including southern right whales (Yablokov, 1994). In addition to biologists working on a number of stocks, geneticists, mathematicians and modellers took part.

Data and analyses were presented from stocks as widely spread as the Auckland/Campbell Islands and the Okhotsk Sea, South Africa and the western North Atlantic, Australia and South America. Included on the agenda were systematics, stock identity, historical and modern catches, biological parameters, abundance and trends, worldwide comparison of population status, factors potentially affecting recovery and whalewatching. As far as possible, discussions dealt with individual stocks or regions; inevitably, as in the case of much historic catch data, that was not always possible.

The Workshop's many recommendations focussed on areas of special interest to the Commission, i.e. the trend and condition of stocks, and measures for their conservation. It confirmed recent increases in several Southern Hemisphere populations, despite the relatively large previously unreported Soviet catches, but not for the western North Atlantic. It emphasised the importance of maintaining research to investigate status and biological parameters, particularly from long-term photo-identification studies and surveys, and (equally important) of processing and analysing the resulting data. Most particularly, it expressed serious concern about the status of western North Atlantic right whales, strongly emphasising the need for research leading directly to a reduction in non-natural mortality such as ship strikes and entanglements in fishing gear. Serious concern was also expressed over the status of eastern North Pacific right whales because of the extremely small population and a lack of information on current human-related threats.

One gratifying consequence of the Workshop was that all its recommendations were endorsed by the full Scientific

Committee and the Commission (IWC, 1999). A further Workshop was held at Woods Hole, Massachusetts, over four days, 24-27 October 1999, specifically to address status and trends in the western North Atlantic stock. In its turn, that Workshop formulated a set of detailed recommendations, in line with those from Cape Town, and emphasised the absolute urgency of making every effort to reduce non-natural mortality to zero in that stock. Once again, the Commission endorsed all the recommendations (IWC, 2001); it is greatly to be hoped that management actions can now be taken, sufficiently and in time, to prevent what some models predict to be that stock's inevitable fate - a slow decline to extinction.

The question of the nomenclature of right whales was raised at the meeting in 1983 and most recently at the Scientific Committee's meeting in Adelaide in 2000 (IWC, 2001). This Introduction is not an appropriate place to discuss this issue in detail but merely to report that we have followed the accepted nomenclature agreed by the Scientific Committee. in this volume i.e. to retain the generic name *Eubalaena* for right whales and to recognise the three species *E. glacialis*, the North Atlantic right whale, *E. australis*, the southern right whale, and *E. japonica*, the North Pacific right whale. Interested readers are referred to IWC (2001), Rice (1998) and Rosenbaum *et al.* (2000).

This Special Issue of the Journal contains the Reports of the Cape Town and Boston Workshops, together with peer-reviewed papers, many of which originated as papers submitted to the Workshops. The papers are arranged by species and stocks, with a further category for techniques applicable generally. The Editors wish to thank the many scientists who undertook the time-consuming but essential task of reviewing the manuscripts. These included: J.L. Bannister, P.B. Best, P. Brodie, M.W. Brown, R.L. Brownell Jr, S.T. Buckland, S.R. Burnell, C. Carlson, H. Caswell, P. Clapham, J.G. Cooke, P. Corkeron, D. DeMaster, G.P. Donovan, N. Friday, A. Hall, P.K. Hamilton, P. Hammond, A.R. Hiby, E.E. Hofmann, L. Hutchings, T. Kasuya, S. Katona, G.P. Kirkwood, A. Knowlton, S.D. Kraus, J.L. Laake, O. Lindquist, M.K. Marx, C.A. Mayo, S. Mizroch, K. Ralls, P. Record, R.R. Reeves, S.B. Reilly, R. Richards, G.J.B. Ross, V. Rowntree, E.R. Secchi, C.T. Tynan, L.G. Underhill, B. Würsig and A. Zerbini.

The editors acknowledge the support provided to the Cape Town Workshop by its major sponsor, MTN Whale Route, by its organising personnel, and by the Commission's administrative and publications staff. Also acknowledged is the assistance of the US Government and the organisers of the Woods Hole Workshop, under its Convenor Dr Phillip Clapham. Between them they have dealt with the mundane, but vital, financial, logistical and editorial production tasks leading to the successful outcomes of both Workshops and the publication of this volume.

Finally, we would like to dedicate this volume to the memory of A.A. Berzin, W.H. Dawbin and J.H. Prescott.

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TECHNIQUES

Report of the Workshop on the Comprehensive Assessment of Right Whales: A Worldwide Comparison

The Workshop was held at the Monkey Valley Beach Resort near Cape Town, South Africa from 19-25 March 1998. It was preceded by a two-day Symposium at the Two Oceans Aquarium, Cape Town.

1. ARRANGEMENTS FOR THE MEETING

1.1 Practical details

Best welcomed the participants to the meeting and took the opportunity to thank MTN Cape Whale Route for their co-sponsorship which had enabled the IWC to increase the number of scientists attending. The list of participants is given as Annex A.

1.2 Terms of reference

At its 1982 annual meeting the Commission had agreed to a pause in commercial whaling (the 'moratorium') from 1986. The relevant amendment to the Schedule had included the clause, 'the Commission will undertake a comprehensive assessment of the effects of this decision on whale stocks and consider modification of this provision and the establishment of other catch limits' (IWC, 1999).

The term 'Comprehensive Assessment' had not been defined by the Commission but was eventually defined by the Scientific Committee as an in-depth evaluation of the status of all whale stocks in the light of management objectives and procedures that would include: (1) the examination of current stock size; (2) recent population trends; (3) carrying capacity; and (4) productivity (e.g. see summary in Donovan, 1992).

In 1997 (IWC, 1997b) the Scientific Committee had appointed an intersessional steering group to plan a Workshop to initiate a worldwide comparative assessment of right whales. It noted that right whales have not been considered in any detail by the Committee since its Workshop held in 1983 (IWC, 1986a), since which time considerable new information has accrued. A striking aspect of the present understanding of right whale populations is the recent increase in Southern Hemisphere stocks and a corresponding lack of any detectable increase in Northern Hemisphere stocks. The Committee had agreed that an attempt to explain this contrast should be a major focus of the Comprehensive Assessment of right whales.

Past experience with other species has shown that such an assessment is almost inevitably an iterative procedure. In that context the Workshop noted that an important aim of the meeting was to identify any gaps in knowledge at both the methodological and data collection level, and to recommend ways in which they could be addressed.

2. ELECTION OF CHAIRMAN

Bannister was elected Chairman.

3. APPOINTMENT OF RAPPORTEURS

Donovan was appointed rapporteur with assistance from Reeves and others. Working Groups appointed their own rapporteurs. Reports of Working Groups are given as Annexes or incorporated into this report under the relevant Agenda Items.

4. ADOPTION OF AGENDA

The adopted Agenda is given as Annex B.

5. REVIEW OF DOCUMENTS AND AVAILABLE MATERIAL

A list of documents is given as Annex C. In addition, several participants provided relevant material and databases from their own datasets.

6. SYSTEMATICS

At the 1983 Workshop (IWC, 1986a), there was considerable discussion over the taxonomy of right whales. Schevill (1986) reviewed the historical development of right whale nomenclature. The 1983 Workshop had agreed to retain the generic distinction between bowhead whales (*Balaena*) and right whales (*Eubalaena*). It had also recommended that morphological distinctions between *Eubalaena glacialis* and *Eubalaena australis* be further examined.

At present (i.e. at the time of this Workshop), the IWC recognises the following:

E. glacialis[1]- Northern right whale;
E. australis[2]- Southern right whale.

However, irrespective of their taxonomic status, North Atlantic and North Pacific right whales are treated separately for the purposes of management and conservation. The Workshop noted that Rice (1998) in his review of the systematics and distribution of marine mammals, considers the Balaenidae to comprise two species: *Balaena glacialis* – the black right whale; and *Balaena mysticetus* – the bowhead whale[3].

The Northern and Southern Hemispheres serve as the geographic units for the classification currently recognised by the IWC and, at present, right whales are the only group of large whales for which such taxonomic distinctions are made. The modern classification of *E. glacialis* and *E. australis* is based upon a single morphological character in the orbital region of the skull (the alisphenoid bone) analysed

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[1] *Balaena glacialis* Borowski 1781; *Balaena japonica* Lacépède 1818; or *Balaena sieboldii* Gray 1864.

[2] *Balaena australis* Desmoulins 1822.

[3] See Schaeff and Hamilton (1999) and Bannister *et al.* (1999). Both disagree with Rice's conclusion, preferring to retain *Eubalaena* and the two species *glacialis* and *australis* on the basis of recent usage, the result of the 1983 Workshop (IWC, 1986a) and this Workshop, genetic information and pending further investigation.

in limited specimens from each hemisphere (Muller, 1954). However, this character appears to be ontogenetic, as it is variable in developmental stages between Northern and Southern Hemisphere specimens (B. Rommel, J. Mead, pers. comm.).

No study to date has examined other sources of character information (morphological or molecular) to assess the validity of the earlier classification based on traditional morphology (Desmoulins, 1822; Muller, 1954). Moreover, representative taxon or population sampling throughout the two species' range has not occurred. Specifically, there has been little or no reproducible information on North Pacific *E. glacialis*, and previous genetic results from *E. australis* have generally been based on one or two populations or geographic regions (Schaeff *et al.*, 1991).

Historically, there has been conflicting taxonomic classification for North Pacific right whales. At various stages, the North Pacific right whale has either been classified as a sub-species of its North Atlantic counterpart (e.g. *E. glacialis sieboldii*) or elevated to full species status (*E. sieboldii* or *E. japonica*). Based primarily on morphometrics, the North Pacific right whale was considered closely related to North Atlantic *E. glacialis*, and both were considered taxonomically distinct from Southern Hemisphere right whales (Ivanova, 1961a; b).

To re-examine the systematics and classification of *Eubalaena*, SC/M98/RW23 examined mitochondrial DNA control region sequences from the three ocean basin forms of right whales (North Atlantic (NA) = 269; North Pacific (NP) = 8; Southern Oceans (SO) = 55). Population Aggregation Analysis (PAA) revealed that each of the three forms is characterised by a small number of diagnostic nucleotide positions (NA = 3; NP = 3; SO = 4). A phylogenetic analysis confirmed the grouping of mitochondrial lineages into three monophyletic clades concordant with the three forms. Furthermore, the phylogenetic analysis indicated that North Pacific right whales are more closely related to Southern Ocean right whales than they are to North Atlantic right whales, which appear ancestral in this phylogeny. The results are inconsistent with the current taxonomy and support an independent taxonomic status for each of the three. The conclusions should be tested further with additional samples from all three ocean areas. Further analysis should include the addition of South Pacific samples (*n* = 45, SC/M98/RW22) as well as historic and current samples from North Pacific animals.

The Workshop recognised that questions of nomenclature are subject to the International Code of Zoological Nomenclature (e.g. see comment in Schevill, 1986). From the perspective of assessing the status of right whales, the Workshop agreed that its discussions under stock identity would provide sufficient basis for progress, irrespective of taxonomic status. It noted that the IWC Scientific Committee only considers questions of changing taxonomic status on the basis of published papers. It **recommends** that the further analyses outlined above are undertaken and that the Scientific Committee revisits the question of the taxonomic status of right whales after the results are published.[4]

7. STOCK IDENTITY: DISTRIBUTION AND POPULATION SEPARATION

There has been considerable discussion in recent years within the IWC regarding the concept of 'stock identity' (e.g. see IWC, 1990a; Donovan, 1991). In summary, from a management perspective, what must be initially determined is the 'unit' that is to be conserved. Such a unit is generally termed a 'management stock' and in ideal circumstances would normally be based on a true biological population, although it may be based on smaller 'groupings' (e.g. feeding aggregations which show strong site fidelity). What comprises a useful management stock cannot be viewed in isolation from the purpose for which it is being defined (e.g. see discussions with respect to the development of the RMP and AWMP, as well as discussion under Item 10.3). The Workshop agreed that it was not appropriate at this meeting to undertake a detailed philosophical review of the 'stock' concept, which in IWC terms has been closely linked to the question of the regulation of whaling operations.

From the perspective of right whales it was agreed that there was value in attempting to:

(1) identify present and past breeding (i.e. mating) and calving grounds as the basic 'management unit' (where possible the identity of true biological populations); and
(2) identify associated feeding areas.

The power and applicability of genetic techniques to identify separate populations has increased dramatically since the previous Workshop (e.g. see IWC, 1991; Dizon *et al.*, 1997). Such information, combined with more 'traditional' approaches to examining stock identity within the IWC Scientific Committee, is discussed below.

The Workshop considered the available genetic information on population structure within each ocean basin according to three habitat classifications: calving grounds, summer feeding grounds and breeding grounds.

7.1 North Atlantic

At the 1983 Workshop (IWC, 1986a), three hypotheses concerning stock identity were considered (essentially an eastern, a central and a western stock). Little direct evidence had been available to support or refute these and that Workshop 'provisionally agreed to divide the North Atlantic, for statistical purposes, into eastern and western sectors and to treat the 60-62°N, 33-35°W area separately' (Fig. 1).

7.1.1 Seasonal distribution

7.1.1.1 WESTERN NORTH ATLANTIC

A combination of survey and some opportunistic data yields a partial description of the seasonal distribution of right whales in the western North Atlantic. A summary of relative abundance by month can be found in Annex D, table 1. SC/M98/RW2 revealed significant gaps in the data, with little survey effort in June, November and December. On average, the catalogue database can only account for about 25% of the total catalogue in any month other than August or September. Furthermore, there is considerable variability between years in areas such as the Great South Channel and the Roseway Basin, where in several years, no whales were observed despite some survey effort (SC/M98/RW30).

From December to March, right whale cows, their newborn calves and some juveniles, are found in the coastal waters of the southeastern USA (i.e. off Georgia/Florida, *ca*

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[4] Editor's note: After a thorough review at the 2000 meeting, the IWC Scientific Committee agreed to retain the generic name *Eubalaena* for right whales, and to recognise three species: *E. glacialis*, the North Atlantic right whale; *E. australis*, the southern right whale; and *E. japonica*, the North Pacific right whale. The Workshop Report published here has been modified to reflect these changes.

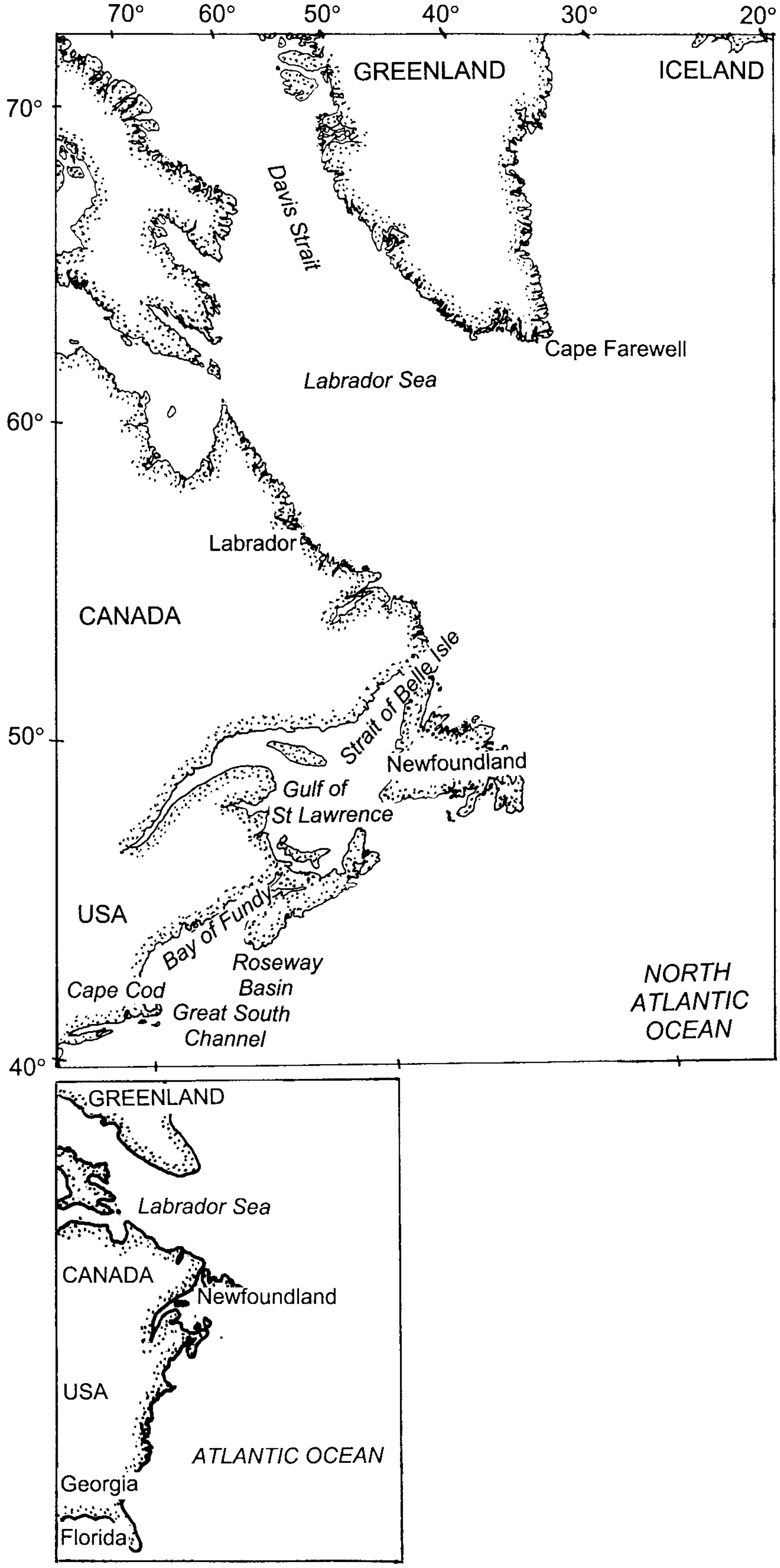

Fig. 1. Western North Atlantic.

27-32°N), the only known calving ground in the North Atlantic. Non-calving adult whales are rarely seen in the area. Calving apparently peaks in January.

In Cape Cod Bay (*ca* 42°N), right whales appear in low numbers in January, abundance peaks in March, April and May, and in most years tails off in June. Some cows with calves pass through the area in April and May. Other adults and juveniles are also represented in the area. In the Great South Channel (*ca* 42°N), right whales are observed from April-July, with a peak in abundance in May and June. Cow-calf pairs are rarely seen in the area, but all other classes are represented.

In the Bay of Fundy (*ca* 45°N), right whales are present from June-November, with a peak in abundance in August, September and early October. Approximately 60% of all known cows bring calves to the Bay of Fundy (SC/M98/RW41). In Roseway Basin (*ca* 42°N), whaling records show that right whales were formerly present from July to November (Reeves and Mitchell, 1986a), with a peak in abundance in August and September. Cow-calf pairs have only been seen here on five occasions during the past 18 years. Adult females are also present in low numbers, as this is predominantly an adult and juvenile male habitat. Since 1992, there has been a significant drop in abundance of right whales in the Roseway Basin area and a concurrent increase in the numbers of whales in the Bay of Fundy.

7.1.1.1.1 GULF OF ST LAWRENCE, GASPÉ, NEWFOUNDLAND

In recent years, a small number of animals have been seen in these areas, including three cows, one of which brought its calf to the Gaspé area in the summer (Lien *et al.*, 1989; Knowlton *et al.*, 1992; SC/M98/RW2).

7.1.1.1.2 GREENLAND/ICELAND/LABRADOR BASIN

There have been three records of right whales in this area in the last 11 years, including one cow-calf pair from the southeastern USA, one single adult previously seen in Roseway Basin and one unidentified whale.

7.1.1.1.3 MID-ATLANTIC MIGRATORY CORRIDOR

Scattered opportunistic sightings, satellite tagging tracks and historic catch records all support the view that the coastal waters of the USA between South Carolina (*ca* 32-34°N) and Rhode Island (*ca* 42°N) represent a springtime northward migratory corridor from the calving ground to the habitats in the Gulf of Maine (*ca* 43°N) (Knowlton, 1997; Slay and Kraus, 1997; SC/M98/RW4).

7.1.2 Movements of identified whales

Photographic re-identifications since the 1980s have supported the hypothesis that the right whales observed in all five of the well-defined habitats along the east coast of North America (i.e. southeast USA, Cape Cod, Great South Channel, Bay of Fundy and Roseway Basin) comprise a single stock. Supplementary satellite tagging work has confirmed the movements between the calving ground and northeastern summering grounds (Slay and Kraus, 1997). Opportunistic observations have led to non-cow photographic matches between: Newfoundland and the Great South Channel; the Labrador Basin and the Bay of Fundy; and the Gulf of St Lawrence and the Gulf of Maine. Schaeff *et al.* (1993) showed that female philopatry occurs in North Atlantic right whales, possibly resulting in summering feeding subgroups within the population. The fact that calving has only been confirmed in the southeastern USA, and cow-calf pairs observed there have been observed summering in the Bay of Fundy, the Gulf of St Lawrence, the Labrador Basin and near Greenland (Knowlton *et al.*, 1992; also supports the hypothesis that western North Atlantic animals probably comprise a single breeding stock. Apparent courtship activity is observed almost year-round but the location of the breeding (i.e. mating) grounds remains unknown.

7.1.3 Historic catches

No new information is available beyond that given at the 1983 Workshop (IWC, 1986a, pp.2-3) and summarised below.

A summer fishery existed in the Strait of Belle Isle (Newfoundland) region, but there are problems with distinguishing between bowheads and right whales in the records. The same applies to records from the Labrador coast, north to the mouth of Davis Strait, also a summer fishery. There was catching east of the Grand Bank and possibly in a mid-ocean area (Maury, 1853). Further summer fisheries occurred east of Cape Farewell (Greenland) centred at 60-62°N, 33-35°E, around Iceland, off North Cape (Norway) and off the British Isles.

The Bay of Biscay was an important winter ground, and catching occurred off the northwest African coast, centred on Cintra Bay (23°N, 16°15’E).

7.1.4 Genetic information

7.1.4.1 WESTERN NORTH ATLANTIC

7.1.4.1.1 CALVING GROUNDS (DECEMBER-MARCH)

It is clear that the primary calving grounds of the animals found in the western North Atlantic are off the southeast USA, (i.e. the Georgia/Florida coast, *ca* 27-32°N). In the absence of any evidence for other extant calving grounds in the North Atlantic, genetic analysis is unlikely to provide additional information for defining this habitat. However, Brown noted that nearly 33% of known reproductively active females remain unsampled genetically due to lack of effort on the calving grounds. This limits interpretation of apparent segregation of maternal lineages on the feeding grounds as discussed below.

7.1.4.1.2 SUMMER FEEDING GROUNDS (JULY-OCTOBER)

The frequency of mtDNA lineages (i.e. haplotypes) has been analysed for heterogeneity based on the pattern of sightings in the Bay of Fundy, the primary summer and autumn study area in the western North Atlantic (Schaeff *et al.*, 1993). For this analysis, females were classified into one of three groups according to their pattern of habitat use in their calving year: (1) always sighted in the Bay of Fundy - ‘Fundy-all’; (2) never sighted in the Bay of Fundy - ‘Fundy-none’; and (3) sometimes sighted in the Bay of Fundy - ‘Fundy-some’. Based on RFLP (Restriction Fragmental Length Polymorphisms) ($n = 96$; Schaeff *et al.*, 1993) and, more recently, control region sequence and Single Stranded Confirmation Polymorphism (SSCP) analyses ($n = 180$, including the 96 used for the RFLP; Malik *et al.*, 1999), significant differences in haplotype frequencies were found among these three groups of females. Thus, the presence of females with calves in known feeding habitats is non-random with respect to mtDNA haplotype. This suggests that certain females with their calves always return to the same feeding area.

7.1.4.1.3 BREEDING GROUNDS (MONTHS UNCERTAIN)

The location of breeding (mating) grounds is unknown. Given that only a single calving ground is known, it is likely that there is only one breeding stock in the western North Atlantic. However, the possibility that two breeding stocks use the single calving ground could be tested by looking for deviation from Hardy-Weinberg equilibrium (i.e. a Wahlund effect) among calves in the southeast US. Further evidence for stock habitat definitions could come from paternity (or parentage) analysis of individuals observed in sexually active groups.

7.1.4.2 EASTERN AND CENTRAL NORTH ATLANTIC

Rosenbaum *et al.* (2000) reported on three historic samples (from the late 19th and early 20th centuries) analysed from the central and eastern region: one from Iceland and two from Scotland. All three match the most common haplotype found in the western North Atlantic. Although this number of samples is too small for statistical interpretation of stock structure, it demonstrates the potential for using further historical samples for that purpose.

7.1.5 Synthesis

The Workshop agreed that only animals found in the western North Atlantic can be considered a functioning extant unit based on current sightings information. Thus, a practical management approach is to consider the animals in the western North Atlantic (largely off the eastern seaboard of the USA and Canada) as a single 'management unit' - the genetic information suggests that this probably corresponds to a 'true' biological population (e.g. see Donovan, 1991; IWC, 1994). The animals found in the eastern North Atlantic may be considered as a 'relict' population or populations.

7.1.6 Research recommendations

The Workshop **recommends** that:

(1) to reduce known bias from regional sampling of July-October feeding habitats and to complete the DNA archive of the western North Atlantic, directed genetic sampling should be undertaken, especially of females on the calving ground and any unsampled animals in Massachusetts Bay (January-May) and the Great South Channel (April-June);

(2) available information on mtDNA haplotypes of individual whales should be examined further to test for heterogeneity in regional resighting probabilities, scarring patterns and reproductive success; the latter could provide some information on differential habitat quality, if local habitat use is influenced by maternal fidelity;

(3) genetic sampling of the 'Fundy-none' females be undertaken - this is particularly important if differential reproductive success is demonstrated by 'Fundy-all' and 'Fundy-none females';

(4) further historical samples from the central and eastern North Atlantic, preferably from prior to the 19th century, should be obtained to test the hypothesis that more than one stock division existed within this ocean.

7.2 North Pacific

At the 1983 Workshop (IWC, 1986a), most discussions concerning stock identity had centred on the historical whaling records. It had been noted that the continuous distributions revealed by the Maury (1853) charts called into question the concept of traditional stock separation. Attention had been drawn to the surprising absence of evidence for coastal calving grounds. That Workshop had agreed to consider the right whales on the eastern and western sides as separate for statistical purposes, noting that the lack of biological evidence precluded conclusions concerning biological populations.

7.2.1 Distribution (see Annex D, table 2)

7.2.1.1 FEEDING GROUNDS

The Okhotsk Sea and the adjacent waters along the Kuril Islands and Kamchatka coast represent a major feeding ground for the species (Fig. 2; SC/M98/RW10, SC/M98/RW11). Historical concentrations of sightings in

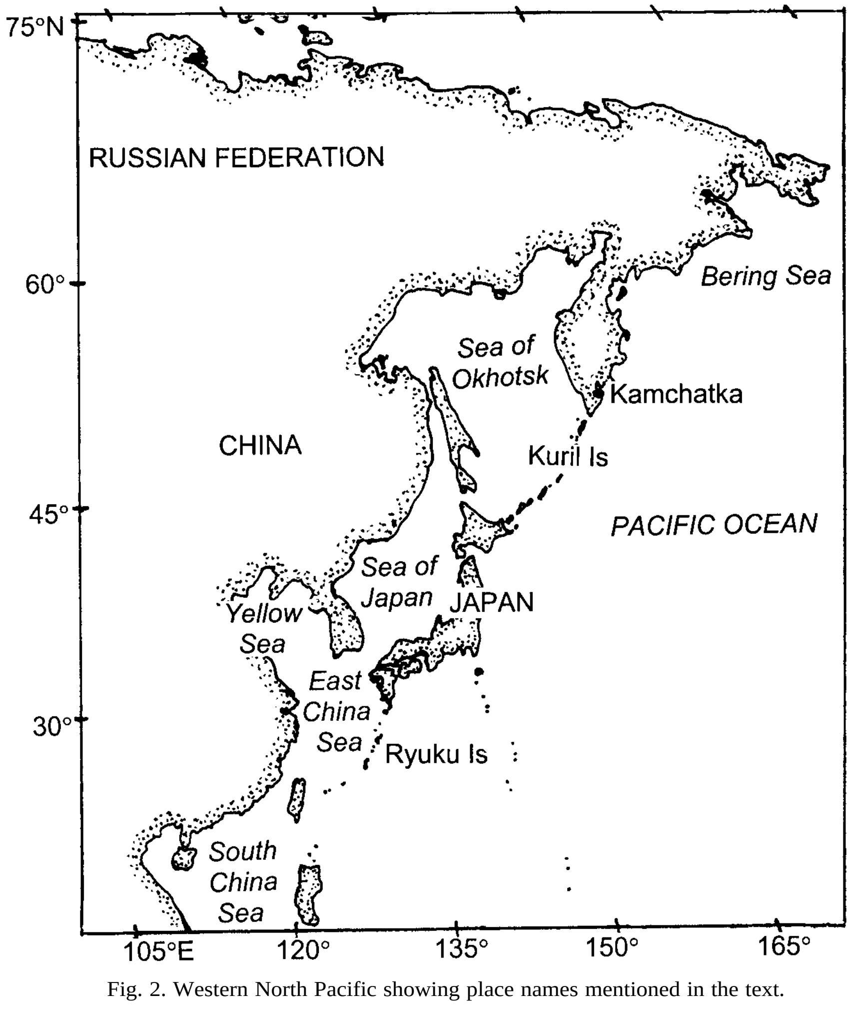

Fig. 2. Western North Pacific showing place names mentioned in the text.

the Bering Sea, together with some recent sightings, suggest that this region was an important summer habitat for eastern North Pacific right whales. Historical evidence also indicates major feeding grounds in the northern Gulf of Alaska (Muller, 1954).

7.2.1.2 BREEDING AND CALVING GROUNDS

In the western North Pacific, various areas have been proposed as breeding and calving grounds, including the Ryukyu Islands, the Yellow Sea, the Sea of Japan and offshore areas (Fig. 2). Overall, mid-winter sightings and seasonal movements in spring and autumn give various degrees of support to all of these suggestions, but the general paucity of winter records makes a definitive assessment impossible.

There is very little information on the winter distribution of right whales in the eastern North Pacific. There are two opinions on the locations of the breeding and calving grounds there: in mid-ocean waters far offshore, or in embayments. If the latter were true it is perhaps surprising that they have not been identified – it seems unlikely that they would have been overlooked on either side of the Pacific, unless perhaps in some remote part of southeastern Asia. One school of thought is that since the biological advantages of coastal calving are not clear, there is no reason to suppose that right whales cannot give birth and perhaps mate far from land. By contrast, it is possible to argue that since right whales in all other ocean areas appear to calve inshore, it would be surprising if those in the North Pacific did not also do so (IWC, 1986a).

7.2.2 Movements

In general, there appears to have been a northward movement to high latitudes in spring, and a similar southward trend in autumn. However, right whales were found across a broad latitudinal range during both seasons, suggesting a non-synchronous migration (Scarff, 1986).

7.2.3 Genetic information

Genetic analysis to date has included sequencing of the mtDNA control region of eight samples (SC/M98/RW43): six[5] collected by biopsy sampling from the southeastern Bering Sea; one historical sample from the Sea of Japan; and another historical one from California (both 19th century baleen). The six biopsy samples included two haplotypes and the two historical samples were each a unique haplotype. All four haplotypes were closely related. The distribution and number of samples collected to date are insufficient for an analysis of population structure.

7.2.3.1 FEEDING GROUNDS

Sampling of animals on feeding grounds has been limited to the southeastern Bering Sea. Since there is little evidence to support the hypothesis of a central stock, the animals found there provide the only likely source of samples from any putative ‘eastern’ stock.

7.2.3.2 CALVING AND BREEDING GROUNDS

There is no genetic information from such areas for any stock.

7.2.4 Synthesis

The question of whether two or more stocks of right whales exist in the North Pacific remains open. However, the Workshop agreed that only the animals found in the western area can be considered a functioning extant unit based on current sightings information (SC/M98/RW10 and RW11). The fact that right whales in the eastern and western North Pacific appear to have different catch and recovery histories supports the hypothesis that once there were at least two stocks, at least with regard to feeding ground divisions.

It has been proposed (Omura, 1986) that the right whales which summer in the Okhotsk Sea represent a discrete population that winters in the Sea of Japan and perhaps the East China Sea. Although it seems unlikely that animals found in such close proximity (notably in the Kuril Islands and Okhotsk Sea) would belong to separate stocks, insufficient data exist to confirm or deny the possibility.

7.2.5 Research recommendations

The Workshop **recommends** that additional analysis of historical samples available in Japan should be undertaken to characterise the western stock. However, there are few known historical samples from the eastern North Pacific and future comparisons are likely to be limited to samples from the Bering Sea. Further biopsy samples should be collected when possible in all regions. Analysis of nuclear DNA using current and historical samples from eastern and western regions could provide some evidence to test the possibility that more than one breeding stock exists or existed in the North Pacific.

7.3 South Atlantic and Indian Ocean coast of Africa

At the 1983 Workshop (IWC, 1986a), most of the discussion on stock identity had centred on the interpretation of historical distribution concentrations from whaling records, and whether these can be used to infer biological stocks. Little agreement on the latter was reached. That Workshop had agreed that the South African and Argentinian animals probably represented separate stocks but the other divisions it had used, such as dividing catches at 20°E (either side of Cape Agulhas), were largely for statistical purposes.

7.3.1 Distribution and seasonality (see Annex D, table 3)

7.3.1.1 CALVING GROUNDS

The following six winter calving grounds can be identified (Fig. 3), based principally on the distribution of current or historical sightings/catches:

(1) Brazil (8-32°S) – surface-active groups extending south to 32°S, and contemporary sightings at the Abrolhos Banks (*ca* 18°S);
(2) Argentina (42-43°S) – biggest concentration around Peninsula Valdes (42°S), but with stragglers occurring both to the north and south;
(3) Tristan da Cunha (mid-Atlantic, *ca* 38°S, 12°E) – possibly including Gough Island;
(4) Three regions of historical catches on the Namibian/Angolan coast (*ca* 16-27°S: southern Angola – Baia dos Tigres; Walvis Bay; Lüderitz) whose separation might simply reflect the logistic difficulties of operating in the areas between them;
(5) South Africa – the coast south of 32°S, between St Helena Bay on the west coast and Port Elizabeth on the east coast;
(6) Mozambique/Natal 20°S – the waters surrounding Maputo Bay (*ca* 26°S: historically known as Delagoa Bay), and including a possible migratory corridor on the Natal coast.

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[5] Until the relevant analysis has been completed, it is not possible to state that these represent six different animals.

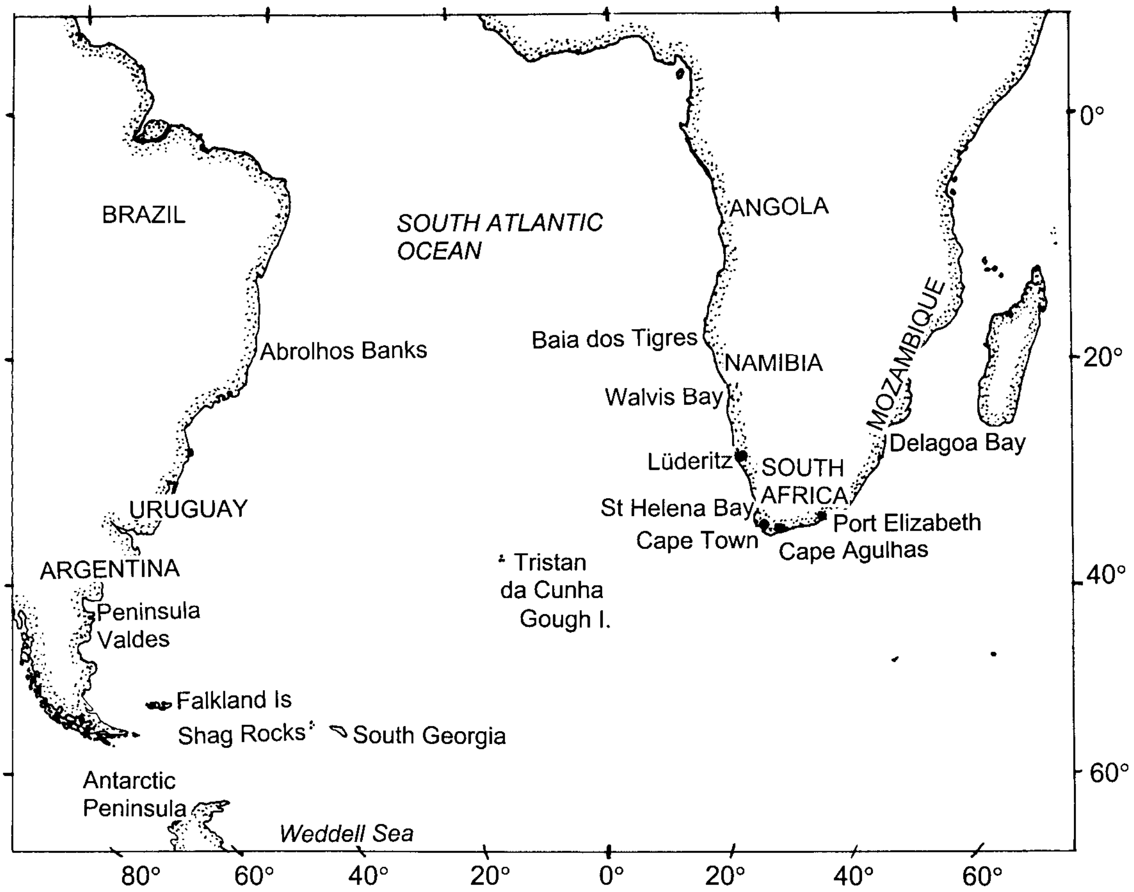

Fig. 3. South Atlantic and Indian Ocean coast of Africa.

7.3.1.2 FEEDING GROUNDS

The following seven summer feeding grounds can be identified (Fig. 3), mainly based on the distribution of catch positions of right whales in 19th century Yankee (Townsend, 1935) or 20th century Soviet whaling (Tormosov *et al.*, 1998):

(1) Brazil/False Banks/Falkland Islands – offshore from southern Brazil, Uruguay and Argentina, between 30° and 55°S, and west of 40°W: seasonality ranging from October-January in the north, to February-May in the south. Soviet catch seasonality was from November-December in the north and March in the south;

(2) South Georgia/Shag Rocks (*ca* 53°S) – an area mainly to the north of South Georgia in which catches were made by modern whalers in the early years of this century, and by Soviet whalers in the 1960s, and where there have been recent sightings (SC/M98/RW26);

(3) Pigeon–Tristan Ground – a concentration of 19th century catches surrounding Tristan da Cunha and extending to the east, from October-January (Soviet catches in the 1960s, mostly in November, indicate that at least the Tristan ground was then still inhabited);

(4) Cape–Tristan – a band of 19th century catches extending from Tristan da Cunha towards Cape Town (30-40°S) from October-January (some Soviet catches were taken in November-December in the 1960s);

(5) South of 50°S – a diffuse area of Soviet catches extending from 50°S to the ice edge and from 10°W to 30°E, seasonality peaked in March but extended from December-April (Townsend, 1935), data showed catches from February-May;

(6) Antarctic Peninsula (*ca* 65°S, 60-70°W) – an area of recent sightings through opportunistic and directed efforts.

In delineating these grounds, the Workshop noted the following caveats:

(a) the catch distributions in time and space may be affected by logistic considerations of the whaling fleets; only for South Georgia were there opportunistic observations for periods outside the southern summer;

(b) the Townsend (1935) plots may exaggerate the size of these grounds because of the author's desire not to overlay positions in areas of dense catching so that *inter alia* the colour coding for each month's catches could be discerned;

(c) the Townsend (1935) data as published are known to contain some errors of position, species identification and number of days on which whales were caught.

7.3.2 Movements

Movements of right whales between calving grounds, or between calving and feeding grounds in the South Atlantic, are known for nine photographically identified individuals (Best *et al.*, 1993, fig. 1; SC/M98/RW26), and Best and Findlay (pers. comm.). These indicate between-year movements from Argentina to Brazil (3 adult females), from Argentina to Tristan da Cunha (1 adult male), from Argentina to South Georgia (1 adult female, 2 adults of unknown sex), from Gough Island to South Africa (1 adult female), and from South Africa to 'south of 50°S' and back (1 adult female).

A comparison of average stable isotopes from seven baleen plates from Argentina with seven plates from South Africa indicated that three of the Argentinian whales had higher nitrogen and carbon values than any of the South African whales (Best and Schell, 1996; SC/M98/RW13). This indicated that they had probably fed in a different region (or at a different trophic level) from whales from South Africa. The other four whales had similar isotope ratios to the seven South African whales and so might have been feeding in the same area (or at the same trophic level in another area) as the South African whales.

7.3.3 Morphology

Comparisons of the incidence of various callosity patterns and dorsal pigmentation types have revealed statistical differences between calving grounds in Argentina and South Africa (Payne *et al.*, 1983; Best, 1990). So far, no such comparisons have been made between right whales off Brazil with those in Argentina or South Africa, although suitable photographs do exist.

Depigmented lesions caused by gull attacks, which persist for up to four years, have so far only been seen in right whales from Argentina, where they are now found on up to one third of the population (Rowntree *et al.*, 1998). No such lesions have been seen on 63 whales examined in Brazilian waters, or in 484 adult females examined in South African waters (Palazzo, Flores, Best, pers. comm.). As such, they might be considered a potential indicator of stock identity.

7.3.4 Parasites

The barnacle *Tubicinella* is universally present in the callosities of right whales over 12 months of age in South African waters (Best, pers. comm.), but has not been recognised on right whales from Argentina (Rowntree, pers. comm.). The presence of barnacles in the callosities of a right whale from South Georgia (Matthews, 1938) might therefore indicate that the animal came from a population other than that wintering off Argentina. Cyamids have not been identified to species in all areas of the South Atlantic. There are apparently higher infestation rates of the orange species *Cyamus erraticus* (which is found on the body surface away from the callosities) in Antarctic waters, than in either Argentina or South Africa (Roussel de Vauzeme, 1834).

7.3.5 Genetic information

7.3.5.1 CALVING GROUNDS

Samples were available for genetic analysis from biopsy samples of whales off South Africa (34°S; $n = 21$) and from stranded or beachcast calves in Peninsula Valdes, Argentina (42°S; $n = 20$). The analysis of mtDNA variation reported in SC/M98/RW23, based on sequencing of the control region, showed significant differentiation between the two calving grounds at both the haplotype and nucleotide level. Estimates of long-term maternal gene flow (2-5 females per generation) were low by demographic standards, often used for management purposes (Donovan, 1991). These results support the historical assumption of stock divisions between these two calving grounds.

7.3.5.2 FEEDING GROUNDS

A sample of eight whales from South Georgia was compared with those from the two calving grounds (SC/M98/RW23). The sample size was considered too small for a statistical test of heterogeneity but included two haplotypes common to both calving grounds, two shared only with Argentina, two shared only with South Africa and two not found on either calving ground. This is consistent with, but not strong evidence for, some mixing of the two stocks during the feeding season.

7.3.5.3 BREEDING GROUNDS

Specific breeding grounds are not known but mating is commonly observed on both calving grounds (SC/M98/RW21). Analysis of nuclear DNA markers (microsatellites) is currently underway (Schaeff, 2001) and will allow a test of the hypothesis of reproductive isolation (i.e. male and female gene flow) between calving grounds.

7.3.6 Synthesis

There are (or were) up to six different calving grounds in the South Atlantic. Currently, three of these are recognised as being substantially populated: Brazil, Argentina and South Africa (see Item 10). In light of the genetic and morphological (and possibly parasite) data, the Workshop agreed that the calving grounds off Argentina and South Africa should be considered as separate management units. Although the gull damage data are indicative of a degree of separation between Argentina and Brazil, the three incidences of photo-identified whales moving from Argentina to Brazil suggest that this separation is not absolute. No comparison of any kind has yet been made between whales from Brazil and South Africa. Photo-identification links have been established between only two of the five suggested feeding grounds and breeding/calving grounds further north, i.e. between South Georgia/Shag Rocks and Argentina, and between ‘south of 50°S’ and South Africa.

7.4 Australia/New Zealand and Indian Ocean excluding East Africa (SC/M98/RW22)

At the 1983 Workshop (IWC, 1986a), Dawbin had considered that two populations existed in the New Zealand area: a New Zealand-Kermadecs population and a Campbell and Auckland islands population (see Fig. 4), largely based on the different catch histories. Although it had been agreed that there was no discontinuity in the catch records, the 1983 Workshop had divided eastern and western Australian catches (at 135°W) for statistical purposes.

7.4.1 Seasonal distribution (see Annex D, table 4)

7.4.1.1 AUSTRALIA - SOUTHWEST

Animals are present from April-November. Cows with calves first appear in June, and are most abundant in August-September, with numbers tailing off into November. There are no records of cows with calves in December. ‘Unaccompanied’ animals (i.e. not cows and their accompanying calves) – either single or in surface active groups – are also present from April-November, but they peak earlier, with high abundance in July and August (Bannister, 1990).

7.4.1.2 AUSTRALIA - SOUTH CENTRAL

Seasonal abundance of cow-calf pairs and ‘unaccompanied’ animals is as for the southwestern region, above. Information is available for individual categories within the latter group: juveniles peak in July/August; adult males and non-calving females in July, tailing off through August/September (Burnell and Bryden, 1997).

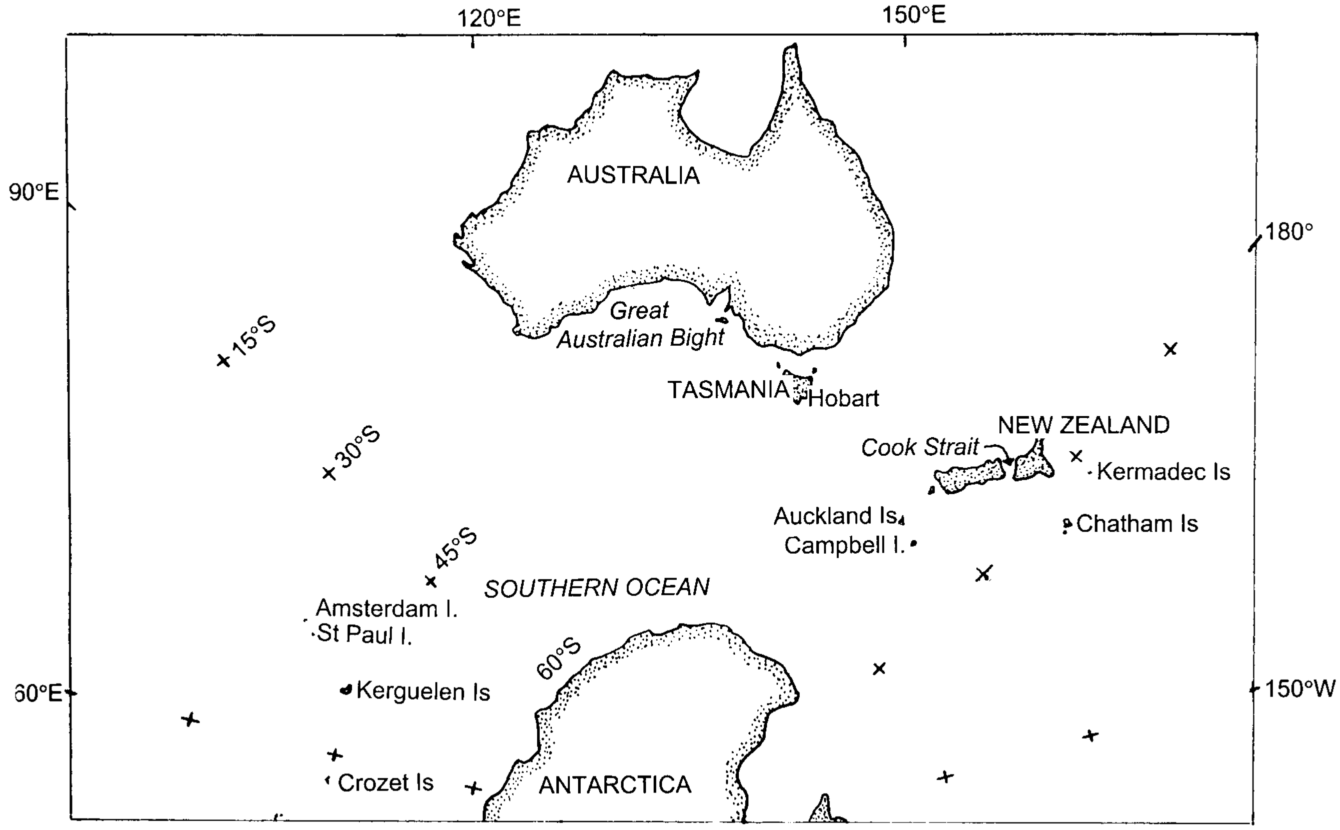

Fig. 4. Australia/New Zealand and Indian Ocean excluding East Africa.

7.4.1.3 AUSTRALIA - SOUTHEAST

Cow-calf pairs have been seen mainly in June-November (but there is one record for January) with a peak in August, but ‘unaccompanied’ animals are present from March to September, peaking in July (Burnell, 1997).

7.4.1.4 SOUTHERN OCEAN (90 - 150°E) EXCLUDING ANTARCTIC

A large concentration of 75 ‘unaccompanied’ animals was seen at 41-44°S in January (Ohsumi and Kasamatsu, 1986) and another 35 animals in the same area – including two cow-calf pairs – in December (Bannister *et al.*, 1997). Marking information exists for two animals around 46°S in summer (November-March). A total of 78 animals was taken south of Tasmania in Soviet operations in March-April (Tormosov *et al.*, 1998).

7.4.1.5 ANTARCTIC (90 - 150°E)

Two ‘unaccompanied’ animals were seen at *ca* 64°S (SC/M98/RW18) in February and a further 23 were taken in Soviet operations between 61° and 65°S from January-March, but mainly in the latter month (Tormosov *et al.*, 1998).

7.4.1.6 MAINLAND NEW ZEALAND (NORTH AND SOUTH ISLANDS)

Current information on the seasonal distribution of southern right whales around the main islands of New Zealand is based exclusively on opportunistic sightings. The movements of right whales facilitate their observation near the coastline, but even so, the reported number of sightings off the mainland is very low - rarely more than two or three reported sightings of individuals or cow-calf pairs per annum (SC/M98/RW20).

Most reports are from the Cook Strait area or from the northeast coast of the North Island, mainly between July and October. The number of whales frequenting the coastline of the North and South Islands is probably fewer than ten each year.

7.4.1.7 SUB-ANTARCTIC ISLANDS (CAMPBELL AND AUCKLAND ISLANDS)

Based on Townsend’s (1935) charts, whales were found near the sub-Antarctic islands in December, March, April, May and June.

Since systematic research work began in 1995, survey effort in the sub-Antarctic has been concentrated in the winter months (June-August). Opportunistic surveys were also conducted in winter 1983 (Campbell Island, June-September) and in spring 1996 (Auckland Islands, September).

Right whales are thought to appear there in May, with a peak in abundance reported in late July/early August. During winter months, all segments of the population are represented on these calving grounds, including cow-calf pairs and surface active groups (SC/M98/RW20; SC/M98/RW33). There have been opportunistic sightings of right whales in small numbers in the Auckland Islands during the summer months. Soviet whaling records reveal large numbers of whales caught in the vicinity of the Auckland Islands during autumn months (March-April; Tormosov *et al.*, 1998). These included males, females and some lactating females.

7.4.2 Movements of identified whales

7.4.2.1 SOUTHERN AUSTRALIA

Historical evidence (Townsend’s 1935 charts) and anecdotes suggest movement from the south towards Tasmania early in the season, i.e. April, followed by westwards movement across the Australian Bight. The bulk of whales were thought to move south from Western Australia in late spring/early summer (October-December) with some evidence of an eastward trend around 40°S. Recent photo-identification records indicate a link between probable feeding grounds at *ca* 42°S and 64°S and calving grounds on the southern Australian coast (summarised in SC/M98/RW18). Records of easterly movement from two recovered marks (Tormosov *et al.*, 1998) are not inconsistent with earlier views but the Antarctic records represent a considerable extension southwards in distribution, by comparison at least with Townsend's (1935) data which showed no catches taken south of 50°S. An additional 108 movements greater than 200km were made by individually identified whales between areas on the southern Australian coast. The large number of movements detected between the three continental Australian regions suggests that the animals found in these areas comprise a single stock. The directions of movement within- and between-years and to offshore locations suggest a generalised westerly movement of whales along the southern Australian coast and an easterly trend on the feeding grounds in summer months (SC/M98/RW18; SC/M98/RW19).

7.4.2.2 NEW ZEALAND SUB-ANTARCTIC ISLANDS

Photographic comparison shows within- and between-year movements of whales between the two New Zealand sub-Antarctic concentrations, at Campbell Island and the Auckland Islands (SC/M98/RW34). There is insufficient information to conclude if there is age- or sex-class sub-division between the two areas. Although the high latitude of the Auckland Islands is more consistent with known right whale feeding grounds in other parts of the world, it appears that this sub-Antarctic region is currently the primary wintering habitat for southern right whales in New Zealand waters.

7.4.3 Historical data

Information is available from coastal and pelagic whaling records; the latter is from American whale ship logbooks per Townsend's (1935) charts and subject to the usual sailing vessel logistic limitations from the effects of wind, weather and currents.

7.4.3.1 AUSTRALIA - SOUTH WEST

Little seasonal information is readily available on local bay whaling operations, but pelagic bay whaling operated from June-October - mainly July-September (Bannister, 1986b) and pelagic offshore whaling from 'late spring to summer' with a peak in November-December. Offshore operations show a latitudinal shift southwards by month, from *ca* 35°S in September to *ca* 45°S in December (SC/M98/RW18).

7.4.3.2 AUSTRALIA - SOUTH CENTRAL

A pelagic bay whaling record (Bannister, 1986a) details a total catch of 33 animals over 79 days in June-August. Offshore records show catching at *ca* 45-50°S in February-March.

7.4.3.3 AUSTRALIA - SOUTH EAST

Dawbin (1986) details substantial catches in the area, particularly in the 1830s-40s, but without seasonal information. Right whales were apparently seen in numbers in the Derwent River, Hobart, Tasmania, between May and November (Dakin, 1963). Pelagic catches show a seasonal distribution off the Australian east coast similar to that off the west coast (SC/M98/RW18), i.e. from *ca* 30°S in September to *ca* 45°S in December. There are records of catch positions yet further south, in February, at *ca* 50°S, in the central Tasman Sea, but it is not clear whether they are referable to animals from the Australian or New Zealand sub-Antarctic (SC/M98/RW18 and Item 7.4.1.7).

Information on the Southern Ocean is included in the above. There is no information on historical catches, if any, south of 50°S (SC/M98/RW18).

7.4.3.4 INDIAN OCEAN (EXCLUDING THE AFRICAN COAST)

On Townsend's (1935) charts, two major catching areas are represented between 40°S and 50°S, the 'Desolation' Ground (Kerguelen Island) at *ca* 70°E, and the 'Crozettes' Ground (Crozet Island) at *ca* 50°E. To the north of the former, including and to the east of St Paul/Amsterdam Island, is an extended area of catching at *ca* 60-80°E, 30-40°S. Catching was recorded at the Crozettes Ground in December-May, with most apparently in February-March. North of the Desolation Ground, most catching was in October-November, but with some, around St Paul Island, in September.

7.4.3.5 MAINLAND NEW ZEALAND (NORTH AND SOUTH ISLANDS) AND KERMADEC ISLANDS

Based on Townsend's (1935) charts, whales appeared to exhibit a general northward migration along the South Island from January-March, that peaked in Cook Strait from May-September then went further northeast to the Kermadec Islands from August-November. The Workshop noted, however, that there may be some doubt over the identity of the Kermadec Islands catches (SC/M98/RW37). Whales were found further south near the Chatham Islands in January and September and off the Chatham Rise in December-January.

7.4.3.6 NEW ZEALAND SUB-ANTARCTIC ISLANDS

Historically, right whales were widely distributed within New Zealand waters. Based on Townsend's (1935) charts, wintering grounds were found mainly east of the Kermadec Islands (but see 7.4.3.5 above), off the Chatham Islands, in Cook Strait and to a lesser extent near the Auckland Islands. Current wintering grounds are limited to the Auckland Islands and Campbell Island.

7.4.4 Genetic information

7.4.4.1 CALVING GROUNDS

Samples were available for genetic analysis from biopsy samples of whales off southwestern Australia (34°S; $n = 20$) and near the Auckland Islands (51°S; $n = 20$) (SC/M98/RW23). As in the South Atlantic, the analysis of mtDNA variation, based on sequencing of the control region, showed significant differentiation between the two calving grounds at both the haplotype and nucleotide level (SC/M98/RW23). Estimates of long-term maternal gene flow (3-5 females per generation) were low by demographic standards. There was no evidence of a strong sex-bias in the haplotype frequencies. These results support the historical assumption of stock separation between these two calving grounds.

7.4.4.2 FEEDING GROUNDS

A sample of five whales from feeding grounds south of Australia (41-44°S) was compared to those from the two calving grounds (SC/M98/RW23). The sample size was too small for a statistical test of heterogeneity but included haplotypes common to both calving grounds. This is consistent with, but not strong evidence for, some mixing of the two stocks during the feeding season.

7.4.4.3 BREEDING GROUNDS

As for the South Atlantic, specific breeding grounds are not known but mating is commonly observed on both calving grounds. Analysis of nuclear DNA markers (nuclear introns and microsatellites) is planned and will allow a test of the hypothesis of reproductive isolation between calving grounds.

7.4.5 Synthesis

The Workshop agreed that the animals found on the Australian coast in winter should be considered as a single management unit and that this probably comprises a true biological population. The offshore sightings and catches as far as 65°S indicate more extensive movements into colder waters than previously believed.

The animals found around the Auckland Islands and to a lesser extent Campbell Island represent the great majority of animals in New Zealand waters. The Workshop **recommends** that the management unit for southern right whales in this region previously described as the Campbell Island population (IWC, 1986a) be referred to as the New Zealand sub-Antarctic population. This is separate from what can be termed the New Zealand-Kermadec management unit and the Australian unit.

Based on Townsend's (1935) charts, major areas of catching in the central Indian Ocean around and to the east of St Paul/Amsterdam Island in September, October and November, and around Kerguelen ('Desolation Ground') in January-May, could indicate a separate Central Indian Ocean management unit. An even more extensive fishery near the Crozet Islands ('Crozettes Ground'), in December-May, could indicate another management unit further east, possibly linked to a small area to its northwest, where catching occurred in September-November. Little information exists on the present occurrence of right whales in those areas (Ohsumi and Kasamatsu, 1986).

7.4.6 Recommendations

Additional genetic samples are needed from existing or suspected feeding and calving areas to improve characterisation of population structure in the Australia/New Zealand region and the central Indian Ocean (see Table 1). In particular, the Workshop recognised that the Auckland Islands and Campbell Island represent the only known current calving grounds in the New Zealand area. It **recommends** that the current research programmes continue and that the relationship between animals found at the Auckland Islands and Campbell Island be further investigated (e.g. by collecting biopsy samples at the latter).

7.5 Southern Hemisphere stocks - general

The Workshop recognised that there are many regions of the Southern Hemisphere from which information is currently unavailable but which are known, from historical records, to have once been occupied by right whales. It was agreed that genetic information would be of considerable value in determining stock separation and migratory interchange among these regions.

Additional genetic sampling is needed to characterise the relationships of whales in regions throughout the Southern Hemisphere, particularly the calving grounds. Samples from feeding grounds are required for more reliable allocation of historical catches to calving grounds (see Item 10). In addition to longitudinal divisions, right whale calving grounds along some continental coasts are distributed over latitudes from approximately 15°S to 50°S. It is important to analyse latitudinal as well as longitudinal components of population structure. To this end, the Workshop **recommends** that the Scientific Committee requests that, where possible, collection of biopsy samples is undertaken from vessels involved in suitable programmes such as: CCAMLR, SO-GLOBEC and BAS krill surveys. It noted that such work is already given priority on IWC SOWER cruises. When possible, biopsy samples should be preserved for multi-disciplinary studies. For molecular genetic analysis, this can be in a salt/DMSO solution or 70% ethanol (Dizon *et al.*, 1997). For *in situ* molecular assays reflecting hormonal and pollutant states (e.g. SC/M98/RW24), a thin, midline section of skin and blubber should be fixed in 10% buffered formalin. Tissues wrapped in solvent-rinsed metal foil and stored at –70°C are also suitable for most purposes.

Table 1

Calving or feeding areas of right whales in the Southern Hemisphere where, based on current abundance, it is considered possible to collect biopsy samples from a minimum of 20 individuals (counting cow/calf pairs as a single individual for purposes of mtDNA analysis).

Region	Samples available?	More needed?	Comment
Calving*			
Argentina	Yes	Yes	
Tierra del Fuego	?	?	
Brazil	?	Yes	Latitudinal component with Argentina
Tristan de Cunha	No	Yes	
South Africa	Yes	?	
Western and South Australia (three areas)	Yes	Yes	
East Australia/Tasmania	No	Yes	
Auckland/Campbell Island	Yes (Auckland)	Yes (Campbell)	
Chile/Peru	?	Yes	
Feeding			
South Georgia	Yes	Yes	
Antarctic Peninsula	Yes	Yes	
>40°S off Australia	Yes	Yes	

*Note that in calving areas sampling should be repeated in at least each of three consecutive years.

The Workshop also noted that stable isotope analysis of baleen plates might provide evidence of the use of differing feeding grounds by right whales from different calving grounds (see SC/M98/RW13) and **recommends** that where possible, such studies be carried out.

7.5.1 Geographic sampling

Following the recommendations for sample sizes for initial descriptions of stock divisions using mtDNA (IWC, 1991), the Workshop **recommends** that priority be given to areas where it should be possible to collect samples from a minimum of 20-50 individuals (Table 1). In calving areas, this sampling should be repeated in at least each of three consecutive years, assuming three calving female cohorts (i.e. 60-150 individuals per area).

However, the Workshop **stressed** that the minimum recommended sample size of 20 individuals per sub-population is sufficient only for an initial description of population structure when the effect size (i.e. genetic isolation) between sub-populations is large. For detecting dispersal rates of interest for demographic management purposes, simulation studies have shown that sample sizes of 80 individuals per sub-population (excluding duplicate samples) are needed to provide unbiased estimates of relevant genetic parameters. This total sample could be accumulated over years and could be chosen to represent the habitat range of the putative population unit of interest. Such sample sizes are also sufficient for multi-disciplinary studies recommended elsewhere in this report (and see SC/M98/RW24).

The Workshop also **recommends** the timely analysis of both extant and future samples, including the large sample (660) from South Africa, which could provide valuable information on breeding habitats, degree of polygyny (estimation of effective population size), female use of calving areas (influence of female-directed philopatry) and estimates of genetic variability and male- and female-directed gene flow. This is not only important for an understanding of South African right whales but also for comparison with the North Atlantic population.

Additional historic specimens from some areas of the Southern Hemisphere (as well as the eastern North Atlantic and North Pacific - see above) could be used to test putative population designations where current abundance is so low that obtaining representative biopsy samples is not practical. In certain situations, such as specimens obtained from bone huts in Namibia, historic material may provide sample sizes (i.e. 20-50) adequate for an initial examination of population structure.

7.6 General recommendations

7.6.1 Population structure

The Workshop **recommends** that an analysis of callosity patterns and dorsal pigmentation types (c.f. Payne *et al.*, 1983; Best, 1990; Schaeff *et al.*, 1999) be carried out comparing the various Southern Hemisphere populations. It also **recommends** that special attention be paid to the question of whether barnacles are present in the callosities of animals in any other populations beside South Africa.

It **reaffirms** that additional genetic samples are needed from other known or suspected feeding and calving areas to improve understanding of population structure/division in the Southern Hemisphere (see 7.4.1 above and Table 1).

7.6.2 Choice of genetic markers and molecular methods

The Workshop noted that the choice of the 5' end of the mtDNA control region has become a standard for studies of population variation and structure for most marine mammals (Dizon *et al.*, 1997). To date, studies of right and other whales have focused on the first 300 base-pairs of the control region (SC/M98/RW21 and SC/M98/RW22). The Workshop **recommends** that this level of resolution should be considered the minimum for future comparable studies. Direct sequencing of samples, although expensive, provides the greatest flexibility for data exchange and comparison.

For studies of nuclear variation, the Workshop **recommends** that microsatellites be considered the markers of choice for individual identification (i.e. DNA profiling), paternity or parentage analysis and estimation of kinship. For analysis of population structure, there is some concern over the problem of distinguishing between identity in size and identity in descent (i.e. homology of alleles). This could positively bias estimation of gene flow (Rosenbaum and Deinard, 1998). Nuclear intron alleles (i.e. non-coding sequences), although less variable than microsatellites, are more likely to be homologous and may prove more useful for systematic studies as well as for some population analyses (Palumbi and Baker, 1994).

7.6.3 Data analysis and reporting

For mtDNA sequences, the Workshop **recommends** that nucleotide and haplotype diversity and their standard errors (with specified equations) be estimated and reported. For these to be meaningful, they must be based on comparable lengths of homologous sequences (i.e. the first 300 base-pairs of the control region). If longer sequences are used, the estimates should also be reported for the comparable minimum or consensus lengths. Statistical analyses of population structure should include both haplotype and nucleotide correlations (e.g. F_{st} and $ø_{ST}$ or their analogues) and tested with a permutation procedure.

As yet, there appears to be no general agreement on standard methods for statistical analyses of microsatellites. The Workshop **recommends** that, at a minimum, the frequencies of alleles should be reported by length and the samples should be tested for deviation from Hardy-Weinberg equilibrium.

8. HISTORICAL AND MODERN CATCHES

8.1 Historical (pre-modern)

Most data from pre-modern whaling are in the form of production statistics (oil or baleen) rather than whales caught. As a result, the numbers of whales killed are estimated rather than known. Different authors have used different yield or catch-per-voyage values, derived from different assumptions and procedures. The same can be said of adjustments for hunting loss, ranging from 1.2-1.5 times the landed catch, depending on the fishery (e.g. IWC, 1986a, p.31).

In the review below, based on a compilation at the Workshop by Reeves, no attempt has been made to standardise estimation methods. Annex L summarises data available for southern right whales.

8.1.1 North Atlantic

The North Atlantic stocks of right whales had already been severely reduced by Basque pelagic whaling and shore whaling prior to the beginning of 'Yankee' pelagic whaling in the mid 18th century (IWC, 1986a). At least dozens of right whales were taken each year in the Bay of Biscay between 1059 and 1650 (Aguilar, 1986; IWC, 1986a). Aguilar (1986) reviewed catch and production data from Basque whaling elsewhere in the North Atlantic, concluding, for example, that some 25,000-40,000 right whales were taken off Labrador between 1530 and 1610. French (and probably other) whalers continued to kill right whales at least opportunistically through the mid-18th century (Du Pasquier, 1986). Shore whaling along the US east coast began in the mid 17th century, with peak catches of right whales from approximately 1680-1730 (Reeves *et al.*, 1999). Estimates of the number of right whales taken off the northeastern USA between 1696 and 1734 range from about 2,000 (based on baleen exported) to 3,800 (based on oil exported). Shore whaling continued, with variable amounts of effort, along portions of the US coast until 1924, with total known catches only in the hundreds for this 190-year period. Catches by pre-modern shore whalers in the 20th century include about ten animals (including struck/lost) off Long Island, New York (Reeves and Mitchell, 1986b); five off North Carolina (Allen, 1977; Allen and Kirkwood, 1977); and one in southeastern Canada (Mitchell *et al.*, 1986). Modern whalers at Iceland and the Faroes took 24 right whales between 1889 and 1898 (Brown, 1986).

The estimated catch of right whales by American pelagic whalers in the North Atlantic between 1855 and 1897 is about 186 (Best, 1987).

8.1.2 North Pacific

Right whales were exploited by net fisheries off Japan beginning in the late 17th century. Omura (1986) estimated that no more than about 50 right whales per year were taken in each of two areas (the Sea of Japan and the Pacific coast of Japan) in the years before about 1850. Thereafter, catches by net whalers declined, presumably because of stock depletion due to pelagic whaling.

Few right whales were taken by shore whalers along the coast of North America. Scarff (1986) found evidence of only 10 catches (and 13 additional sightings) between 1856 and 1886.

Pelagic whaling for right whales began in the Sea of Japan in the 1820s (Omura, 1986), on the ‘Northwest’ or Kodiak grounds in the central and eastern North Pacific in 1835 (Kugler, 1986), and in the Okhotsk Sea in 1845 (Kugler, 1986). Best (1987) estimated a total catch of about 14,500 right whales by American pelagic whalers in the North Pacific (including the Okhotsk Sea) between 1835 and 1904, of which more than 90% were taken in 1840-59. These cannot be allocated to grounds.

The catches summarised above make no allowance for hunting loss, and they do not include catches by British, French and other European whalers.

8.1.3 Southern Hemisphere

Shore-based catches in the Southern Hemisphere can be allocated to management units, based primarily on locations of winter calving grounds. Pelagic catches, however, have often been compiled in a coarser manner and therefore cannot readily be allocated to particular units. In the Tables and text below, the Southern Hemisphere catch data are presented in mixed format, with catches by shore whalers grouped by coastal wintering area, catches by offshore whalers assigned to coastal wintering areas when possible (‘bay whaling’), and the rest only to ocean basin.

8.1.3.1 SOUTH PACIFIC

Best (1987) estimated that American whalers took about 14,700 right whales in the South Pacific between 1815 and 1909. He made no attempt to allocate these catches to specific grounds, but Dawbin (1953; 1988) used the same data (from Starbuck, 1878) to estimate American catches off New Zealand totalling 4,487 in 1832-1901 (all but four before 1850). Although shore whaling began in Australia as early as 1805, catch records are available only beginning in 1827. Shore-based catches peaked in the 1830s and 1840s, with a total of 10,148 from 1827-53 for South Australia, Victoria, New South Wales and Tasmania, combined. New Zealand shore whaling began in 1829 and peaked in the 1840s. The shore whalers based in New Zealand took 2,715 right whales from 1830-1930. In addition, whalers from Australia took at least 2,638 right whales in New Zealand waters from 1833-68 (Dawbin, 1986). French whalers took an estimated 3,871 near southern Australia, Tasmania and New Zealand in 1835-41 (Du Pasquier, 1986).

Pre-modern catches of right whales along the west coast of South America have not been well documented. It is known that French whalers took about 2,372 on the Coast of Chile ground in 1817-37 (Du Pasquier, 1986) and some of the catches attributed by Best (1987) to the South Pacific would have been off South America.

None of the above estimates includes allowance for hunting loss. Nor are returns from British and German whaling in the South Pacific fully taken into account.

8.1.3.2 SOUTH ATLANTIC

The estimated total catch of right whales by American whalers in the South Atlantic from 1805 to 1914 is 28,532 (Best, 1987). Best and Ross (1986) estimated a total catch of 1,580 by shore whalers in southern Africa between 1792 and 1912. Estimates of catches by French whalers can be apportioned to different grounds (Du Pasquier, 1986): 1,252 off southern Africa, 1785-1837; 382 at Tristan da Cunha, 1830-37; 2,369 on the Brazil Banks/Falkland Islands, 1785-1837; and 624 on unspecified grounds (summarised here from IWC, 1986a, p.29).

Richards (1993) attempted a comprehensive compilation of catches on the Brazil Banks/Falklands grounds by pelagic whalers from France, Britain, the USA and Spain between 1765 and 1812, and summarised the literature of Brazilian shore whaling. Shore whaling, which targeted mainly females and calves, began in 1603. By 1678, and for a century following, 4-6 (or more) shore stations took 20-30 whales each year. After 1770, total annual catches were as high as 1,000 but soon declined, averaging only 190 per year in 1793-96. By the 1820s only a few tens of whales were being taken per year, and the shore operations ceased.

Richards (1993) estimated a combined total catch, including that of the shore whalers in Brazil and that of the multinational fishery on the Brazil Banks/Falklands grounds offshore, at about 29,500 right whales between 1772 and 1814. This estimate partially overlaps those of Best (1987) for the American whalers and Du Pasquier (1986) for the French.

None of the above estimates allows for hunting loss.

8.1.3.3 INDIAN OCEAN

Comparatively little pre-modern whaling for right whales has been documented for the Indian Ocean. Shore whaling in Madagascar began in the mid-1750s, and French whalers hunted right whales in Delagoa Bay, Mozambique, beginning in 1789 (IWC, 1986a). Du Pasquier (in IWC, 1986b, p.30) indicated that at least 103 were taken there in 1789-91 and that substantial whaling effort continued until at least 1803. Catches from Delagoa Bay between 1785 and 1805 by a multinational fleet are included in Richards and Du Pasquier (1989).

American pelagic whalers hunted right whales intensively on the Coast of New Holland Ground, offshore western Australia, in 1838-49 (Bannister, 1986a). Bannister (1986a) also estimated that at least 266 (possibly 311) right whales were taken by local bay whalers in SW Australia in 1836-66. Major whaling grounds were at St Paul/Amsterdam Island and Kerguelen Island (Desolation Ground). Another important right whale ground was at the Crozet Islands, where American whaling began in the early 1830s and ended by about 1848 when the ground was fished out (Richards, 1990). At least 1,080 right whales were taken by the American whalers at ‘the Crozettes’ in 1841-45 (Richards, 1990). Best (1987) estimated a total catch of about 12,500 in the Indian Ocean by American whalers between 1830 and 1909. Of this total, more than three-quarters were taken in the period 1835-44. It is important to note that the estimate by Richards (1990) is subsumed in the ocean-wide estimate by Best (1987).

None of the above estimates allows for hunting loss.

8.2 Modern

8.2.1 North Atlantic, 1900-1967

About 140 right whales were taken in the eastern North Atlantic between 1902 and 1967, including about 100 killed off the Shetlands, Hebrides and Ireland in the years 1906-1910 (Brown, 1986). This intense episode of whaling seems to have had a catastrophic effect on the right whale population in the eastern North Atlantic.

Two right whales were killed by shore whalers in Newfoundland: one in 1937 and one in 1951 (Mitchell *et al.*, 1986).

8.2.2 North Pacific, 1900-1970

Catch data for the North Pacific since 1900 were summarised in SC/M98/RW10. Between 1911 and 1946, Japanese whalers took 160 right whales in the western North Pacific (Omura, 1986), and an additional 18 animals were taken between 1915 and 1946 (SC/M98/RW10). In the 1950s, 10 whales were taken for scientific research by Soviet whalers off the Kurils, and two for scientific research by Japanese whalers off eastern Japan. Two were taken for scientific research by Japan in the Okhotsk Sea in 1968, two by China in the Yellow Sea before 1978, and one by Korea in the Sea of Japan in 1974 (SC/M98/RW10).

In the eastern North Pacific, about 28 right whales were taken in the Gulf of Alaska, Bering Sea and British Columbia waters between 1911 and 1938 (SC/M98/RW10). One animal was taken off California in 1924, one off British Columbia in 1951, and ten in the Gulf of Alaska and Bering Sea in the 1960s (SC/M98/RW10). All but one of the latter were taken for scientific research by Japan.

Of special importance is the discovery that large illegal catches were made by Soviet whalers between 1958 and 1964. Two factory ships built specifically for the North Pacific, the *Vladivostok* and the *Dalnij Vostok*, began operations in 1963 and killed close to 200 right whales in the eastern North Pacific in 1964 (SC/M98/RW10). There is also evidence that ‘hundreds’ of right whales, including bowheads (SC/M98/RW10), were taken in the Okhotsk Sea in the 1960s and that additional unreported catches were made from shore stations in the Kuril Islands between 1948 and 1970 (Yablokov, 1994; SC/M98/RW10).

8.2.3 Southern Hemisphere

Relatively few right whales were officially reported as taken by modern whaling in the Southern Hemisphere. Catches of 63 at Campbell Island in 1909-13 (Dawbin, 1986), 38 in New Zealand between 1915 and 1959 (IWC, 1986b, p.30, citing Cawthorn, unpubl.; Dawbin, 1986), and occasionally in New South Wales through 1930 (Dawbin, 1986) were apparently made by open-boat shore whalers. At least 105 were taken in southern Africa, in the period 1908-75 (Best and Ross, 1986), 649 at South Georgia, the South Shetlands and Kerguelen, in 1900-1920 (Tønnessen and Johnsen, 1982), and 309 off Chile, in 1900-20 (Tønnessen and Johnsen, 1982). Catches from shore stations in Brazil occurred from at least 1950 to 1973, totalling approx. 350 (Palazzo and Carter, 1983).

Of particular significance are the previously unreported illegal Soviet catches during the period 1951/52-1971/72, totalling at least 3,349 (Tormosov *et al.*, 1998). The largest documented catch was 1,335 whales off Patagonia in 1961/62. Large catches were also made in the southeast Atlantic (total 704, 1961/62-1967/68), the southwest Pacific (372, 1963/64-1969/70) and the southwest Indian Ocean near Crozet Island (309, 1962/63-1967/68).

9. BIOLOGICAL PARAMETERS

9.1 Data collection: field and analysis techniques

The Workshop agreed that it was important to try to standardise data collection and data fields to allow for comparisons among and between datasets on specific research questions. It reviewed the nature of the datasets maintained by some participants, and recognised that most studies maintained comparable datasets. It was agreed that as long as the data can be searched in a comprehensive manner, it is unnecessary to standardise all data fields. The Workshop did not attempt a comprehensive assessment of methodology and techniques of all data collection, but rather addressed specific categories of particular importance, i.e. photo-identification, biopsy and necropsy.

9.1.1 Photo-identification data

The focus of discussion on photo-identification data was the coding of the quality/detail of photographed sightings for comparison of matches within and among catalogues quantitatively, either to help to establish the level of confidence in a given match or to quantify the risk of missing a match. This is important when trying to obtain unbiased estimates of biological parameters or abundance (e.g. see Hammond, 1986). Currently there are no accepted standard methods for quantifying such risks but any that are developed will be more reliable if they are based on measures of quality for each sighting. The Workshop recognised that such estimates will be easier to derive for automated matching systems. It particularly **encourages** those groups anticipating future automation of their catalogues to initiate or expand the recording of quality measures.

Hiby demonstrated an automated system for matching aerial photographs of callosity patterns, as described in SC/M98/RW38. The system, developed with joint funding from IFAW and IWC, is being used to automate the catalogue of photographs from Argentina and the programs were provided to participants from South Africa and Australia at the Workshop.

9.1.1.1 CODING OF PHOTOGRAPHED SIGHTINGS

To quantify the quality of photographs (i.e. one or more photographs), five assessment categories with associated numerical codings (in parentheses) were agreed:

(A) Head obscured by water and/or glare:
  Quality: good (1), medium (2), poor (3), unmatchable (4).
(B) Focus/image size:
  Quality: good (1), medium (2), poor (3), unmatchable (4).
(C) Angle/foreshortening:
  Quality: good (1), medium (2), poor (3), unmatchable (4).
(D) Viewpoint:
  Left side only (1), right side only (2), topside/both sides (3).
(E) Distinctiveness of individual:
  Good (1): even with poor quality photographs, animal is distinctive enough to match.
  Average (2): with average quality photograph, animal is distinctive enough to match.
  Poor (3): generic/indistinct animal. Even with high quality photos, confirming match is difficult.

Because each study area uses different image types, it was agreed that rather than try to develop a standard assessment for these criteria, each research group should decide what photographs typify each of these categories. Ten or so example photographs should be printed by each group to ensure consistency in photograph coding over time and between individual researchers.

The Workshop recognised the value of long-term photo-identification studies (IWC, 1990b) in providing essential data for assessing and monitoring the status of right whale populations. It **recommends** the continuance of existing programmes and the establishment of new programmes where appropriate.

Given the value of the historical information contained in the various photo-identification catalogues, it also **recommends** that the images in catalogues be digitised and archived in a secure way (see IWC, 1990b, pp.9-10 for details).

9.1.2 Biopsy data

The Workshop discussed a range of topics pertinent to the collection of skin and blubber biopsy samples from right whales for both genetic and organo-chemical and biochemical analyses. The type and efficacy of various sampling systems were discussed along with other variables potentially affecting sample collection (e.g. angle and range of shot, class of animal, type of vessel).

A brief review of the methodology used and the number and location of samples currently available from different geographic areas is given in Annex E.

9.1.2.1 STERILISATION OF BIOPSY TIPS

The importance of sterilisation of biopsy tips was noted both for the whale (issues of infection) and for meaningful analyses (cross contamination). For DNA (skin) samples it was noted that either ethanol rinse and flaming and/or bleach would suffice. However, for organo-chemical (blubber) analyses it is important to clean the tip with solvent after flaming (see SC/M98/RW24)

Wherever possible, enough tips should be taken into the field to sample for the entire day, allowing tips to be used on only one animal before undergoing thorough sterilisation overnight or onshore.

9.1.2.2 REACTION OF RIGHT WHALES TO BIOPSY

All research groups have noted a range of apparently short-term reactions to biopsy darting. The frequency and extent of reaction is highly variable and is influenced by group size, activity of whale and possibly sex of whale. It was noted that females with calves show more reaction than do their calves.

Importantly, it was highlighted that the reaction to the vessel from which biopsy is being undertaken often exceeds the reaction to the biopsy darting itself.

The possibility and potential of alternative sampling methods is discussed below.

(a) *Sloughed skin.* Some difficulty was reported with accurately identifying the individual whale from which the sample comes. The quality and quantity of DNA in such samples is low (Whitehead *et al.*, 1990) and may potentially limit analysis.

(b) *Scrub scrapes.* A system of using sterile nylon scrub pads to collect skin was described. Such a system has been successfully used on dusky and Hector’s dolphins in New Zealand (Patenaude, pers. comm.) and on sperm whales (Whitehead *et al.*, 1990). It was suggested that such ‘non-penetrative’ techniques may be useful for demographic studies where multiple sampling of individuals may be required.

(c) *Hand scrapes.* It was suggested that peeling skin can be collected by hand from whales alongside boats. The method’s feasibility for large whales is unknown, and there is the risk of sample contamination from the collector.

It was noted that none of these alternative techniques would provide blubber samples and that the small size of the samples may be restrictive for some types of DNA analysis.

9.1.2.3 PERMITS AND REGULATIONS

The Workshop highlighted the fact that calves typically show less reaction to biopsy darting than the mother and agreed that there is considerable scientific merit in obtaining samples from calves. Such samples can provide valuable data not otherwise available (e.g. sex ratio at birth, paternity analyses) and the Workshop **recommends** that, where possible, such samples should be obtained.

Permits for the acquisition and export or import of biopsy samples are subject to the requirements of domestic legislation, sometimes requiring public advertisement and comment. Researchers should therefore ensure that in planning research trips or distribution of samples, adequate time is allocated for fulfilling the requirements of the permitting process.

The Workshop **recommends** that IWC member nations should be asked to facilitate the transfer of skin/blubber biopsy samples between research institutions in different countries to assist collaborative analyses, and that the IWC Secretariat approaches the CITES Secretariat to determine the best way to facilitate the exchange of such material.

9.1.3 Necropsy data

The Workshop **recommends** that, where possible, necropsies should be conducted to determine the cause of death (SC/M98/RW8; SC/M98/RW25) and to collect biological samples relevant to studies of the recovery of right whale populations. Detailed necropsies should follow protocols described by Blaylock *et al.* (1996). At a minimum, collections should include: standard morphometric measurements; skin (or other tissue if skin is not present) in salt-saturated DMSO; skin/blubber interface in formalin; internal organ tissue in 10% neutral, buffered formalin; parasites in 70% alcohol; and dried baleen (for genetic and isotope analysis).

In addition, there are a number of important ongoing studies that could be further addressed through necropsy data. A brief description of these, the sampling technique to be used and the researcher to contact for further information is given in Annex F.

9.2 Methodology and estimates

The Workshop first examined data and methodologies in the context of the assumptions underlying the models used and their likely reliability.

9.2.1 Data types

A number of points were noted that were applicable to all of the analyses used at the Workshop.

(1) Biological parameters for all populations were estimated on the basis of repeated photo-identification of individual whales usually from aerial, shore-based, or ship-based surveys.

(2) In the Southern Hemisphere, analyses were generally confined to cow-calf pair data; however, in the North Atlantic and all areas in the Southern Hemisphere apart

from South Africa, individuals of all ages and both sexes are photographed.

(3) There is a potential lack of comparability among areas in observed calving events, because the relative timing and duration of surveys differ, as do the observation platforms.

(4) Assessing the quality of photo-identification catalogues and the extent of whale approachability will lead to improved population parameter estimates by enabling questions of heterogeneity in recapture probability to be better addressed (e.g. Hammond, 1986; IWC, 1990b). The question of photograph quality is discussed under Item 9.1. It was suggested that measuring the time necessary to photograph an individual could provide an index of approachability. Inter-individual differences will introduce heterogeneity which may lead to biased estimates as discussed below.

Two further issues pertinent to the estimation of age at first parturition were identified.

(1) All analyses use observations of mothers first identified as calves, taking into account the possibility that a first calf may have been missed and that insufficient time may have passed for some animals to have yet had their first calf.

(2) For Argentinian and South African whales, a subset of animals was used, because these were easier to re-identify. It is assumed that this subset is representative of the whole group of maturing females.

9.2.2 Parameter estimation methodology

The following papers containing estimates of biological parameters were presented.

SC/M98/RW12 uses a model that is an extension of one used in an earlier paper for animals off Argentina (Payne *et al.*, 1990). It uses a maximum likelihood approach. The total population is forced to follow an exponential rate of increase, while allowing each yearly calving group to be of different sizes. This allows more flexibility for fitting the model and providing estimates of inter-calf interval, population rate of increase and mortality rate for calving females. Tests for time trends in mortality rate and in population rate of increase are also made. The model is extended to estimate age at first parturition, by requiring that a maximum value for that age be specified.

SC/M98/RW16 applies the method of Payne *et al.* (1990) to animals off South Africa, to estimate inter-calf interval, population rates of increase and survival rates, and is extended to estimate age at first parturition for females. The authors then use the balance equation to explore the likelihood of different possible values of population rate of increase on the assumption that juvenile survival should not exceed that of adults.

SC/M98/RW3 also uses a maximum likelihood approach, somewhat comparable to that of Payne *et al.* (1990). Sighting histories of all categories of individuals (i.e. juveniles, mature males, calving and non-calving females) in the western North Atlantic population are used. The model estimates annual survival probability, given different hypothesised patterns of sighting probability: constant; variable over time; or depending on an index of ‘offshore’ habitat use. Tests for time trends in survival rate are made.

SC/M98/RW15 uses a Bayesian approach to estimate the size of the mature female population off South Africa and the population rate of increase. The estimation method requires a prior distribution for the starting population size and a ‘first guess’ for initial rate of increase. Survival rate values for each three-year interval are obtained from the mark-recapture program SURGE, which uses a maximum-likelihood approach similar to that in the three papers above, and is based on the assumption of a fixed three-year calving cycle.

SC/M98/RW1 presented estimates for certain biological parameters (e.g. mortality rate) for the western North Atlantic based on a six-year running total of catalogued animals (i.e. animals seen during the period, excluding known deaths). Two problems identified with this straightforward approach are that: (a) some animals that are alive may not be seen during the six-year period; and (b) changes in geographical coverage over the period will affect the likelihood of sighting animals.

Best and Kishino (1998) use a regression approach to obtain estimates of mortality rate for calving females off South Africa. It was noted that the methods used, although robust, are subject to bias of known direction but of unknown magnitude.

Underlying assumptions of the estimation methods presented, their biological significance and the effects of their violation, are given in Table 2; assumptions shared by all estimation methods are listed first, followed by the particular assumptions of each model. The importance of the effects of violations of these assumptions can be tested using the different methodologies on synthetic datasets.

9.2.2.1 RECOMMENDATIONS AND CONCLUSIONS

The Workshop agreed that of all the potential biases arising from possible violation of the assumptions listed in Table 2, those related to probable differences in parameter values by sex and age in the analysis presented in SC/M98/RW3 potentially introduced the most serious bias into results. It **recommends** that the authors continue to develop their methodology to allow for these factors (and see Item 9.2.2 below).

It also **recommends** that:

(1) the effects of problems in re-identification from catalogue photographs on estimates of sighting probability be tested (e.g. if the catalogue admits photographs showing only part of the callosity pattern, a new partial pattern will not be accepted as a new whale because it will not be comparable to the entire catalogue, but may be accepted if it matches an existing partial pattern);

(2) the effects of differential approachability of individuals on their inclusion in the dataset be examined;

(3) the effects of dependence between successive calving cycle lengths on the estimation methods of SC/M98/RW12 be examined;

(4) the different models presented be used to examine the same datasets (and *vice-versa*) in order to understand better their differences and similarities – any inconsistencies between results should be thoroughly investigated (e.g. see Item 10).

9.2.2.2 AGE AND GROWTH

Maximum lengths of males and females, and ranges in calf size are given in Table 3.

9.2.2.2.1 NORTH ATLANTIC

There is limited information available on longevity based on photo-identification records (Hamilton *et al.*, 1998). Only seven catalogued animals were first identified over 20 years ago. One animal fortuitously identified from a photograph

Table 2

Assumptions used in the papers addressing biological parameters (see text).

Assumptions	Assumption biologically appropriate? Relevant data
General/all methods	
Calving (= potential sighting) intervals independent of each other for the same individual	May be incorrect if calves are lost and not observed. Australia: observation that certain females are seen to calve at more regular intervals than others. The effects of violations of this assumption have not been checked.
No heterogeneity in sightings probability among individuals	Incorrect if a shift in geographical distribution is undetected. Potential problem of recognition of photographed individuals from catalogue. Some individuals are less approachable, so less likely to be photographed. Some individuals may be photographed more due to clear markings, thus are more likely to be 'resighted' and re-identified, especially if observed in large groups. North Atlantic: use of all members of the population regardless of age or sex can lead to erroneous parameter values; heterogeneity in sightings probability between cow/calf pairs and females in their non-calving years. Violation of this assumption may affect estimation of absolute population size and mortality rate; possibly low effect on inter-birth interval estimate; population trend estimate likely unbiased unless heterogeneity levels change with time.
'Mortality' includes death, emigration and reproductive senescence	No evidence of senescence in Argentinian population. North Atlantic: 1 female with 29 years of reproductive history. Russian data: lower % pregnant in the largest females, but low sample size (not statistically significant count at 5% level). In general, observation periods are not long enough to detect signs of senescence. In bowhead whale catch data, anatomical signs of senescence.
'Mortality' excludes immigration	Immigration of individuals would not bias mortality rate estimate downward from true value, but would bias the population rate of increase upwards. Probable heterogeneity in sighting probability between cow/calf pairs.
SC/M98/RW12 - Argentina	
Constant trend in population rate of increase over time used in estimating other parameter estimates	In SC/M98/RW16 evidence for a three-year cycle in estimated number of calves/year, contrary to assumption of constant trend in increase over time; unlikely to cause bias in survival and rate of increase estimates, but may affect precision.
SC/M98/RW15 - South Africa	
Bayesian; uses a prior distribution on population size at beginning of time series + first guess at initial rate of increase and survival rate	Posterior distributions not very sensitive to choice of first guesses of rate of increase and survival rate in South African case.
Three-year cycle in sighting availability of calving females	Probably little effect if a small deviation from this cycle.
Best and Kishino, 1998 - South Africa	
Constant sightings probability over time	In both Argentina and South Africa lower effort now than at start of the study has lowered sighting probability over time.
If individual not resighted within nine years after first sighting, it is assumed dead	Argentina: about 50% sighting probability/year/individual, resulting in a 12% chance of no sighting over nine years if still alive. S. Africa: ~75% sightings probability giving a 2% chance of no sighting if still alive. Assumption critical, and survival probability is very sensitive to it; however the bias produced is in a known direction (mortality biased upward).
SC/M98/RW3 - North Atlantic	
Survival rate equal in a given year irrespective of sex, age and breeding status (i.e. calving or not)	From other mammal species, survival not constant over age; early year(s) likely to have lower survivorship. Effect of breeding status on survival estimate unknown. Some neonatal mortality will happen before sighting.
Same assumption for sightability	Calving and non-calving females have different sightability. In North Atlantic mature females have different sightability from males and juveniles.
Effect of spatial distribution assumed to be adequately modelled by offshore index	Offshore index takes into account shift in sightings effort over time, but not potential shifts in population structure. Observed shifts in geographical distribution on feeding grounds in the 1990s and influx of newly mature females violate this assumption. Differentials in distribution of different age classes at different distances offshore could cause the estimated changes in demographic parameters over time.

Table 3
Summary of maximum length data for right whales.

Species	Males	Females	Calves (mean length at birth)
North Atlantic	12.9m (Allen, 1916)	59ft (18m) Thompson (1928)	*ca* 4m
North Pacific	17.1m (Klumov, 1962)	18.3m (Klumov, 1962)	6m (Ohsumi, 1981)
Southern Hemisphere	>16m (Tormosov *et al.*, 1998)	53.7ft (16.5m) (Best and Ross, 1986)	6.1m (Best, 1994)

taken in 1935 was re-photographed over 60 years later. A female photographed with a calf in 1967 was also seen with a calf 29 years later, in 1996.

Hamilton *et al.* (1998) also presented information on the age-structure of the population in 1996, both with and without presumed mortalities being taken into account. Juveniles and calves accounted for 26-31% of the population, considerably less than the estimate of 56-58% given for the Bering-Chukchi-Beaufort Seas stock of bowhead whales by Zeh *et al.* (1993).

9.2.2.2.2 NORTH PACIFIC

Little information exists for North Pacific animals, other than that for maximum lengths given in Table 3.

9.2.2.2.3 ARGENTINA

An age-length key for animals aged up to 10 years (albeit with wide confidence intervals) was published by Whitehead and Payne (1981). The longest active reproductive span from the photo-identification catalogue is 26 years.

9.2.2.2.4 SOUTH AFRICA

Best and Rüther (1992) measured 72 cow-calf pairs photogrammetrically in 1988 and 1989. Adult females ranged from about 12.4-15.5m. Presumed primiparous females were smaller on average than those believed to have had at least two calves (13.5m versus 14.3m). Primiparous females also appeared to give birth to smaller calves (5.4m versus 5.9m). Calf growth rates were of the order of 2.8cm per day (±0.7cm) and calves grew to about half their mother’s length by mid-October.

From stable isotope analysis of baleen plates, Best and Schell (1996) concluded that growth in body length slowed markedly after weaning. Best speculated that the presence of distinct modes in the length composition at 9-12m (SC/M98/RW25 and Tormosov *et al.*, 1998) suggested that a spurt in growth preceded sexual maturity.

9.2.2.2.5 AUSTRALIA

The longest active reproductive span identified thus far is 25 years (Burnell, pers. comm.).

9.2.2.2.6 WESTERN NORTH ATLANTIC

SC/M98/RW1 reported a mean mortality rate of about 0.031 (SD = 0.017) for the period 1986-97. Methodological concerns regarding the approach used are given above and under Item 10.

Additional methodological work is recommended under Item 9.2 with respect to the technique for estimating survivorship given in SC/M98/RW3. The Workshop **recommends** that the results of this work be presented to the IWC Scientific Committee as soon as possible, given the possibility raised in the preliminary analysis that survival rates may have declined in recent years.

9.2.2.2.7 ARGENTINA

SC/M98/RW12 estimates adult female annual mortality as 0.020 (SE = 0.005) for the period 1971-90. The authors had found no evidence for any trend over the time period. From a balance equation, an estimate of 0.92 (SE = 0.11) was derived for survival of females from birth to first parturition.

9.2.2.2.8 SOUTH AFRICA

SC/M98/RW16 provides an estimate of adult female survivorship of 0.99 (95% CI 0.975, 1.005) for the period 1979-96, using similar methodology to that given in SC/M98/RW12.

SC/M98/RW15 provides an alternative estimate of survivorship based on a duck hunting mark-recapture approach. Annual adult female mortality was estimated as 0.978 (95% CI 0.969, 0.985). SC/M98/RW16 also provides an estimate of juvenile survivorship. Although the point estimate (1.02) is biologically not feasible, the 95% CI (0.504, 4.59) is wide; the authors also noted that some 75% of neonatal mortality occurred before the survey period, which would naturally have led to a higher estimate of juvenile survival.

9.2.2.3 REPRODUCTIVE PARAMETERS

9.2.2.3.1 AGE AT SEXUAL MATURITY

Western North Atlantic

Based on resightings information ($n = 19$), Hamilton *et al.* (1998) estimated the median age at first parturition to be 9.5 years. Observed ages ranged from 5-14 years. The authors also investigated the question of missed calvings.

Argentina

SC/M98/RW12 estimated mean age at parturition as 9.0 years (SE = 0.3). The modal age at first calving was also nine years, with about 50% of first calvings occurring at this age. Observed ages ranged from seven to an inferred maximum of 11 years.

South Africa

SC/M98/RW16 estimated 9.1 years as the age at which 50% of first calvings occur (95% CI 7.3, 31.4). Observed ages ranged from 6-13 years ($n = 123$). Further analyses taking into account the proportion of marked animals at each age that had not reached parturition age would reduce the upper confidence limit.

Australia

The only available information is from two females observed with their presumed first calves, giving ages at first conception of eight years and nine years (Bannister, pers. comm.).

9.2.2.3.2 PREGNANCY RATE AND CALF PRODUCTION

North Atlantic

SC/M98/RW1 reported a mean gross annual reproductive rate (GARR) of 0.0423 (SD = 0.0186) for the period 1986-1997.

Argentina

SC/M98/RW12 estimated a pregnancy rate of 0.339 (SE = 0.006).

Southern Ocean

Aggregated data from Soviet catches (Tormosov *et al.*, 1998) obtained from three factory ships in 1960/61-1967/68 gave increasing pregnancy rates for a series of size classes from 12-12.4 to 15.5-15.9m of 4.0-39.0%. For the largest females, > 16m, the rate was 16.7%, but this estimate was based on a small sample, and not statistically significantly different from the rates reported for immediately smaller animals. Some of the low rates in the smaller size intervals above 12.5m probably reflect the presence of some immature animals in the sample.

Auckland Islands

The percentage of calves observed over three years averaged 11.8% (range 9.4-13.8%) of the total number of animals observed (SC/M98/RW20).

9.2.2.3.3 REPRODUCTIVE CYCLE/SEASONALITY

North Atlantic

For the western North Atlantic, Knowlton *et al.* (1994) gave a mean interval of 3.67 (SE = 0.11, $n = 86$, range 2-7) years. The Workshop noted that there had been an increase over time in recent years (SC/M98/RW1). The rates were variable but for 1985-1997 there was a significant increase ($p < 0.001$) from 3.33-5.36 years. The variable intervals had been shown not to be affected statistically by sampling.

SC/M98/RW29 reported that changes in calving rate could be correlated statistically with the Southern Oscillation Index (SOI), with low calving years one year after minima in the SOI, which indicate El Niño years. With an intense El Niño in 1998, a low calving rate would be expected in 1999.

South Atlantic

For Argentina, there was no detectable time trend in calving interval (SC/M98/RW12). The mean interval was 3.35 years (SE = 0.05). The mean calving interval estimated using the same model for South Africa (SC/M98/RW16) was 3.12 years (95% CI 3.05, 3.17). The probability distribution of calving intervals differed from that for right whales off Argentina in that it contained more three-year intervals (0.85 *vs* 0.692) and fewer five-year intervals (0.03 *vs* 0.131). Payne *et al.* (1990) suggested that the high probability for a five-year interval off Argentina reflected animals losing their calves soon after birth (and before being sighted), and then changing from a three- to a two-year cycle. However, the Workshop could offer no explanation of why the South African situation should differ.

Australia

Observations at Head of the Bight, South Australia (SC/M98/RW19), gave an interval of 3.3 years (SE = 0.1, $n = 57$). A larger sample, including animals from a wider area of the Australian southern coast, gave an estimate of 3.64 years (SE = 0.13, $n = 117$). The Workshop noted that the estimates were not directly comparable with those derived using a modelling approach as in SC/M98/RW12.

10. ESTIMATES OF ABUNDANCE AND TRENDS

In presenting estimates of abundance and population trends for the southern right whale, the Workshop agreed to divide the Southern Hemisphere into 11 management units based on the breeding stocks given under Item 7: sub-Antarctic New Zealand, Australia, Central Indian Ocean, Mozambique, South Africa, Namibia, Tristan da Cunha, Brazil, Argentina, Chile/Peru and mainland New Zealand/Kermadec. Current best estimates of certain demographic parameters and population sizes for each of these regions are summarised in Table 4.

10.1 Population trends

10.1.1 Increase rates - Southern Hemisphere

10.1.1.1 AUSTRALIA

SC/M98/RW18 provides aerial survey data at the peak of the season (mid-August to mid-September) for three sections of the southern coast of Australia: (A), (B) and (C) in increasing extent along the coast from east to west (SC/M98/RW18, fig. 2). The areas were selected to cover the main areas of whale concentration, initially off the southern Western Australian coast (Areas (A), (B)) and later extended eastwards to South Australia to embrace the major area of coastline along which coastwise movements had been detected (Area (C)). For each dataset, information is provided for three classes of whale: (a) all animals; (b) 'unaccompanied' animals; (c) cow-calf pairs. Data for areas (A) and (B) are provided for the 15-year period 1983-97, excluding two years in (A) and four years in (B) (*ibid* table 1) and for the five-year period 1993-97 for (C). Regressions of the natural logarithms of

Table 4

Summary of estimates of certain demographic parameters and current abundance levels for different breeding stock population units used for the modelling exercise described in Item 10.3. A dash indicates no information.

Breeding unit	Growth rate r	Annual survival S	Age at first parturition tm	Most recent population estimate of mature females	'1997' estimate of mature females used in model[1]	'1997' total population (i.e. all animals) estimate used in model
New Zealand	-	-	-	69 (1997)	70	330
Australia	0.0825	-	-	220 (1995)	254	1,197
Central Indian Ocean	-	-	-	-	0	0
Mozambique	-	-	-	< 10	0	0
South Africa	0.072	0.98-0.99	9.1	613 (1996)	659	3,104
Namibia	-	-	-	< 10	0	0
Tristan da Cunha	-	-	-	20 (1985)[2]	48	226
Brazil	-	-	-	25 (1995)	29	137
Argentina	0.071	0.98	9.0	330 (1990)	547[3]	2,577
Chile/Peru	-	-	-	< 10	0	0
NZ/Kermadec	-	-	-	-	0	0
Total					1,607	7,571

[1] Estimates calculated assuming a growth rate of 0.075 for all areas. [2] Upon review later in the meeting, it was felt that this number was probably too high.

[3] This is entirely extrapolation-based, as data are available only to 1990.

maximum counts of cow-calf pairs for all three areas are significantly different from zero ($p = 0.0001$-0.025) for the data for the two (smaller) areas (A) and (B), but not for the larger area (C) (*ibid* table 3 (c)).

The Workshop agreed that the increase rate for Area (A)(c) was the best available at this time for the following reasons:

(1) the final two years, 1996 and 1997, of all the datasets are likely to be less comparable with the remainder because of a change in pilot and observer following the death of the pilot employed for all flights until 1995; the effect is relatively greater for the short five-year dataset (C) than for the others (there is also concern that the 1997 results include some undercounting because of bad weather); and

(2) although Area (B) traverses somewhat more of the coastline than (A), the probability level for the regression is lower ($p = 0.025$ cf. 0.0001) and the 95% confidence interval much wider (0.128-0.1297) than for Area (A), despite the lower estimated increase rate, of 7.12%.

The Workshop agreed that the current best estimate of the rate of increase for this population was 0.0825 (95% CI 0.510-0.1140) for the period 1983-97.

10.1.1.2 SOUTH AFRICA

SC/M98/RW15 estimated an annual increase rate of 0.0733 (SE = 0.41%) per annum for right whales off South Africa, based on a regression analysis of numbers of cow-calf pairs seen during annual aerial surveys off the southern coast of South Africa from 1969-1996. This estimate would be negatively biased if survey efficiency declined with time. Two alternative estimates are available. Based on the model of Payne *et al.* (1990) for estimating a trend in the number of calvings produced, SC/M98/RW16 estimated an annual rate of increase from 1982-1996 as 0.081 (95% CI 0.06, 0.97). However, this estimate is thought to be biased upwards because it is clearly sensitive to the last data point (for 1996) which reflects a stronger cohort in the breeding group. SC/M98/RW15 also uses a Bayesian approach to estimate values which yield values for current population growth rate in the range 0.071-0.073. The Workshop agreed that an increase rate of 0.072 represented the best estimated annual increase for this population.

10.1.1.3 ARGENTINA

The annual rate of increase for the breeding female component of the Argentinian concentration was estimated at 0.071 (SE = 0.8%) in SC/M98/RW12 for the period 1971-1990. This is a maximum likelihood estimate based on resightings of females with calves only, and the Workshop agreed that it represented the best estimate of increase rate for this population.

10.1.1.4 OTHER REGIONS

There was no information available for other areas.

The Workshop **recommends** that two additional datasets should be investigated in the future: (1) the sightings data collected by Japanese scouting vessels (JSV) in the Antarctic during the years 1965/66-1981/82, some of which has been analysed by Ohsumi and Kasamatsu (1986); and (2) the data from the Japanese Antarctic Research Programme which began in 1987/88.

10.1.2 Increase rates - Northern Hemisphere

10.1.2.1 WESTERN NORTH ATLANTIC

Best commented that population simulations of the Western North Atlantic right whales suggest that some recovery must have taken place following protection in 1935, and that this slow recovery seemed to have continued at least until the 1980s (Reeves *et al.*, 1992).

SC/M98/RW1 provided population size estimates based on a six-year running total of catalogued animals (see Item 9.2). The values were used to obtain an annual rate of increase (range −0.039 to +0.031) for each of the years 1987-1996. A regression estimate obtained using all the data is probably negatively biased (0.01, SE = 0.0232 although the SE needs to be adjusted to account for the fact that the data are correlated) because of reduced sampling effort in recent years.

Annex G summarises three alternative methods used to obtain estimates of the rate of increase for this population. The first provides an estimate of 0.0159 (CI −0.0246, 0.0564) with the caveat that the result is likely to underestimate the rate of increase for the 1980s because the calving interval has increased significantly in recent years. The second looks only at parous females and shows an increase between 1985 and 1997 (0.035, 95% CL 0.024-0.045) but with an apparent long-term oscillation in recruitment. The third (based on the approach outlined in SC/M98/RW3) suggests that 0.043 is an upper bound to the population growth rate. Although actual growth rates are likely to be considerably less than that, the figure serves to illustrate that the growth rate of the North Atlantic right whale is both low and substantially less than that of southern right whale populations.

In view of the methodological concerns expressed under Item 9.2, the Workshop did not believe it was in a position to reach any firm conclusions as regards recent population trends.

Given concerns expressed about the status of this population (see Item 11) the Workshop **recommends** that as a matter of urgency further work is carried out to provide quantitative information on population trends. For example, more complex models (which allow for parameters such as calving rate to vary with time) should be explored to test for any possible changes in trend. In addition, the use of stochastic models should be explored: stochasticity is particularly important when considering small populations. The Workshop also noted that there are indications of a decrease in growth rates in recent years, as suggested by a statistically significant increase in the calving interval and three years of poor calf production (SC/M98/RW1). Further concerns were related to a major change in the feeding grounds that is thought to have occurred, as well as to an increase in reported ship strikes and potentially fatal entanglements in recent years.

10.1.2.2 NORTH PACIFIC

No information on trends is available. Given the concerns expressed under Item 11 about the status of right whales in the North Pacific, the Workshop **recommends** that studies designed to assess population trends be implemented as a matter of urgency.

10.2 Estimates of current abundance

The estimates reported below refer to adult females where no direct estimates of total population size had been carried out. For modelling purposes (see Item 10.3) ‘best’ annual estimates of the number of females have in some cases been multiplied by a factor of three under the assumption that there is a fixed three-year calving cycle and hence three separate cohorts. Item 10.3 indicates how the estimates may be converted for certain cases to total population numbers for use in simulations.

The estimates of abundance given below and in Table 4 have different levels of reliability. They can be divided into four categories:

(1) based on regular research surveys over an extended period: Australia, South Africa, Argentina;
(2) based on limited research: New Zealand sub-Antarctic, Brazil, Tristan da Cunha;
(3) based upon opportunistic sightings: Mozambique, Namibia, Chile/Peru, Mainland New Zealand/ Kermadecs;
(4) no recent information: Central Indian Ocean.

10.2.1 Southern Hemisphere

10.2.1.1 SUB-ANTARCTIC NEW ZEALAND

No surveys aimed at estimating absolute population size have been carried out. A crude estimate of 23 females per year can be obtained from the average maximum count of females obtained during directed research in the Auckland Islands in 1996 and 1997 (SC/M98/RW20). This is probably a minimum estimate because of uncertainty as to the timing of the peak season in this area and the presence of an unsurveyed area.

10.2.1.2 AUSTRALIA

SC/M98/RW18 provides estimates of the number of cow-calf pairs observed during aerial surveys of Southern Australia, between Cape Leeuwin, Western Australia and Ceduna, South Australia during 1993-97. As noted under Item 10.1, estimates for 1996 and 1997 are likely to be biased downwards. However, during the earlier period and within the area surveyed, the counts are likely to represent only a slight undercount of the absolute number of adult reproductive females visiting the coast each year because: (1) the cow-calf pairs are relatively sedentary and easily visible; (2) surveys are conducted during the period of peak abundance; and (3) aspects of the survey methodology were changed as little as possible over the years (see SC/M98/RW18). In 1995, 65 cow-calf pairs were counted in the survey area. Based on an incidental flight network for photo-identification off southeastern Australia, the estimated minimum number of cow-calf pairs sighted in coastal waters between Sydney and Coffin Bay (South Australia) in 1995 was six (Burnell, 1997). Furthermore, an additional two cow-calf pairs were sighted off the west coast of Western Australia in 1995 (Bannister, pers. comm.), yielding a 'best' population estimate of 73 reproductive females for 1995.

10.2.1.3 CENTRAL INDIAN OCEAN

There was no information available for this area.

10.2.1.4 MOZAMBIQUE

No right whales were seen during a winter survey of the coastal waters of southern and central Mozambique in 1991 (Findlay *et al.*, 1994). The absence of any current sightings of cow-calf pairs in the area suggests that the current population size is zero. However, a few individual right whales were sighted moving up the Natal coast during several months of intensive humpback whale surveys during 1990 (K. Findlay, pers. comm.) and it is possible that the area may be restocked in the future from the South African population.

10.2.1.5 SOUTH AFRICA

Aerial surveys for cow-calf pairs have been carried out since 1969. SC/M98/RW15 provides an estimate, based on a Bayesian approach, of 613 (95% CI 583-646) adult females in the South African population in 1996. Results presented in SC/M98/RW16 can be used to derive a rough 1996 population size estimate of 453, based on summing estimates of the number of adult females present for each of the previous three years. Although the Workshop agreed that the former estimate was based on a more thorough analysis, it expressed some concern at the extent of the difference between the two approaches and **recommends** further investigation (see also Item 9.2).

10.2.1.6 NAMIBIA

No surveys have been carried out. There have been 1-2 incidental sightings per year of cow-calf pairs there (Best, pers. comm.). However, the Namibian coast is generally very isolated and the actual number of whales present may be greater. For simulation purposes only, an estimate of < 10 cow-calf pairs was adopted.

10.2.1.7 TRISTAN DA CUNHA

No surveys designed to estimate absolute population size have been carried out. The only available information is derived from aerial surveys conducted on a single day in each of the years 1985-89. Although the daily surveys were fairly comprehensive in terms of their coverage of the three islands, they were subject to factors such as poor weather conditions. The maximum number of cow-calf pairs seen on any of the days surveyed was two, suggesting that the total number of reproductive females in this population over this period was very low.

10.2.1.8 BRAZIL

No surveys designed to estimate absolute population size have been carried out. Fixed-wing surveys were undertaken off southern Brazil in 1987 and 1988, producing counts of 29 adults and 6 calves, and 12 adults and 8 calves, respectively (Best *et al.*, 1993). Aerial surveys of right whales off southern Brazil in 1993, 1994 and 1997 (Palazzo and Flores, pers. comm.) yielded counts of cow-calf pairs of 6, 10 and 9 (Table 5).

Table 5

Summarised information on aerial surveys of right whales off southern Brazil, 1993-94 (Palazzo and Flores, unpublished data).

Year	Month	No. flights	Distance surveyed (N ↔ S)	No. whales sighted	No. cow/calf pairs
1993	Late Aug.	01	400km	17	6
1994	Late Aug.	01	400km	27	10
1997	Late Sep.	01	400km	24	9

10.2.1.9 ARGENTINA

Aerial surveys have been carried out in the Peninsula Valdés region since 1971. SC/M98/RW12 provides an estimate of 330 (95% CI 274-386) for the size of the breeding female component in 1990. This is a maximum-likelihood estimate based on resightings of females with calves only.

10.2.1.10 CHILE/PERU

No surveys designed to estimate absolute population size have been carried out. Sightings of right whales off the coasts of Chile and Peru appear limited to approximately 10 sightings since 1984 (Aguayo and Torres N, 1986; Van Waerebeek *et al.*, 1992). Three or four of these were of cow-calf pairs.

10.2.1.11 MAINLAND NEW ZEALAND/KERMADECS

One or two opportunistic sightings of cow-calf pairs in the past ten years suggest that this population is very small.

10.2.2 Northern Hemisphere

10.2.2.1 WESTERN NORTH ATLANTIC

From SC/M98/RW1, a total population estimate of 300 can be derived for 1993 (the year midway through the last six years) based on all animals seen that year plus the previous five years, but excluding all those known to have died over the period (see Item 9.2). Two sources of negative bias are associated with this estimate: (a) some animals might not have been seen in the six-year period; and (b) some areas were not surveyed in the later years and hence a portion of the population might not have been seen. The adult female component was estimated at 74 in 1997. Greater confidence can be attached to the estimate of the number of adult females because the surveys (which maintained a constant level of effort) provided complete coverage of the inshore areas in which the females occur. With respect to (a), so-called ‘suburban whales’ may comprise a small component of the North Atlantic population. Because they occur only intermittently in the areas surveyed, the estimates above may be biased downwards (SC/M98/RW2).

10.2.2.2 EASTERN NORTH ATLANTIC

There have been only sporadic sightings in this area (Brownell, 1986).

10.2.2.3 WESTERN NORTH PACIFIC

Data from Japanese sightings cruises conducted during 1989, 1990 and 1992 provide estimates of abundance of right whales in the Okhotsk Sea (SC/M98/RW11). A total of 2,688 n.miles of track lines uniformly covered the research area (50°-56°N, 143°E, Kamchatka Peninsula). The surveys had been designed to estimate minke whale, not right whale abundance (Buckland *et al.*, 1992; Miyashita and Shimada, 1994). The hazard rate model was applied for sixteen primary right whale sightings within a perpendicular distance of 1.5 n.miles and the effective search half-width was estimated at 0.940 n.miles (CV = 0.217). The mean school size corrected for size-bias was 1.75 (CV = 0.169). Abundance in the research area was estimated at 922 (CV = 0.433; 95% CI 404, 2,108). This estimate is biased downward because: (a) the Russian territorial waters (12 n.miles zone), where right whales are known to occur, were not surveyed; (b) the probability of detection on the track line ($g(0)$) was assumed equal to one; and (c) the survey was conducted in closing mode. One factor was noted as possibly positively biasing the estimate: sightings in the eastern area were conducted in August whereas those in the western area were conducted more in September, so that there was a possibility of double countings if there was westward migration over this period.

The Workshop notes the wide confidence intervals associated with the above estimate of abundance. It believed it was important to clarify the status of this population which had been thought to be at very low levels. It therefore **recommends** that a further sightings survey be undertaken following the guidelines for surveys adopted by the Scientific Committee (IWC, 1997c). It **recommends** that the Committee requests the Commission to urge relevant member nations to cooperate in this exercise and in particular that the Russian Federation is urged to grant permission for vessels to survey within 12 n.miles of the Okhotsk Sea coast.

10.2.2.4 EASTERN NORTH PACIFIC

Recent sightings of small groups of right whales in the eastern North Pacific are encouraging, but no confirmed sightings of calves have been recorded this century.

10.3 Estimates of initial abundance

The Workshop agreed that there was some merit in attempting to obtain an estimate of the initial population size for southern right whales by extrapolating backwards from estimates of current abundance using a modelling approach similar to that previously used by the Scientific Committee. Previously published estimates of initial population size are given in Table 6.

Table 6

Published (and other available) estimates of initial population size for right whale populations

Area	No. whales	Time	Reference
S. Atlantic	At least 17,000	1830	IWC (1986:9)
New Zealand	10,000	ca. 1829	Dawbin in RW37
Australia	15,000	?	Dawbin in RW37
NW Atlantic	12,000-15,000	1530	Gaskin (1991)
NW Atlantic (US)	> 1,000	1680s	RW4

The population simulation approach adopted requires:

(1) agreement on a population model and required population parameters;
(2) estimates of current abundance;
(3) an agreed catch history.

The Workshop agreed that it was only possible to attempt the above analysis for the entire Southern Hemisphere combined. Although in principle it could also be attempted for specific breeding populations within the Southern Hemisphere, that would necessitate historical catches being assigned to these different populations. Discussions under Item 7 revealed that assigning catches made outside the breeding grounds would be extremely difficult and was certainly not a task that could be achieved at this meeting.

10.3.1 The model

To obtain an estimate of the initial pre-exploitation size K of a population, the following difference equation was used to describe the dynamics of a whale stock:

$$P_{t+1} = P_t + r P_t \left(1 - \left(\frac{P_t}{K}\right)^{\mu}\right) - C_t \qquad (1)$$

where:

P_t is the total population size in year t;
r is the intrinsic growth rate (the maximum the population can achieve, when its size is very low);
μ is 2.39 (this sets the *MSY* level, $MSYL = 0.6K$ as conventionally assumed for such analyses by the IWC Scientific Committee); and
C_t the total catch (in terms of number of animals) in year t.

Assuming $P_0 = K$, and given values for the parameter r as well as a catch history series, equation (1) can be used to generate population size estimates P_t corresponding to a particular value of K for each of years $t = 0, \ldots t_{current}$ where year 0 corresponds to the pre-exploitation period and $t_{current} = 1997$. Given a population size estimate $P_{t^*}^{obs}$ for a recent year t^*, where $t^* \leq t_{current}$, a 'best' estimate for K can be found by successively substituting different values for K until the difference between the model estimate $\hat{P}_{t^*}^{obs}$ and observed population size estimate $P_{t^*}^{obs}$ is sufficiently small.

Equation 1 is the population model used in the *Catch Limit Algorithm* of the Revised Management Procedure (IWC, 1993). This provides a good approximation to the sex-and-age structured model 'BALEEN II' (de la Mare, 1989) conventionally used by the Scientific Committee for stock assessment computations. The approach described above is an example of what is described as 'Hitting with fixed MSYR' in such exercises.

Since it was not possible to carry out the analyses by management unit, an average of the growth rate estimates in Table 4 of $r = 0.075$ was assumed. For comparative purposes, computations were also performed using $r = 0$ and $r = 0.04$. The scenario using $r = 0$ is equivalent to a method for estimating K by simply summing all historical catches plus the current population size estimate, i.e. assuming zero surplus production. Performing computations over a range of r values therefore effectively provides a means of assessing to what extent the surplus production characteristics of the resource were able to compensate for population decreases as a result of whaling.

10.3.2 Current population size

t^*_{current} was set at 1997 and, where necessary, female population size estimates were adjusted to a '1997' estimate by assuming an annual growth rate of 0.075. An estimate of the total number of adult females in the Southern Hemisphere in 1997 was obtained by combining the population estimates for the different breeding stocks (Table 4). The estimate obtained (1,607 adult females) is negatively biased because: (a) it excludes contributions from areas about which no information on current abundance is available; and (b) the population size in areas with recent population estimates of < 10 adult females was set at zero. However, it may also be larger than appropriate because: (a) the value used for the relatively large Argentinian population involves an extrapolation over a seven year period; (b) the higher of two estimates for the relatively large South African population was adopted; and (c) the value used for Tristan da Cunha may be too high (see footnote in Table 4).

Current population size estimates for the various breeding stocks in the Southern Hemisphere are all expressed in terms of the number of reproductive females (and therefore exclude the number of males and immature females).

Let N_0 be the number of newborn whales, N_1 be the number of one year old whales, N_2 the number of two year old whales in a particular year and so on. Given the survival rate s and the growth rate r, N_{i} can be represented in terms of N_0 as follows:

$N_1 = N_0 se^{-\mathrm{r}}$
$N_2 = N_1 se^{-\mathrm{r}} = N_0 se^{-\mathrm{r}} se^{-\mathrm{r}}$
$N_3 = N_2 se^{-\mathrm{r}} = N_0 se^{-\mathrm{r}} se^{-\mathrm{r}} se^{-\mathrm{r}}$, and so on.

An annual average estimate of $s = 0.98$ (see Table 4) was assumed for simulation purposes. Furthermore, an average estimate of the age of first parturition of $t_m = 9$ years (Table 4) was also assumed.

Using the above estimate of t_m, the number of juveniles in the population is calculated as the sum of N_0, N_1, ... N_8, yielding $N_0 x$, where x is given by:

$$x = 1 + R + R^2 + \ldots + R^8$$

and $R = se^{-\mathrm{r}}$.

The number of adults in the population is calculated as the sum of N_9, N_{10}, ... N_∞, yielding $N_0 y$, where y is given by:

$y = R^9(1/1\text{-}R)$.

The ratio $x/(x+y)$ then gives the proportion of females which are juvenile or calves.

Let N_i^T denote the total number of whales in the population in year i. This is obtained from the number of adult females in the population using the relation:

$$N_i^T = 2N_i^F (x + y) / y,$$

where N_i^F denotes the number of females in the population in year i. The conversion equation above assumes a 50:50 sex ratio and a constant survival rate after birth.

In this case, the ratio of juveniles and calves to adults is estimated to be about 1.4:1. It is important to note, however, that this relatively high ratio is a consequence of the relatively high population growth rate. In the North Atlantic, juveniles and calves account for only 26-31% of the population (see Item 9.2.1).

The estimates of total population size obtained for each of the breeding stock areas included in the analysis are presented in Table 4. Together they provide an estimate for P_{1997}^{obs} of 7,571 whales in the Southern Hemisphere for use in the population model. However, noting the coarseness of many of the assumptions used to arrive at this figure, the Workshop emphasised that the current best estimate of the total number of right whales in the Southern Hemisphere is preferably expressed as 'about 7,000'.

10.3.3 Historical catches

Catch data for the Southern Hemisphere were considered under Item 8. These data have been revised (because some of the catches indicated to have occurred in a particular area are subsumed within estimates given for another area) to obtain estimates of the total Southern Hemisphere catch by decade (Table 6). Catch data were modified further by adjusting for struck and lost (and presumed dead) rates, which ranged from 1.2-1.5 times the landed catch, depending on the fishery (IWC, 1986a, p.31). A base-case catch history series was obtained by assuming an average loss rate of 1.35 (Table 7). Where there was ambiguity as to whether or not catches were duplicated in the various series available, the base-case catch history assumed the average of the two extremes of assuming no duplication at all and of assuming duplication for every instance that this was suspected. 'High' and 'low' series of catches were also developed based on these two extremes (of possible duplication) together with extreme values of the range for struck and lost. In all instances the catch data per decade were converted to annual estimates by assuming an even distribution of catches over each ten-year period.

It is important to note the following caveats:

(1) the available catch data do not include substantial British catches whose total magnitude is unknown - in some cases, e.g. off Brazil and South Africa, where they were large, they have been included whereas in others, e.g. off Australia and New Zealand, they have not, and might have comprised around one tenth of the total, i.e. around 10,000;

(2) the composition of the catches was assumed to comprise equal proportions of males and females. Because female whales constituted a larger proportion of many of the catches (particularly those taken by shore whalers) and because their selective removal would have had a greater impact on a population's rate of growth, by ignoring a sex disaggregation of catches the analysis above gives a likely lower bound for *K*;

Table 7

Grand totals for Southern Hemisphere catches by decade (see Item 8) – Base-case, High case and Low case.

	Estimated removals[1]		
Decade	Base-case	High case	Low case
1770s	8,197	8,197	8,197
1780s	11,390	11,990	11,390
1790s	12,893	14,173	12,839
1800s	10,559	12,739	9,312
1810s	3,837	4,336	3,436
1820s	14,069	15,689	12,273
1830s	53,091	59,821	48,230
1840s	21,488	24,380	19,730
1850s	4,901	5,528	4,458
1860s	2,639	2,965	2,387
1870s	1,029	1,158	931
1880s	1,012	1,138	916
1890s	290	338	276
1900s	753	798	718
1910s	677	686	675
1920s	104	110	104
1930s	122	123	122
1940s	2	2	2
1950s	163	164	163
1960s	3,099	3,099	3,099
1970s	60	60	60

[1] Large catches in some areas by British (and possibly other European) whalers in the late 18th and 19th centuries are not fully taken into account.

(3) catches were assumed to have been taken in proportion to the different components of the population (including calves), which therefore ignores any disaggregation of catches on the basis of age.

10.3.4 Results

Fig. 5 shows the results of this population modelling exercise for the base-case catch series and for various values of *r*. The assumption of no historical surplus production suggests an initial total population size of about 160,000, but this drops to about 60,000 if the level of surplus production suggested by current growth rates ($r = 0.075$) is taken into account. This points to the importance of incorporating surplus production considerations into estimates of initial abundance.

Fig. 6 shows trajectories for the case $r = 0.075$ for each of the base, high and low historic catch scenarios. Only the early part of the estimated population trajectory changes to any marked extent, suggesting that the uncertainties in catch history considered translate into a possible range for initial total population size of 55,000-70,000 whales.

Fig. 7 shows the $r = 0.075$ trajectory for the base-case catch series on an expanded scale over the period from 1880. Overall this trajectory illustrates: (i) the rapid depletion of the stock following the substantial catches of the early-mid 1800s; (ii) the almost complete lack of any sign of a recovery after 1850, for almost 100 years, followed by a gradual recovery after protection in 1935; and (iii) the effects of the illegal Soviet catches of the 1960s in delaying further recovery by about 20 years.

The trajectory also indicates that the entire Southern Hemisphere population reached a low point of about 300 animals in 1920, corresponding to an adult female population of about 60 individuals only. Intuitively, this

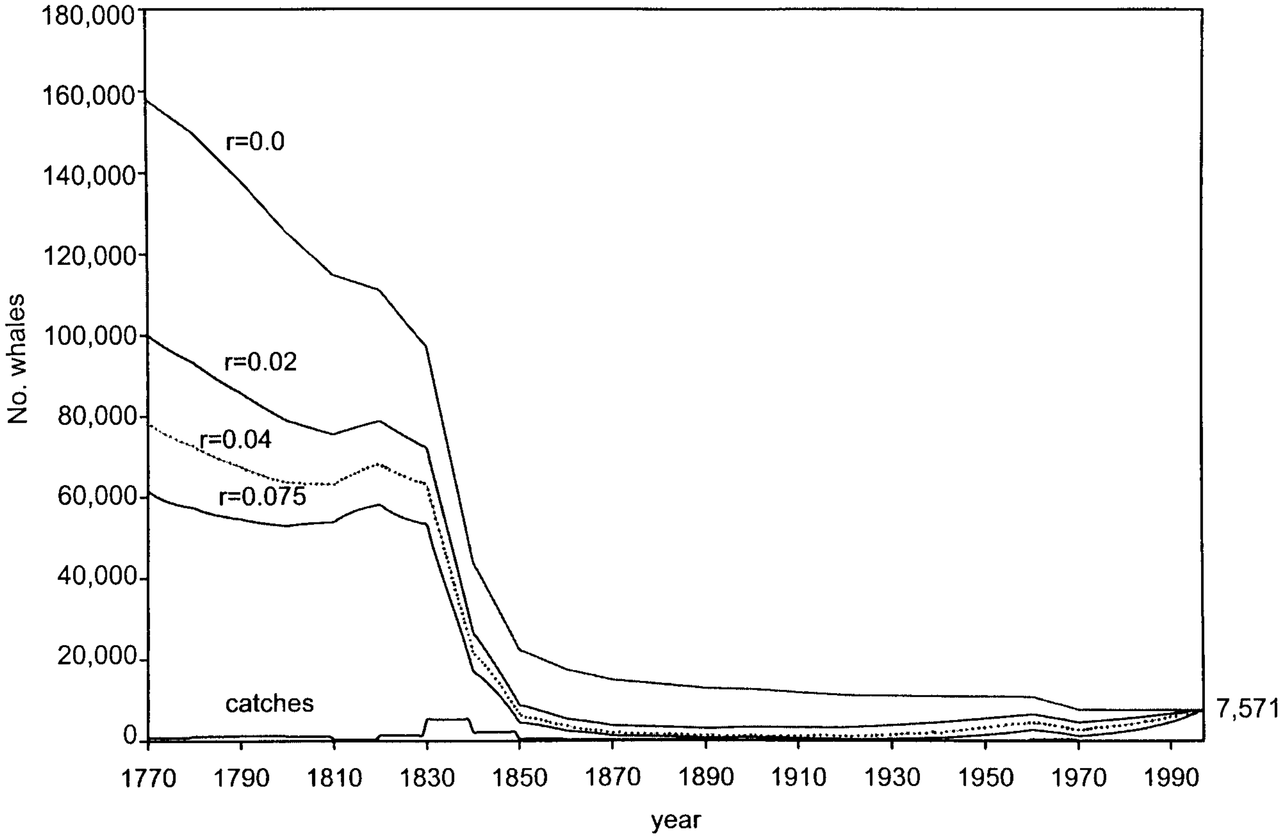

Fig. 5. Total population size and catches (all Southern Hemisphere combined).

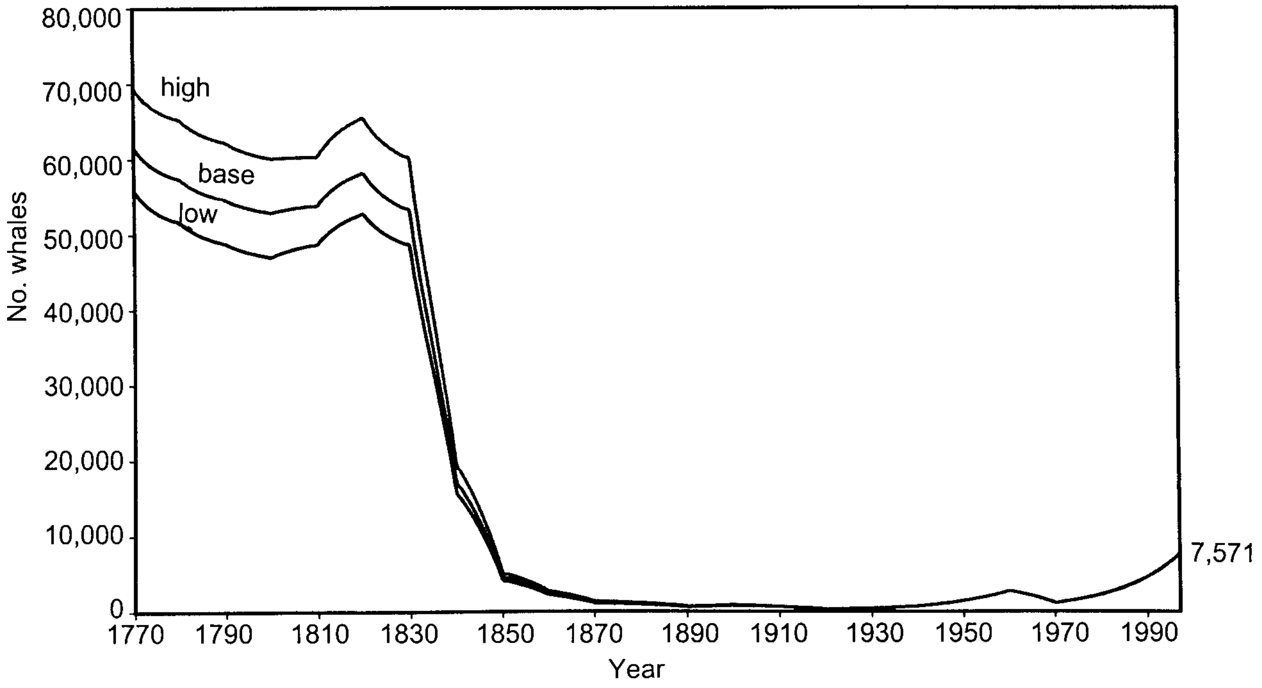

Fig. 6. Total population size (all Southern Hemisphere combined).

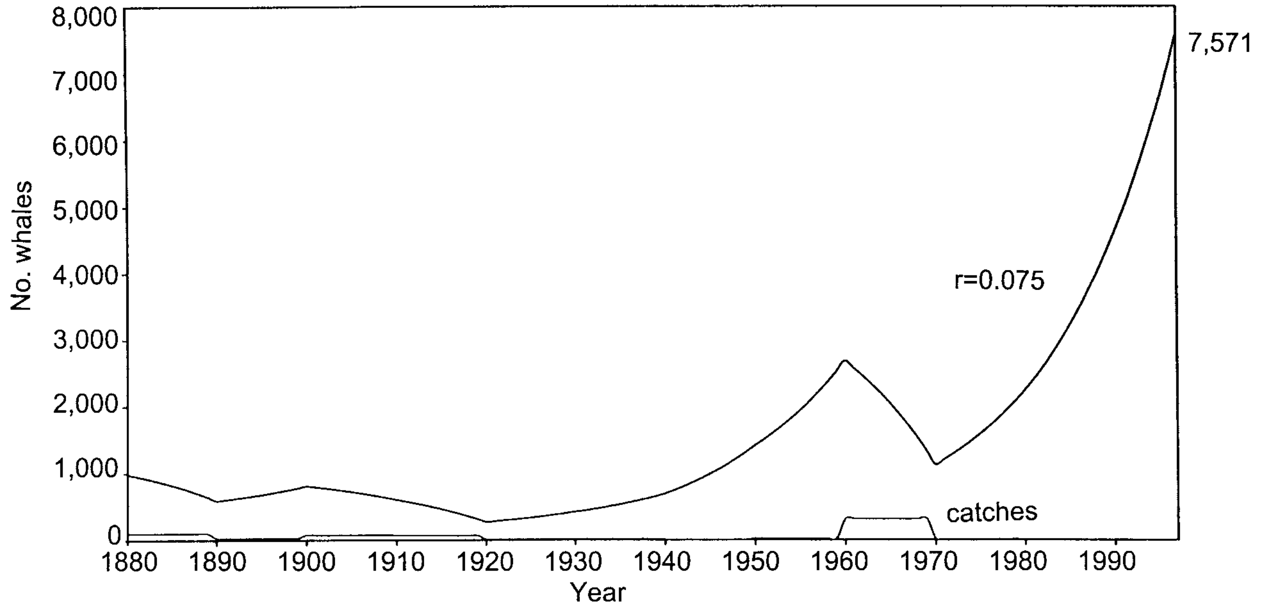

Fig. 7. Total population size and catches for 1880-1997 (all Southern Hemisphere combined).

number seems very low, but as, for instance the first right whale sightings for the whole Australian coast during the 20th century were reported only for the 1950s in the scientific literature (Chittleborough, 1956), right whale numbers in at least some of the current major concentration areas must have been very low. Alternatively, if there had been depensation effects (not allowed for in the current model), the minimum number in 1920 would have been higher than 300. However, the Workshop noted that there were still uncertainties surrounding both the historical catch series and the current projection and that aggregating the different breeding populations as in the current computations might distort impressions of lowest sizes; the exact numbers generated by the model should therefore be treated with caution.

In summary, the population modelling exercise confirms that the Southern Hemisphere population of right whales is still heavily depleted, perhaps at about 10% of its initial size (but see the caveats discussed above). The population model used suggests that the current growth rate should continue for some time before any marked density-dependent reduction might come into play, implying that the population as a whole should continue to grow with a doubling time of about 10 years for at least the next decade.

The Workshop recognised that the exercise above merely represented an initial attempt to determine the population trajectory and initial population size for southern right whales. It **recommends** that at least the following three modifications of the analysis above should be attempted in the future.

(1) Hypotheses need to be developed to permit catch data to be allocated to management units based on breeding stocks. This will enable estimation of initial abundance for each of the breeding stocks for which there is considered to be sufficient information.
(2) The BALEEN II (and HITTER-FITTER) models should be used to take sex and maturity disaggregation of historic catches into account.
(3) The consequences of depensation at low population size should be explored.

11. WORLDWIDE COMPARISON OF POPULATION STATUS

The Workshop noted that several Southern Hemisphere populations (those off Argentina, Australia and South Africa) are increasing at annual rates of the order of 7-8%. There is evidence that the New Zealand sub-Antarctic population has increased (at least at the Auckland Islands) since the 1940s. However, systematic research in the area has not yet been carried out for long enough to estimate whether the population is currently increasing. Nevertheless, there are other areas where major whaling operations were conducted for which there is no sign of recovery, although recent information is either absent or incomplete. The Workshop **recommends** that research be undertaken to determine the current status of right whales in these areas. For the three best known areas (Australia, Argentina and South Africa), the current estimated total abundance is about 7,000 (see Item 10.2 and Table 4). Should these populations continue to grow at 7-8% they will double in ten years. There have been no catches in the Southern Hemisphere since the early 1970s and there is no evidence that human-related mortality is affecting population recovery.

The situation in the North Pacific differs greatly between the western and eastern populations. Sightings survey estimates for the summer feeding ground indicate an abundance of around 900 (95% CI 404; 2,108) in the Sea of Okhotsk. However, the Workshop expressed considerable concern about the situation in the eastern North Pacific. Over the past forty years, most sightings have been of single whales. During the last few years, small groups of right whales have been sighted in the eastern North Pacific. This is encouraging but there have been no confirmed sightings of calves in the 20th century and the North Pacific animals are known to have been subjected to large illegal Soviet catches in the early 1960s. The Workshop **recommends** that research efforts to better understand the status of this population and any human-related problems it may have should be greatly expanded as a matter of urgency.

The situation in the North Atlantic gives great cause for concern. The eastern North Atlantic population probably numbers only in the low tens of animals and its future remains questionable. The Workshop expressed considerable concern about the situation of the western North Atlantic population. Whereas it may have increased since protection in 1935 (e.g. see Reeves *et al.*, 1992) and may have been still increasing at a modest rate (about 2.5%) in the 1980s (Knowlton *et al.*, 1994), more recent data (near-failure of calf production from 1993-95, increased calving interval, and a relatively large number of human-induced mortalities) suggest that this modest recovery rate (by comparison with the Southern Hemisphere) may not have continued in the 1990s. North Atlantic parous females show an increase between 1985 and 1997 but with an apparent long-term oscillation in recruitment (Annex G). These features, together with the lack of significant increase in calving rates, support the need for age-structured models to account for the complexity of this population's dynamics. It is now unclear whether the population is declining, stationary, or increasing and the best estimate of current population size is only 300 animals (see Item 10.2). The Workshop **recommends** that, as a matter of urgency, increased efforts be undertaken to determine the recent trajectory of this population.

The Workshop noted the high rate of known entanglement and ship strikes in the western North Atlantic; not all dead whales are recorded, especially when they die, or are killed, offshore. In addition to these physical mortality factors, the western North Atlantic population shows a significantly increased calving interval and decreased fecundity compared with the Southern Hemisphere. The Workshop agreed that inbreeding, organic chemical exposure and nutritional factors need further study (see Item 12). It **recommends** that comparative studies are undertaken to try and determine factors that may explain the difference between Northern and Southern Hemisphere reproductive parameters.

The Workshop concluded that any human-related mortality could be detrimental to the long-term survival of the western North Atlantic population. Efforts to reduce human-induced mortality are of the **greatest urgency** if the chances of the western North Atlantic population recovering are to be maximised. The Workshop **draws the Commission's attention** to its recommendations under Item 14.

12. FACTORS POTENTIALLY AFFECTING RECOVERY

12.1 Genetic diversity and genetic problems in small populations (inbreeding depression)

12.1.1 Context and definitions

The Workshop noted that the amount of variation in a population is a consequence of long-term effective population size, and the mutation rate and selective coefficient of the genetic marker under analysis. Loss of genetic variation in small populations is an inevitable consequence of drift and can be modelled with simple equations that assume selective neutrality and random mating. In general, when populations are small (i.e. less than 500 census individuals) there is an increased chance of individuals sharing alleles that are identical by descent. This process is termed inbreeding. However, the distinction between loss of variation, inbreeding and inbreeding depression requires clarification. Inbreeding depression is an observed phenomenon where reduced reproductive fitness is correlated with a loss of genetic variation. This is generally a greater problem in formerly large, outbred populations which have been subsequently reduced in size. Although inbreeding depression is almost invariably associated with populations with reduced levels of genetic variation, there are populations with low levels of measured variability which are not known to suffer from a loss of reproductive success.

The Workshop examined the evidence concerning low genetic variation in some right whale populations and in particular whether there is evidence to link low genetic variation with reduced reproductive success in the western North Atlantic population. Currently, only anthropogenic problems facing this population can be addressed through management efforts (see Item 14). However, an understanding of the likelihood of inbreeding depression will be important in assessing the population's vulnerability.

12.1.2 Genetic diversity

Estimates of diversity were available from a number of papers presented at the Workshop or previously published (SC/M98/RW5, 21, 23; Schaeff *et al.*, 1991; 1993; 1997; Malik *et al.*, 1999).

Available data involved the following molecular methods/diversity estimation: fingerprinting/bandsharing; microsatellites/%polymorphic loci; average number of alleles per locus; and heterozygosity.

The Workshop noted that mitochondrial sequence data allow estimation of genetic diversity at two levels (resolutions): nucleotide diversity which incorporates nucleotide divergence between haplotypes; and haplotype diversity which considers only categorical differences between haplotypes (Nei, 1987).

12.1.3 Estimating changes in genetic diversity

12.1.3.1 HISTORICAL RECONSTRUCTIONS

The Workshop reviewed two papers that presented theoretical models for examining probable loss in genetic diversity (Amos, 1996; Seger, 1998). Whilst these models were considered instructive within themselves, it was agreed that they were not entirely applicable to the situation for right whales. It was also noted that modelling based on heterozygosity alone may be an insensitive measure of variation loss.

The Workshop discussed the results in Rosenbaum *et al.* (2000). Sequence data from the mtDNA control region of six samples from the eastern and western North Atlantic in the late 18th/early 19th century were compared with extant samples from the western North Atlantic. Of the five haplotypes found among the extant samples, four were also represented in the historical samples. The levels of haplotypic diversity among historical versus extant samples were found to be comparable. Because no unique alleles were identified among the historical samples, the study provides no evidence of loss of diversity in the western North Atlantic during the last hundred years. However, given the confidence limits associated with the maximum likelihood estimate from the small sample size, some loss of genetic variation may have occurred that would not be detected.

12.1.3.2 CURRENT ESTIMATES OF DIVERSITY AND VALIDITY OF COMPARISONS

The Workshop considered genetic diversity comparisons that have been made between the western North Atlantic and the southwest Atlantic/southwest Pacific using estimates from multilocus fingerprinting, microsatellites and mtDNA sequence data. Fingerprinting data (Schaeff *et al.*, 1997) showed significant differences in genetic diversity between presumably unrelated right whales in the western North Atlantic and South Atlantic. Preliminary microsatellite analyses also suggested a lower level of genetic diversity among western North Atlantic right whales (SC/M98/RW5). Available mtDNA sequence data showed similar levels of nucleotide diversity for the South Atlantic (SC/M98/RW21) and the western South Pacific (SC/M98/RW23), but which were considerably higher than those for the western North Atlantic (SC/M98/RW5). Comparisons of haplotype diversity between the western North Atlantic and South Atlantic also showed lower levels in the western North Atlantic, although western South Pacific haplotype diversities were comparable to those for the western North Atlantic. These results all point to a lower level of overall genetic diversity in the western North Atlantic, at least relative to the South Atlantic. The Workshop identified two possible and not mutually exclusive explanations for this: (1) western North Atlantic diversity may always have been lower than the South Atlantic; (2) a loss of diversity may have occurred in the western North Atlantic as a result of a long period of exploitation (i.e. population bottlenecks). The difference in haplotype diversity estimates between the southwest Atlantic and the southwest Pacific might be similarly explained.

12.1.4 Recommendations for improving diversity estimates

The Workshop **recommends** that further theoretical modelling should be undertaken that considers multiple measures of diversity and the use of appropriate models for the molecular marker chosen. Theoretical models (e.g. PVA) should be used to account for multiple population bottlenecks in accordance with the exploitation history of right whales and stochastic factors.

The Workshop agreed that the best measure of a loss of genetic diversity would involve analysis of historical samples *versus* extant samples. It noted the potential for use of samples from the years 1530-1610 in the western North Atlantic (Cumbaa, 1986), although obtaining a sufficient sample size for the analysis may be difficult. It **recommends** that the feasibility of such a study be examined. Based on the available data, the first priority for genetic analysis of historical diversity should be to sequence the mtDNA control region for comparative purposes.

Because estimates of haplotype diversity are dependent on the length of sequence examined, a longer segment of DNA is likely to reveal more haplotypes. The Workshop **recommends** that the effects of using differing sequence lengths for comparisons of haplotype diversity estimates be explored by sensitivity analysis.

The Workshop also noted that different estimates of haplotype mtDNA diversity in the western North Atlantic have resulted from two different sampling schemes: (1) the direct assignment of haplotypes from sequence data of sampled individuals ($n = 180$); (2) the direct plus inferred assignment of haplotypes using sightings records of photo-identified individuals ($n = 269$; SC/M98/RW5; Malik *et al.*, 1999). It **recommends** that further consideration be given to the choice of sampling scheme for current as well as historical comparisons of diversity.

12.1.5 Inbreeding depression

The Workshop identified a number of trends that would be consistent with inbreeding depression in a population:

(1) high juvenile mortality (non-anthropogenic);
(2) low fertility (proportion of reproductive females);
(3) low fecundity;
(4) decreases in recruitment rates;
(5) decreases in population increase rates;
(6) increases in diseased animals.

Many of these expected trends have been identified in the western North Atlantic population (SC/M98/RW44; Knowlton *et al.*, 1994; Schaeff, 2001) but it is difficult to link them directly with an inferred loss of genetic variability. Correlations between observed trends and genetic diversity estimates may lend further support to the hypothesis of inbreeding depression. For example, Schaeff *et al.* (1993) observed lower than expected bandsharing among first degree relatives which could be a consequence of unsuccessful matings between genetically similar individuals (a direct measure of inbreeding depression). Incest avoidance could also account for this pattern (SC/M98/RW44). Since the expected value in Schaeff *et al.*

(1993) was based on matings between presumably unrelated animals, such inbreeding avoidance would also require that right whales avoid mating with animals that are not close relatives but nonetheless share common alleles.

12.1.5.1 RECOMMENDATIONS

The Workshop agreed that current evidence for inbreeding depression in the western North Atlantic population of right whales is inconclusive. An improved understanding of the extent of inbreeding depression in this population could be gained through detailed pedigree analysis similar to that used to quantify inbreeding depression in captive breeding colonies (Ralls *et al.*, 1979). To this end, the Workshop **recommends**:

(1) estimating levels of heterozygosity among females and correlating them with female reproductive success as measured by all relevant reproductive parameters (parallel correlations of male reproductive success and heterozygosity could be performed if information on paternity is available, see (2));
(2) paternity analysis using microsatellite loci to estimate male effective population size and reproductive success;
(3) testing for an excess of heterozygotes among offspring of known parentage to corroborate the findings of Schaeff *et al.* (1997) that homozygote offspring are less viable.

12.2 Trophic relationships and body condition

12.2.1 Trophic relationships

The trophic structure and productivity of a habitat profoundly affect distribution, behaviour and fitness (SC/M98/RW29, SC/M98/RW30, SC/M98/RW31 and SC/M98/RW39). Relevant indices of fitness in right whales include reproductive parameters discussed elsewhere in this report (Item 9.2.3) and body condition. Food density studies suggest that, in the western North Atlantic, plankton patch condition could be used to evaluate the quality of right whale feeding habitat (SC/M98/RW7 and SC/M98/RW45). However, with few exceptions (Tormosov *et al.*, 1998), direct observations of feeding are not available from most of the presumed feeding areas. Isotope analyses of baleen and prey may be useful in identifying feeding areas.

12.2.2 Body condition

Reduction in habitat quality in the western North Atlantic could be reducing fecundity in northern right whales. Studies of land mammals indicate that fertility is affected by an insufficiency of body fat (Thomas, 1990), thus measurement of fat stores may be an index of fertility. It is now possible to measure blubber thickness of live animals at sea (SC/M98/RW27). From Soviet catch records it appears that there may be little seasonal variation in blubber thickness in individuals (Tormosov *et al.*, 1998), however it has been hypothesised that there may be variation in blubber thickness between those that are and are not reproductively successful. In a preliminary comparison of blubber thickness in northern and southern right whales, Moore suggested that blubber may be thinner in western North Atlantic right whales than predicted by regressions of blubber thickness and body length based on Soviet catch data for southern right whales (Tormosov *et al.*, 1998).

12.2.3 Recommendations

The Workshop **recommends** that:

(1) further studies of isotope ratios in baleen and prey species be carried out to try and link calving to feeding areas (and see Item 7.5) so that issues of habitat degradation can be examined in the context of population parameters;
(2) studies be undertaken on the trophic structure and productivity of right whale habitat (and see Item 12.3.4) for the assessment of possible prey availability limitations, habitat quality and feeding thresholds, causes of occupation and desertion of habitats, prediction of habitat use patterns (including remote sensing to predict as yet unidentified habitats);
(3) a comparative study be carried out on blubber thickness and lipid content in cow-calf pairs in the western North Atlantic and southern right whale populations;
(4) appropriate girth and blubber thickness measurements be made wherever possible during the examination of all right whale mortalities (see Item 9.1.3).

12.3 Anthropogenic factors

12.3.1 Chemical pollution

Contaminant data on right whales (Woodley, 1991; SC/M98/RW24) have been restricted to those from biopsy-derived samples apart from one necropsy sample. Wet-weight values were all in the parts per billion range. These data appear to be relevant to the whole animal given that lipid-normalised contaminant burden is comparable between different blubber depths and locations in large whales (Gauthier *et al.*, 1997), although such an extrapolation was earlier questioned for fin whales (Aguilar and Borrell, 1991). No obvious geographic chemical trends were evident in samples from South Georgia and the western North Atlantic. Notwithstanding these low concentrations of accumulated organic compounds, a biochemical assay for cytochrome P450 1A (CYP1A) in biopsied dermal endothelia was significantly elevated in right whales feeding in the Bay of Fundy, Canada, as compared to those from calving habitats in both hemispheres, and from a southern feeding habitat near South Georgia (SC/M98/RW24). This may reflect chronic exposure of the Bay of Fundy animals to non-bioaccumulating compounds such as petroleum-derived polynuclear aromatic hydrocarbon or possibly natural compounds.

The Workshop **recommends** that:

(1) extant and future necropsy and biopsy samples should be analysed for PCBs, pesticides and dioxins;
(2) routine monitoring of CYP1A expression in right whales should be implemented;
(3) copepod and krill samples from known or presumed feeding habitats in both hemispheres should be analysed for PCBs, pesticides and dioxins.

It also **recommends** that local, regional and national authorities responsible for right whale habitat should develop contingency plans for oil and chemical spills.

12.3.2 Entanglement in fishing gear

A summary of available data on entanglements is given in Table 8. It should be noted that since most entanglement events go unreported, these are minimum values. Rates of entanglements can be monitored over time through examination of photographs of entanglement scars collected primarily from shipboard surveys (SC/M98/RW28). Data from South Africa (SC/M98/RW25), Brazil and the western North Atlantic (SC/M98/RW28) indicate that in most cases whales free themselves. However, in damaging and/or persistent entanglements, deaths have been reported (SC/M98/RW8 and RW25). The greatest impediment to successful rescue is lack of entanglement reporting. Disentanglement efforts greatly improve the whale's chances of survival if trained disentanglement teams are available (SC/M98/RW47). A number of steps have been taken to reduce the likelihood of right whale entanglement, including: (a) gear modifications (or proposed modifications) to reduce the likelihood of entanglement and to facilitate the whale freeing itself (USA); (b) time and area closures of certain fisheries (USA); (c) complete prohibition of fishing activities in protected areas (Head of the Bight, Australia and state waters in Florida, USA). In addition, data from observers that accompany fishing operations help lead to quantification of entanglement rates by fishery operation observers (USA).

The Workshop **recommends** that:

(1) research continues on methods to reduce right whale entanglements in fishing gear;
(2) entanglement rates and the success of steps to reduce entanglement are determined and monitored (e.g. through periodic analysis of scarring rates and levels of severe entanglement in photo-identification databases);
(3) if the above monitoring indicates that protective measures are insufficient, they are upgraded as appropriate;
(4) disentanglement programmes (including training from experienced persons) are established where appropriate;
(5) consideration is given to the prohibition of any gear that might entangle right whales in high use habitats, and especially in calving, breeding or feeding areas and sanctuaries.

12.3.3 Shipping

Right whale injuries and mortalities are attributed to ship strikes on the basis of external signs of trauma and necropsy results indicating internal trauma. External evidence of vessel collision has been documented on living and dead right whales in both hemispheres (Annex H).

Propeller lacerations demonstrate that vessels of various sizes strike right whales, but that large vessels are most often associated with fatal encounters, based on the presence of larger propeller cuts, broken bones, severed flukes and broad areas of blunt trauma (SC/M98/RW8 and SC/M98/RW28). Of over 40 known or suspected encounters, on only three occasions has a particular vessel been identified as killing right whales and information on vessel speed is known for only two of these events (Annex H).

Right whale behaviour may make them more vulnerable to ship strikes than other large whale species. It has been observed that right whales engaged in surface active behaviour, skim feeding and nursing, seem to make no effort to avoid the approach of small boats. Other general factors that may increase whale vulnerability to shipping include reduced ship noise in front of the bow and hydrodynamic effects of ships which could draw a whale into the ship (Knowlton *et al.*, 1997). Little is known about right whale behaviour in the vicinity of large ships.

In the western North Atlantic, where ship strikes have been of increasing concern, efforts are underway to reduce them. Efforts include aerial surveys to notify mariners of the location of right whales on a real-time basis (SC/M98/RW6), educational pamphlets distributed to mariners, delineation of major right whale habitats on nautical charts, broadcast Notices to Mariners, and the inclusion of information in the Coast Pilot and Sailing Directions (documents that must be on the bridge of all large vessels), describing right whale distribution and precautionary measures. Other possibilities that have been explored are measures through the International Maritime Organisation (IMO) such as mandatory ship reporting and ship routing. These measures have to be proposed by a member country and approved by the IMO.

12.3.3.1 RECOMMENDATIONS

The Workshop **recommends** that the Scientific Committee requests the Commission to:

(1) urge its member nations to:
    (a) initiate or expand preventative measures including Notices to Mariners, notifications on charts and informational brochures in or to other areas where right whales and high levels of shipping overlap;

Table 8

Right whale entanglement in fishing gear.

Location	Number of known/ reported entangled	Known (or presumed) mortality	Type of gear	Entanglement scarring in the population (%)	Successful disentanglement (by humans)	Source
South Africa	14 (7 more possible) (1963-1997)	5 (1 of these 'possible')	Crayfish trap lines, longlines, shark nets; spearfishing float lines; boat anchor lines	3-4	7	RW25
Brazil - Santa Catarina	approx. 4/yr (1989-1997)	1 calf (1986) 1 unconfirmed calf (1996)	Fixed nylon gillnets of artisanal fishery for sharks and sciaenids	None observed	-	Palazzo, pers. comm.
	4 (1982-93)	-	Unknown	-	-	Lodi *et al.* (1996)
Brazil - Sao Paulo Coast	1 (1996)	1	'Evidence of entrapment'	-	-	RW35
	2 (1982-83)	-	Unknown	-	-	Lodi *et al.* (1996)
Brazil - Rio de Janeiro	3 (1981-92)	-	Unknown	-	-	Lodi *et al.* (1996)
Argentina	3 (1969-90)	0	1 rope through baleen; 2 seed mussel ropes	<2.6%	-	RW13
Australia	4 (1991-1997)	0	Rope/netting; 1 individual towing buoy; pot line	None observed	1 reported	Burnell, pers. comm.
Auckland Islands	2 (1995-1997)	-	1 heavy rope around tailstock; 1 unknown	None observed	-	Patenaude, pers. comm.
North Pacific	2 (1986,1992)	1	1 salmon drift gillnet around tail stock; 1 thick 'rope' around tail	No data	-	RW10, RW11
W. North Atlantic	24 (1980-1998)	2 known, 8 presumed	Lobster gear; pelagic driftnets; sink gillnets	61.6 (from shipboard)	6 (estimated)	RW8, RW28

(b) develop mitigating options, areas to be avoided, early warning systems, sonar detection of whales, acoustic deterrents, and the shifting of shipping lanes and reductions in ship speed;

(2) seek cooperation from the IMO to provide protection for right whales, including but not limited to mandatory ship reporting and ship routing, especially where commercial vessels are entering calving, breeding or feeding areas.

It also **recommends** that studies be undertaken to determine how whales respond to approaching ships to determine the acoustic characteristics, vessel speeds or other features of ships that put right whales at particular risk.

Given the serious concern over the status of western North Atlantic right whales (see Item 11), the Workshop developed specific recommendations for that area. These are given in Annex I.

12.3.4 Habitat loss

The Workshop identified four categories of right whale habitats (these are not necessarily mutually exclusive):

(1) feeding - areas developing copepod and krill densities that routinely elicit feeding behaviour and are visited seasonally;
(2) calving - areas routinely used for calving and neonatal nursing;
(3) nursery - aggregation area(s) where nursing females feed and suckle;
(4) breeding - locations where mating behaviour leading to conception occurs. Breeding areas are not known for any population.

Given the conservation problems associated with the western North Atlantic stock (Item 11), the Workshop agreed that fine scale characterisation of the area is a priority. Information on southern right whale habitats is also necessary both as a reference for northern right whales and as a baseline for future Southern Hemisphere development (SC/M98/RW14). It can be assumed that there is some level of threshold for various stressors, above which habitat abandonment would occur. Anthropogenic stressors possibly important in displacing right whales from chosen habitat include: noise from close vessels or aircraft; seismic exploration; low frequency active sonar; oil, gas and mineral exploration and production. Food webs may be altered by eutrophication, coastal development and contaminants. Dredging, filling, aquaculture, fishing and recreational activities may also be significant stressors.

12.3.4.1 RECOMMENDATIONS

The Workshop recognised the importance of quantitative studies of right whale habitats. It noted the increasing importance that the Scientific Committee has placed on environmental change and habitat studies (e.g. IWC, 1998). In this context it **recommends** that the Committee considers convening a workshop to develop approaches to quantify key features of whale habitats, including trophic structure; right whales should be considered as a potential key species. Such a workshop would involve a variety of disciplines.

With respect to right whales, particular attention should be paid to comparative studies of Northern and Southern Hemisphere populations. Such studies should: (1) identify the most important parameters characterising right whale habitats and standardise methods to measure them; (2) assess ‘threshold’ levels of disturbance (including noise, temperature, food availability); (3) identify potential sources of disturbance.

Given the potential of noise pollution to affect right whales, the Workshop recognised the importance of understanding the anatomy and physiology of right whale hearing. It noted that such studies are being undertaken by D. Ketten (Woods Hole, USA). It **recommends** that where possible, suitable samples (frozen or fixed middle and inner ears) be collected for Southern Hemisphere animals, following the protocol given in Blaylock *et al.* (1996).

12.3.5 Other

The Workshop recognised three other important issues relevant to the question of the recovery of right whale populations.

12.3.5.1 GULL HARASSMENT

Kelp gull harassment of right whales off Peninsula Valdés, Argentina (Rowntree *et al*., 1998 and SC/M98/RW13) has grown substantially worse in parallel with increasing areas of open waste disposal sites and concomitant growth in gull populations. Avoidance reactions of the whales significantly impact their behaviour and perhaps their distribution (SC/M98/RW13). The Workshop **recommends** that the Commission be asked to urge relevant member governments that these disposal sites be aggressively regulated.

12.3.5.2 CLIMATE CHANGE

SC/M98/RW29 and SC/M98/RW30 considered the impact of climate change on right whales. The issue of climate change has recently been considered in depth by the Scientific Committee (IWC, 1997a). The Workshop **reaffirmed** that the issue may well be of concern with respect to the recovery of right whale populations.

12.3.5.3 MONITORING HUMAN ACTIVITIES

Recognising in particular that the entire known breeding population of New Zealand sub-Antarctic southern right whales concentrates in a very small area and that adverse effects of human-related activities could potentially have a serious impact on this recovering population, the Workshop **recommends** that the Commission be asked to urge the New Zealand Government to carefully evaluate and monitor any existing or proposed human-related activities (e.g. whalewatching, oil or gas exploration, vessel traffic and fishing operations) in the New Zealand sub-Antarctic for any potential negative effects.

12.4 Health and pathology

The Workshop had little specific information available on this topic, but it noted that chronic skin lesions of diverse types including crater-like welts and white patches with indistinct edges have been described in the western North Atlantic. Most welts and patches resolve over a period of months (Hamilton *et al.*, 1995). Scars may remain. No material from this condition has been obtained to date as necropsy derived samples tend to be heavily compromised by decomposition.

12.4.1 Recommendations

The Workshop **recommends** that coordinated studies of health in right whales should be undertaken, from both biopsy- and necropsy-derived samples. Where possible, researchers should:

(a) obtain biopsy and/or necropsy samples of skin lesions for histology and microbiology;

(b) examine histology samples and necropsy data from all right whale mortalities.

Such studies will be greatly enhanced if all workers follow a standard approach to reporting necropsies (see Item 9.1).

13. WHALEWATCHING

The Workshop established a Working Group to consider issues related to right whales and whalewatching. Its report is given as Annex J. The Working Group considered the following: positive and negative aspects of whalewatching; legislation, regulations and guidelines; management recommendations. Recommendations are discussed under Item 14.

14. MANAGEMENT IMPLICATIONS

The Workshop discussions resulted in a number of recommendations that require management action to attempt to reduce or eliminate non-natural mortality of right whales and disturbance to their habitat. These are particularly important for those stocks for which the Workshop has expressed concern over their status.

14.1 Mortality

Under Item 12, the Workshop identified ship strikes and incidental entanglements in fishing gear as the most significant cause of human-induced mortality of right whales.

With respect to ship strikes (see Item 12.3.3), given the serious concern over the status of western North Atlantic right whales (see Item 11), the Workshop **strongly recommends** that the Committee urges the Commission to make every effort to encourage the adoption by relevant governments of the specific recommendations for this area given in Annex I.

In more general terms the Workshop (see Item 12.3.2) **recommends** that the Scientific Committee requests the Commission to:

(1) urge member nations to
    (a) initiate or expand preventative measures including Notices to Mariners, notifications on charts and informational brochures in or to other areas where right whales and high levels of shipping overlap; and
    (b) develop mitigating options, areas to be avoided, early warning systems, sonar detection of whales, acoustic deterrents, and the shifting of shipping lanes and reductions in ship speed;
(2) seek cooperation from the International Maritime Organisation to provide protection for right whales, including but not limited to mandatory ship reporting and ship routing, especially where commercial vessels are entering calving, breeding or feeding areas.

With respect to entanglements (see Item 12.3.2), the Workshop **recommends** that the Scientific Committee requests the Commission to urge member governments to ensure that:

(1) research continues on methods to reduce right whale entanglements in fishing gear;
(2) entanglement rates and the success of steps to reduce entanglement are determined and monitored (e.g. through periodic analysis of scarring rates and levels of severe entanglement in photo-identification databases);
(3) if the above monitoring indicates that protective measures are insufficient, they are upgraded as appropriate;
(4) disentanglement programmes (including training from experienced persons) are established where appropriate; and
(5) consideration is given to the prohibition of any gear that might entangle right whales in high use habitats, especially in calving, breeding or feeding areas and sanctuaries.

14.2 Disturbance and habitat issues

The Workshop **recommends** that the Scientific Committee requests the Commission to request member nations to urge local, regional and national authorities responsible for right whale habitat to develop contingency plans for oil and chemical spills, where these do not exist (see Item 12.3.1).

The Workshop also made specific recommendations on habitat related issues that require management action by individual governments (see Item 12.3.5). The Workshop **recommends** that the Committee requests the Commission to ask the relevant governments to take the necessary action.

14.3 Facilitation of research

The Workshop **recommends** that the Committee requests the Commission to urge member governments to provide funding for the research items it has identified (see Item 15). In addition, the Workshop draws attention to the following **recommendations** that require action but not funding *per se*.

14.3.1 Sample collection

The Workshop has made a number of research recommendations with respect to the collection of biopsy samples. It **recommends** that the Scientific Committee requests the Commission to urge member governments to facilitate the issue of national permits to collect sufficient biopsy samples from adult and calf right whales to address the research recommendations identified in this report (see Items 7 and 9).

14.3.2 Necropsies

The Workshop has noted the need for detailed necropsies of right whales, particularly for those populations for which there is concern over their status. It **recommends** that the Scientific Committee urges the Commission to request that member governments ensure that appropriate programmes are initiated and, where necessary, permits granted to enable this work to take place (see Item 9.1.3).

14.3.3 Surveys in territorial waters

The Workshop identified the need for a further research cruise to assess the abundance of right whales in the western North Pacific. It **recommends** that the Scientific Committee requests the Commission to urge relevant member nations to cooperate in this exercise and in particular that the Russian Federation be urged to grant permission for vessels to survey within 12 n.miles of the Okhotsk Sea coast (see Item 10.2).

14.3.4 Whalewatching

The Workshop endorsed the IWC's general principles for whalewatching (IWC, 1997b, p.105) and **recommends** that these be applied to all whalewatching activities involving right whales. It was agreed that it was critical to: (1) manage the development of new and fledgling whalewatching operations to minimise the risk of adverse affects; and (2) take appropriate regulatory measures in areas where directed research demonstrates negative impacts on whales from established whalewatching activities.

The Workshop agreed that special protected areas provide a framework for the implementation of site-specific regulations for whalewatching and that such areas are important in conserving coastal habitats. It therefore **recommends** that studies be undertaken to assess the establishment of special protected areas in areas of known right whale concentration (e.g. the Central-South Coast of Santa Catarina, Brazil).

15. FUTURE RESEARCH

During its discussions of the various Agenda Items, the Workshop made a number of recommendations for future research (Table 9). It **reiterates** the value it attaches to all of those recommendations. However, as at previous IWC Workshops, it recognises the need to assign priority to research items in the context of the Commission's interests. In particular, this applies to questions associated with the 'trend and condition of whale stocks' and 'measures for the[ir] conservation' (Article IV of the Convention), as reaffirmed in the Terms of Reference for this meeting (Item 1.2).

Table 9

Specific research recommendations by Agenda Item.

Research	References in text (Agenda Items)
Taxonomy	6
Genetics	7.1.5, 7.2.5, 7.3.7, 7.4.6, 7.6.1, 7.6.2
Sampling	7.1.5 (1, 3), 7.4.6, 7.5.1, 12.4 (1a), 9.1.2.1, 9.1.2.3
Comparisons	7.2.5, 7.3.7, 751, 9.1.2
Photo-identification	9.2, 12.3.2 (2), 9.1.1.2
Mortality reduction	12.3.1 (3), 12.3.2 (1, 3, 4), 12.3.3
Habitat studies	12.3.4, 12.2.1
Feeding	12.2.1 (1.3)
Contaminants	12.3.1 (1, 2, 3)
Population parameters	10.3 (1, 2) 9.2.3, 10
Modelling trajectories	10.3
Health and pathology	12.4, 9.1.3
Surveys	7.1.5, 7.5, 7.5.1

15.1 Trends and status

The Workshop confirms the view already expressed by the Scientific Committee on several previous occasions (e.g. IWC, 1990b) of the extreme importance of maintaining research effort when investigating trends in both abundance and in biological parameters. It therefore stresses that **high priority** should be given to the continuation of both demographic photo-identification studies (Item 9) and surveys designed to improve knowledge of absolute abundance and current trends (see Item 10). Similarly, **high priority** should be given to the processing and analysis of such data. This is particularly important for the western North Atlantic where there are serious concerns over the status of the stock (see Item 11).

The Workshop also notes the need to initiate and improve such studies in areas of identified concentrations where they are either absent or in their infancy. **High priority** should be given to those areas where it is believed there is most chance of success.

In order to interpret data on trends and abundance it is important to determine appropriate management units. In this context, **high priority** should be given to stock identification studies that will answer questions believed to be hindering the Committee's ability to address important conservation questions (see Item 7). Genetic sampling programmes should be initiated where needed, and maintained in areas where increased sample sizes are needed for statistical validity.

15.2 Measures for conservation

The Workshop agreed that **high priority** should be given to research that will lead directly to improved methods of reducing anthropogenic mortality (e.g. reducing ship strikes and fishing gear entanglements) for stocks for which there is concern over their survival (see Item 11).

Priority should also be given to research examining environmental factors that affect the fecundity and mortality rates of right whale populations (e.g. food limitation, pollution, see Item 12). Such research should ultimately lead to improved recommendations for appropriate and effective management action. Comparative studies between stocks that are recovering and stocks that do not appear to be (see Item 10) may be particularly valuable in this context. Studies that improve information on feeding grounds in the Southern Hemisphere will facilitate such comparisons.

From the genetic standpoint, two questions are of high priority:

(1) what are the implications of the low haplotype diversity detected in certain populations; and
(2) is the effective population size of right whales significantly lower than the abundance estimates?

16. PUBLICATION

The Workshop agreed that the papers submitted were of sufficient quality to warrant the publication of a special issue. Details will be discussed at the next meeting of the Editorial Board.

17. ANY OTHER BUSINESS

Payne presented a proposal for the creation of a global right whale catalogue, to facilitate, *inter alia*, a study of the degree of mixing between populations of right whales worldwide. He believed that such a comparison was becoming more practicable given the development of computerised callosity pattern matching aids (e.g. SC/M98/RW38). The Workshop agreed that consideration of this proposal should be included within the context of a broader proposal for a Southern Hemisphere Right Whale Consortium (Annex K and below).

It was noted that prior to this Workshop, few opportunities had existed for cooperation and collaborative research in the Southern Hemisphere. In contrast, the foundation of the North Atlantic Right Whale Consortium in 1986 had provided the framework for a collaborative and uniform approach to the research and conservation of right whales in the western North Atlantic.

The Workshop recognised that creation of a similar framework for collaborative research could provide similar benefits for southern right whale research. A Southern Hemisphere Consortium might also serve as a vehicle for identifying and seeking support for right whale research worldwide.

Some concern was expressed over the scientific rationale behind the concept of a 'global' catalogue for right whale photo-identifications. The Workshop preferred to support the facilitation of inter-catalogue comparisons which would in time permit promotion of a single 'global' catalogue, should it be deemed necessary.

The objectives of a Southern Hemisphere Right Whale Consortium could include:

(1) standardisation of data collection;
(2) facilitation of regional inter-catalogue comparisons of photo-identifications;
(3) development of comparable analytical methods;
(4) sharing of resources, especially sophisticated and expensive laboratory techniques (e.g. for genetic, isotopic and pollutant analysis);
(5) exchange of scientific personnel and samples;
(6) where appropriate, assistance in the development of joint management strategies and policy.

The Workshop **agreed** that there was merit in the proposal and **recommends** that the Scientific Committee approves the principle of establishing a Southern Hemisphere Right Whale Consortium and that it consequently recommends it to the Commission. Subject to such approval, it was agreed that a Steering Committee, comprising representatives of each Southern Hemisphere nation currently involved in right whale research, should be established to develop the details of the proposal. In this regard, funding should be sought from, *inter alia*, the IWC, national governments and other sponsors to convene a meeting of interested parties to formally establish a Southern Hemisphere Right Whale Consortium with appropriate terms of reference.

18. ADOPTION OF REPORT

The Workshop accepted all the available draft sections of the report but agreed that Donovan, Bannister, Best and Brownell should carry out final editing of the report to ensure its completeness, clarity and consistency.

It agreed that considerable progress had been made at the Workshop. In accordance with the Terms of Reference it had identified the current data available for carrying out the Comprehensive Assessment and undertaken some preliminary analyses. In that light it had identified both further theoretical work and additional data required. It had not been possible in the time available to develop a timetable for the work and hence for the completion of the Comprehensive Assessment.

The success of the Workshop was aided by the extremely hard work of the local convenor, Peter Best and his staff, particularly Desray Reeb, Margaret Best and Leonie Juritz. Thanks are also due to: MTN Cape Whale Route, especially Darden Lotz, not only for their sponsorship but also for logistical support; the Two Oceans Aquarium who hosted the symposium; IFAW for facilitating the attendance of three participants; Mondi (SA) for donation of photocopying paper; and Price Forbes for donation of document bags. The hospitality shown by Rodger Bunney and his staff at the Monkey Valley Beach Resort was much appreciated. Thanks are also due to Moira Dykes who cheerfully typed the report and dealt with the administration of the meeting.

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Annex B
Agenda

1. Arrangements for meeting
   1.1 Practical details
   1.2 Terms of reference

2. Election of Chairman

3. Appointment of rapporteurs

4. Adoption of agenda

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10. Estimates of abundance and trends
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13. Whalewatching

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15. Future research

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Annex C
List of Documents

* = Revised and published in this volume.

SC/M98/RW1. KRAUS, S., HAMILTON, P.K., KENNEY, R.D., KNOWLTON, A. and SLAY, C.K. Status and trends in reproduction of the North Atlantic right whale.*

SC/M98/RW2. HAMILTON, P.K., KENNEY, R.D., KNOWLTON, A.R., KRAUS, S.D., MARX, M.K., MAYO, C.A. and SLAY, C.K. The North Atlantic Right Whale Catalogue: the strengths and limitations of using photo identification to assess population parameters.

SC/M98/RW3. CASWELL, H., FUJIWARA, M. and BRAULT, S. Declining survival probability and its implications for the North Atlantic right whale.

SC/M98/RW4. REEVES, R.R. Progress report: catch history, historical abundance and distribution of right whales in the western North Atlantic.*

SC/M98/RW5. BROWN, M.W. Genetic aspects of the western North Atlantic right whales.

SC/M98/RW6. SLAY, C.K., KRAUS, S.D., HAMILTON, P.K., KNOWLTON, A.R. and CONGER, L.A. Early warning system 1994-1997. Aerial surveys to reduce ship/whale collisions in the North Atlantic right whale calving ground.

SC/M98/RW7. MAYO, C.A. and GOLDMAN, L. Fine scale characteristics of copepod patches foraged by the northern right whale (*Eubalaena glacialis*).

SC/M98/RW8. KNOWLTON, A.R. and KRAUS, S.D. Mortality and serious injury in North Atlantic right whales.*

SC/M98/RW9. SILBER, G.K. and PAYNE, P.M. Implementation of the Northern Right Whale Recovery Plan.

SC/M98/RW10. BROWNELL JR., R.L., CLAPHAM, P.J., MIYASHITA, T. and KASUYA, T. Conservation status of North Pacific right whales.*

SC/M98/RW11. MIYASHITA, T. and KATO, H. Recent data on the status of right whales in the NW Pacific Ocean.

SC/M98/RW12. COOKE, J.G., PAYNE, R. and ROWNTREE, V. Updated estimates of demographic parameters for the southern right whales (*Eubalaena australis*) observed off Peninsula Valdés, Argentina.*

SC/M98/RW13. ROWNTREE, V.J., PAYNE, R.S. and SCHELL, D.M. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) identified on the nursery ground at Peninsula Valdés, Argentina.

SC/M98/RW14. PALAZZO JR, J. and FLORES, P.A. de C. Right whales (*Eubalaena australis*) in southern Brazil: a summary of knowledge and research needs.

SC/M98/RW15. BEST, P.B. and UNDERHILL, L.G. Population size, growth rate and survival of southern right whales (*Eubalaena australis*) off South Africa, 1979-1996.

SC/M98/RW16. BEST, P.B., BRANDAO, A. and BUTTERWORTH, D. Demographic parameters of southern right whales off South Africa.*

SC/M98/RW17. FINDLAY, K. Aspects of whale watching for right whales off South Africa.

SC/M98/RW18. BANNISTER, J. Status of right whales off Australia.*

SC/M98/RW19. BURNELL, S.R. Aspects of the reproductive biology and behavioural ecology of right whales off Australia.*

SC/M98/RW20. PATENAUDE, N.J. and BAKER, C.S. Population status and habitat use of southern right whales in the sub-Antarctic Auckland Islands of New Zealand.*

SC/M98/RW21. PORTWAY, V.A., SCHAEFF, C.M., BEST, P.B., ROWNTREE, V., PAYNE, R., MOORE, M.J. and HAMILTON, P.J. Genetic population structure of South Atlantic right whales (*Eubalaena australis*).

SC/M98/RW22. BAKER, C.S., PATENAUDE, N.J., BANNISTER, J.L., ROBINS, J. and KATO, H. Distribution and diversity of mtDNA lineages among southern right whales (*Eubalaena australis*) from Australia and New Zealand.

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Annex D
Summaries of Relative Abundance of Right Whales by Month

This Annex is an attempt to summarise what is known or surmised about the present (last decade) distribution and relative abundance of right whales by month based upon both survey and opportunistic data. The first table for each region summarises the relative abundance and the second provides information on the mean number and range of whales and information on survey effort. It is important to remember that the first table indications of abundance refer to relative abundance to the total in the area at the time, not to the total population size.

Table 1

Western North Atlantic. Key: Opp. = opportunistic; Dir. = directed; C/c = cow-calf; Juv.= juvenile; Ad-F = adult female; Ad-M = adult male. Popn = population component; 0 = none; 1 = low; 2 = high; ? = unknown.

	Southeast						Mid-Atlantic corridor				Great South Channel			
	Effort		Popn				Effort		Popn		Effort		Popn	
	Opp.	Dir.	C/c	Juv.	Ad-F	Ad-M	Opp.	Dir.	C/c	Other	Opp.	Dir.	C/c	Other
Jan.	Yes	2	High	High	Low	Low	Yes	0	?	Low	0	1	0	0
Feb.	Yes	2	High	Low	Low	Low	Yes	0	?	Low	0	1	0	0
Mar.	Yes	2	Low	Low	Low	Low	Yes	0	Med.	Low	0	1	0	Low
Apr.	Yes	1	0	0	0	0	Yes	0	Med.	Low	0	2	0	Low
May	Yes	0	0	0	0	0	Yes	0	0	Low	0	2	Low	High
Jun.	Yes	0	0	0	0	0	Yes	0	0	Low	0	2	Low	Med.
Jul.	Yes	0	0	0	0	0	Yes	0	0	Low	0	2	0	Low
Aug.	Yes	0	0	0	0	0	Yes	0	0	Low	0	1	0	0
Sep.	Yes	0	0	0	0	0	Yes	0	0	Low	0	1	0	0
Oct.	Yes	1	0	0	0	0	Yes	0	0	Low	0	1	0	0
Nov.	Yes	1	Low	0	0	0	Yes	0	0	Med.	0	1	0	0
Dec.	Yes	2	Med.	Med.	Med.	Med.	Yes	0	0	Med.	0	1	0	0

	Cape Cod Bay				Roseway Basin					Bay of Fundy					
	Effort		Popn		Effort		Popn			Effort		Popn			
	Opp.	Dir.	C/c	Other	Opp.	Dir.	C/c	Ad-M	Ad-F	Opp.	Dir.	C/c	Juv.	Ad-F	Ad-M
Jan.	No	1	0	Med.	0	0	?	?	?	No	0	?	?	?	?
Feb.	No	1	0	Med.	0	0	?	?	?	No	0	?	?	?	?
Mar.	Yes	2	0	High	0	0	?	?	?	No	0	?	?	?	?
Apr.	Yes	2	Med.	High	0	0	?	?	?	No	0	?	?	?	?
May	Yes	2	Med.	Med.	0	0	?	?	?	No	0	?	?	?	?
Jun.	Yes	2	Low	Low	0	2	0	?	?	Yes	1	Low	Low	Low	Low
Jul.	Yes	2	0	0	0	2	0	?	?	Yes	2	Low	Low	Low	Low
Aug.	Yes	2	0	0	0	2	0	High	Low	Yes	2	High	High	High	High
Sep.	Yes	2	0	0	0	2	0	High	Low	Yes	2	High	High	High	High
Oct.	Yes	2	0	0	0	2	0	?	?	Yes	2	Med.	Med.	Med.	High
Nov.	No	0	0	?	0	2	0	?	?	No	1	Low?	Low?	Low?	Low?
Dec.	No	1	0	Low	0	0	?	?	?	No	0	?	?	?	?

Number of identified right whales observed seasonally in the known habitats of the western North Atlantic.

Location	Months observed	Range	Mean	Years included	Years surveyed
Southeast USA	Dec.-Mar.	6-83	29	1984-96	1984-96
Cape Cod	Jan.-Jun.	21-78	41	1983-96	1983-96
Gt. S. Channel	Mar.-Jul.	0-94	22	1980-96	1980-92
Bay of Fundy	Jun.-Nov.	23-185	76	1980-96	1980-96
Roseway Basin	Aug.-Sep.	0-118	39	1980-96	1983-92, 1997

Table 2

North Pacific. Key: Opp. = opportunistic; Dir. = directed; C/c = cow-calf; Juv.= juvenile; Ad-F = adult female; Ad-M = adult male. Popn = population component; 0 = none; 1 = low; 2 = high; ? = unknown.

Western North Pacific

	Yellow Sea			Japan					NW Pacific					Kuril Islands			Okhotsk					W. Aleutians		
	Effort			Effort		Popn			Effort		Popn			Effort		Popn	Effort		Popn			Effort		Popn
	Opp.	Dir.	All	Opp.	Dir.	C/c	Juv.	Adult	Opp.	Dir.	C/c	Juv.	Adult	Opp.	Dir.	All	Opp.	Dir.	C/c	Juv.	Adult	Opp.	Dir.	All
Jan.	Yes	1	?	Yes	1	Low	?	?	Yes	0	?	?	?	No	0	0	No	0	0	0	0	No	0	0
Feb.	Yes	1	Low	Yes	1	?	?	?	Yes	1	0	0	0	No	0	0	No	0	0	0	0	No	0	0
Mar.	Yes	1	?	Yes	1	?	?	?	Yes	1	0	0	0	No	0	0	No	0	0	0	0	No	0	0
Apr.	Yes	0	?	Yes	0	?	Low	Med.	Yes	0	?	?	?	No	0	0	No	0	0	0	0	No	1	Low
May	Yes	0	?	Yes	1	?	?	High	Yes	1	?	?	Low	No	1	?	No	1	?	?	?	No	2	Med.
Jun.	Yes	1	0	Yes	1	?	?	Med.	Yes	0	?	?	Low	No	0	?	No	0	?	?	?	No	2	Low
Jul.	Yes	1	0	Yes	2	0	0	Low	Yes	1	?	?	?	No	1	Med.	No	0	?	?	?	No	2	?
Aug.	Yes	2	0	Yes	2	0	0	0	Yes	2	Low	?	Low	No	1	?	No	2	?	Low	High	No	2	?
Sep.	Yes	2	0	Yes	2	0	0	0	Yes	2	?	?	?	No	1	?	No	2	?	?	High	No	1	?
Oct.	Yes	0	0	Yes	2	0	0	0	Yes	0	?	?	?	No	0	?	No	0	?	?	Med.	No	0	?
Nov.	Yes	0	0	Yes	1	?	?	Low	Yes	0	?	?	?	No	0	?	No	0	?	?	?	No	0	?
Dec.	Yes	0	0	Yes	1	?	?	?	Yes	0	?	?	?	No	0	?	No	0	?	Low	?	No	0	?

Eastern North Pacific

	Hawaii			West Coast					NE Pacific			Northwest Ground			Eastern Aleutians			Bering Sea		
	Effort		Popn	Effort		Popn			Effort		Popn	Effort		Popn	Effort		Popn	Effort		Popn
Month	Opp.	Dir.	All	Opp.	Dir.	C/c	Juv.	Adult	Opp.	Dir.	All	Opp.	Dir.	All	Opp.	Dir.	All	Opp.	Dir.	All
Jan.	Yes	0	?	Yes	0	?	?	Low	No	0	?	Yes	0	?	No	0	?	No	0	?
Feb.	Yes	0	?	Yes	0	?	?	Low	No	0	?	Yes	0	?	No	0	?	No	0	?
Mar.	Yes	0	High	Yes	0	?	?	High	No	0	?	Yes	0	?	No	0	?	No	0	?
Apr.	Yes	0	?	Yes	0	?	?	Med.	No	0	?	Yes	0	?	No	0	?	No	0	?
May	Yes	0	?	Yes	1	?	?	Low	No	1	?	Yes	1	?	No	2	?	No	1	?
Jun.	Yes	0	?	Yes	1	?	?	?	No	2	Low	Yes	2	?	No	2	High	No	2	Med.
Jul.	Yes	1	Low	Yes	2	?	?	?	No	2	Med.	Yes	2	High	No	2	Med.	No	2	High
Aug.	Yes	1	?	Yes	1	?	?	Low	No	2	High	Yes	2	High	No	2	?	No	2	Med.
Sep.	Yes	1	?	Yes	1	?	?	Low	No	1	?	Yes	0	?	No	1	?	No	1	Low
Oct.	Yes	0	?	Yes	0	?	?	?	No	0	?	Yes	0	?	No	0	?	No	0	?
Nov.	Yes	0	?	Yes	0	?	Low	?	No	0	?	Yes	0	?	No	0	?	No	0	?
Dec.	Yes	0	?	Yes	0	?	?	?	No	0	?	Yes	0	?	No	0	?	No	0	?

Table 3

South Atlantic. Key: Opp. = opportunistic; Dir. = directed; C/c = cow-calf; Juv.= juvenile; Ad-F = adult female; Ad-M = adult male. Popn = population component; 0 = none; 1 = low; 2 = high; ? = unknown.

	Brazil (8°-32°S)			P. Valdes, Argentina (42°S)				Tristan/Gough (38°S)			South Africa (34°S, 18-27°E)				Mozambique/Natal (20°S)			S.R./S. Georgia (53°S, 42-35°W)			Antarctic Peninsula (~65°S, 60-70°W)		
	Effort		Popn	Effort		Popn		Effort		Popn	Effort		Popn		Effort		Popn	Effort		Popn	Effort		Popn
	Opp.	Dir.	All	Opp.	Dir.	C/c	Other	Opp.	Dir.	All.	Opp.	Dir.	C/c	Other	Opp.	Dir.	All	Opp.	Dir.	All	Opp.	Dir.	All
n=			10-60			1-126	1-126			<10			10-150	20-150			<10			1-30			1-10
Jan.	Yes	0	0	Yes	0	0	Low	Yes	0	0	Yes	0	0	0	Yes	0	0	Yes	2	Med.	Yes	2	Low
Feb.	Yes	0	0	Yes	0	0	Low	Yes	0	0	Yes	0	0	0	Yes	0	0	Yes	2	High	Yes	2	Low
Mar.	Yes	0	0	Yes	0	0	Low	Yes	0	0	Yes	0	0	0	Yes	0	0	Yes	2	High	No	2	?
Apr.	Yes	0	0	Yes	0	0	Low	Yes	0	0	Yes	0	0	0	Yes	0	0	Yes	0	Low	No	0	?
May	Yes	1	Low	Yes	0	Low	Low	Yes	0	0	Yes	0	0	Low	Yes	0	0	Yes	0	Low	No	0	?
Jun.	Yes	1	Med.	Yes	2	Low	Med.	Yes	0	0	Yes	0	Low	Med.	Yes	2	Low	Yes	0	Low	No	0	?
Jul.	Yes	2	Med.	Yes	2	Low	Med.	Yes	0	Low	Yes	0	Med.	Med.	Yes	2	Low	Yes	0	Low	No	0	?
Aug.	Yes	2	High	Yes	2	High	Med.	Yes	0	Low	Yes	0	High	High	Yes	2	Low	Yes	0	Low	No	0	?
Sep.	Yes	2	High	Yes	2	High	Med.	Yes	0	Low	Yes	0	High	High	Yes	2	Low	Yes	0	0	No	0	?
Oct.	Yes	2	High	Yes	2	High	Med.	Yes	0	High	Yes	2	High	Med.	Yes	2	Low	Yes	0	Low	No	0	?
Nov.	Yes	1	Med.	Yes	2	Low	Low	Yes	0	Low	Yes	0	Med.	Low	Yes	0	0	Yes	0	Low	Yes	0	0
Dec.	Yes	0	Low	Yes	2	Low	Low	Yes	0	Low	Yes	0	Low	0	Yes	0	0	Yes	2	Low	Yes	0	0

Number of identified right whales observed seasonally in the known habitats of the South Atlantic.

Location	Season	Max. daily count	Max. photo-id/yr	Years included	Years surveyed
Brazil	May-Dec.	27	12	1982-97	1987-88, 92-94, 97
Valdes*	Jun.-Dec.	374	193	1970-97	1971-97
Tristan	Jun.-Dec.	*ca* 4	4	3 since 1983	1983, ?, ?
South Africa	Jun.-Dec.	447	130 C/c pair	1969-1997	1969-97
Shag Rocks/ S. Georgia	Jan.-Feb.	15	19	1997	1997

* Maximum count is for 1997. Maximum photo-identified is for 1973.

Table 4

Australia/New Zealand and Indian Ocean excluding East Africa. Key: Opp. = opportunistic; Dir. = directed; C/c = cow-calf; Juv.= juvenile; Ad-F = adult female; Ad-M = adult male. Popn = population component; 0 = none; 1 = low; 2 = high; ? = unknown.

	South/West Australia				South/Central Australia							South/East Australia				Mainland New Zealand				Auckland Islands							Campbell Islands					S. Ocean (90°-150°E)				Antarctic (90°-150°E)			
	Effort		Popn		Effort		Popn					Effort		Popn		Effort		Popn		Effort		Popn					Effort		Popn			Effort		Popn		Effort		Popn	
	Opp.	Dir.	C/c	Other	Opp.	Dir.	C/c	Juv.	Ad-F	Ad-M	Ad?	Opp.	Dir.*	C/c	Other	Opp.	Dir.	C/c	Other	Opp.	Dir.	C/c	Juv.	Ad-F	Ad-M	Ad?	Opp.	Dir.	C/c	Juv.	Ad?	Opp.	Dir.	C/c	Other	Opp.	Dir.	C/c	Other
n=			10-100	10-100			10-100	10-100	<10	10-100	10-100			<10	10-100			<10	<10			10-100	10-100	10-100	10-100	10-100			<10	<10	10-100			<10	10-100			0	10-100
Jan.	Yes	0	0	0	Yes	0	0	?	?	?	0	Yes	0	vLow	0	Yes	0	0	0	Yes	0	?	?	?	?	Low	No	0	?	?	?	No	2	0	High	No	2	0?	Low
Feb.	Yes	0	0	0	Yes	0	0	?	?	?	0	Yes	0	0	0	Yes	0	0	0	Yes	0	?	?	?	?	Low	Yes	1	?	?	Low	No	2	0	0	No	2	0?	Low
Mar.	Yes	0	0	0	Yes	0	0	?	?	?	0	Yes	0	0	Low	Yes	0	0	Low	No	0	Low*	?	Med.*	Med.*		Yes	1	?	?	Low	No	2	0	Low	No	2	0?	High
Apr.	Yes	0	0	Low	Yes	0	0	?	?	?	Low	Yes	0	0	Low	Yes	0	0	0	No	0	Low*	?	Med.*	Med.*		No	0	?	?	?	Yes	0	Low	Low	No	0	?	?
May	Yes	0	0	Low	Yes	0	0	?	?	?	Low	Yes	0	0	Low	Yes	0	0	0	Yes	0	?	?	?	?	Low	Yes	0	Low	?	Low	No	0	?	?	No	0	?	?
Jun.	Yes	0	Low	Low	Yes	2	Low	Med.	Med.	Low	Low	Yes	2	Low	Low	Yes	0	0	0	Yes	0	?	?	?	?	Low	Yes	2	High	High	High	No	0	?	?	No	0	?	?
Jul.	Yes	1	Med.	High	Yes	2	Med.	High	High	High	High	Yes	2	Med.	High	Yes	0	0	High*	Yes	2	High	High	High	High	High	Yes	2	High	High	High	No	0	?	?	No	0	?	?
Aug.	Yes	2	High	High	Yes	2	High	High	Med.	Med.	Med.	Yes	2	High	Med.	Yes	0	High	0	Yes	2	High	High	High	High	High	Yes	2	High	High	High	No	0	?	?	No	0	?	?
Sep.	Yes	2	High	Med.	Yes	2	High	Med.	Low	vLow	Med.	Yes	2	Med	Low	Yes	0	High	High	Yes	1	Low	?	?	?	Med.	Yes	1	High	High	High	No	0	?	?	No	0	?	?
Oct.	Yes	2	Med.	Low	Yes	2	Med.	Low	0	0	Low	Yes	2	Low	0	Yes	0	0	High	No	0	?	?	?	?	?	Yes	0	?	?	Low	No	0	?	?	No	0	?	?
Nov.	Yes	1	Low	Low	Yes	0	Low	?	?	?	Low	Yes	0	0	0	Yes	0	0	0	No	0	?	?	?	?	?	No	0	?	?	?	No	1	?	Low	No	0	?	?
Dec.	Yes	0	0	0	Yes	0	0	?	?	?	0	Yes	0	0	0	Yes	0	0	0	No	0	?	?	?	?	?	No	0	?	?	?	No	2	High	High	No	0	?	?

* To be confirmed

Number of identified right whales observed seasonally in the known habitats of Australia/New Zealand and Indian Ocean excluding East Africa.

Location	Season	Max. daily count	Max. photo-id/yr	Years included	Years surveyed
SW Australia	Apr.-Nov.	143	~70	1976-97	1977-97
SC Australia	Apr.-Nov.	102	101	1991-97	1991-97
SE Australia	Mar.-Oct.	none	39	1995-97	1995-97
Mainland NZ	Mar.-Oct.	~5	~2	1975-98	none
Auckland Is	Jan.-Sep.	80-146	125	1950-97	1950-70, 95-97
Campbell I.	Feb.-Oct.	44	31	1983-97	1983, 95-97
S. Ocean	Nov.-Apr.	75	5+	1981-96	1981-82, 93, 1995-96
Antarctic	Jan.-Mar.	22**	2+	1963-67	1963-67, 96

** Catch records, cumulative.

Annex E
Review of Biopsy Sampling Methods and Available Samples

A summary of some of the methodologies and equipment used by different groups in different areas is given below. Success rate refers to the frequency of obtaining a sample following a successful ‘hit’ on the whale.

FLORIDA/GEORGIA

Slay reported on biopsy of western North Atlantic right whales on a calving ground using a 70lb longbow with long shafted arrows and Larsen tips (30mm length, 5mm internal diameter, three rearward facing barbs, Palsbøll *et al*., 1991), fired from onboard a 6m inflatable boat. Successful samples were taken at ranges up to and exceeding 20 metres. No retrieval was used. There was injection moulded flotation on the arrow, also serving as the stop collar. 100% success rate ($n = 9$) had been obtained; all samples contained skin and blubber. The Larsen bolt and tip with flotation costs approximately US$60-80.

BAY OF FUNDY/ROSEWAY BASIN

Brown described a system using an Excalibur ‘Vixen’ crossbow (68kg prod with longer track than the ‘wildcat’ bow described below) using Larsen (as above) or North Atlantic tips (30mm length, 6mm internal diameter, centre single barbed pin), with a 25mm diameter stop collar and 13kg test retrieval line (Brown *et al*., 1991). The Larsen tips were considered more effective (90% success rate, $n = 40$) than the North Atlantic tips which ‘stuck’ more often, provided blubber samples only 30% of the time and had a lower overall success rate (70%, $n = 430$). 85% of biopsy darting was undertaken from a 9m boat at average range 5-15m, aiming for a perpendicular strike to maximise the chance of a blubber sample. The cost of the North Atlantic bolt and tip was approximately US$30.

AUCKLAND ISLANDS, NEW ZEALAND/ AUSTRALIA/SOUTH GEORGIA

Patenaude used a Barnett ‘Wildcat’ crossbow (68kg prod) and tips from the North Atlantic right whale project with a 19mm stop collar. Most attempts were made at ranges of 5-15 metres and a 18kg test retrieval line was used due to 95% of darts ‘sticking’ in the whale. There was a 90% success rate from a 5m inflatable boat ($n = 195$). Perpendicular strikes were aimed to maximise the chance of a blubber sample. It was noted that the use of the Larsen tips did not reduce the incidence of darts ‘sticking’ in this study.

Researchers from South Georgia and Australia described similar experiences with darts sticking using the same or very similar equipment. Using this equipment, Bannister reported a 66% success rate using rear oblique shots off Western Australia ($n = 25$).

SOUTH AFRICA

Best described the ‘PAXARMS’ rifle system used in South Africa. A .22 calibre rifle cartridge is used to propel a short dart from a 12 gauge shotgun barrel. The standard floating, plastic dart from PAXARMS was used with a custom made tip (25mm length, 3mm internal diameter) and no retrieval line. The propellant charge can be varied and the system is accurate at ranges up to 40 metres. There was a 90% success rate from small boats and 33% of samples included blubber. Most attempts are made obliquely from the rear of the animal. The cost of a rifle was US$650 and the dart and tip US$25.

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Palsbøll, P.J., Larsen, F. and Hansen, E.S. 1991. Sampling of skin biopsies from free-ranging large cetaceans in West Greenland: development of new biopsy tips and bolt designs. *Rep. int. Whal. Commn* (special issue) 13:71-9.

Table 1

The number, location/date and archive location of right whale skin samples currently available from different geographic areas. Years in parentheses represent the range of years in which biopsies have been collected.

Sampling location/date	No. skin samples[1]	Skin/ blubber[2]	DNA archive location[3]
Western North Atlantic (1988-97)	470	82	1
North Pacific (1997)	6	0	2
Argentina (1989)	17	0	1
(1994-96)	21	-	3
South Georgia (1997)	8	3	1, 3, 4
South Africa (1995-97)	~660	80	3
Madagascar (1997)	1	0	5
Western Australia (1993-95)	25	0	6, 7
Southern Ocean (South of W. Australia) Japan/IWC (1995-96)	5	0	6, 7
Southern Ocean (Areas IV and V) IDCR/JARPA (1995-98)	6-8	0	8
South Australia (1992)	4	0	9
Auckland Islands, NZ (1995-97)	195	17	7

[1] Not necessarily equal to the number of individuals. [2] Formalin fixed, paraffin embedded; archived at Woods Hole Oceanographic Institute. [3] Institutions: 1 = McMaster University, Canada; 2 = Southwest Fisheries Science Centre, USA; 3 = American University, Washington DC, USA; 4 = Woods Hole Oceanographic Institute, USA; 5 = American Museum of Natural History, USA; 6 = Western Australia Museum, Australia; 7 = Auckland University, New Zealand; 8 = Institute of Cetacean Research, Japan; 9 = South Australian Museum, Australia.

Annex F
Ongoing Studies that could be Assisted by Necropsy Data

BLUBBER ASSESSMENT

Worldwide assessment of individual body condition, contaminant burdens and effects can be furthered by a uniform collection of data and samples. In addition to basic body measurements, dorsal, lateral and ventral blubber thickness should be measured at three or more stations evenly spaced from the blowholes to the peduncle. They should be measured on the cut face of the blubber after the removal of the adjacent coat. Maximum girth should also be measured after decomposition gasses have been vented. The blubber/muscle interface should be regarded as the first white fibrous layer at the base of the blubber and the skin should be included (if flensing is not undertaken, a 15cm diameter core should be cut out and measured). Additionally, a measurement should be made at the mid-lateral flank perpendicular to the anus for comparison with Soviet whaling data. For contaminant analysis, a full core of blubber removed from the dorsal, lateral and ventral surface at the middle of the back region should be removed and frozen at –20°C. Any available kidney and liver tissue should also be collected and frozen at –20°C. Contact: M. Moore.

BARNACLES

Barnacles (*Tubicinella)* have been found embedded in the callosities of right whales only off South Africa. Because these animals may be obscured by cyamids and may not be visible from photographs of live animals, particular attention should be made during necropsies of right whales from other areas to inspect the callosities for barnacles. Stable isotope ratios of barnacle shells may also provide evidence of migration. Samples of barnacles should be stored dry or in 70% alcohol. Contact: P. Best.

ISOTOPE RATIO ANALYSES OF BALEEN AND PREY

Baleen plates of adult whales can provide a chronological record of feeding and migratory behaviour over a period of 10-15 years (Schell *et al.*, 1989). Comparisons of the carbon and nitrogen isotope ratios of baleen with that of the whales' prey in various geographic locations can estimate the whales feeding grounds (Schell *et al.*, 1989; Best and Schell, 1996; SC/M98/RW13). Given the difficulty in accessing the feeding grounds of the Southern Hemisphere and North Pacific right whales, it would be valuable to use isotopic ratio analyses to help identify right whale feeding grounds and to identify the relationship between the calving and feeding grounds. Prey samples (copepods, euphausiids) necessary for these analyses may already exist in fishery departments that have surveyed Southern Hemisphere oceans. Prey samples and baleen plates from adult right whales should be contributed to isotopic analyses wherever possible. One of the longest baleen plates from any non-calf whale should be collected with the gum and be stored dry. Prey should be stored dry or in 70% alcohol. Contact: V. Rowntree.

MIDDLE AND INNER EAR

Discussed under Item 12.3.3. Contact: D. Ketten.

REFERENCES

Best, P.B. and Schell, D.M. 1996. Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Mar. Biol.* 124(4):483-94.

Schell, D.M., Saupe, S.M. and Haubenstock, N. 1989. Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of ageing and habitat usage. *Ecol. Stud.* 68:260-9.

Annex G

Estimating Population Rate of Increase of the North Atlantic Right Whale (see Item 10.1)

METHOD 1

Brault attempted to obtain an index of population rate of increase using the number of cow-calf pairs identified in each year in all observation areas in the northeast, as presented in Table 1, column 1 below.

Table 1

Number of cow-calf pairs observed every year from 1982 -97 in the western North Atlantic.

Year	No. of cow-calf pairs	No. of parous females
1982	11	
1983	9	
1984	13	
1985	11	41
1986	13	46
1987	11	50
1988	8	52
1989	19	51
1990	12	51
1991	17	51
1992	12	52
1993	8	54
1994	9	57
1995	7	57
1996	22	66
1997	20	74

The natural log of the number of cow-calf pairs from 1982-1997 were regressed against time, with the following results:

ln(no. of pairs) versus year
$n = 16$
$R^2 = 0.048$
Slope = 0.0159, SE = 0.0189, *p* value = 0.41
95% CI of slope estimate = [-0.0246, 0.0564]

It was noted that this regression would result in an underestimate of the rate of increase for the 1980s period of relatively even conditions, because the calving interval has significantly increased during the observation period.

METHOD 2

A simple linear regression of the number of parous females by year (Table 1, column 2, taken from SC/M98/RW1) shows an increase between 1985 and 1997 of 0.0345 (95% CI 0.0238, 0.0452).

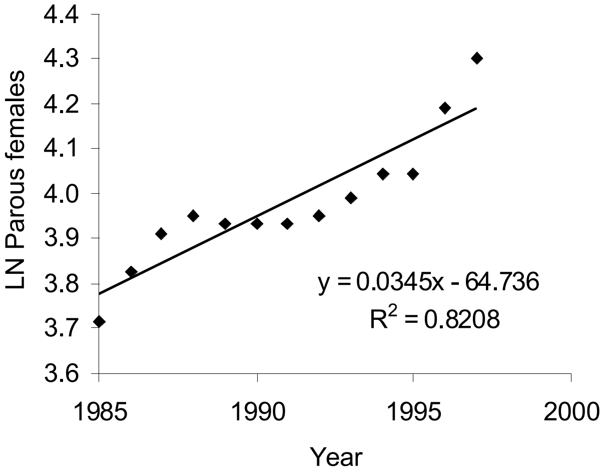

Fig. 1. Regression on the number of parous females against year (see text).

METHOD 3

In SC/M98/RW3, equation 17 provides rates of increase values calculated from: (1) an upper bound of annual survival ($S = 0.99$) and the lower bound ($S = 0.94$) of the estimates from the analysis in that paper; and (2) an annual reproductive output per individual, *m*, itself calculated from three quantities:

(1) the inter-calf interval *T* of breeding females: 3.7 years from early years of observation, and 5 years from the recent period;
(2) the proportion *R* of females in the population, taken at 0.5;
(3) the proportion *M* of these females that are mature. A value of 0.38 was used from an estimate from Brown (1994) (see point 3 below for alternative value of 0.40 calculated from the North Atlantic catalogue data at the meeting) such that:

$$m = (1/T) * R * M = 0.051 \text{ (for } M = 0.40,\ m = 0.054).$$

The lambda value of 1.041 in equation 17, is equivalent to an annual rate of increase of 4.1%. Using the alternative *M* value, the rate of increase is 4.3%, which can then be interpreted as an upper bound to the population growth rate for the North Atlantic right whale. However this approach works on the assumption of stable population increase, i.e. that the population has been increasing at a steady rate prior and during the observation period. For that reason this exercise should only apply the 1980s portion of the observation period, given the increase in calving interval and the change in geographical distribution in the 1990s.

ANALYSIS OF THE NORTH ATLANTIC RIGHT WHALE CATALOGUE AS OF MARCH 24 1998

1986

244 whales had been seen from the beginning of the observation period to the end of 1986. Two of those had died, making a total of 242 whales in 1986, of which 48 were parous females. Given a 50% sex ratio, the proportion of females that are parous in this population is:

$48 / (242 \times 0.5) = 0.40$

1989

299 whales had been seen by the end of 1989. Three of those had died, making a total of 296 whales in 1989, 59 of which were parous females.

$59 / (296 \times 0.5) = 0.40$

Calculations do not include:

(1) presumed mortalities;
(2) known mortalities of unidentified individuals; or
(3) calves that were born but not photo-identified.

Calculations are not comparable to those in SC/M98/RW1 (table 1).

REFERENCES

Brown, M.W., Kraus, S.D., Gaskin, D.E. and White, B.N. 1994. Sexual composition and analysis of reproductive females in the North Atlantic right whale, *Eubalaena glacialis*, population. *Mar. Mammal Sci.* 10(3):252-65.

Annex H

Fatal and Non-Fatal Ship Collisions

Date seen injured/dead (last date seen uninjured)	Animal's fate	Age (or range) when struck	Sex	Geographical area injury or mortality was documented	Date survivors most recently seen	Remarks
Western North Atlantic*						
30 Jan. 1972	Fatal	Calf	U	Texas	n/a	Body severed ~1m forward of tail stock. Only documentation is a photograph published in a local newspaper (Brazosport Facts) in Freeport, TX.
15 Apr. 1976	Fatal	Calf	M	Massachusetts	n/a	Large area of bruising observed behind skull. Scientist noted as probable ship collision.
5 Nov. 1976	Fatal	Unknown	U	Maine	n/a	Severe lacerations observed on back.
5 Mar. 1979	Fatal	Juvenile	M	New York	n/a	Tail severed.
28 May 1980	Non-fatal	Unknown	M	Great South Channel	5 Sep. 1989	Cut along back crossing spine ~1.5m long, 15cm deep.
13 Aug. 1980	Non-fatal	Unknown	M	Bay of Fundy	8 Mar. 1997	Series of 8 propeller cuts running along left flank and over back. Max. ~1.2m length and 15cm deep.
21 Feb.1983 (18 Sep. 1981)	Fatal	2 years	M	New Jersey	n/a	Severed tail.
5 Aug. 1984	Non-fatal	Unknown	U	Browns Bank	29 May 1988	Series of 5 propeller cuts ~60cm long, 10cm deep on left flank and near spine.
14 Aug. 1986 (May 1984)	Presumed fatal	7 years (5-7 years)	F	Bay of Fundy	3 Oct. 1986	1m diameter necrotic wound ~1m behind blowholes. Last seen 3 Oct. 1986 in Cape Cod Bay. Status: poor – slow swimming, orange cyamids, infection.
7 Aug. 1986 (9 Sep. 1985)	Fatal	1 year	F	Massachusetts Bay	n/a	2 propeller cuts, max. ~4.5m long, 1m deep running longitudinally along body. Severed spine.
14 Feb. 1987	Non-fatal	Calf	F	Southeast US	26 Aug. 1997	Series of 5 propeller cuts ~30cm long and 8cm deep on left fluke tip. Fluke tip eventually came off because of cuts.
9 Jul. 1987	Fatal	Juvenile	M	Nova Scotia	n/a	2-3 observed propeller cuts on left flank, 20-25cm deep, shallow gash and swelling observed on right flank. Animal buried without a necropsy.
28 Aug. 1987	Non-fatal	Unknown	U	Browns Bank	28 Sep. 1997	~1m of right fluke tip missing. Severed by propeller.
11 Feb. 1991	Non-fatal	Calf	F	Southeast US	1997	Series of 3 propeller cuts, max. 1.2m long, 15cm deep on left flank. Cuts healed.
12 Mar. 1991 (21 Feb. 1991)	Fatal	2 years	F	Florida	n/a	Seen in Bay of Fundy, Oct. 1990 with line, gillnets and buoys wrapped around tailstock. Seen off the coast of Florida on 21 Feb. 1991 with skin lesions on head. Swimming laboriously. Stranded on 12 Mar. 1991 in Florida. Flensed carcass revealed a shattered skull, from ship strike.
5 Sep. 1992 (23 Aug. 1992)	Fatal	Adult	F	Bay of Fundy	n/a	No external sign of injury. Necropsy revealed extensive internal haemorrhaging caused by impact from ship. Carcass flensed, no broken bones.
5 Jan. 1993	Fatal	Calf	M	Florida	n/a	Two series of large propeller cuts from a twin engine, 82 foot Coast Guard cutter. Max. depth 40.5cm, max. length 104cm. Animal not seen by vessel operators before impact. Vessel struck whale at a speed of 15 knots. Carcass not recovered until 8 Jan., full necropsy 9 Jan.
6 Dec. 1993	Fatal	Unknown	F	Virginia	n/a	Found floating belly up, back side not observed. Not retrieved. Large straight gash running from right ventral to right lateral surface anterior to flukes.
	Fatal	Unknown	U	Virginia	n/a	Another dead floating right whale found on same day, 28 miles to the south. Cause of death undetermined. Carcass not retrieved.
22 Feb. 1994 (27 Jan.1994)	Presumed fatal	Calf	U	Florida	-	Several deep cuts on head and lower lip regions from line or cable. Probable propeller cuts on both sides of dorsal flukes. Injury maybe while fishing vessel retrieving gear.
13 Aug. 1995 (22 Mar. 1992)	Unknown	Adult	F	Gulf of Maine	-	Cut ~60-90cm deep on right side of head below rostrum and cutting into the lower lip and extending down for undetermined length. Orange cyamids on tail and along lip edge, greying of skin. Status: poor.
16 Sep. 1995 (8 Sep. 1995)	Non-fatal	4 years	M	Bay of Fundy	1997	Series of propeller cuts, max. ~1m long, 8cm deep on tail stock and tail. Fishing gear through mouth was partially removed.
19 Oct. 1995 (8 Oct. 1995)	Fatal	Unknown	M	Bay of Fundy	n/a	4.8m long gash in back, broken vertebral discs. Full necropsy impossible as whale found on inaccessible beach.
30 Jan. 1996	Fatal	Adult	M	Georgia	n/a	No external sign of impact. Broken skull, vertebrae and ribs found when carcass floated. Blunt impact from ship.

cont…

Table cont.

Date seen injured/dead (last date seen uninjured)	Animal's fate	Age (or range) when struck	Sex	Geographical area injury or mortality was documented	Date survivors most recently seen	Remarks
9 Mar. 1996 (3 Oct. 1995)	Fatal	Unknown	M	Massachusetts	n/a	3.3m long gash in back, broken skull. Lobster line including a trap caught through mouth and around tail. Entanglement occurred in Dec. in Bay of Fundy. Carcass severely decomposed.
19 Aug. 1997	Fatal	Unknown	F	Bay of Fundy	n/a	No external sign of injury. Necropsy revealed 6m long haematoma along left side and broken right mandible. Carcass flensed, no other broken bones observed.
Brazil						
1989 (several times, days prior)	Fatal	Juvenile	U	Rio Grande do Sul	n/a	Stranded with propeller cuts on head. Sighted several times during two weeks prior to stranding.
1991	Fatal	Unknown	U	Rio Grande do Sul	n/a	Two halves of a right whale were found approximately ½ mile apart.
1992	Unknown	Unknown	U	Rio Grande do Sul	n/a	Trawler reported striking a right whale. No other information.
Oct. 1993	Fatal	Unknown	U	Rio Grande do Sul	n/a	Right whale stranded 16km south of Rio Grande (32°08'S) with four propeller cuts on tail stock.
South Africa						
27 Jul. 1983	Fatal	Adult	F	Beachview, Port Elizabeth	n/a	Died at sea. Five apparent propeller marks. Shark bites also noted.
8 Feb. 1984	Fatal	Adult	U	Jakkalsfontein	n/a	Seen from air. Major damage around the midlength. Possible ship strike.
16 Oct. 1984	Fatal	Calf		East London Harbour	n/a	Crew of cargo ship reported the presence of cow/calf pair of right whales at the harbour entrance. Despite this, the calf was later struck, at 0730 hours, by a hopper dredge leaving the harbour. The dredge captain reported the pair surfaced suddenly off his bow. Vessel speed unknown.
21 Nov. 1986	Non-fatal	Unknown	U	-	-	Fisheries vessel struck whale causing some damage to whale and boat. Vessel abandoned but later towed in. Whale cut but apparently OK.
10 Sep. 1988	Fatal	Adult	M	25km E of Sundays River	n/a	On 7 Sep. 1988, nine whales were sighted ahead of roll-on/roll-off ferry M/V *Barrier* as it gained speed leaving Port Elizabeth harbour at 0653 hours. They apparently did not react to the approaching vessel, which was travelling 12-13 knots. Impact was felt by crew and blood was observed in the water. Two whales stranded 10 Sep. 1983, on a beach 15 n.miles from strike. One had propeller slashes and damaged rostrum. One showed no outward sign of impact.
10 Sep. 1988	Fatal	Adult	M	25km E of Sundays River	n/a	See above.
16 Aug. 1993	Fatal	Calf	U	Between Long Beach and Koppie Alleen	n/a	Found dead, blubber and appendages. Tail cut off. Possible ship strike.
10 Oct. 1993	Fatal	Calf	F	Lekkerwater, De Hoop	n/a	Found dead, decomposing. Tail cut off. Possible ship strike.
22 Sep. 1994	Fatal	Juvenile	F	Kabeljoubank, Breede River	n/a	Found dead. Bystanders claimed that there had been a boat struck in the adjoining bay 2-3 days before and that the animal had cuts across the back. Possible ship strike.
10 Nov. 1994	Fatal	Juvenile	M	Shell Bay, St Helena Bay	n/a	Found dead. Diagonal slash through the blubber near the genital aperture through which viscera protruded. Possible ship strike.
6 Jan. 1995	Non-fatal	Unknown	U	-	-	Boat damage, whale apparently survived.
28 Jul. 1996	Fatal	Adult	F	Scarborough, Cape Peninsula	n/a	Stranded dead. No external signs of injury but when the skeleton was later being prepared for museum display the rostrum was found to be broken and skull fragments were missing. Possible ship strike.
6 Sep. 1997		Unknown	U	-	-	Boat damage, whale apparently survived.

* Vessel strikes resulting in propeller cuts less than 8cm in depth are not included.

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Tønnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling.* C. Hurst and Co., London. I-xx+798pp.

Tormosov, D.D., Mikhalev, Y.A., Best, P.B., Zemsky, V.A., Sekiguchi, K. and Brownell Jr, R.L. 1998. Soviet catches of southern right whales, *Eubalaena australis*, 1951-1971; biological data and conservation implications. *Biol. Conserv.* 86(2):185-97.

Annex I

Specific Recommendations for Reducing Ship Strikes (see Item 12.3.3 and Item 14)

WESTERN NORTH ATLANTIC

Southeast USA

Calving right whales give birth and overwinter in the coastal waters between Savannah, Georgia (GA) and West Palm Beach, Florida (FL). The primary aggregation occurs along 80 n.miles of coastline between Sapelo Island, GA and St. Augustine, FL. Most sightings of right whales occur west of 81°00W (Kraus *et al.*, 1993; SC/M98/RW6). Three major shipping channels serve three commercial ports and two military bases located within this area of aggregation. These are the Brunswick Harbour entrance (Brunswick, GA), the St. Marys River entrance (Fernandina Beach, FL) and the St. Johns River entrance (Jacksonville, FL).

The Workshop **recommends** that these three channels be extended due east, from their respective sea-buoys, to 81°00W. During the calving season (December to March), all vessels greater than 25m in length, using these channels, should travel the entire length of the channels. All vessels greater than 25m in length should operate at less than 10 knots (or minimum safe steerage) while in the federally designated critical habitat. The Workshop further **recommends** that a mandatory ship reporting system be implemented to acquire information on the numbers of vessels transiting this area.

Bay of Fundy

Right whales are present in the Bay of Fundy from June to November, with a peak in August and September. In recent years, cow-calf pairs, juveniles and adults identified in the Bay represent some two-thirds of the catalogued population. The aggregation of right whales overlaps with the outbound shipping lane from Saint John, New Brunswick, and the inbound vessel lane for ports in Maine and New Brunswick. These lanes are monitored by a Vessel Traffic System. Since 1992, there have been three mortalities from ship collisions in the Bay of Fundy (SC/M98/RW8).

To reduce the potential for ship/whale collisions the Workshop **recommends** that the shipping lanes be narrowed and moved about 10km to the east away from right whale aggregations.

Roseway Basin

Roseway Basin is an offshore feeding habitat which has been observed with high numbers of right whales from July to September. Although no shipping lanes transit the area and no mortalities have been documented, ship traffic has been observed transiting this habitat.

The Workshop **recommends** that this high-use area be designated as an area to be avoided by shipping.

Great South Channel

Right whales are present in high numbers in this offshore area from April to June. Shipping traffic to/from Boston Harbour use the shipping lanes in the Great South Channel. Other Gulf of Maine shipping traffic traverses the entire breadth of the Great South Channel. Little is known about the level of ship traffic and how it overlaps with right whale habitat use.

The Workshop **recommends** that a mandatory ship reporting system be implemented to acquire information on the numbers of vessels transiting this area and to provide these ships with information on real time sighting locations obtained of right whales observed from aerial surveys.

Cape Cod Bay

Right whales are present in limited numbers in this area from December to May. An unknown level of vessel traffic transits through this high-use area.

The Workshop **recommends** that a mandatory ship reporting system be implemented to acquire information on the numbers of vessels transiting this area and to provide these vessels with information on right whale sighting locations obtained from aerial and shipboard surveys.

High speed ferries

The Workshop expressed serious concern over the proposed use of large (>100ft) high speed (>30 knot) ferries transiting right whale migration corridors and habitat, and **recommends** consideration of ship/whale collision risks in permit review.

OTHER AREAS

The Workshop agreed that many of the problems faced by North Atlantic right whales with regard to ship traffic either currently or potentially exist in other parts of the world where right whales concentrate.

For areas where there is information on right whale distribution and densities, or critical habitats have been defined, the control of shipping activity should be investigated. This may include:

(a) moving shipping lanes to areas of lower right whale densities;
(b) slowing ship speeds;
(c) educating mariners on right whale distribution and vulnerability;
(d) assessing regions where there is increased potential for whale/ship interaction with increasing or expanding right whale populations.

REFERENCE

Kraus, S.D., Kenney, R.D., Knowlton, A.R. and Ciano, J.N. 1993. Endangered right whales of southwestern North Atlantic. p.69. *In:* Final Report, Minerals Management Service Contract No. 14-35-0001-30486. Edgerton Research Laboratory, New England Aquarium, Boston, MA.

Annex J
Report of the Whalewatching Working Group

Members: Findlay (Convenor), Brown, Burnell, Carlson, Donoghue, Flores, Juritz, Knowlton, Lotz, Mayo, Palazzo Jr, Patenaude, Payne, Reeb, Rowntree, Silber, Slay, Swartz.

1. ELECTION OF CHAIRMAN

Findlay was appointed Chairman.

2. ELECTION OF RAPPORTEURS

Carlson and Donoghue were appointed Rapporteurs.

3. ADOPTION OF THE AGENDA

The adopted agenda is given as Appendix 1.

4. REVIEW OF AREAS

The group reviewed areas where watching of right whales occurs around the world and noted that regulation of whalewatching activities varied greatly between countries. It did not have adequate information to provide precise numbers for boats operating in many areas; broad estimates were provided where exact numbers were not known.

5. POSITIVE AND NEGATIVE ASPECTS OF WATCHING RIGHT WHALES

5.1 Positive aspects

Positive aspects of watching right whales were discussed under the following general categories: education (IFAW, 1996; Orams, 1996); research (IFAW, 1995); economic (Hoyt, 1995; Findlay, 1997; IFAW, 1998); protection (IFAW, 1999); political; and benefits to whales.

5.1.1 Education/emotional response/public awareness

The group agreed that right whales, like other whale species, can be effective in highlighting issues of ocean conservation. The coastal habits of right whales in some areas increase their visibility to the public and as a result may facilitate protection of coastal and marine environments. Right whales are of great interest to the public and provide a sense of awe in whalewatchers, thus providing advocacy for wider protection of the marine environment upon which the whales depend.

5.1.2 Research

Whalewatching vessels can be excellent platforms for data collection. Mayo noted that in New England, considerable research and entanglement data have been collected from whalewatching vessels, however, data collection has been limited by the 500-yard approach regulation. Participants noted that in Argentina, operators provide information on photo-identification, entanglements and carcasses, and in Brazil, tourists and locals provide sighting data for researchers.

Patenaude noted that levies are charged on commercial dolphin-watching vessels in the Bay of Islands, New Zealand. There is no such levy for right whalewatching operations. However, in some cases, whalewatching operators have provided salaries for researchers and support for research through the sale of souvenirs.

5.1.3 Economics

Several communities around the world have derived economic benefits from whalewatching industries. In such cases, numerous aspects of community life benefit (Hoyt, 1995; IFAW, 1998).

It was noted that the Mobile Telephone Network (MT) believes their sponsorship of the Cape Whale Route in South Africa provides more public interest than their sponsorship of high profile sporting events.

Shore-based whalewatching in Santa Catarina, Brazil is being promoted as the main winter alternative for coastal tourism which is otherwise very scarce. In at least one location in Australia, shore-based whalewatching and general tourism has resulted in increased opportunities for terrestrial and marine conservation as a result of revenues generated. Although Peninsula Valdés, Argentina is remote, over 44,000 tourists took whalewatching trips in 1994. Because the local community is earning money from whales, they are protective of the resource and associated infrastructure.

The group recognised that there are examples of economic benefits to local communities from whalewatching activities based on other species, such as gray whales.

5.1.4 Protection

Shore-based whalewatching may provide extra protection to right whales because any vessels interacting with the whales are more easily observed, promoting self-regulation. In the Bay of Fundy, Canada, boat-based whalewatching is self-regulated by a code of ethics agreed by the operators. There is also self-regulation by boat operators in Argentina. Community monitoring and local pressures in these areas may be more effective than legislation alone.

5.1.5 Political

Whalewatching is a significant way to generate political support for increased protection of whales. For example, Burnell noted that the Head of the Bight Right Whale Sanctuary in Southern Australia gained increased political support when it was realised that the revenues from whalewatching could equal or exceed previous revenues from fishing.

5.1.6 Potential benefits to whales

Whalewatching can be an important element in habitat protection. In areas where populations are recovering, whales may be reoccupying previously used habitats, parts of which are now severely degraded (e.g. western North Atlantic). Political pressure, much of it generated by whalewatching, can result in better protection of such habitats.

As a further example, Payne reported that right whales in Peninsula Valdés, Argentina seek the shelter of whalewatching boats to escape gull harassment.

5.2 Potential negative aspects

5.2.1 Short-term impacts

There are few studies which demonstrate short-term, negative effects of whalewatching activities. The group noted that short-term effects may depend on: the vessel (number, duration of encounter, speed, angle of approach, type and acoustic signature of vessel); the whales (behaviour, group composition, past experience with vessels); and the environment (habitat type, sea state and water depth). It was noted that short-term effects may include changes in dive times, respiration, swimming speed and direction, and behaviour including acoustic behaviour.

5.2.1.1 BOAT-BASED WHALEWATCHING

Studies in Peninsula Valdés, Argentina showed that individuals without calves in Golfo Nuevo (whalewatching permitted) exhibited greater swimming speeds than individuals without calves in Golfo San Jose (protected; no whalewatching), whereas whales with calves did not (Colombo *et al.*, 1990). SC/M98/RW32 describes evasive responses by whales to ‘threatening’ approaches by boats (e.g. circling, chasing). Palazzo noted that threatening approaches in Brazil resulted in the temporary displacement of right whales to adjacent bays, whereas more careful approaches often resulted in whales approaching boats. Patenaude reported that small boat approaches in the Auckland Islands often resulted in the disturbance of cow-calf pairs when the boat was closer than 20m, but the whales quickly resumed normal behaviour after the boat left the immediate area.

Payne reported that right whales are more easily disturbed when approached by vessels on calm days. In the Bay of Fundy, right whales appear not to notice approaching vessels when the whales are resting on the surface or participating in surface active groups.

5.2.1.2 AERIAL WHALEWATCHING

Payne noted a general lack of response in Argentinian right whales exposed to fixed-wing aircraft during surveys. However, helicopters appear to cause disturbance. Burnell reported that in southeast Australia, research aircraft are not permitted to fly lower than 250m over whales. Voluntary protocols restrict each encounter to three circuits. If required, further encounters are made after a minimum five-minute delay. It has been noted that photography becomes progressively more difficult after the first encounter/session as whales remain submerged for a longer period.

A number of studies have examined the effects of aircraft and boats on marine mammals, although the relevance of these results to whalewatching activities is not known. The group discussed several cases. For example, bowhead whales frequently react to circling aircraft at 305m or less. Reactions include hasty dives, increased respiration, change of direction or dispersal from the area of disturbance (Richardson *et al.*, 1995).

5.2.2 Long-term effects

The group noted the difficulty of linking long-term effects to whalewatching given the relatively few directed studies.

Although no long-term effects are known, the group acknowledged that they may result in: shifts in distribution or habitat use; lowered reproductive success (e.g. missed mating opportunities; separation of cow-calf pairs); changes in mortality/recruitment or feeding/energetics.

The group discussed the issue of repeat approaches and noted that this may result in habituation. It was suggested that habituation may increase the likelihood of ship strikes.

5.2.2.1 BOAT-BASED WHALEWATCHING

The group noted that there were no observed long-term negative effects of whalewatching on right whales.

In Peninsula Valdés, Argentina, cow-calf pairs have moved from the outer coast and a bay where whalewatching is not allowed, to an area in Golfo Nuevo that is adjacent to the centre of the whalewatching industry. These whales have therefore moved from an area of less human disturbance to one of more disturbance (SC/M98/RW13). However, the 1994/1997 cohort of calving females moved 50km away from the whalewatching area to an area with considerable boat activity and severe gull harassment of the whales. The reasons for this movement are unclear. It may be attributed to social cohesion, environmental factors or disturbance from whalewatching activities.

The group then discussed other species. Swartz noted that there had been changes in gray whale migratory corridors off California, USA. Increasing levels of recreational whalewatching were thought to be the reason for the shift, but a definitive link had not been established. He also noted that, unlike the other three bays, whalewatching in one of the four breeding lagoons in Mexican waters, Northern Magdalena Bay, was not regulated, and that gray whales appear to have abandoned this area as a result. Again, a clear cause-effect relationship had not been established.

The group noted that well-documented studies on humpback whales in New England (Mayo and Carlson, pers. comm.) and Glacier Bay, Alaska (Baker and Herman, 1989) had shown that initial concerns that whales had vacated these areas because of vessel traffic had later been demonstrated to be unfounded. Thus, distributional shifts cannot be attributed to whalewatching in all cases, and such shifts need to be carefully investigated.

Mayo noted that research on seasonally returning humpback whales conducted for the past 22 years has shown no long-term effects of boat-based whale-watching. In particular, the reproductive success of known individuals apparently has not been negatively affected.

5.3 Other identified effects

Environment

Mayo suggested that motor vessel traffic has an effect on the density of surface plankton patches, and therefore may affect right whale prey acquisition in Cape Cod Bay. The effect of this on right whales is not clear.

Research

The group noted that there are locations where cetacean tourism activities had interfered with research. These included examples from the Bay of Islands, New Zealand, Witsand and Hermanus, South Africa and New England, USA.

Economics/political

Burnell noted that political influence based on economic motivation can affect whale conservation. For example, in Australia, the fishing industry has applied significant political pressure to inhibit legislation designed to protect whales. He stressed the importance of highlighting to politicians the economic value of whalewatching.

Swimming with whales

Payne noted that right whales provide a unique opportunity to generate increased support for whale conservation through close contact but recognised that this activity would have to be carefully regulated.

6. REVIEW OF LEGISLATION, REGULATIONS AND GUIDELINES

The group reviewed present legislation, regulations and guidelines which pertain to the watching of right whales around the world. The majority of these are presented in Carlson (1996).

6.1 Protected areas

The group noted that marine protected areas exist in certain parts of the world and identified a number of protected areas bearing on the protection of right whales. The extent of regulation within protected areas differs between nations or areas. Not all of these protected areas were established as a result of whalewatching or to protect right whales.

Canada

The Bay of Fundy and Roseway Basin Right Whale Conservation Areas were designated by the Federal Government of Canada. These areas encourage voluntary compliance for vessel approach guidelines. The areas provide a means for mariner awareness and education, but provide no *a priori* protection for right whales.

USA

National Marine Sanctuaries are generally designated for a particular marine resource or species, and serve to raise public awareness, rather than limit human activities. Although there are no sanctuaries established specifically for right whales, the range of the North Atlantic right whales includes the Gerry E. Studds Stellwagen Bank National Marine Sanctuary and Gray's Reef National Marine Sanctuary.

RIGHT WHALE CRITICAL HABITAT

Three Critical Habitats have been designated for right whales on the eastern seaboard of the USA. Designation of a Critical Habitat does not restrict human activity or mandate management action, but it does contribute to species conservation by raising public awareness about the importance of the area, and provides specific guidance for the regulation of federal activities in the area.

Argentina

Argentina created the first marine sanctuary for right whales. Golfo San Jose was declared a Provincial Marine Park in 1974 to maintain the pristine nature of the area as an important nursery area for right whales.

Australia

The South Australian Government established the Head of the Bight Right Whale Sanctuary in 1996, restricting all industrial, commercial and boat-based access. The Commonwealth Government has proposed a large complementary Marine Park surrounding the whale sanctuary to cover a total of 21,000km^2, restricting access for the six-month period when right whales are in coastal waters and providing strict controls over access for the remainder of the year.

Sub-Antarctic

The Auckland Islands Marine Mammal Sanctuary includes all waters within a 12 n.mile radius of the Auckland Islands. Currently all commercial fishing is prohibited within this area, and further regulations are able to be promulgated by the Minister of Conservation.

Other

The Southern Ocean Whale Sanctuary and Indian Ocean Sanctuary have been designated by the IWC but the only provisions are for the prohibition of whaling.

7. RECOMMENDATIONS FOR MANAGEMENT

The group endorsed the IWC's general principles for whalewatching and **recommended** that these be applied to all whalewatching activities involving right whales. The group agreed that it was critical to: (1) manage the development of new and fledgling whalewatching operations to minimise the risk of adverse affects; and (2) take appropriate regulatory measures in areas where directed research demonstrated negative impacts on whales from established whalewatching activities.

The group agreed that special protected areas provide a framework for the implementation of site-specific regulations for whalewatching and that such areas are important in conserving coastal habitats. It is therefore **recommended** that studies be undertaken to assess the establishment of special protected areas in areas of known right whale concentration (e.g. the central-south coast of Santa Catarina, Brazil).

8. ADOPTION OF REPORT

The report was adopted at 10:30am on Sunday 22 March.

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Annex K
Proposal for the Establishment of a Southern Hemisphere Right Whale Consortium

BACKGROUND

Dedicated research has been carried out on southern right whales in Argentina, South Africa and Western Australia for the past thirty years or so (Whitehead *et al*., 1986; SC/M98/RW15). Recent studies have included work in Southern Australia, New Zealand sub-Antarctic, South Georgia and Brazil (Baker *et al*., 1997; Burnell, 1997; SC/M98/RW26; SC/M98/RW14). However, prior to this IWC-convened Right Whale Workshop, few opportunities existed for cooperation and collaborative research, and consequently the national programmes that have been developed have not shared common methodologies for data collection and analysis. Further, information on stock structure and life history parameters have only been partially elaborated because of the localised nature of study areas.

By contrast, in the North Atlantic, a collaborative research consortium has been formed, consisting of representatives from five independent research institutions, two national governments and their appropriate agencies and four US state agencies (see Appendix 1). This consortium was formed in 1986, when research teams from various institutions recognised the need to bring together the information that had been collected from study programmes on right whales in five different locations on the east coast of North America, and to standardise data collection protocols and methods for analysis. Additionally, establishment of the consortium has allowed the pooling of resources, the sharing of key personnel and the development of a broader overview of the biology and conservation requirements of the North Atlantic right whale.

PROPOSAL

Here we propose the establishment of a multinational consortium for the study of right whales in all oceans of the Southern Hemisphere. Such a multinational effort will provide insights into stock structure, population dynamics and conservation requirements that no single national research effort could hope to obtain. The consortium objectives might be:

(1) standardisation of data collection;
(2) facilitation of inter-catalogue comparisons of photo-identifications between regions;
(3) development of comparable analytical methods;
(4) sharing of resources, especially sophisticated and expensive laboratory techniques (e.g. for genetic, isotopic and pollutant analysis);
(5) exchange of scientific personnel and samples;
(6) and where appropriate, assistance in the development of joint management strategies and policy.

Membership

Members of such a consortium might include (but not be limited to) the following.

Government Agencies
Brazil – IBAMA (National Environmental Authority).
Argentina – Advisory Committee on Right Whales as a Designated National Monument.
Chile – Ministry for the Environment.
South Africa – Department of Sea Fisheries.
Australia – Environment Australia.
New Zealand – Department of Conservation.

Provincial Agencies
Brazil – State Secretariat of the Environment, Santa Catarina.
Argentina – Organismo Provincial de Turismo, Chubut.
Western Australia – Department of Conservation and Land Management South Australia.

Academic Institutions
University of Auckland.
Western Australia Museum.
University of Sydney.
MRI, University of Pretoria.
British Antarctic Survey.

Independent Research Organisations
Whale Conservation Institute.
International Wildlife Coalition.
Fundacion Patagonia Natural.
CODEFF (Chile).

Additionally, the proposed Southern Hemisphere Consortium would benefit from the active involvement (at least in the early stages) of some members of the North Atlantic Right Whale Consortium, for example, the New England Aquarium and the National Marine Fisheries Service (NMFS).

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Appendix 1

MEMBERS OF THE NORTH ATLANTIC RIGHT WHALE CONSORTIUM

National Government Agencies

Canada
Department of Oceans and Fisheries
Ministry of Transport
Canadian Coastguard

USA
National Marine Fisheries Service
US Coastguard
US Navy
US Army Corps of Engineers
US Environmental Protection Agency

US State Agencies

Florida
Department of Marine Resources

Georgia
Department of Natural Resources

Massachusetts
Division of Marine Fisheries

Maine
Department of Marine Resources

Private Institutions

New England Aquarium
Centre for Coastal Studies
Woods Hole Oceanographic Institution
University of Rhode Island
McMaster University

Annex L
Summary of Available Catch Data for Southern Right Whales

Table 1

South Atlantic right whale catches, by decade and area. For explanation of what is missing, redundant etc. see text. Square brackets denote that the indicated catch is subsumed within an estimate given in another column.

Period	S. African shore (inc. Natal)		Brazil shore[2]	Brazil shore[3]	Total pelagic Brazil/ Falkands[4]*	French pelagic Brazil/ Falkands[5]	US pelagic S. Atlantic[6]	S. Africa bay whaling [7]**	French pelagic [8]	French pelagic unspecified[9]	Modern (S. Georgia S. Shetlands)[10]	Illegal Soviet		Modern German pelagic[12]
												SW	SE	
1770-9	-	-	7,450	-	747	-	-	-	-	-	-	-	-	-
1780-9	-	-	4,700	-	3,690	[205]	-	*ca* 600/season (1785-1805)	-	-	-	-	-	-
1790-9	128	-	1,950	-	4,329	[238]	-	-	-	360	-	-	-	-
1800-9	266	-	650	-	5,396	[0]	[1,849]	-	-	-	-	-	-	-
1810-9	378	-	154	-	504	[119]	[149]	-	-	11	-	-	-	-
1820-9	304	-	-	-	-	1,064	8,085	-	-	204	-	-	-	-
1830-9	270	-	-	-	-	743	14,564	-	382	49	-	-	-	-
1840-9	64	-	-	-	-	-	1,113	-	-	-	-	-	-	-
1850-9	49	-	-	-	-	-	940	-	-	-	-	-	-	-
1860-9	24	-	-	-	-	-	860	-	-	-	-	-	-	-
1870-9	16	-	-	-	-	-	481	-	-	-	-	-	-	-
1880-9	16	-	-	-	-	-	329	-	-	-	-	-	-	-
1890-9	41	-	-	-	-	-	67	-	-	-	-	-	-	-
1900-9	23	7-8	-	-	-	-	67	-	-	-	258	-	-	-
1910-9	1	39	-	-	-	-	18	-	-	-	390	-	-	-
1920-9	-	39	-	-	-	-	-	-	-	-	-	-	-	-
1930-9	-	15	-	-	-	-	-	-	-	-	-	-	-	1
1940-9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1950-9	-	4	-	150	-	-	-	-	-	-	-	-	-	1
1960-9	-	1	-	150	-	-	-	-	-	-	-	1,408	767	-
1970-9	-	-	-	60	-	-	-	-	-	-	-	-	-	-

* Estimates in this column include an adjustment for hunting loss (x1.2). ** Walvis Bay, Delagoa Bay; i.e. includes some Indian Ocean catches. [1] Best and Ross (1986). [2] Richards (1993). [3] Palazzo and Carter (1983; see IWC 1986, p.29). [4] Richards (1993). [5] Du Pasquier (1986 p. 30). [6] Best (1987). [7] Richards and Du Pasquier (1989). [8] Tristan da Cunha, Du Pasquier (1986). [9] Du Pasquier (1986). [10] Tønnessen and Johnsen (1982). [11] Tormosov *et al.* (1998) 233 in 1951/52-1959/60 and 237 in 1960/61-1970/71, some proportion of which would have been taken in this ocean. [12] Kock (1996); Barthelmess *et al.* (1997).

Table 2

South Pacific.

Period	Coast of Chile[1]	Early shore and bay whaling, S. Australia, NSW, Tasmania, Victoria[2]	19th century US pelagic[5]	NZ bays [6]	French whaling NZ/Australia[9]	Illegal Soviet SW Pacific[10]
1815-9	31	-	1,958	-	-	-
1820-9	69	323	535	-	-	-
1830-9	2,211	6,777	5,580	2,237	2,723	-
1840-9	70	3,089	5,027	2,394	1,148	-
1850-9	-	431	740	347	-	-
1860-9	-	232	385	100	-	-
1870-9	-	62[3]	109	62[7]	-	-
1880-9	-	62[3]	308	62[7]	-	-
1890-9	-	62[3]	-	62[7]	-	-
1900-9	118	3[4]	10	30[8]	-	-
1910-9	191	2[4]	-	30[8]	-	-
1920-9	33	2[4]	-	30[8]	-	-
1930-9	104	-	-	3	-	-
1940-9	1	-	-	1	-	-
1950-9	7	-	-	2	-	-
1960-9	4	-	-	-	-	372
1970-9	0	-	-	-	-	-

[1] Includes French pelagic (Du Pasquier, 1986, as summarised in IWC, 1986, p.30) for 19th century, Tønnessen and Johnsen (1982) for 1900-20 and IWC (1986, p.30) for 1920 onwards. [2] Dawbin (1986). [3] Dawbin (1986) lists a total catch of 185 for 1870-1900. [4] Dawbin (1986) lists a total catch of 7 for 1901-30. [5] Best (1987). [6] Dawbin (1986), IWC (1986, p.30); including catches in New Zealand by whalers from NSW or Tasmania, and also Campbell Island catches. [7] Dawbin (1986) lists a total catch of 186 for 1870-1900. [8] Dawbin (1986) lists a total catch of 89 for 1901-30. [9] Du Pasquier (1986). [10] Tormosov *et al.* (1998).

Table 3

Indian Ocean.

Period	Best (1987)	W. Australia bay whaling[1]	Kerguelen[2]	Illegal Soviet whaling[3]	
				Crozet (SW)	Other[4]
1830-9	6,161	50	-	-	-
1840-9	4,360	121	-	-	-
1850-9	1,276	84	-	-	-
1860-9	438	11	-	-	-
1870-9	69	-	-	-	-
1880-9	9	-	-	-	-
1890-9	26	-	-	-	-
1900-9	154	-	1	-	-
1910-9	-	-	-	-	-
1920-9	-	-	-	-	-
1930-9	-	-	-	-	-
1940-9	-	-	-	-	-
1950-9	-	-	-	-	-
1960-9	-	-	-	309	25
1970-9	-	-	-	-	-

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Report of the Workshop on Status and Trends of Western North Atlantic Right Whales

1. INTRODUCTORY ITEMS

The meeting was held at the Northeast Fisheries Science Center (NEFSC), Woods Hole, Massachusetts, USA from 24-27 October 1999.

Dr John Boreman (Deputy Science Director of the NEFSC) welcomed participants to the NEFSC and noted the importance of the Workshop to the management of right whales by the US National Marine Fisheries Service.

Donovan welcomed the participants on behalf of the IWC and thanked them for coming to the meeting. He noted the great importance attached by both the Scientific Committee and the Commission to the status of the western North Atlantic right whale, particularly since the 1998 Workshop held in Cape Town (IWC, 2001), hereafter referred to as the Cape Town Workshop.

In 1998, an Intersessional Steering Group had been set up by the Scientific Committee to review ongoing work in relation to the status and trends of the North Atlantic right whale population, and to consider whether sufficient progress had been made to hold a workshop on this topic (IWC, 1999b). This was in response to recommendations made at the Cape Town Workshop.

At the 1999 Scientific Committee meeting (IWC, 2000a), discussion first centred around a recently published analysis of trends in the survival probability of North Atlantic right whales (Caswell *et al.*, 1999). That analysis estimated a decrease in annual survival rate from 0.99 in 1980 to 0.94 in 1994 and an expected time to extinction of less than 191 years. An earlier version of the analysis had been submitted to the 1998 Cape Town Workshop.

The Committee had concluded that whilst it had some questions on the approach used, these did not alter the Committee's conclusion of 1998 that there are 'serious concerns over the status of the stock'. Those concerns were based on *inter alia*: the small size (300-350 animals) of the stock; an increase in calving interval from an average of 3.67 years in the 1980s to over 5 years in the 1990s; poor recent calf production; the possibility of an unusually high degree of female senescence (only 38% of females are reproductively active); and the level of anthropogenic mortality. Under these circumstances the Committee had strongly recommended that the Comprehensive Assessment of this stock should remain of high priority.

Clapham (Convenor) welcomed participants to the meeting, and thanked Sara Wetmore for the considerable assistance she had given in the organisation of the Workshop. Clapham reiterated the terms of reference for the Workshop given by the Scientific Committee (IWC, 1999c), that:

> ...the Comprehensive Assessment of the western North Atlantic right whale should be a priority topic... with its objectives being to establish the current status and dynamics of the population.

Bannister was elected Chairman. Clapham, Hammond and Taylor agreed to act as rapporteurs with assistance from Donovan and others where appropriate. Donovan, Clapham, Hammond and Bannister edited the final report.

A list of participants is given as Annex A.

2. AGENDA

The draft agenda developed by the Steering Group was adopted as shown in Annex B.

3. REVIEW OF DOCUMENTS

A list of documents considered by the Workshop is given in Annex C.

4. REVIEW OF AVAILABLE DATA

Hamilton summarised the available data from the North Atlantic Right Whale Catalogue (NARWC, curated at the New England Aquarium), which details any sighting of a right whale for which the animal was positively photo-identified. NARWC data include dates, times and locations of sightings, sex, age (in years) and age class of the individual, its reproductive history (if female), genotype information, behaviour and identifying characteristics. By July 1999, there were more than 14,000 photographically identified sightings of 396 individuals, 11 of which are known to be dead (an additional mortality of an identified animal occurred in October 1999). The earliest record is from 1935.

The five major areas of effort (Fig. 1) have been the southeastern USA (the only known calving ground), Massachusetts Bay/Cape Cod Bay, Great South Channel, the Bay of Fundy and Browns Bank/Roseway Basin (also referred to as the Scotian Shelf). The period of most consistent effort is from 1983 to date, with variability among areas. In particular, effort essentially ceased in the Great South Channel in 1990 and did not resume until 1998, and beginning in 1993, right whales abandoned Roseway Basin, resulting in a subsequent lack of effort in that area. There has been no systematic coding for photograph quality or individual distinctiveness in the NARWC. Although there are sightings for which photographic quality and distinctiveness make it impossible to establish individual identity in that case, it is unlikely that the population contains individuals with insufficient markings to be identifiable (i.e. are not uniquely marked).

Sightings probability through photo-identification is affected by the chances of encountering whales, selection of whales to be photographed, obtaining adequate photographs and matching to the existing catalogue. Variation in these processes can introduce heterogeneity in sightings probability, which primarily biases estimates of population size and to a lesser degree, estimates of survival rate (e.g. Hammond *et al.*, 1990). Annual sighting histories of whales were constructed based on the composite result of all sampling throughout the year in all regions. The composite nature of the sampling should reduce the effects of heterogeneity somewhat by increasing overall sightings probability. However, heterogeneity in sightings probability has been identified through goodness-of-fit tests (SC/O99/RW5) for time dependent models.

A Working Group established under Laake (Annex D) identified various sources of heterogeneity in sightings probability from each aspect of the photo-identification process. The mark-recapture models in SC/O99/RW2 and SC/O99/RW7 incorporate features such as sex, age or stage, and spatial/temporal distribution patterns to model heterogeneity in sightings probability. Those covariates are useful proxies for the sources of variation in the photo-identification process identified in Annex D.

Kenney summarised the North Atlantic Right Whale Database (NARWD, curated at the University of Rhode Island). This contains all sightings (approximately 15,000 sightings of from 1-40+ animals per sighting) of right whales, whether the animal was photographed or not; it also contains sightings of other species. Effort sources are either dedicated or opportunistic; information on the type and extent of effort is generally available for dedicated surveys, but there are gaps for some areas in some years. Although an SPUE-type analysis might be possible with these data, there is currently no consistent and standardised measure of effort that could be utilised in an identifications per unit effort analysis.

White summarised the genetic database, which is curated at McMaster University, Canada. For each individual, this includes sex, mitochondrial DNA haplotype, genotype at nine microsatellite loci and at four MHC loci. Comparisons of genotype and photo-identification data indicate a very low error rate in either. There are 253 identified individuals which have been biopsied; in addition, biopsies exist for 45 animals not matched to an individual in the NARWC because either no photographs (or inadequate photographs) were obtained at the time of sampling or the animal was a dead neonate or adult for which no individual identification was possible.

Additional available data on right whales include those on blubber thickness, contaminants, stable isotopes, fatty acids, tagging and entanglements; these are not included in the centralised databases described above, but can be linked to

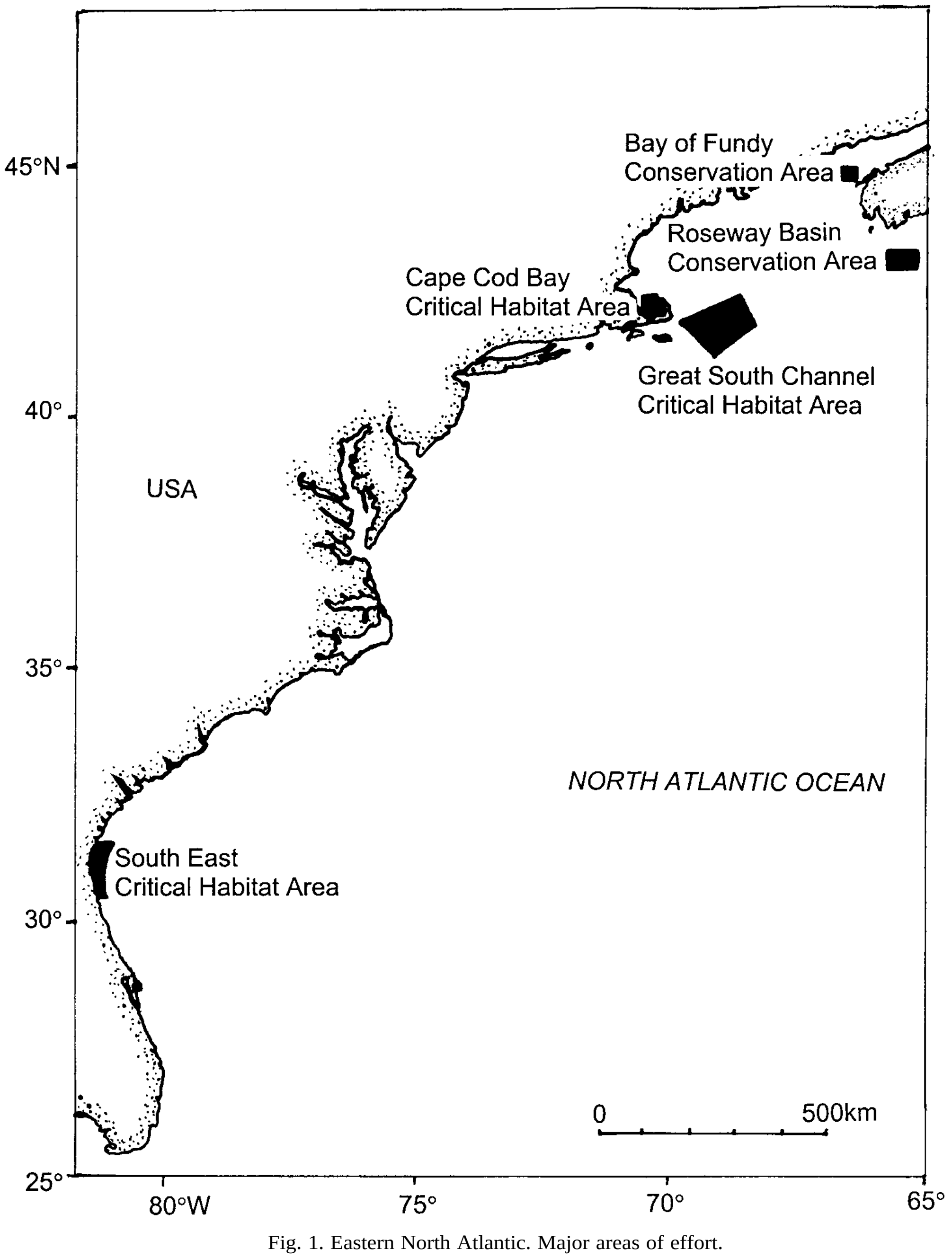

Fig. 1. Eastern North Atlantic. Major areas of effort.

individuals in the NARWC. There is also information on dead right whales, often including necropsy data. In addition, identification photographs can be used for the purpose of health assessment, for example from scars, fungal-like growths or lesions (Hamilton *et al.*, 1995).

All the data noted above are accessible through the North Atlantic Right Whale Consortium, which has established formal protocols for data access. Further information is available from Kraus (address in Annex A).

4.1 Recommendations

The Workshop **recommends** that goodness-of-fit tests be conducted for models developed in SC/O99/RW2 and SC/O99/RW7, to evaluate whether additional heterogeneity remains. Further theoretical development for the goodness-of-fit test may be required for the model in SC/O99/RW7. If there is further evidence of heterogeneity, covariates should be used that describe whale distinctiveness and photographic quality through time. This will require retrospective inspection of the catalogue and will require a major effort.

The Workshop also **recommends** that from now on, the quality and distinctiveness codes identified during the Cape Town Workshop (IWC, 2001) should be used to classify photographs in the existing catalogue. Any changes (e.g. reassignments of animals, retrospective assignments of identifications or sex) should be documented within the database.

The Workshop noted that Burnell had developed a semi-automated matching process for southern right whales (Burnell *et al.*, 2001), and **recommends** that its applicability to northern right whales should be investigated.

5. REVIEW OF AVAILABLE MODELS

Previously, the Scientific Committee had reviewed the analysis of Caswell *et al.* (1999) on trends in the survival probability of the North Atlantic population (IWC, 2000b). Questions were raised with regard to the statistical approach and the certainty that could be attached to the results. The Committee had recommended that further work be conducted, including the development of stage-structured models and those that attempted to incorporate additional spatial heterogeneity. That work has now been undertaken, and under this item the Workshop discussed the aims, data requirements, assumptions and limitations of each model available. An overview is given in Table 1.

Fujiwara reported on a model (SC/O99/RW7) that examined the effects of heterogeneity due to sex and developmental stage on estimates of survival and transition probabilities. The model classified individuals by sex and as calves, immature, mature (at least nine years old, or females known to have reproduced), and for females as mature with calf. Transition probabilities among stages were estimated using multi-stage mark-recapture methodology with maximum likelihood, and models were compared using the Akaike Information Criteria, AIC (Akaike, 1973). Animals of unknown sex or stage contributed to the likelihood function according to weighted averages of the likelihoods for males and females (assuming a 50:50 sex ratio) or for juveniles and mature animals (assuming proportions derived from a time-invariant model). Transition probabilities for each stage were allowed to vary as polychotomous logistic functions of time. Stage-specific sightings probabilities were allowed to vary as a function of time and/or of sampling effort. The best description of sightings probability according to AIC was obtained, allowing all transition probabilities to vary as logistic functions of time. Then the best transition model was selected using the best sightings model.

The transition model was turned into a two-sex female-dominant population projection matrix by noting that the transition from mature to female with calf produces a new calf. The resulting model was analysed using standard projection matrix methodology to compute population growth rates, stable stage distributions, and sensitivity and elasticity of growth rate. Absorbing Markov chain theory

Table 1

Comparison of available models for estimation of survival (ϕ), sighting probability (p), inter-birth interval and finite population growth rate (λ). Each method relies on photo-identification data and the mark-recapture models all require the assumptions summarised in Hammond (1986) with appropriate modifications relating to homogeneity of survival and sighting probabilities. A=Crude ϕ, B=Stage-specific ϕ; C=Sex specific ϕ; D=Annual p; E=Stage p; F=Sex p; G=Spatial p and ϕ; H=Inter-birth interval; NA=North Atlantic; SA=South Atlantic.

	Parameters										
Model	Population	A	B	C	D	E	F	G	H	λ	Comments
Mark-recapture: 2-sex multi-stage transition model (SC/O99/RW7)	NA only		x	x	x	x	x		x	x	Uses translated exponential distribution for inter-birth interval; all calving intervals exceed 2 years.
Mark-recapture: 3-stage model, adult females only (SC/O99/RW5)	NA and SA		x	x	x	x	x		x		Uses translated exponential distribution for inter-birth interval; all calving intervals exceed 2 years; used only sightings of females with calves.
Mark-recapture: Crude survival, sighting probability function of spatial location (Caswell *et al.*, 1999)	NA	x			x			x		x	Survival probability function of time, sighting probability a function of tendency of individual to be seen offshore. Population growth rate calculated from crude survival and birth-intervals reported by Kraus *et al.* (2001).
Mark-recapture: Inter-birth interval model (SC/O99/RW1)	NA and SA		x	x	x	x	x		x	x	Inter-birth interval proportions through age 5 are free parameters with an exponential decline beyond age 5; used only sightings of females with calves in southeast US, Bay of Fundy, and Massachusetts Bay.
Mark-recapture: Cormack-Jolly-Seber model with spatial component (SC/O99/RW2)	NA only		x		x			x			Spatial heterogeneity incorporated by clustering whales of similar spatial sighting distribution and using the clusters as strata in the mark-recapture analysis.
Back calculation (SC/O99/RW3)	NA only	x									Any individual not observed for 6 years is presumed dead; some sighting histories removed to accommodate reduction in effort in offshore regions.

was used to compute life expectancy, net reproductive rate, generation time, and expected number of lifetime reproductive episodes. The model was then transformed into a multitype branching process to compute extinction probabilities under demographic stochasticity and the probability distribution of time to extinction.

In discussion, a question was raised regarding whether stage-structured models were inferior to age-classified models because of the greater degree of precision associated with the latter. It was noted that a comparison of stage- and age-classified models for a single data set, on killer whales, showed broad agreement between them (Brault and Caswell, 1993); however, it should be borne in mind that age-structured models tend to be over-parameterised. In any stage-structured model there will inevitably be variability amongst animals within stages and in age-classified models there will be variability (e.g. reproductive versus non-reproductive) among animals within age classes. Potentially significant bias could be investigated by sensitivity analyses. Variability among animals within stages will be reflected in the precision of parameter estimates. More important is misclassification of animals into stages, which may cause errors in estimation or parameterisation.

Brault summarised the results of a recent Workshop held at the Woods Hole Oceanographic Institution, WHOI, (SC/O99/RW5), which examined the performance of different models. Recommendations of the WHOI Workshop for future work included: examination of the potential effect of data post-stratification on model estimation; use of within-year information to attempt classification of individuals by capturability; and simulation of capture histories to investigate the impact of heterogeneity on existence and detectability of a decline in survival. The model developed by Cooke *et al*. (2001) for analysis of southern right whale data was applied to sightings data of females with calves in the North Atlantic; its high sensitivity to annual fluctuations in number of births subsequently led to modifications of the model and its conclusions as presented in SC/O99/RW1. A model for mature females only was developed by Fujiwara to compare the demography of North Atlantic and southern right whales. Preliminary results show lower survival of females with calves in the North Atlantic than in the Southern Hemisphere, as well as a higher interbirth interval. Overall, alternative analyses to that of SC/O99/RW7 tend to support the finding of a decrease in survival (see Item 6.5).

In discussion, a number of clarifications were made. The analysis using program MARK introduced a stage for unknown sex; the Fujiwara model allocated unknown sex animals to sex in a 1:1 ratio. All models considered in SC/O99/RW5 accounted for heterogeneity in capture probabilities over time. Biological differences among individuals were not modelled except in groups in the stage-structured models. No models used data stratified by area but a model for the Bay of Fundy only was run. It was noted that this model would not necessarily reduce spatial heterogeneity because of the wide range of capture histories observed in that area, and could actually increase it. The best-fitting model in Caswell *et al.* (1999) did include the ‘offshore indicator’ variable. It was noted that for spatial heterogeneity, the most important aspect was whether there were trends over time because this may lead to a trend in estimates of survival rate.

SC/O99/RW1 provided a comparative analysis of the demography of the calving female components of the South Atlantic and North Atlantic right whale populations, using a model originally developed for analysis of the southern right whale photo-identification data. The model provides estimates of the distribution of calving intervals (implicitly corrected for missed calvings) the mean age at first calving, the survival rate of reproductive females and the rate of population change. The sightings of females with calves by year were grouped into two areas (Bay of Fundy/Massachusetts Bay and the southeastern USA calving ground) and the model assumed homogeneity of sighting probabilities within each area in each year. Since the model makes use only of identifications of females with calves, it is not optimal for the northern right whale for which these records constitute less than 10% of the total data set.

SC/O99/RW3 presented a preliminary analysis of a study to examine the impact of heterogeneity and presumed mortality on the estimation of population parameters. The study concluded that the apparent increase in mortality rate in recent years was largely attributable to heterogeneity combined with spatial sampling bias.

In discussion, questions were raised relating to the use of data on presumed mortalities and on the potential use of effort data to aid the assignment of animals to inshore or offshore categories. The Workshop **agreed** that it was inappropriate to use presumed mortalities when estimating survival. However, it noted that the examination of observed intervals between sightings might be useful in assessing the validity of model predictions and investigating those individual animals that had longer than predicted intervals between sightings.

SC/O99/RW2 investigated the influence of spatial heterogeneity among areas on estimated survival rates. Sightings data for individually identified right whales between 1980 and 1997 were examined by cluster analysis to form groups of whales with similar spatial distributions, using the proportion of years out of the total when animals were seen in each of the five main habitat areas. The following clusters were used:

(a) Massachusetts Bay/southeastern USA/Bay of Fundy (MASS/SEUS/BOF);
(b) Scotian Shelf/Great South Channel (SS/GSC);
(c) Bay of Fundy (BOF);
(d) Bay of Fundy/Scotian Shelf (BOF/SS).

Mark-recapture analysis was performed on the grouped sighting histories with the program MARK, using a general form of the Cormack-Jolly-Seber model. Three different sighting probability models were examined with sightings probability varying by: (1) year; (2) group; and (3) group and year. Six different survival probability models were examined for non-calf survival: (1) survival constant; (2) varying by year; (3) varying through time by a logistic model as in Caswell *et al.* (1999); (4) varying by group but constant across years; (5) varying by year and by group; and (6) varying through time by a different logistic model for each group. Calf survival was initially assumed to be constant. These 18 possible models were compared using AIC. Once the best models for sightings probability and survival had been selected, year-dependent and logistic trend in calf survival were compared to constant calf survival.

In general discussion, two features emerged that might be implied from the observed data but may not be captured in the models. The first was the suggestion that sightings probabilities for females in the years following a calf year had decreased with an associated increase in calving interval. Assuming a typical reproductive cycle might lead to an increase in ‘missing’ whales. The second was that estimated calving intervals appeared to be lower than observed ones. This might be a result of sampling effort tending to focus on 'Surface Active Groups', which comprised sexually active animals. The Workshop noted that the Fujiwara model (SC/O99/RW7) estimated capture probabilities and survival rates for different reproductive classes, and that an important feature of the Wade and Clapham model (SC/099/RW2) was that it addressed spatial aspects without discarding data.

After the presentation of the individual models, Taylor gave a brief presentation on the aim of models in assessing the status and trends of endangered populations and the use of simulation models to test model assumptions and parameter estimates. She noted that the models discussed at the Workshop were useful in estimating trends and population parameters, but that they did not explicitly seek to identify sources of risk in an endangered population. She further cautioned that models designed for use on large, potentially harvestable populations (such as minke whales) are often inappropriate for examining the dynamics and trends of small, critically endangered populations such as right whales where demographic stochasticity is often greatly magnified. She suggested two stages in modelling: (1) models to evaluate levels and trends in risk and (2), if increased risk is plausible, models that try to identify the source of increased risk and that are structured to rank needed research and management options. She noted that the models discussed in this Workshop have been generally at the first stage of risk identification. Given that increased risk is plausible and probable, the second stage should now proceed. The Workshop noted that the analyses of Caswell *et al.* (1999) and SC/O99/RW7 do incorporate their parameter estimates into demographic models and permit some quantification of risk and include demographic stochasticity. The value of incorporating genetic data into future models is discussed under Item 6.1.1 and in Annex E.

Taylor suggested a method to proceed that began with listing plausible sources for observing increased risk which include: re-distribution (poor conditions leading to a reduction in both calf production and capture rate of adult females), ship strikes, entanglement and direct mortality through poor environmental conditions. Models can then consider various hypotheses and evaluate their plausibility according to the compatibility of the model results with the various types of data (photographic and genetic) and the distribution of risk factors such as fishing gear and shipping traffic. The results could be used to eliminate hypotheses, strengthen conclusions about status and trends, prioritise research and guide management decisions. The difficulty in setting plausible bounds on simulation models used to assess hypotheses or model assumptions was acknowledged but it was noted that such problems had been successfully addressed previously within the IWC by assembling a group to recommend suitable bounds.

6. OVERVIEW OF EXISTING KNOWLEDGE OF POPULATION PARAMETERS

6.1 Stock and sub-stock structure

Under this Item, the Workshop considered only information additional to that presented at the Cape Town Workshop (IWC, 2001).

White summarised SC/O99/RW6 and other recent genetics papers on this population (Malik *et al.*, 1999; 2000; Waldick *et al.*, 1999). Sightings data indicate the existence of two subsets of mature females, both of which are observed in the southeastern USA but only one of which is resighted in the Bay of Fundy in summer. Mitochondrial DNA (mtDNA) data suggest that these two groups show significant differences in haplotype/allele frequencies, a phenomenon which is probably due to maternally directed philopatry. Current work focuses on: population substructure; the mating system; effective population size; size of population since exploitation; census size of the population; paternity/maternity analyses of individuals of unknown relatedness; and MHC (Major Histocompatibility Complex) variation relative to reproductive success. There are five mtDNA haplotypes in the population, with greatly varying frequency. Summary measures of allelic frequency suggest a bimodal distribution in a subset of Bay of Fundy animals which is not found in the 'non-Fundy' group (i.e. those animals not photographically identified in the Bay of Fundy). Simulations suggest that there is not random mating within the population, and that two mating areas may exist with a somewhat different population composition. Pedigree analysis suggests that the population contains some individuals that have yet to be sampled. An investigation of paternity suggests that approximately 85% of calves have different fathers. This is consistent with a mating system dominated by sperm competition but inconsistent with one dominated by a few males.

A question was raised regarding whether the 'missing' animals in the population could be accounted for by photo-identified animals that had yet to be biopsy sampled. White responded that mathematical analyses suggested that the population was somewhat larger than is assumed, even when non-biopsied individuals were accounted for. It was suggested that a breakdown of mtDNA data by sex might show immigration of males from other areas. The Workshop noted, however, that a certain level of discovery of 'new' animals is to be expected in any population. It also agreed that it is not possible to assess from the genetic data whether the apparent increase in mean calving intervals is due to senescence. Three historic specimens from the eastern North Atlantic (see Rosenbaum *et al.*, 2000) had been found to be of the most common haplotype in the current western population, as was the individual observed recently in Arctic Norway (see below). However, the different exploitation histories and recovery (or lack thereof) suggest that for present management purposes (as opposed to evolutionary/ecological timescales), the two populations be considered discrete.

Concerns have been raised over the genetic diversity of North Atlantic right whales (Schaeff *et al.*, 1997). Low genetic diversity can lead to a lowering of population fitness via the expression of deleterious alleles or the reduction of heterozygosity at loci such as MHC, which confers the ability to respond to disease. However, low diversity does not always indicate an unhealthy population. For example, several apparently healthy populations of cetaceans, such as sperm whales and pilot whales in all ocean basins, have even lower genetic diversity than observed for North Atlantic right whales. Comparing levels of genetic diversity across species may provide insight about differences that exist between species, but it is not possible to attribute hypothetical changes in gene diversity in one population from the level of genetic variation in another (Rosenbaum *et al.*, 2000). The likelihood of a population expressing deleterious alleles depends on the number of such alleles remaining in the population, which itself depends on population history. Populations reduced to very low levels (typically fewer than 50 effective individuals) very rapidly lose genetic diversity without sufficient time for selection to purge deleterious alleles. On the other hand, populations that remain at low levels for long periods of time lose diversity and the potential for selection to purge deleterious alleles. Loss of allelic diversity can also result in the loss of beneficial alleles, such as MHC loci, which cannot be easily restored in small populations because low population size can support only low genetic diversity.

Several lines of research may help resolve whether reduction in fitness is likely, including research on MHC genotyping to see whether MHC loci are randomly transmitted. The Workshop concurred with the conclusions of the Cape Town Workshop that low genetic variation in North Atlantic right whales can best be interpreted through an analysis of historical versus extant samples and **encourages** further work along these lines. The Workshop also **encourages** further research examining whether a population bottleneck is likely. SC/O99/RW6 had found no heterozygote excess that would suggest a bottleneck in the last 150 years (using the analytical program 'Bottleneck'). However, the Workshop noted that the evolution of microsatellites is only partially understood. Further examination of mutational processes is desirable since this will improve interpretation of genetic data with respect to the plausibility of bottlenecks.

There was discussion of how genetic data should be incorporated into modelling exercises. The Workshop recognised that appropriate methods need to be developed. Analysts should consider the use of genetic data both for individual-based models and for group-based analyses, for example to investigate survival of individuals by mtDNA haplotype (see recommendation below).

Hamilton summarised sighting data relevant to population structure. Of 396 individuals identified, 25 have never been seen in any inshore habitat, and 117 were never seen offshore. In addition, 11 of 95 known mothers have never been observed in the only known calving ground in the southeastern USA; it is not clear whether this indicates the existence of a second calving area, or simply missed animals in the southeast.

Marx briefly summarised sightings of right whales in the eastern North Atlantic since 1960. Of particular interest in this regard was the sighting of a right whale in a Norwegian fjord in September 1999 that had been seen off Cape Cod in May 1999 (Øien and Marx, pers. comm.). Since 1960, there have been eight confirmed sightings (11 animals) in the eastern North Atlantic.

Rosenbaum *et al.* (2000) summarises ongoing genetic work on the question of the separation of eastern and western North Atlantic right whales.

6.1.1 Recommendations (and see Item 8)

The Workshop noted a number of important considerations with respect to analyses of the genetics data and their incorporation into population models. It **strongly recommends** that a Workshop on Right Whale Genetics be held in October 2000. Participants should include demographic modellers (see Item 7.2.1), cetacean biologists, genetics modellers and geneticists to: (1) explore a range of population genetic analytical techniques; (2) develop analytical techniques to estimate model parameters specific to right whale conservation models; and (3) identify the best approaches for future genetic research in terms of needed sampling, potential additional markers and development of future analytical techniques. Further details and rationale for this Workshop are given in Annex E.

The Workshop identified a number of ongoing genetic analyses that should ideally be completed before the Genetics Workshop takes place. It **recommends** that this work continues expeditiously:

(1) complete multi-locus genotypes to discriminate between individuals and determine paternity for all available biopsy samples;
(2) complete genotyping of MHC loci for direct testing of whether right whales may be genetically compromised, in order to examine possible effects on reproductive success and resistance to disease.

It also **recommends** continued analysis of historical specimens to examine questions of population structure, and of early exploitation levels of genetic variation (especially at MHC loci) to test the hypothesis that reduced variation has a negative impact on reproduction. Samples have been obtained from the western North Atlantic 16th century Basque right and bowhead whale fishery in Red Bay, Labrador, Canada. The right whale samples should be examined, together with any other historical samples that can be obtained. It is essential that published methodological safeguards to eliminate false positives associated with sample handling and laboratory data collection of historical samples are adhered to.

The Workshop also reviewed the following recommendations for genetic work made at the Cape Town Workshop (IWC, 2001).

(1) Reduction of known bias from regional sampling in July-October feeding habitats and completion of the archive of western North Atlantic.

Over the last two years, genetic sampling has continued annually from July to September in the Bay of Fundy. This does not represent a separate research effort but is carried out as part of vessel photo-identification surveys. There has been minimal sampling effort in Cape Cod Bay in winter and spring (~3 days per season). There has been virtually no sampling effort in the southeastern USA calving ground or in the Great South Channel because of a lack of funding.

The Workshop **recommends** that the current programme continue and be expanded. In particular, high priority should be given to obtaining samples from the calving ground, especially from females who do not take their calves to the Bay of Fundy.

(2) Examination of available information on mtDNA haplotypes, microsatellite and MHC genetic profiles with respect to habitat use, resighting probabilities, scarring patterns, and reproductive success.

The Workshop **recommends** that this work be undertaken.

(3) Transfer of samples under CITES regulations.

The Workshop noted that whilst not confined to samples for genetic analysis, transfer of samples under CITES regulations is still very difficult and can constitute a major impediment to research on critically endangered species such as northern right whales. It repeats the Cape Town Workshop **recommendation** that IWC member nations be **strongly urged** to facilitate the transfer of such samples, and that the IWC Secretariat approach the CITES Secretariat to consider expediting permits for *bona fide* institutions conducting conservation-related research on endangered species.

6.2 Population size

Hamilton summarised estimates of population size from NARWC data. The rate of discovery of newly identified individuals reached an asymptote in 1982; relatively few new (non-calf) whales have been added in recent years.

The Workshop **agreed** that there were at least 263 animals alive (of which 56 were known to be mature females) in 1996. This is based on an examination of the NARWC and represents the number of identified animals seen in 1996 plus any animals that were seen both before and after 1996. It is thus a minimum direct count and not an estimate.

The mark-recapture analyses discussed at this meeting were designed to estimate survival rates, not abundance. It is more difficult to reliably estimate population size using mark-recapture data (e.g. see Buckland, 1990), as this requires calculation of the number of animals not seen in the sample. A number of estimates using mark-recapture techniques or involving various assumptions about presumed mortality of individuals are discussed in Annex F. It was **agreed** that estimation of current population size or trends in population size using those techniques is unlikely to provide reliable information on the status of this stock. Despite these caveats it was **agreed** that the results given in Annex F suggest that the overall abundance in 1996 is unlikely to have been considerably greater than 263. A total of 338 known individuals was observed between 1988 and 1997.

The appropriateness of a population estimate depends on the use to which it is to be put. The Workshop **agreed** that in response to general queries it is reasonable to state that the current population size of the western North Atlantic right whale population is probably around 300 animals (±10%).

Unlike North Atlantic right whales, a number of other whale populations have apparently recovered from very low observed abundance (e.g. Southern Hemisphere right whales, eastern North Pacific gray whales, some Southern Hemisphere humpback whales). However, data to reliably estimate minimum historic abundance are invariably incomplete. North Atlantic right whales, like Southern Hemisphere humpback and right whale populations, may have gone through a genetic bottleneck. Since North Atlantic right whale numbers had not increased as in the Southern Hemisphere, there is the possibility of the occurrence of the ‘Allee effect,’ where population growth rate declines at low population size. Whether or not this is the case is cannot be evaluated with the available data. White noted that analyses reported in SC/O99/RW6 suggested that North Atlantic right whales may have been at a low level for hundreds of years and that investigations into the possibility of such an effect were continuing.

6.3 Age composition

Hamilton summarised the available data on age composition in the NARWC. There are records of 385 individuals (157 males, 153 females and 75 individuals of unknown sex). There are 69 known juveniles (less than nine years old), 298 adults and 18 of unknown age; in total, 11 individuals are known to have died, and 87 have not been sighted for six years or more (in certain analyses such animals are presumed dead, although as noted under Item 6.5 this is not a reliable means of estimating mortality). He noted that the proportion of juveniles in the population has dropped from 44% in 1990 to 23% in 1998. This decline is not unexpected in a longitudinal study, although it is perhaps somewhat surprising given the high effort on the calving grounds and the fact that many calves would therefore be expected to be recruited into the NARWC population. It was noted that the figures given presumed that all animals included in the total were alive but had not all been sighted in the year (1998) for which calculations were undertaken.

6.4 Reproduction

Kraus *et al.* (2001) present the most recent analysis of reproduction in this population. Two measures of reproduction, Gross Annual Reproductive Rate (GARR) and Calves per Mature Female per Year (CMFY), were estimated, giving mean values of 0.049/0.043 for GARR (depending on methodology) and 0.25 for CMFY. Interbirth intervals have increased from 3.67 years in 1992 to 5.8 years in 1998, and this does not appear to be an artefact of sightings effort. However, the analysis is contingent upon a number of assumptions regarding the probability of unobserved calving. It is also possible that some females may have given birth to calves that died prior to the mother being observed.

The results of the interbirth interval model given in SC/O99/RW1 were largely consistent with a conclusion of increasing intervals in recent years. A statistically significant increase (from 3.28 years in the 1980s to 4.44 years in the 1990s) of estimated mean calving interval was obtained. The distribution of calving intervals indicates a shift from 3-year intervals in the 1980s towards 5+ year intervals in the 1990s, with the proportion of 4-year intervals little changed. The data are thus consistent with the hypothesis of an increased pre- or neonatal mortality in the 1990s, on the assumption that pre- or neonatal mortality tends to be followed by a 2-year interval whereas successful weaning tends to involve a 3-year interval following birth.

The Workshop **agreed** that calving intervals had indeed increased. It was not possible to assess whether this was due to lengthened intervals between births or to loss of an unrecorded neonate in the years between observed births. It is important to note that this analysis does not include the many mature females that have calved only once or not at all; thus, actual intervals are likely to be even greater than calculated. The Workshop noted that the question of whether this could be due to sampling bias, notably in offshore areas which were either abandoned by whales (Roseway Basin) or the subject of diminished effort (Great South Channel) during the period in which intervals had apparently increased, requires further investigation.

Calving interval information alone does not provide an estimate of the average reproductive rate of the entire mature female population, because of the possibility that some females are not reproductively active (Brown *et al.*, 1994 and as alluded to under Item 6.1). Therefore the Workshop considered (i) direct estimates of the reproductive rate of the mature female population; and (ii) estimates of the proportion of mature females that are reproductive in the sense of having calved at least once.

Table 2 presents calf production by year in the 1990s from the animals known to be at least nine years old (and thus assumed to be mature) and which are presumed female; the latter was estimated as the known females plus half the animals of unknown sex. Support for an approximately 50:50 ratio among the unknown sex animals is given in SC/O99/RW7. The average annual calf production rate per mature female is 0.13 but substantial annual variation is observed.

Thus in 1996, there were 94 presumed live, known/presumed females known to be at least nine years old. Of these, 66 had been observed to calve at least once. This gives a conservative (due to missed calvings and some females reaching maturity after nine years of age) estimate of

70% for the proportion of mature females that are reproductively active. Using the direct estimate of apparent mean calving interval in the 1990s of 4.6 years (Kraus *et al.*, 2001), which is very similar to the statistically 'corrected' estimate of 4.4 years (SC/O99/RW1), the implied average reproductive rate for mature females is 0.7/4.6 = 15%, which is within the range shown in Table 2.

Table 2

Right whale calf production (for explanation see text).

	Adults presumed alive				
Year	Female (F)	Unknown (U)	F+0.5U	No. calved	Percent calves
1990	57	18	66	11	16.67
1991	60	20	70	16	22.86
1992	62	20	72	10	13.89
1993	69	20	79	5	6.33
1994	72	18	81	6	7.41
1995	76	18	85	6	7.06
1996	85	18	94	19	20.21
1997	87	18	96	18	18.75
1998	90	18	99	5	5.05
Total			742	96	12.94

It is not possible to provide comparable estimates of average reproductive rate for the 1980s because animals need a sufficiently long sighting history to be determined to be at least nine years of age. However, in view of the increase in mean calving intervals in the 1990s relative to the 1980s, the Workshop **agreed** that it is very likely that the average reproductive rate was lower in the 1990s. It also noted with concern that the estimate of average reproductive rate was less than half of that obtained for the southern Atlantic populations (Best *et al.*, 2001; Cooke *et al.*, 2001). Given that in the 1990s most North Atlantic right whale calves were seen on the calving grounds, as in the Southern Hemisphere, the estimates for the two hemispheres are directly comparable.

Several possible explanations for the increased interbirth intervals in multiparous females were discussed. One proposed mechanism involved a decreasing food supply. Moore noted that the preliminary results of acoustic profiling for blubber thickness (SC/O99/RW4) suggest that northern right whales have significantly thinner blubber than Southern Hemisphere animals. However, the data have not been normalised *inter alia* for length and analysed sample sizes are small. Some participants believed that this was consistent with a hypothesis that food limitation might be responsible for the increase. They also referred to a purported correlation between reproductive rate and climatological changes that potentially affected the abundance and distribution of prey patches. Others believed that since *Calanus* is the most common zooplankton in the North Atlantic and that present right whale abundance is greatly below historic levels, the proposal that food limitation was the major factor seemed questionable.

Other ideas considered included the possibilities that:

(a) observed increasing frequencies of skin lesions may be indicative of poor health that could compromise reproduction;

(b) there is an unstable age structure, which includes an increasing number of reproductively senescent animals (although senescence has not been reported for baleen whales – e.g. see review in Lockyer, 1984 – and has rarely been documented in mammals, this may reflect lack of effort rather than lack of occurrence).

The Workshop **agreed** that the available data do not allow the identification of a cause for the increase in interbirth interval. It noted that it might well be the result of a combination of factors.

The Workshop noted that knowledge of length and (by possible inference) age is important for demographic analyses, including longitudinal studies of growth rate and of reproduction. Given that the technology exists to accurately measure individuals (e.g. Gordon, 1990; Best and Rüther, 1992), it **recommends** that this work be conducted on right whales, preferably in the form of an annual survey.

6.5 Survivorship

Caswell and Fujiwara presented stage-specific survival and sightings probability for the best fitting model from SC/O99/RW7. The most dramatic result was the trend in the estimated survival of females with a calf that had fallen from about 0.95 to about 0.65 from 1980 to 1995. There were also decreases over time in the estimated survival of immature females and mature males. The capture probability for females with a calf was estimated to be constant but to have increased over time in all other stages, reflecting an increase in effort.

Questions were raised about the high constant capture probability of females with a calf; constant capture probability was neither supported by the data nor by results from Cooke's model (SC/O99/RW1). Fujiwara responded that choosing lower constant capture probabilities for this stage had little effect on estimates of survival rate and that if capture probability had increased over time, the downward trend in survival rate would be even steeper. However, he noted that this might be more important with respect to estimates of birth interval. Although a time trend in birth interval was not selected in the best model fit, he noted that this was not the most appropriate model structure to investigate this factor. He commented that the model in which all parameters are time dependent also shows a declining survival rate in females with a calf but noted that this has too many parameters to be useful. Caswell noted that the estimated constant capture probability had a wide confidence interval and that this aspect was being investigated further.

There was some discussion about the desirability or otherwise of modelling trends over time in survival rate when the lower estimates in recent years may be the result of chance events in one or more years rather than a smooth trend. Caswell noted that the fully time-dependent models in Caswell *et al.* (1999) and SC/O99/RW2 did not fit as well as modelling trends over time and believed that in principle it was better to fit a trend and investigate what might be causing that trend than to focus on particular events. Others believed that it was important to investigate particular atypical events (such as the high mortality in 1992); inspection of residuals around a trend was one way to do this. The Workshop **agreed** that modelling most parameters as trends but allowing survival of females with a calf to vary over time would be a useful exercise.

It was noted that in the absence of independent information, estimates of survival are always confounded with any emigration. The possibility that spatial structure in the population and sampling had resulted in animals becoming unavailable for sampling rather than dying could not be completely ruled out, but the model used in SC/O99/RW2 that did incorporate spatial structure also showed an overall decline in survival rate.

In SC/O99/RW1, the model incorporating a trend in survival over time had the best AIC. The estimate of trend was negative but not precise. This was not surprising because the model only used a subset of the data (those for reproductively active females). Nevertheless, the estimated magnitude of the declining trend over the period 1980-1997 was consistent with that estimated by Caswell *et al.* (1999) but had lower precision. The survival rate estimated for this model was for reproductively active females in all years (calf and non-calf years) whereas the estimate in SC/O99/RW7 was for females in the year in which they had a calf.

The cluster analysis presented in SC/O99/RW2 identified four groups of individuals. The two groups containing animals primarily seen in offshore areas were male dominated whilst two groups containing animals seen in the southeastern US were female dominated. The Bay of Fundy/Scotian Shelf group contained animals formerly seen on the Scotian Shelf but seen mainly in the Bay of Fundy from 1993 onwards.

Models allowing capture probability to vary by group as well as year gave consistently better fits to the data. The best model for survival rate included variation among groups and a logistic trend over time. Estimated capture probabilities reflected changes in effort over time. For the offshore group (SS/GSC), there was a peak in the late 1980s followed by much lower values. Other groups showed increases over time. Overall, non-calf survival showed a downward trend over time. When heterogeneity in capture probabilities over groups was not accounted for, poorer fits to the data were obtained and estimates of survival were lower. The estimates from Caswell *et al.* (1999) were lower, reflecting differences in the analyses; they estimated crude survival rate (including calves) and used data only through 1996.

The best fitting survival model showed the greatest decline in the MASS/SEUS/BOF group (83% female); this was consistent with the results from other analyses presented. There were also declines estimated for the SS/GSC and BOF/SS groups but Wade expressed the concern that these might be artefacts because of a decline in sampling effort in SS and GSC after 1990 and the decline in use of Roseway Basin (in SS) after 1993. There was a slight increase in survivorship in the BOF group (57% female); the group for which the greatest and most consistent effort data exist.

In discussion it was noted that whales in the offshore (SS/GSC) group were mostly seen in other areas after 1990 and that this implied there was still significant spatial heterogeneity present in this group. Attention was also drawn to the comparability of the results in SC/O99/RW2 with those in Caswell *et al.* (1999) that included the ‘offshore index’ covariate, although the estimated decline in survival in SC/O99/RW2 was only about half of that in Caswell *et al.* (1999) and was found by the AIC to apparently account for more spatial heterogeneity than the offshore index approach.

Fujiwara presented preliminary results for North Atlantic and Southern Hemisphere right whales from a stage-specific model for reproductively active females. It was noted that differences in the time of year when animals were typically sighted in the two areas introduced difficulties in interpreting the results. Nevertheless, the Workshop **agreed** that this was a valuable approach and should be pursued.

The Workshop **agreed** that survival rate had declined from relatively high levels in the 1980s to lower levels in the 1990s. A summary of the results presented to the Workshop are given in Table 3 and Fig. 2. The greater declines estimated for females with calves might indicate that there were particular problems with this class of animals. However, results from stage-specific models for particular stages should be interpreted with some caution and declines in other stages should not be ignored. Females with calves may be vulnerable because of increased energetic requirements but calves were also vulnerable. There was limited information on calves because they are typically not identified at time of first capture. Nevertheless the best model fit from SC/O99/RW2 included constant calf survival.

7. ASSESSMENT OF STATUS AND TRENDS

7.1 Results from population modelling

Caswell presented the results from a stage and sex specific demographic model (SC/O99/RW6), which were not widely divergent from those of the previously published aggregated model (Caswell *et al.*, 1999). Life expectancy declined from about 40 to 20 years from 1980 to 1995. Expected lifetime reproductive events (the mean number of times that a female will give birth over her lifetime) similarly declined over the same period from about 6 to 2 for newborn animals and about 9 to 2.5 for animals at maturity. The net reproductive rate declined from about 3 to less than 1. The population growth rate declined from 1.03 to 0.98. Projected time to extinction varies by how long it is assumed a mother must survive to ensure survival of her calf; if this is one year, the population is predicted to be extinct within 200 years. Improving the survival rate of mature females would make most difference to the predicted fate of the population; preventing the deaths of 2-3 animals would bring the population growth rate above 1.0. However, the estimated survival rate is already 0.99 and can, therefore, increase only slightly.

The survival rate estimates for North Atlantic right whales in the 1980s are similar to survival estimates of about 0.98 from the Southern Hemisphere (SC/O99/RW1; Best *et al.*, 2001). However, survival rate estimates for North Atlantic right whales in the 1990s are lower, while the Southern Hemisphere rates appear to have remained constant (SC/O99/RW1).

The Workshop **agreed** that the population modelling results (Table 3) indicated that survival had declined in the 1990s relative to the 1980s.

7.1.1 Recommendations

It was recognised that the incorporation of even crude measures of effort into population modelling provided better fits to data and allowed some examination of heterogeneity. Accordingly, more detailed and standardised effort data would probably permit more refined analyses. The Workshop **recommends** that an effort be made to tabulate effort by area, platform, type (dedicated versus opportunistic, vessel versus aerial) and by year. Kenney and Wade agreed to cooperate to achieve this before the next North Atlantic Right Whale Consortium meeting and in time for the multidisciplinary Workshop discussed under Item 8.1.2. It should include entry of raw effort data where necessary.

The Workshop also **recommends** the continued development of population models into which demographic parameter estimates can be incorporated. One of the goals of such models should be estimation of risk, and they should include exploration of demographic stochasticity (as in Caswell *et al.*, 1999 and SC/O99/RW6), environmental stochasticity (especially in reproductive rates) and spatial structure. Linking these models to genetic factors will be one of the goals of the proposed Genetics Workshop (see Item 6.1.1 and Annex E).

7.2 Results from population monitoring

Knowlton presented the total number of individuals observed by year (Table 4). She noted an increase in the number of individuals recorded starting in 1994, and attributed this to a redistribution of animals from Roseway Basin into the Bay of Fundy, together with higher effort in other inshore areas.

The Workshop **agreed** that the available data from the NARWC and the NARWD alone could not be used to estimate trends in population size. In this context their value was in providing data for the modelling exercises discussed above. Although it appears unlikely to be practical, the

Table 3

Summary of the results of models presented at the Workshop.

Source	Sighting model	Measure of survival	Conclusion
Caswell *et al.* 1999	Time	Crude survival	Survival has declined
Caswell *et al.* 1999	Time, location (offshore/onshore)	Crude survival	Survival has declined
Caswell *et al.* 1999 model; Lebreton analysis at Woods Hole Workshop	Time, corrected for trap-happiness and quasi-transients	Crude survival	Survival has declined ($p < 0.1$)
Caswell *et al.* 1999 model; Lebreton analysis at Woods Hole Workshop	Time, corrected as above, location (BOF)	Crude survival	Survival has declined ($p<0.02$)
SC/O99/RW7	Time, effort, sex, stage	Sex-stage-specific survival	Calf survival constant Immature female survival declining Mature female survival constant Cow survival declining Immature male survival increasing Mature male survival declining
SC/O99/RW7	Time, effort, sex, stage (calf, juvenile, mature, cow)	Computed crude survival	Survival has declined
SC/O99/RW7	Time, effort, sex, stage (calf, juvenile, mature, cow)	Computed non-calf survival	Survival has declined
SC/O99/RW2	Time, location (4 regions), stage (calf, non-calf)	Non-calf survival	Survival has declined in three of four clusters
SC/O99/RW2	Time, location (4 regions), stage (calf, non-calf)	Non-calf survival, pooling areas	Survival has declined
Cooke and Glinka	Time, location (2 regions)	Adult female survival	Survival has declined

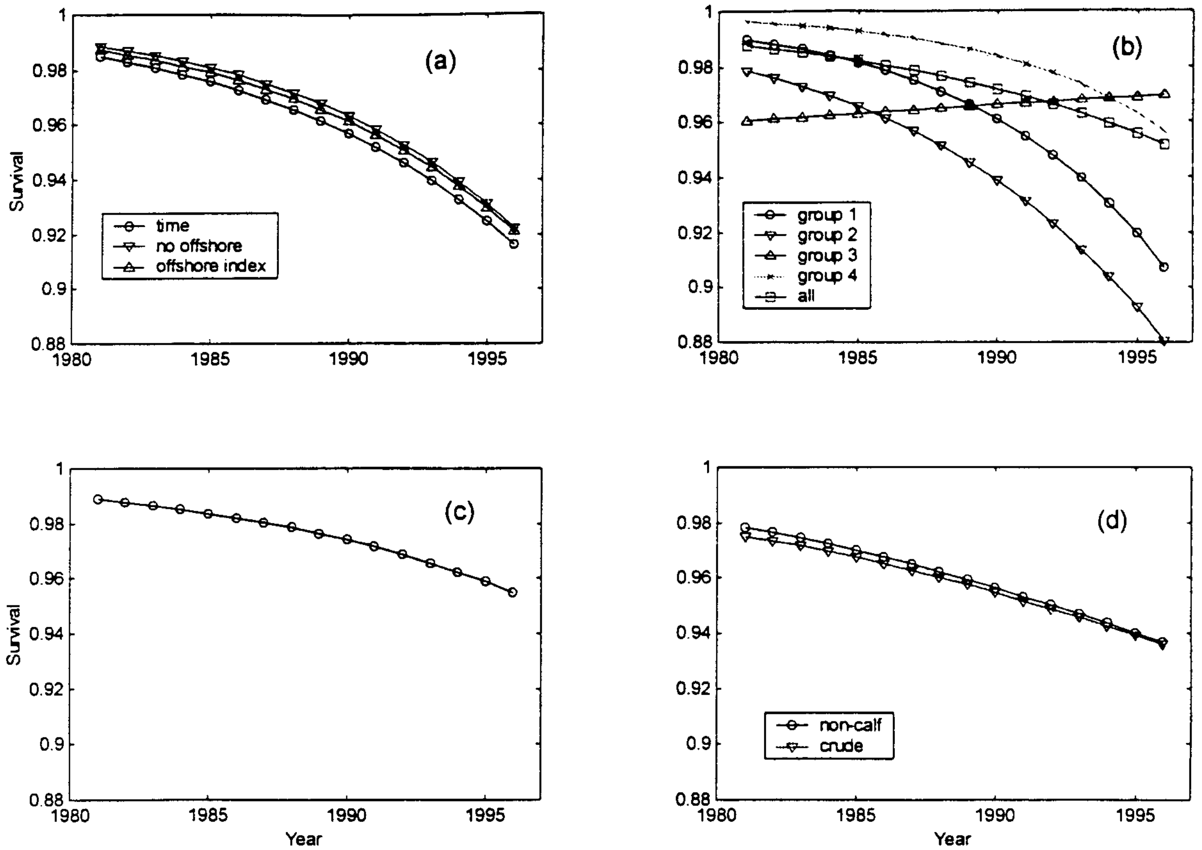

Fig. 2. This figure shows trends in survival probability from various models of the North Atlantic right whale. (a) Crude survival from three sighting models: one a function of time only, one a function of time but eliminating all ‘strictly offshore’ whales from the data, and one a function of time and of an offshore index as an individual covariate (from Caswell *et al.*, 1999). (b) Group-specific non-calf survival with sighting a function of group and time (group 1 = MASS/SEUS/BOF; group 2 = SS/GSC; group 3 = BOF; group 4 = BOF/SS) and an estimate of non-calf survival pooled over all four groups (from SC/O99/RW2). (c) Mature female survival with sighting a function of time and location (from SC/O99/RW1). (d) Crude survival and non-calf survival computed from the stage-sex-specific model of SC/O99/RW7. Sighting probability is a function of time, effort, sex, and stage. Crude and non-calf survival probabilities calculated as weighted averages of sex-stage-specific survival probabilities.

Table 4

Summary of annual sightings of total numbers of individuals and numbers of individuals sighted in each area. Note: one individual can be sighted in numerous areas in a given year but will only be counted once in the total number of individuals. Abbreviations: SEUS, southeast U.S.; MB, Massachusetts Bay; GSC, Great South Channel; BOF, Bay of Fundy; BB, Browns Bank/Roseway Basin; North, North and east of Browns Bank/Roseway Basin; Mid Atl., mid Atlantic between South Carolina and Cape Cod.

			No. of individuals photographed							
Year	Sightings	Individuals	SEUS	MB	GSC	BOF	BB	North	Mid Atl.	Other
1980	120	62	0	5	19	23	13	0	2	17
1981	336	103	2	8	62	56	0	1	0	7
1982	405	99	3	13	20	52	30	0	2	9
1983	280	76	3	30	7	26	26	0	2	4
1984	423	114	15	28	22	54	29	0	5	11
1985	332	103	6	53	31	31	11	0	2	12
1986	907	152	23	54	27	42	80	0	5	6
1987	458	152	14	39	40	31	82	2	2	1
1988	579	197	9	29	94	44	118	0	0	10
1989	899	206	41	21	39	74	115	2	4	8
1990	502	148	32	29	0	68	47	1	1	9
1991	384	158	20	33	9	51	90	0	1	2
1992	584	130	26	45	0	72	17	1	0	9
1993	608	177	53	41	0	148	0	1	5	7
1994	1,147	206	25	27	2	186	0	1	3	13
1995	1,543	216	25	64	2	187	5	1	1	2
1996	1,539	216	98	78	4	168	0	2	5	45
1997	2,170	230	46	57	10	199	3	1	0	9
1998	979	188	27	85	22	106	0	9	13	8

Workshop **recommends** investigation of the feasibility of conducting a dedicated, standardised survey to assess right whale population size and trends.

Given the central importance of the NARWC to population assessment and to the monitoring of the effectiveness of management actions, the Workshop **strongly recommends** continued funding for this effort, its compilation, and the fieldwork that underpins it.

7.3 Factors affecting trends

7.3.1 Direct anthropogenic interactions

The Workshop strongly believes that reducing the impacts of anthropogenic activities (fishing and shipping) on the North Atlantic right whale population should be the primary focus of future research and management actions (see Item 8). Mortalities and serious injuries of right whales have been documented since 1970 (Knowlton and Kraus, 2001). The data suggest that the level of mortalities attributable to human activities has been increasing over time, however this increase could be due to increased reporting of carcasses and increased efforts to retrieve and necropsy them. The total number of mortalities documented between 1970 and 1999 is 45 (16 due to ship collisions, 3 due to entanglement, 13 neonates, and 13 of unknown cause).

Knowlton and Kraus (2001) developed a set of criteria for defining a serious injury from entanglement or ship strike to assess how many animals have suffered injuries that could lead to death. For entanglement, this includes any animal carrying line, any animal with a wound deeper than 8cm caused by entanglement, or any animal that appears to be in poor health from entanglement. For ship strikes, seriously injured animals are those with propeller cuts or gashes deeper than 8cm, evidence of bone breakage determined to have occurred pre-mortem, or evidence of haemorrhaging or haematoma. These serious injuries were further subdivided into impact levels of fatal, possibly fatal and non-fatal. Under these criteria, 56 serious injuries have been documented between 1970 and 1999: 31 from entanglement and 25 from ship strikes. Nineteen were fatal (16 ship strikes, 3 entanglements), 13 were possibly fatal (2 ship strikes, 11 entanglements), and 24 were non-fatal (7 ship strikes, 17 entanglements).

The annual rate of increase of all serious injuries and mortalities is 5.65% (95% CI = 1.32-9.98% – 1970-1998). This rate exceeds the estimated average annual rate of increase of the population, which has ranged from 4.4% to –2.4% (Caswell *et al.*, 1999). This suggests that this increase in serious injury and mortality is not correlated with population size. The data also indicate that anthropogenic interactions are responsible for a minimum of two thirds of the confirmed and possible mortalities of non-neonate animals. The estimates do not take into account changing effort.

The recommendations of the Workshop are given under Item 8.

7.3.2 Habitat degradation

Kenney summarised results of the South Channel Ocean Productivity Experiment (SCOPEX), which concluded that successful right whale feeding depends on extremely dense zooplankton patches (e.g. Kenney *et al.*, 1986; Wishner *et al.*, 1988; Mayo and Marx, 1990; Kenney and Wishner, 1995). Patch development is primarily a physical rather than biological phenomenon. Consequently, changes in oceanographic conditions can alter extent, location, timing and persistence of acceptable or optimal feeding grounds. Overall non-tidal circulation in the Gulf of Maine is driven by the influx of Scotian Shelf Water across the shelf south of Cape Sable, Nova Scotia and at depth inward through the Northeast Channel. An analysis of oceanographic affects on right whale distribution (Kenney, 2001) concluded that the absence of right whales in the Great South Channel in 1992 resulted from the greatly reduced abundance of *Calanus* that resulted from significantly lower water temperatures and consequential hydrographical changes. The underlying cause was an unusually large influx of cooler and fresher Scotian Shelf Water, observed on Georges Bank in April for the first time, possibly exacerbated by the global cooling effect from the 1991 eruption of the Mt Pinatubo volcano.

Kenney also described another analysis (SC/M98/RW29), correlating calving rate with the annual mean Southern Oscillation Index (SOI) lagged by one year, with low calving years tending to occur one year after El Niño events. Another correlation was found between calving rate and the North Atlantic Oscillation (NAO) lagged by two years. A regression model including both variables predicted eight calves would be born in 1999, when the observed number was four. Hindcasting from the model back to 1982, the absolute value of the difference between predicted and observed was 2.4, ranging from 3.5 higher than observed in 1995 to 8.1 lower than observed in 1996. Updating the model to include the 1999 calves and atmospheric data, plus a recent NARWC correction for 1984, the significant effects are still from SOI lagged one year and NAO lagged two years. It predicts 14 calves in 2000. The observed increase in calving intervals was primarily between 1992 and 1993 rather than a gradual trend, coinciding in time with observed distributional shifts (i.e. the abandonment of Roseway Basin). This is consistent with a hypothesis that changes in oceanographic conditions have altered foraging grounds. Kenney suggested that energy limitation is an underlying cause of the reproductive changes.

As noted under Item 6.4, the Workshop could reach no conclusions on the food limitation hypothesis.

Kenney also hypothesised (Kenney *et al*., 2001) that the present population is a remnant on the periphery of its historical range that has not re-occupied the original core of the range because of strong maternally-directed site fidelity. Such a peripheral segment of a population might be expected to undergo fluctuations in feeding and reproductive success with environmental variation, which might over the long term maintain low abundance. As with the previous hypothesis, insufficient data are available to confirm or refute this hypothesis.

Moore summarised results of work on right whale blubber thickness (SC/O99/RW4). Blubber thicknesses of necropsied northern right whales were consistently less than observed in southern right whales (Tormosov, 1998) when blubber thickness is plotted against body length. It was noted that because the sampled northern right whales were mostly ship-struck their blubber thickness would not have been compromised by reduced health prior to death. A small sample of randomly selected blubber thickness measurements obtained acoustically in 1999 from adults from the above two species (for methods, see Moore *et al.*, 2001) also revealed that northern right whales had lower blubber thickness than their southern counterparts. Although no relationship was found between acoustically measured blubber thickness and age in male northern right whales, females' blubber thickness increased with age. Those females that had calved showed a correlation between increasing blubber thickness and number of years since calving.

Moore discussed the possibility of using blubber biopsy contaminant burdens of halogenated hydrocarbons, and related biochemical indices, to predict potential internal organ toxicological risk (SC/M98/RW24). Both northern and southern right whales, from different ocean basins, have consistently low organochlorine burdens, as predicted by other studies in right whales and other mysticetes. However, the induction of endothelial cytochrome P 450 1A (CYP1A) was elevated in samples from feeding northern right whales, as compared to calving northern right whales, and to calving and feeding southern right whales. Since these assays detect presence of chemicals that are not accumulated, positive findings indicate current and continuing exposure. Moore concluded that these levels warrant further monitoring. The Workshop noted that further work is required to interpret how pollutant levels relate to the health of marine mammals (Reijnders *et al.*, 1999).

The Workshop also noted that there are a number of widely used compounds only recently recognised as potentially toxic or endocrine-disruptive at ambient oceanic levels including tributyltins (anti-fouling compounds used on ships worldwide), nonylphenols (dispersants used widely in detergents), polybrominated biphenyls, polybrominated diphenyl ethers and phthalates (plasticisers). Few of these have been tested in marine mammals, and none have been tested in right whales.

Marx described three different types of skin lesions seen. There is clear evidence of a steady increase of such lesions through time. Animals have been observed to recover from them. Their cause remains unknown and it was **recommended** that in addition to the veterinarians already consulted, dermatologists be employed to diagnose the whales' condition. Lesions and scars were also discussed at a New England Aquarium workshop on the effects of tagging in October 1999. Its report will be made available to the Scientific Committee in 2000.

7.3.2.1 RECOMMENDATIONS

The Workshop endorsed the previous **recommendations** of the Cape Town Workshop (IWC, 2001) that coordinated studies of health in right whales should be undertaken, from using both biopsy- and necropsy-derived samples. Where possible, researchers should:

(a) obtain biopsy and/or necropsy samples of the skin lesions for histology and microbiology;
(b) examine histology samples and necropsy data from all right whale mortalities.

Such studies will be greatly enhanced if all workers follow the standard approach to reporting necropsies discussed at Cape Town (IWC, 2001).

The Workshop also **recommends** that:

(1) methods of assessing the health of right whales be investigated, including continued monitoring of the prevalence and incidence of skin lesions;
(2) the feasibility of applying techniques designed to investigate stress in other cetacean species using skin biopsies and faecal samples (e.g. by the Southwest Fisheries Science Center) be explored with regard to their applicability to right whales; and
(3) an evaluation of the feasibility and efficacy of medical interventions for right whales in extreme circumstances be undertaken.

With respect to pollutant studies, the Workshop **endorsed** the three following (slightly modified) recommendations from the Cape Town Workshop (IWC, 2001) that:

(1) extant and future necropsy and biopsy samples should be analysed for PCBs, pesticides and dioxins, as well as certain newer contaminants such as tributyltins, phthalates and nonylphenols;
(2) routine monitoring of CYP1A expression in right whales should be implemented;
(3) copepod and krill samples from known or presumed feeding habitats in both hemispheres should be analysed for PCBs, pesticides and dioxins.

However, the Workshop recognised the importance of continuing parallel studies of cause-effect relationships in contaminants, without which interpretation of levels is impossible. Sample sizes from right whale studies alone will inevitably be too small. Thus, the Workshop **strongly recommends** support for the Commission's POLLUTION 2000+ project (IWC, 1999a) and agrees that right whale studies should be linked to those ongoing investigations.

Given the probable link between body condition and reproductive success, the Workshop **recommends** that seasonal and annual body condition dynamics in each habitat and reproductive class should be studied and that girth and blubber thickness measurements be taken during all right whale necropsies. Such information will also be of value in interpreting the results of pollutant analyses.

Finally, the Workshop endorsed the Cape Town Workshop **recommendation** (IWC, 2001) that local, regional and national authorities responsible for right whale habitat should develop contingency plans for oil and chemical spills.

7.3.3 Population structure and recruitment

Both sightings and genetic data support the possibility of maternally directed philopatry to the Bay of Fundy and to an alternative (currently unidentified) nursery area (SC/O99/RW7). Genetic data also suggest restricted gene flow between the Bay of Fundy and the non-Fundy group, and raises the possibility of the existence of two mating grounds.

Genetic analyses have attempted to assign the first-order relatedness of animals of unknown age to other individuals in the population; these have produced a surprisingly low match rate, which suggests that more calving events are being missed than is assumed. It is not clear whether this is due to mother/calf pairs being unrecorded in the southeastern USA, to the existence of another calving ground, to the appearance in the population of individuals born and not observed in the earlier part of the study period (as suggested by population models), or to a slightly larger population size.

The Workshop **agreed** that information on genetic structure of different feeding areas should be incorporated into future risk analyses for those areas. This is discussed further in the context of the proposed genetics Workshop (Annex E).

7.3.4 Inbreeding

Results from reproductive analyses showing that the North Atlantic right whale has a lower birth rate and longer interbirth intervals than the southern right whale might indicate the existence of inbreeding (mating between animals that are related by descent). However, there is no evidence from completed kinship analyses of paternity assignments to sampled mother/calf pairs to indicate inbreeding in this population. This is further supported by the lack of heterozygote deficiency in the population, which indicates no departure from the Hardy-Weinberg equilibrium (Ralls *et al.*, 1986).

MHC analysis in humans indicates that foetuses which share the same MHC type as their mother are more likely to be aborted than those with different genotypes. Analysis of MHC diversity in northern right whales may provide insights into whether this is a possible explanation for the depressed reproduction in this population.

The Workshop noted that analysis of microsatellites suggests that this population has not gone through a bottleneck within the last 150 years. Additional analyses further suggest that the population has been small for several hundred years; if true, this may have resulted in the purging of deleterious alleles, but may have compromised MHC diversity. Predictions from this hypothesis include: that females with low fecundity in this population should show the most common MHC haplotypes; and that 16th century specimens from Red Bay, as well as South Atlantic right whales, should both show higher MHC diversity than the current North Atlantic population.

7.4 Comparison with other populations

Best *et al.* (2001) calculated demographic parameters of southern right whales off South Africa. Results included a mean calving interval of 3.12 years (95% CI 3.07-3.17), an adult female survival rate of 0.983 (95% CI 0.972-0.994), median age at first parturition 7.88 years (95% CI 7.17-9.29), first-year survival rate of 0.913 (95% CI 0.601-0.994), and instantaneous population increase rate of 0.071 (95% CI 0.059-0.082). These biological parameter estimates were compatible with the observed increase rate of the population without the need to postulate immigration.

The data presented in Table 2 indicate a relatively low rate of reproduction in the North Atlantic. Although strictly comparable data are not available for the Southern Hemisphere, by inference reproductive rates for the latter are higher. There is a significant number of North Atlantic right whale females that never calve. In contrast, the reproductive rate in southern right whales precludes this possibility in that population.

8. CONCLUSION AND RECOMMENDATIONS

In discussing Recommendations, the Workshop agreed to separate out at least two aspects of the issues being discussed when deciding a strategy for the future. These can be seen as:

(1) research that enables us to document and gain scientific insights into population dynamics and ecology of a whale population that has been reduced both to very low absolute numbers as well as a small fraction of its original population size;
(2) research that will permit implementation of appropriate management actions and evaluation of their performance.

Whilst both the above are important, and recommendations for both have been developed, it was **agreed** that the **highest priority** must be accorded to the latter category. Despite the improvements that can and should be made in terms of refining the modelling of this population, it is clear that none of those refinements will lead to a change in the conclusion that:

> *by any management criteria applied by the IWC in terms of either commercial whaling or aboriginal subsistence whaling, there should be no direct anthropogenic removals from this stock.*

The evidence that this population (possibly the only potentially viable population of this species) is in serious danger is compelling, and the need for further research under category (1) above should not be seen as a reason for delaying immediate and highest priority action under (2). In short, this population:

(a) is at very low absolute abundance and thus highly vulnerable to stochastic variation in population dynamic processes;

(b) is, unlike a number of Southern Hemisphere populations, not recovering despite protection from whaling since the 1930s;
(c) appears to be decreasing at present as a result of
  (i) a decreased rate of survival in the 1990s versus the 1980s;
  (ii) an increase in effective calving interval in the 1990s;
(d) is subject to known direct anthropogenic removals (ship strikes and entanglements in fishing gear) that have been increasing in recent years.

In addition, there is some evidence that the overall health of the population has decreased since the 1980s (e.g. as witnessed by increased incidence of skin lesions).

Given all the above, the Workshop **agreed** that it is a matter of absolute urgency that every effort is made to reduce anthropogenic mortality to zero. This is perhaps the only way in which the chances of survival for this population can be directly improved. Research directed at this aim should be given immediate priority.

8.1 Research

8.1.1 General

A number of recommendations were developed and are discussed under the relevant Agenda Items. Table 5 summarises these, their aims and their relevance to the two research categories noted above. The Workshop believes that all of the recommendations are of importance. However, it **agrees** that given the present status of this population as documented above, it is important to assign levels of priority to the research recommendations, as shown in Table 5.

8.1.2 Highest priority

Records of deaths and injuries indicate that two-thirds of non-calf mortality events could be due to entanglements and ship strikes (Knowlton and Kraus, 2001). Given the failure of current methods to eliminate all sources of mortality from shipping and fishing in North Atlantic right whales, the Workshop recognises that only drastic measures, such as total restrictions on fixed fishing gear and shipping, would immediately accomplish the goal of zero mortality. Since such total restrictions are not feasible, research is urgently needed on the development of methods to eliminate both sources of mortality. Nevertheless, the Workshop **strongly emphasises** that there is no need to wait for further research before implementing any currently available management actions that can reduce anthropogenic mortalities.

In that context, the Workshop **recommends** that the highest priority be assigned to research into means of reducing mortality from entanglements and vessel collisions. It further **recommends** that an international multidisciplinary Workshop be held to review progress and to identify priorities for further work and the most promising approaches to management action to reduce mortality. That multidisciplinary Workshop will review ongoing work on *inter alia*:

(1) the determination of risk factors for collisions and entanglements (such as analyses of vessel traffic and fishing activity patterns with respect to right whale distribution and risk);
(2) use of modelling to identify areas or classes of animals that are subject to particularly high risk;
(3) the use of shipborne, aerial and fixed (acoustic) surveys for real-time monitoring of right whale concentrations;
(4) the efficacy and feasibility of different approaches to managing shipping movements for right whale avoidance, such as ship rerouting and/or speed reductions, using both computer simulations and field trials;
(5) the awareness of mariners in the region to right whale issues and their response to information and directions relating to right whale avoidance;
(6) cross-disciplinary evaluation of disentanglement and gear modification technologies.

It is essential that every effort be made to ensure that requisite data are available. At a minimum this must include, for the entire east coast of North America, good temporal and geographical information on vessel traffic, fishing gear effort and distribution. The Workshop **recommends** that the Commission urges the relevant governments to ensure that such data are recorded, collated and made available. In this context, the Workshop **recommends** that a Geographic Information System (GIS) project be conducted to overlay effort data (see Item 7.2.1) onto information on right whale distribution together with that of fishing gear, shipping activity and other threats.

For the multidisciplinary Workshop to be successful it is important that relevant national and international organisations are invited as well as experts in right whale biology, shipping technology, fishing gear, etc. It was **agreed** that Knowlton and Kraus should identify an appropriate Steering Group to *inter alia*:

(1) identify potential participants and request papers;
(2) identify a suitable venue and time;
(3) draw up an agenda and structure for the meeting.

Notwithstanding that the above recommendation should be accorded highest priority, the Workshop also recognises that reduced calving success may reflect the impact of a variety of human activities that alter coastal habitats (e.g. altered food resources, elevated contaminant levels and behavioural disruption). It therefore **recommends** that research on these and other habitat quality issues be intensified and that the habitat Workshop referred to under Item 7 evaluate the impact and mitigation of habitat stressors.

8.2 Management

The Workshop reiterates that it is a matter of absolute urgency that every effort is made to reduce anthropogenic mortality in this population to zero. This is perhaps the only way in which its chances of survival can be directly improved. There is no need to wait for further research before implementing any currently available management actions that can reduce anthropogenic mortalities.

Knowlton noted that an information document to shift shipping lanes in the Bay of Fundy had been submitted to the International Maritime Organisation (IMO). To reduce the potential for ship/whale collisions, the Workshop **recommends** that a document summarising right whale sightings data, corrected for effort, be presented as a proposal to IMO for consideration of alternate routing of vessels away from areas of high right whale density.

In light of the recently implemented Mandatory Ship Reporting System in this area, the Workshop **recommends** that the data on number of ships entering the area and the speeds at which they are travelling be investigated. It further **recommends** that the distribution of whales be overlaid with traffic distribution and shipping lanes to assess the need and feasibility of further regulatory actions related to ship routing and reduction of ship speed.

In addition to those described above, the following actions have been taken regarding recommendations made by the

Table 5

Summary of recommendations (high priority marked with an asterisk). (Cat.1 = research that enables us to document and gain scientific insights into the population dynamics and ecology. Cat. 2 = research that will enable us to carry out appropriate management actions and evaluate their performance.)

Agenda Item	Brief objective	Cat. 1	Cat. 2	Priority	Timescale	Comments
Anthropogenic removals (highest priority)						
8.1.2	Workshop on ship strikes and entanglements		Yes	A*	*Ca* 1 year	Aim for ?? date ??
7.1.1	Tabulating effort data	Yes	Yes	A	1 year	Relevant to shipstrike and entanglement workshop
8.1.2	GIS analysis of right whale distribution relative to geographic and risk factors	Yes	Yes	A	1 year+	Relevant to shipstrike and entanglement workshop
8.1.2	Collect/collate good temporal and geographical information on vessel traffic, fishing gear	Yes	Yes	A	1 year	Relevant to shipstrike and entanglement workshop
NARWC - related long-term monitoring						
7.2.1	Continuation of NARWC and related field effort	Yes	Yes	A*	Ongoing	Relevant to all work - very high priority
4.1	Code identification photographs for distinctiveness and photo quality	Yes	Yes	A	Ongoing	
4.1	Goodness of fit testing for heterogeneity	Yes		C	Unclear	
4.1	Automated matching	Yes		C	1 year	
Genetics - related studies						
6.1.1	Genetics workshop	Yes	Yes	A*	1 year+	Aim for October 2000
6.1.1	Multilocus genotyping of all individuals, and use of markers to determine substock structure	Yes	Yes	A	1 year	Completion required before genetics workshop
6.1.1	Genotyping at MHC loci for correlations with reproductive success and health	Yes		A	1 year	Completion required before genetics workshop
7.1.1	Continued development of population models	Yes	Yes	A		Relevant to genetics workshop
6.1.1	Conducted directed biopsy sampling, especially in the southeastern USA	Yes	Yes	A	Ongoing	
6.1.1	Genetic analysis of historical specimens to examine population structure and genetic diversity	Yes		B	Unclear	Relevant to genetics workshop
6.1.1	Conduct genetic analysis with respect to habitat use, scarring patterns, reproductive success and resighting probabilities	Yes	Yes	B	2 years	Relevant to genetics workshop
Health - related studies						
7.3.2.1	Evaluate possible methods for health assessment, including monitoring of skin lesions	Yes	Yes	A	1 year (prelim)	
7.3.2.1	Feasibility study on stress investigation	Yes		B	?	
7.3.2.1	Evaluation of medical interventions		Yes	B	?	
Pollutant - related studies						
7.3.2.1	Link of pollution studies to POLLUTION 2000+	Yes	Yes	A	5 years	
7.3.2.1	Collect and analyse right whale samples for contaminants	Yes	Yes	B	Years	
7.3.2.1	Monitor CYP1A expression	Yes	Yes	B	Years	
7.3.2.1	Collect and analyse zooplankton samples for study of contaminants	Yes	Yes	C	Years	
Habitat - related studies						
8.1.2	Conduct habitat workshop	Yes	Yes	A	2 years+	See SC environment group
6.4.1	Obtain length measurements of individual right whales for use in assessments of health, age and blubber thickness	Yes		A	Years	
7.3.2.1	Blubber thickness studies	Yes	Yes			
Other						
7.2.1	Examine feasibility of a coordinated dedicated assessment survey	Yes		C	1 day	

Cape Town Workshop (see IWC, 2001c, appendix 1 of annex O):

(1) Movement of major shipping channels in the southeastern USA calving ground: this remains in discussion.

(2) Consideration of risks to right whales in permit review for high-speed ferry operations: this is legally complex but is being investigated further.

9. OTHER BUSINESS

The Workshop offered its warm thanks to Clapham and the NEFC Science Center for their courtesy and the provision of excellent facilities. The Chairman, despite avoiding the final session, was applauded for his usual firm but fair and good-natured chairing of the meeting. Thanks are also due to the Steering Group and the Rapporteurs, and to Clare Last and Martin Harvey of the IWC Secretariat who assisted with the administration.

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Annex B
Agenda

1. Introductory items

2. Agenda

3. Review of documents

4. Review of available data
    - 4.1 Recommendations

5. Review of available models

6. Overview of existing knowledge of population parameters
    - 6.1 Stock and sub-stock structure
        - 6.1.1 Recommendations (and see Item 8)
    - 6.2 Population size
    - 6.3 Age composition
    - 6.4 Reproduction
    - 6.5 Survivorship
    - 6.6 Conclusion

7. Assessment of status and trends
    - 7.1 Results from population modelling
        - 7.1.2 Recommendations
    - 7.2 Results from population monitoring
    - 7.3 Factors affecting trends
        - 7.3.1 Direct anthropogenic interactions
            - 7.3.1.1 Recommendations
        - 7.3.2 Habitat degradation
            - 7.3.2.1 Recommendations
        - 7.3.3 Population structure and recruitment
        - 7.3.4 Inbreeding
    - 7.4 Comparison with other populations

8. Conclusion and recommendations
    - 8.1 Research
        - 8.1.1 General
        - 8.1.2 Highest priority
    - 8.2 Management

9. Other business

Annex C
List of Documents

SC/O99/RW

1. Cooke, J. and Glinka, S. A comparative analysis of the demography of the Southwest Atlantic and Northwest Atlantic right whale populations from photo-identification of calving females.
2. Wade, P.R. and Clapham, P.J. The influence of sighting probabilities on survival estimates for North Atlantic right whales.
3. Hain, J.H.W., Kenney, R.D., Knowlton, A.R. and Kraus, S.D. Heterogeneity, sampling, presumed mortality, and the estimation of population parameters for the North Atlantic right whale.
4. Miller, C. and Moore, M. Blubber thickness in Atlantic *E. glacialis* and *E. australis*.
5. Brault, S. and Caswell, H. Draft report of the first Woods Hole workshop on right whale demography.
6. White, B.N., Waldick, R., Tomlinson, C., Malik, S., Brown, M., Hamilton, P., Knowlton, A., Slay, C. and Kraus, S. The status of the North Atlantic right whale as determined from genetic data.
7. Fujiwara, M., Brault, S. and Caswell, H. Stage-structured demographic analysis of the North Atlantic right whale.

For Information Papers

1. Hain, J.H.W., Ellis, S.L., Kenney, R.D. and Slay, C.K. 1999. Sightability of right whales in coastal waters of the United States with implications for the aerial monitoring program. pp.191-207 In: *Marine Mammal Survey and Assessment Methods.* A.A. Balkema, Rotterdam.
2. Rosenbaum, H.C., Egan, M.G., Clapham, P.J., Brownell, R.L. Jr., Malik, S., Brown, M., White, B.N., Walsh, P. and DeSalle, R. 2000. World-wide genetic differentiation of Eubalaena: questioning the number of right whales species. *Mol. Ecol.* 9(11):1793-1802.
3. Best, P.B., Brandão, A. and Butterworth, D.S. 2001. Demographic parameters of southern right whales off South Africa. [Published in this volume].
4. Portway, V., Best, P.B., Clapham, P.J., Hamilton, P.K., Moore, M.J., Payne, R., Rowntree, V., Rivarola, M. and Schaeff, C.M. 2000. Mitochondrial DNA differentiation between two wintering populations of southern right whales (*Eubalaena australis*) off South Africa and Peninsula Valdes, Argentina. *Mar. Ecol. Progress Ser.* (In press).
5. Weinrich, M.T., Kenney, R.D. and Hamilton, P.K. 2000. Right whales (*Eubalaena glacialis*) on Jeffreys Ledge: an unrecognized habitat? *Mar. Mammal Sci.* 16 (In press).
6. Waldick, R.C., Brown, M.W. and White, B.N. 1999. Characterization and isolation of microsatellite loci from the endangered North Atlantic right whale. *Mol. Ecol.* (In press).
7. Malik, S., Brown, M.W., Kraus, S.D., Knowlton, A.R., Hamilton, P.K. and White, B.N. 1999. Assessment of mitochondrial DNA structuring and nursery use in the North Atlantic right whale (*Eubalaena glacialis*). *Can. J. Zool.* 77: 1-6.
8. Malik, S., Brown, M.W., Kraus, S.D. and White, B.N. 2000. Analysis of mitochondrial DNA diversity within and between North and South Atlantic right whales. *Mar. Mammal Sci.* 16 (In press).
9. Knowlton, A.R. and Kraus, S.D. 2001. Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. [Published in this volume].
10. Kraus, S.D., Knowlton, A.R., Hamilton, P.K., Deney, R.D. and Slay, C.K. In review. Status and trends in reproduction in North Atlantic right whales. *J. Cetacean Res. Manage.* [See Kraus *et al.*, this volume.]
11. Moore, M.J., Miller, C.A., Weisbrod, A.V., Shea, D., Hamilton, P.K., Kraus, S.D., Rowntree, V.J., Patenaude, N. and Stegeman, J.J. 1998. Cytochrome P450 1A and chemical contaminants in dermal biopsies of northern and southern right whales. [SC/M98/RW24].
12. IWC. 1999. Extract from SC/51/4, Report of the Scientific Committee.
13. IWC. 1998. Extracts from the Cape Town meeting report.

Annex D
Working Group on Heterogeneity in Sighting Probability

Members: Burnell, Donovan, Friday, Hamilton, Knowlton, Laake (Convenor), Marx, McMillan, Pace.

1. TERMS OF REFERENCE

(1) Identify factors of the photo-identification sampling and matching process that may introduce heterogeneity in sighting probability.
(2) Identify existing data (covariates) that may be used to reduce/model heterogeneity in sighting probability.
(3) Develop strategy for explaining/modelling heterogeneity in existing and future photo-identification data collection.

2. IDENTIFY FACTORS OF THE PHOTO-IDENTIFICATION SAMPLING AND MATCHING PROCESS THAT MAY INTRODUCE HETEROGENEITY IN SIGHTING PROBABILITY

Sighting probability through photo-identification is affected by the chances of encountering whales, selection of whales to be photographed, obtaining adequate photographs, and matching to the existing catalogue. Variation in these processes can introduce heterogeneity in sighting probability that primarily biases estimates of population size and to a lesser degree, estimates of survival rate (Hammond *et al.*, 1990). The Working Group identified the following potential sources of heterogeneity in sighting probability within each of the aspects of the photo-identification process given below.

I. **Whale encounter probability** depends on:

(a) spatial and temporal (within and between year) distribution of whales relative to the spatial and temporal distribution of sampling; and
(b) ability to sight whales which depends on the survey platform, observer ability, whale diving behaviour, group size and a variety of other factors that affect sightability.

II. **Selection of whales to photograph** depends on:

(a) group size of the whales (e.g. large groups may be selected more often); and
(b) survey platform and logistics of sampling the survey region (e.g. aerial surveys in offshore regions are less likely to sample individual whales).

III. **Obtaining adequate photographs of a whale in a single encounter** depends on:

(a) *whale behaviour*, which may vary for the following reasons:
    (1) behavioural response to the survey platform (e.g. diving as an aversive response to a circling aircraft, or avoiding a motorised boat);
    (2) predominant whale activity (e.g. social or skim feeding) as it affects the display of head, tail, lip callosities, etc.;
    (3) individual variation in behaviour; and
    (4) group size.
(b) *researcher experience*;
(c) *time spent with the whale(s) and number of photographs taken*;
(d) *various factors that may affect photo quality* such as approach distance, weather, lighting, etc.;
(e) *survey platform*, which may limit the amount of time available to spend with a whale;
(f) *group size*, which affects the number of photographs obtained per whale and the ability to link different photos of the same whale.

IV. **Successful matching to the existing catalogue or adding a newly identified whale** depends on:

(a) *features of the photos* obtained during the encounter:
    (1) photo quality (e.g. contrast, image size, sharpness);
    (2) number of different aspects (e.g. head, back, tail, etc.) photographed; and
    (3) distinctiveness of the whale (e.g. amount and shape of scars, pigment discoloration, callosities and their distribution across the body, uniqueness of the callosity pattern – broken versus continuous). Temporary characteristics such as skin sloughing, cyamids, and callosity topography are used for matching within season but they are not useful for between-year matches.
(b) *the same features of the existing whale photographs in the catalogue at the time the new set of photographs are matched*, which depends on the number of previous sightings of the whale;
(c) *experience of the individual matching the photographs* which may interact with the quality of the photograph. For the right whale catalogue, more than one experienced matcher examines all matches and non-matches of photographic events. However, proposed matches are given higher priority to avoid

false positives and whilst non-matches are reviewed they are done so with a lower priority. This creates a time lag in adding new whales.

2. IDENTIFY EXISTING DATA (COVARIATES) THAT MAY BE USED TO REDUCE/MODEL HETEROGENEITY IN SIGHTING PROBABILITY

The Working Group recognised that some of the features such as sex, age or stage, and spatial/temporal distribution patterns used in the analyses of SC/O99/RW2 and SC/O99/RW7 should be useful variables to model variability in encounter probability and as proxies for various behavioural differences that affect success in obtaining photographs. The Working Group also recognised that there were limits to modelling heterogeneity and that some factors may not be easily quantified.

Typically, annual sighting histories of whales have been constructed based on the composite result of all sampling throughout the year in all regions. The composite nature of the sampling should reduce the effects of heterogeneity somewhat by increasing overall sighting probability. However, the composite sampling complicates the identification and definition of covariates for most aspects involving sampling (I, II) and photography (III). For example, an effort measurement is difficult to define for the composite sampling of whalewatching boats and dedicated vessel and aircraft surveys. Likewise, in general it will be difficult to define covariates for any factor related to individual photographic events. The Working Group considered such measures as the number of photographs taken but noted that these types of measures do not always adequately reflect matchability (e.g. experienced researchers will often take very few photos of a very distinctive whale) and they are inappropriate because they are the result of sighting and not a predictor of sighting success.

The primary determinant of matching success is the distinctiveness of the whale and the type and quality of the photographs in the catalogue. Some caution is necessary in defining variables such that they are not influenced by the accumulation of photographs over years; otherwise, bias may be introduced because more photographs will be collected from survivors. If matches were only made in a year with the photographs available prior to that year, then the quality, distinctiveness, and number of photographs available in the catalogue at that time could be used as a predictor for that year. As the number and quality improved over time, the value of the predictor for ensuing years would change. This approach requires documentation of these features through time - this does not currently exist. In addition, matches in the existing sighting histories have been determined backwards in time (i.e. using photographs from year t to establish a match in year t-x), so the matching probability of previous years depends on future years which can only occur for survivors. The current database does have a defined field for quality of the photos in the catalogue but it has not been updated to include more recent photographs and its definition did not distinguish adequately between distinctiveness of marking and photo quality.

Matches of photographs taken from aerial and vessel surveys are often difficult to match. An easily constructed and possibly important covariate may be the source of existing photographs in the catalogue (i.e. vessel, aerial, or aerial and vessel). This covariate will not require a re-evaluation of photographs but does need to be reconstructed through time.

3. DEVELOP STRATEGY FOR EXPLAINING/ MODELLING HETEROGENEITY IN EXISTING AND FUTURE PHOTO-IDENTIFICATION DATA COLLECTION

Heterogeneity in sighting probability has been identified through goodness-of-fit tests (SC/O99/RW5) for time dependent models. The Working Group proposes that similar tests be conducted for models that incorporate sex, stage, and spatial covariates as appropriate to determine if additional heterogeneity remains. If those covariates do not remove all of the heterogeneity, further consideration should be given to devising covariates that would describe whale distinctiveness and photographic quality through time. The Working Group recommends that the quality and distinctiveness codes identified during the Cape Town Workshop should be used for the existing catalogue and carried forward in time in the database with documentation of matching.

REFERENCE

Hammond, P.S., Mizroch, S.A. and Donovan, G.P. (eds.). 1990. *Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters*. International Whaling Commission, Cambridge, UK. [vi]+440pp.

Annex E

Proposal for a Workshop on Right Whale Genetics

1. RATIONALE

Preliminary analyses indicate that the understanding of right whale dynamics can be significantly improved through consideration of genetic data. Demographic models indicate that calving intervals have increased, that survival rates of certain components of the population have decreased (particularly among reproductively active females) and that survival rates differ for groups of whales utilising different areas. Genetic data indicate that there is female philopatry to different feeding areas that is passed on to calves that results in significantly different genetic profiles in different areas. Some possible uses of genetic data are: to delineate groups exposed to different levels and types of risks, to estimate the level of female and male dispersal between different areas, to estimate the magnitude of whales that may never be available for photographic sampling by examination of paternity (identification of missing fathers), to identify the plausibility of more than one calving ground and multiple breeding grounds, the relative plausibility that current genetic patterns could have resulted from a bottleneck, a population that has remained rare for a long period or a population that has been recently reduced, and to assess the plausibility of reduced long-term fitness.

Future models are urgently needed to identify the source of increased risk. Model results could be used to eliminate risk hypotheses, strengthen conclusions about status and trends, prioritise research and guide management decisions. Although genetic data can play an essential role in such management models, the use of genetic data to estimate demographic parameters and evaluate risk hypotheses is novel. As demonstrated by the demographic analyses already completed the understanding of data can be most quickly accomplished through numerous researchers approaching the problem.

2. TERMS OF REFERENCE

The following draft terms of reference are proposed:

(1) explore a range of population genetic analytical techniques;

(2) develop new analytical techniques to estimate model parameters specific of right whale conservation models; and

(3) identify the best approaches for both future genetic research both in terms of needed sampling, potential additional markers and development of future analytical techniques.

3. STEERING GROUP

Taylor (Convenor), Brault, Brownell, Clapham, Donovan, Rosenbaum, White.

4. DATES AND VENUE

White indicated that the outstanding genetic analyses should be completed in one year. It is proposed that the Workshop be held in New England after the 2000 meeting of the Right Whale Consortium in order to reduce travel expenses.

Annex F
Estimates of Current Abundance

Table 1 shows estimates of recent (1995-96) population size obtained by various methods. The method of calculation for each count or estimate is given below. Catalogued animals known to have been alive in 1996 provide a firm lower bound of 263 for total abundance in that year. The statistical approaches (Caswell *et al.*, 1999; SC/O99/RW2) are sensitive to violations of their assumptions when used to provide abundance estimates, and are expected to provide negatively biased estimates because of heterogeneity in sightings probabilities by area. It is therefore not surprising that the 'best' estimates produced by these methods are less than the lower bound of 263. The high estimated sighting probabilities from these methods do, however, suggest that the overall abundance in 1996 is unlikely to have been much greater than the 263 lower bound.

A lower bound on the reproductive female component is provided by the 58 animals known to have calved by 1996 who are also known to have been alive in 1996 (i.e. seen in 1996 or both before and after 1996). For the same reasons, the true number is considered unlikely to be much in excess of this.

The statistical analyses to date have concentrated primarily on the estimation of survival and sighting probability. Further research is required before definitive recommendations can be offered as to the best approach to estimate abundance from the photo-id data.

1. *n/p* MARK-RECAPTURE METHOD FROM CASWELL *ET AL.* (1999) [CASWELL AND FUJIWARA]

The Cormack-Jolly-Seber model used by Caswell *et al.* (1999) produces estimates of sighting probability $p(t)$ as a function of time (year). We also computed 95% profile

Table 1

Summary of population counts/estimates from photo-identification data.

Method	Component	Year	Count	Estimate	(95% CL)	Reference
Catalogued, known to be alive	Total	1996	263			
Catalogued, presumed alive	Total	1996	296			
As above + suspected missed	Total	1996	314			
Cormack-Jolly-Seber	Total	1995		230	(220-242)	Caswell *et al.* 1999
n/p by cluster	Total	1996		250	(194-321)	SC/O99/RW2
Catalogued, known to be alive	Calving female	1996	58			
Catalogued, presumed alive	Calving female	1996	70			
Southern right model	Calving female	1996		57	(52-98)	SC/O99/RW1

(a) Minimum population estimates based on annual counts (1990-1997)

Year	No. seen in year + No. seen in years before and after	Year	No. seen in year + No. seen in years before and after
1997*	248 (230 + 18)	1993	253 (177 + 76)
1996	263 (216 + 47)	1992	252 (130 + 122)
1995	258 (216 + 42)	1991	249 (158 + 91)
1994	259 (206 + 53)	1990	250 (148 + 102)

*This estimate is likely biased downward because of limited post 1997 data.

(b) Abundance as of December 1996

No. in catalogue	374
Animals seen only prior to 1979	–5
Mortalities of identified whales	–9
Whales mortally injured	–4
1995/96 calves not catalogued	+13
Subtotal	369
Presumed mortality 1979-1993	–5
Presumed mortality 1994-1996	–38
'Mid' estimate	**296**
Conservative correction for unlikely presumed mortality (based on individuals with 'offshore signature')	+18
'Best' estimate	**314**

likelihood confidence limits (pointwise) on $p(t)$. Assuming that all whales have identical sighting probabilities, and that the probability of first sighting is the same as the probability of re-sighting, we estimated total population size as:

$$\hat{N}(t) = \frac{n_{\mathrm{obs}}(t)}{\hat{p}(t)}$$

where $n_{\mathrm{obs}}(t)$ is the number of whales observed in year t. An approximate standard error of $\hat{N}(t)$ is:

$$\mathrm{SE}(\hat{N}(t)) \approx \frac{n_{\mathrm{obs}}}{\hat{p}(t)^2}\mathrm{SE}(\hat{\mathrm{p}}(\mathrm{t}))$$

We approximated SE(p) as ¼ of the width of the 95% profile likelihood interval.

The resulting estimates are shown in Fig. 1. The estimates agree closely with the projected trend in fig. 7 of Caswell *et al.* (1999), when that trend is conditional on beginning at $\hat{N}$ (1980).

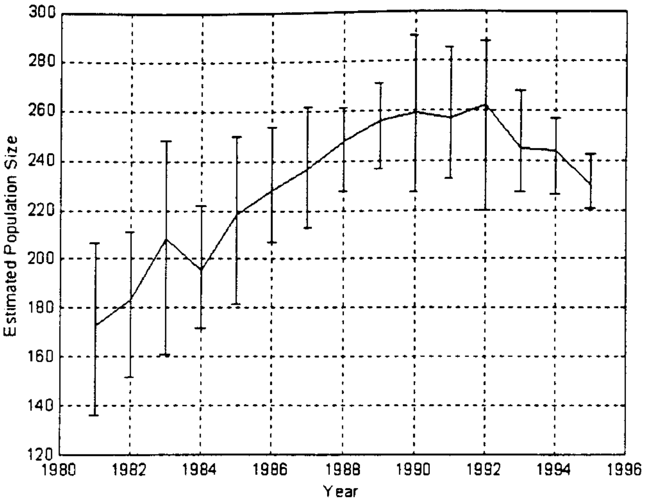

Fig. 1 Population estimates and 95% CL by year from Caswell *et al.* (1999).

The assumptions required to make this estimate are very strong. Such estimates are generally considered to be more sensitive to violation of mark-recapture assumptions than are estimates of survival or transition rates.

2. POPULATION ESTIMATES FROM THE WADE-CLAPHAM MODEL (WADE)

2.1 *n/p* mark re-capture method

Abundance can be estimated by taking the number of captured animals (n) and correcting it by the inverse of the probability of capture ($1/p$). To use estimated capture probabilities from Wade and Clapham (SC/O99/RW2), this must be done for each group and then summed across groups. For 1996, the number of captures for clusters 1-4 were 32, 9, 84, and 80 (total of 205), with estimated capture probability in 1996 of 0.930, 0.328, 0.900, 0.850. The estimated population size was therefore 249.8 (95% CI 194.3, 321.3). The lower confidence limit is less than the number of identified individuals in 1996 (205), so this method does no better in providing a lower bound than simply using that number. This method can be negatively biased by individual heterogeneity in sighting probability.

2.2 Correction for whales not seen 1991-96

293 individual whales were identified in the years 1991-1996. This does not account for whales that may not have been seen in those years. Estimated capture probabilities from Wade and Clapham (SC/O99/RW2) can be used to make this correction. The probability of not being seen for those 6 years is the product of one minus the capture probability in each year. This probability (taking the weighted average across groups) is 0.0057. One minus that quantity is the probability of being seen in any of those years (0.9943). One over this probability becomes the correction: $1.0058*293 = 294.7$. This method does not take account of whales seen within the years 1991-1995 that might have died by the year 1996.

3. POPULATION ESTIMATES USING THE SOUTHERN RIGHT WHALE MODEL (COOKE)

This model estimates the size of the breeding female population (females who have had at least once calf in their lifetime) along with survival and calving rates as described in SC/O99/RW1. Since the model does not use sightings of animals in years when they do not calve, it is possible for the point estimate to be less than the minimum number of animals known (on the basis of the full data set) to be alive. The estimates are liable to be biased low through unaccounted-for heterogeneity.

4. DIRECT COUNTING METHODS FROM THE CATALOGUE (KNOWLTON)

The back-counting method defined by Knowlton *et al.* (1994) combined with criteria defined in Hain *et al.* (SC/O99/RW3) to estimate presumed mortality in years when survey effort was limited or stopped in offshore areas was carried out to provide a maximum and mid population estimate for 1996. A minimum population for 1996 was estimated by counting the number of animals seen in 1996 plus the number not seen in 1996 but seen both before 1996 and after 1996. The latter provides the minimum number definitely known to have been alive in 1996.

4.1 1996 estimates

'Best' estimate - 314: total catalogued animals minus presumed dead (1979-1996), mortalities of known animals, and mortally injured known animals; plus calves born in 1995/1996 (not yet catalogued) and unlikely presumed mortalities (1994-1996) based on individuals with an 'offshore signature'.

'Standard' estimate - 296: total catalogued total catalogued animals minus presumed dead (1979-1996), mortalities of known animals, and mortally injured known animals; plus calves born in 1995/1996 (not yet catalogued).

'Minimum estimate' - 263: number of animals photographed in 1996 plus the number of animals photographed both before and after 1996 and not in 1996.

4.2 Potential biases

The 314 estimate is biased down if our correction for presumed mortalities is too conservative, and up if it is not conservative enough. The accuracy of this correction factor may be tested in the future as offshore surveys are resumed and the need to utilise it at all may be eliminated if offshore surveys are maintained and expanded.

The 296 estimate may be biased upwards by dead animals that are unreported and/or animals that have died but have not yet become presumed dead; downwards if presumed dead criteria are violated.

The 263 estimate is a hard minimum and is likely biased downward from the best estimate because of the limited time frame after 1996 to resight animals seen prior to 1996. Also the lack of effort in the offshore areas during the 1990s would reduce the chance of animals first sighted in the 1980s, when survey effort was high, to be resighted after 1996.

Each of these estimates are biased down by animals that exist but are not catalogued.

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Aspects of the reproductive biology, movements and site fidelity of right whales off Australia

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ABSTRACT

Between 1991 and 1997 right whales were studied on their wintering grounds on the southern coastline of Australia, predominantly at the Head of the Great Australian Bight, where over 350 individuals have been identified. The observed mean inter-calf interval for females was 3.33±0.10 years (±SE, $n = 57$) at the Head of the Bight and 3.64±0.13 years (±SE, $n = 117$) in the wider Australian population. When inter-calf intervals of six or more years were excluded, the mean intervals became 3.28±0.09 years (±SE, $n = 56$) and 3.28±0.06 years (±SE, $n = 107$), respectively. Inter-calf intervals of two years were recorded following the early death of a neonate on two separate occasions and the implications of these 'shortened' intervals and of calvings that were not observed are discussed. The mean age at which yearlings were observed to be fully weaned was calculated to be 365±8 days (±SE, $n = 18$) from the estimated birth dates of individual calves and subsequent associations, or lack of them, between the yearlings and their cows the following year. A total of 108 movements greater than 200km in length were made by individual whales. The mean within-year movement was 730±84 km, made over 34±4 days (±SE, $n = 18$), whilst the mean between-year movement was 1,036±45km (±SE, $n = 87$), made over a mean interval of 3.3±0.3 years (±SE, $n = 90$). The number and direction of coastal movements observed suggest that the right whales off southern Australia comprise a single population which may undertake an almost circular, anti-clockwise migration to the south of the Australian continent. A significantly greater proportion of females displayed a level of between-year fidelity to the Head of the Bight aggregation area (92%, $n = 61$) than did males (68%, $n = 19$) or whales of unknown sex (63%, $n = 8$).

KEYWORDS: RIGHT WHALE; REPRODUCTION; MOVEMENTS; SITE FIDELITY; AUSTRALASIA

INTRODUCTION

Right whales (*Eubalaena* sp.) in both hemispheres were subject to severe hunting pressure prior to the twentieth century. Australia was no exception, with shore-based and pelagic whaling taking at least 26,000 right whales from the region between 1822 and 1930 (Dawbin, 1986).

Population levels prior to exploitation have proved impossible to estimate with any confidence (see IWC, 2001b), although Braham and Rice (1984) suggest a world-wide abundance for the genus of between 100,000 and 300,000 prior to the 15th century with an estimated 80% of these in the Southern Hemisphere. Southern right whales (*E. australis*) winter on the southern coastlines of the African, South American and Australian continents, along with the coast of New Zealand and oceanic islands such as the Tristan da Cunha, Auckland and Campbell Island groups. The extent of the species' migration and the location of the summer feeding grounds have never been known with any certainty. The long delay in recovery of the Australian population between its supposed protection in 1935 and the first sign of any measurable recovery in the late 1970s has been puzzling, particularly given the fact that whaling for the species off Australia virtually ceased in the mid 1800s. However, the recent evidence of extensive and illegal whaling operations carried out by the former Soviet Union throughout the 1950s, 1960s and early 1970s (Yablokov, 1994; Tormosov *et al.*, 1998) may have effectively solved this puzzle.

The southern right whale remains classified as 'vulnerable' by the World Conservation Union (IUCN) and is a listed species under Australia's Endangered Species legislation. The protection and monitoring of the recovering southern right whale population is considered a high priority by Australian Government conservation authorities (e.g. Bannister *et al.*, 1996).

Right whales are found close to the southern Australian coastline during the austral winter, between May and November. One of the largest and most consistent aggregation areas lies at the Head of the Great Australian Bight, on the west coast of South Australia (31°28'S, 131°08'E) where shore-based observations of right whales have been undertaken since 1991 (Burnell and Bryden, 1997).

Reproduction

The small sizes of the remnant populations, combined with complete protection, have meant that long-term studies of living right whales are required to determine reproductive parameters such as reproductive rates, age at first parturition and the duration of gestation and lactation. Such studies, carried out in the North and South Atlantic, and Southern Oceans, have found female reproductive (inter-calf) intervals of three years to be the most common in both the southern and North Atlantic right whale (*E. glacialis*), with intervals of two and four or more years being detected much less frequently (Bannister, 1990; Best, 1990a; Payne *et al.*, 1990; Knowlton *et al.*, 1994; Best *et al.*, 2001; Cooke *et al.*, 2001). Post-partum ovulation does not appear to occur in right whales and no published record exists of a female right whale giving birth in consecutive years.

Most mysticetes are thought to wean their young within a year (Lockyer, 1984). Data collected during whaling operations indicated a mean age of weaning of 10.5 months for Southern Hemisphere humpback whales, *Megaptera novaeangliae* (Chittleborough, 1958) and 6-9 months for Pacific gray whales, *Eschrichtius robustus* (Rice and Wolman, 1971; Yablokov and Bogoslovskaya, 1984). Until recently, the only such whaling data available from right whales was Klumov's (1962) estimate of 6-7 months for the age of weaning in the northern right whale in the North Pacific. This estimate was based on the presence of copepods in the stomachs of two immature whales killed and assumed from their length (approximately 11 metres) to have been born the previous winter. However, recent data from illegal Soviet catches in the 1960s showed lactation to last at least 7-8 months (Tormosov *et al.*, 1998). Further, Hamilton *et al.* (1995) describe three juvenile northern right whales in the northwest Atlantic that were weaned between 8 and 17 months after the estimated peak of calving in that population. The only well documented age of weaning in right whales is based on the photo-identification of a single neonate and its subsequent resighting the following year, as described by Thomas and Taber (1984). This individual was a minimum of 412 days old when weaned at Peninsula Valdes, Argentina.

Movements and fidelity

Although right whales range along the entire temperate coastline of Australia during the winter and spring months, their spatial distribution is quite clumped. Several aggregation areas are characterised by their consistent use by relatively dense concentrations of right whales. Bannister (1990) reports the high incidence of right whales off four broad, but distinct, regions of the south coast of Western Australia. Similarly, sightings off southeastern Australia, particularly of calving females, appear to be clumped (Ling and Needham, 1991; Burnell, 1997; Burnell and Bryden, 1997).

The occurrence or nature of any population sub-division within the 'Australian' population is unknown. The delineation of a southeastern and southwestern Australian stock has been proposed (Brownell *et al.*, 1986), although this was biologically unfounded and appears to have been done primarily for management purposes. What it is that attracts right whales to particular areas on these coastlines is still not well understood. Fidelity to calving and feeding grounds has been observed in a range of mysticetes and is summarised well in Donovan (1986). Individual gray and right whale females are known to return repeatedly to specific coastal areas during winter to calve and rear their young; gray, humpback, bowhead (*Balaena mysticetus*) and North Atlantic right whales have been observed to return consistently to core feeding areas also (Darling, 1984; Donovan, 1986). Site fidelity can be displayed on a wide range of scales, from a small lagoon or aggregation area to whole ocean regions (10s-100,000s km^2), although the geographic level to which fidelity is displayed is difficult to quantify and thus rarely attempted.

This paper reports on several aspects of the reproductive biology, movements and site fidelity of right whales along the southern Australian coast. In particular, data are presented on: the reproductive capacity of the population; the age at which yearlings are weaned; medium- and long-range coastal movements; and the relative fidelity shown to the Head of Bight aggregation area by individual right whales.

METHODS

The majority of data collection was undertaken at the Head of the Great Australian Bight between 1991 and 1997. This site represents one of the largest and most consistent aggregation and calving areas for this species on the Australian coast, with around a third of all known calves born there. Between 1991 and 1997, more than 350 individual right whales were photographically identified at this site.

Although utilising the same naturally-occurring identifying features, the methodology of photo-identification of individual right whales used at the Head of the Bight differed from most previous studies (Payne *et al.*, 1983; Kraus *et al.*, 1986a; Bannister, 1990; Best, 1990a) in that all identification photography was carried out from shore-based positions. The sea-cliffs at the Head of the Bight aggregation area provide an excellent photographic platform up to 65m above sea level, with identification photography enhanced by the willingness of the whales to approach very close to shore at the base of these cliffs.

A benefit of the photographic methodology employed during this study (see Burnell and Bryden, 1997) was the very high resolution achieved, due to both the stability of the photographic platform and the use of super-telephoto lenses. In addition, individual whales were available for photography over longer time periods, due to the lack of any time restrictions imposed by the increased cost and logistical difficulties of aircraft- and vessel-based operations. This resulted in the successful collection of a range of individual specific markers for most of the whales identified, including the determination of the sex of many adults that were not accompanied by calves and of many of the calves themselves. Due to the reduced likelihood of achieving a positive resight based on photographs of the callosities alone, the use of all individual specific identification cues is critical when identifying calves, as noted by Kraus *et al.* (1986a). Possible matches detected from the callosity pattern were quickly and unquestionably confirmed if a direct match of the unique ventral blaze was also made.

Right whales show no dorsally obvious sexual dimorphism. Determination of the sex of males can only be determined through direct observation/photography of the ano-genital configuration and/or the penis itself, and for females through direct observation/photography of the ano-genital configuration or via the continued close accompaniment of a calf. The extended periods of observation and proximity of the whales meant that the determination of sex was possible for the majority of non-calf whales identified at the Head of the Bight. Although the use of behavioural cues can be, and has been used to infer the sex of individuals (eg. Payne and Dorsey, 1983), these were not used in this study as they often produced an incorrect classification.

All young-of-the-year were classified as 'calves' with the term being reserved for that age-class. A definitive maximum size, in terms of the relative length of one individual to another, was not used to assign 'calf' status. This was due to the large size range possible for southern right whale calves in their birth year (Best and Rüther, 1992); returning yearlings could be of similar size to the larger calves. The duration and frequency of observation produced numerous within-year resightings of most female-calf pairs allowing accurate designation of calves. Similarly, repetitive behavioural observations combined with morphological differences, particularly of the head, meant that large calves were very unlikely to be mistaken for returning yearlings during this study. Immature whales (based on relative length, girth and morphology of the head) were referred to as 'sub-adults' when their age was not known, or as yearlings, two-year-olds etc., when an individual had been identified in its birth year and was thus of known age.

Adult whales not accompanied by a calf were termed 'unaccompanied adults'. This status category contained males, non-calving females and animals of unknown gender; for most analyses all sub-adults and known age juveniles were also included. Females accompanied by calves were termed 'cows' with the combined unit usually referred to as a 'cow-calf pair'.

Reproduction

The inter-calf (reproductive) intervals of females were determined through longitudinal identification studies which recorded the years in which females were observed accompanied by calves and those in which they were not. The status of individual whales identified at the Head of the Bight was recorded on each sighting occasion, with the survey regime usually allowing many confirmations of a female's reproductive status in any given year. To determine the calving interval within the wider population, additional data were available from aerial photographs collected from the Western Australian coastline between 1979 and 1997 (Bannister, 1997) and from identification photographs and data collected off southeastern Australia between 1995 and 1997 (Burnell, 1997). Some additional sightings of females identified in the current study but made at the Head of the Bight aggregation area between 1984 and 1990 (Ling and Needham, 1985) were also included.

The calculated 'age at weaning' represents the age of the individual when it was first observed to be independent of the cow. The use of the date of first sighting of a neonatal calf as its birth date has a tendency to reduce the observed age at weaning, whereas the delay in sighting the independent yearling will tend to increase the observed age at weaning. Both these sightability biases are predicted to be small and they may effectively negate each other. The observed 'age at weaning', although possibly analogous to the 'duration of lactation', is a more accurate description of what has been documented in this study and is thus the preferred descriptor.

Coastal movements

Movements made by individual right whales around Australia's southern coastline are described and the implications of these movements for the migration and stock delineation of the Australian right whale population discussed. Australia's southern coastline represents an approximate great circle distance of 3,200km and a coastal distance of well over 5,000km, so movements along this coastline can potentially be similar in distance to the long-range oceanic movements described by Best *et al.* (1993). The distance between resightings made in different calendar years was calculated using the great circle route between the two points, due to the high probability of one or more long-distance, latitudinal migrations to the sub-Antarctic summer feeding grounds taking place between the two coastal sightings (Bannister *et al.*, 1999). Although the time period between the two sightings may have been less than 12 months, the sightings were made in different calendar years, and few if any right whales are sighted in Australian coastal waters during the austral summer (December-February). For convenience, these were termed 'between-year movements', although it is clear that they represent only a small proportion of the individual whale's actual movements between the two sightings.

Movements that occurred within a winter season are predicted to have been made in coastal waters, and the distance between within-year sightings (made in the same calendar year) was calculated using the shortest sea-route (great circle route avoiding land), and termed a 'within-year movement'. For these analyses, a distance of 200km was chosen as the minimum distance and resightings made less than 200km apart have not been included. This distance clearly separates such longer range movements from the short range meanderings and daily movements that whales can make within and around aggregation areas, and which rarely exceed 50km. The southern Western Australian coastline is referred to as the 'southwest' region; the South Australian coastline to the west of 135°E, or approximately Port Lincoln, and including the Head of the Bight aggregation area, is referred to as the 'south central' region; and the coastline east of 135°E to Sydney in New South Wales, and including Tasmania, as the 'southeast' region, see Fig. 1.

Determining fidelity

An attempt was made to determine the relative fidelity of individual right whales to the Head of the Bight aggregation area by comparing the number of sightings made within the aggregation area against the combined total number of sightings made at other locations on the Australian coastline. Individual whales were assumed to be displaying some level of fidelity to the Head of the Bight aggregation area when an individual whale has been seen there in at least two separate years, and if so, that the individual has been seen at the Head of the Bight on more occasions than the number of sightings at all other localities combined. For example, a whale seen three times at the Head of the Bight, once at Albany, Western Australia and once at Port Lincoln, South Australia was considered to be displaying some level of fidelity to the Head of the Bight, whereas a whale that has been seen twice at the Head of the Bight as well as at Albany and Esperance in Western Australia and Victor Harbor, South Australia was not considered to be showing any observable fidelity to the Head of the Bight aggregation area (see Fig. 1). Whales that have only ever been seen once at the Head of the Bight and nowhere else were not included as their relative fidelity was indeterminable.

RESULTS

Reproductive biology

Inter-calf interval at the Head of the Bight

Between 1991 and 1997, 47 individually identified females were recorded with calves at the aggregation area in two or more separate study years, providing a total of 57 inter-calf intervals for analysis.

Of the 57 inter-calf intervals recorded, two (3.5%) were of two years duration, 41 (72%) were of three years, eight (14%) were of four years, five (9%) were of five years and one (1.5%) was of six years, giving a mean interval of 3.33±0.10 years (±SE, $n = 57$), for the inter-calf intervals observed during this study. A mean inter-calf interval of 3.33 years equates to a calf production rate of 0.30 calves per mature female per year.

Inter-calf interval in the wider Australian population

The Head of the Bight aggregation area does not represent a closed population, a fact highlighted by the extent of interchange between coastal regions documented during this study.

The inclusion of data in the form of photographs and sighting details from other regions on the Australian coastline and from the Head of the Bight prior to 1991 allowed an assessment of the inter-calf interval in the wider Australian population. A total of 70 females for which two or more calvings were observed provided 117 inter-calf intervals for analysis.

With the inclusion of these additional data, the mean inter-calf interval observed increased to 3.64±0.13 years (±SE, $n = 117$). A mean inter-calf interval of 3.64 years equates to a calf production rate of 0.275 calves per mature female per year.

Early calf mortality, 'missed' calvings and two and five year inter-calf intervals

During this study, two females were observed and photographed whilst accompanied by a neonate, and then observed later in the same season without the calf. One of these females 'lost' her calf in two of the three years in which she was observed to calve at the aggregation area, providing data on a total of three neonatal mortalities.

In 1992, female 9216 was observed with a calf on 2 July and then sighted and photographed with the same calf on at least four separate days up to and including 16 September. She was next sighted on 27 September with no accompanying calf and then resighted subsequently on ten separate days up to 6 October, again with no calf. Following the death of her calf in 1992, female 9216 calved again at the aggregation area in 1994. In that year, when first observed on 30 June, she was accompanied by a neonate and then was subsequently sighted on at least six separate days up to and including 1 August accompanied by the calf. On 4 August she was observed alone, and then on at least 13 separate days up to and including 6 September was again observed without a calf. She calved again at the Head of Bight aggregation area in the first week of July 1996, another two year inter-calf interval. Although survey coverage in 1996 was less than in 1992 or 1994, observations were made of 9216 and calf over several days in early July and again on several occasions at the end of August at which time the calf appeared normal in all respects. These observations suggest that the death of a neonate within the first six weeks may have resulted in the female concerned adopting a two year interval prior to the next calving.

A third early calf mortality was observed at the Head of the Bight but it is unknown if the female concerned subsequently exhibited a two year interval. On 27 July 1993, female 9324 was seen alone and then on 10 August was sighted accompanied by a calf estimated to be less than 3 days old (based on size, colouration, presence of foetal skin folds etc.) with which she was observed and photographed over four separate days up to and including 16 August. This female was then seen and photographed over two separate days up to 20 August with no accompanying calf.

Five females recorded a five year inter-calf interval at the Head of the Bight during this study. However, in between these calvings, four of the five were sighted without calves at an interval of three years.

Maximum age at weaning

Between 1992 and 1995, 17 calves were resighted at the Head of the Bight aggregation area in the year following their birth there. An additional three calves born at the Head of the Bight were resighted as yearlings at other localities on the Australian coastline. Of these 20 yearlings, 13 were resighted alone or interacting with other whales but no sighting of the cow was made in that year, indicating they were already fully weaned at the time of resighting. The cows of another two yearlings were sighted at the aggregation area although never in the company (within

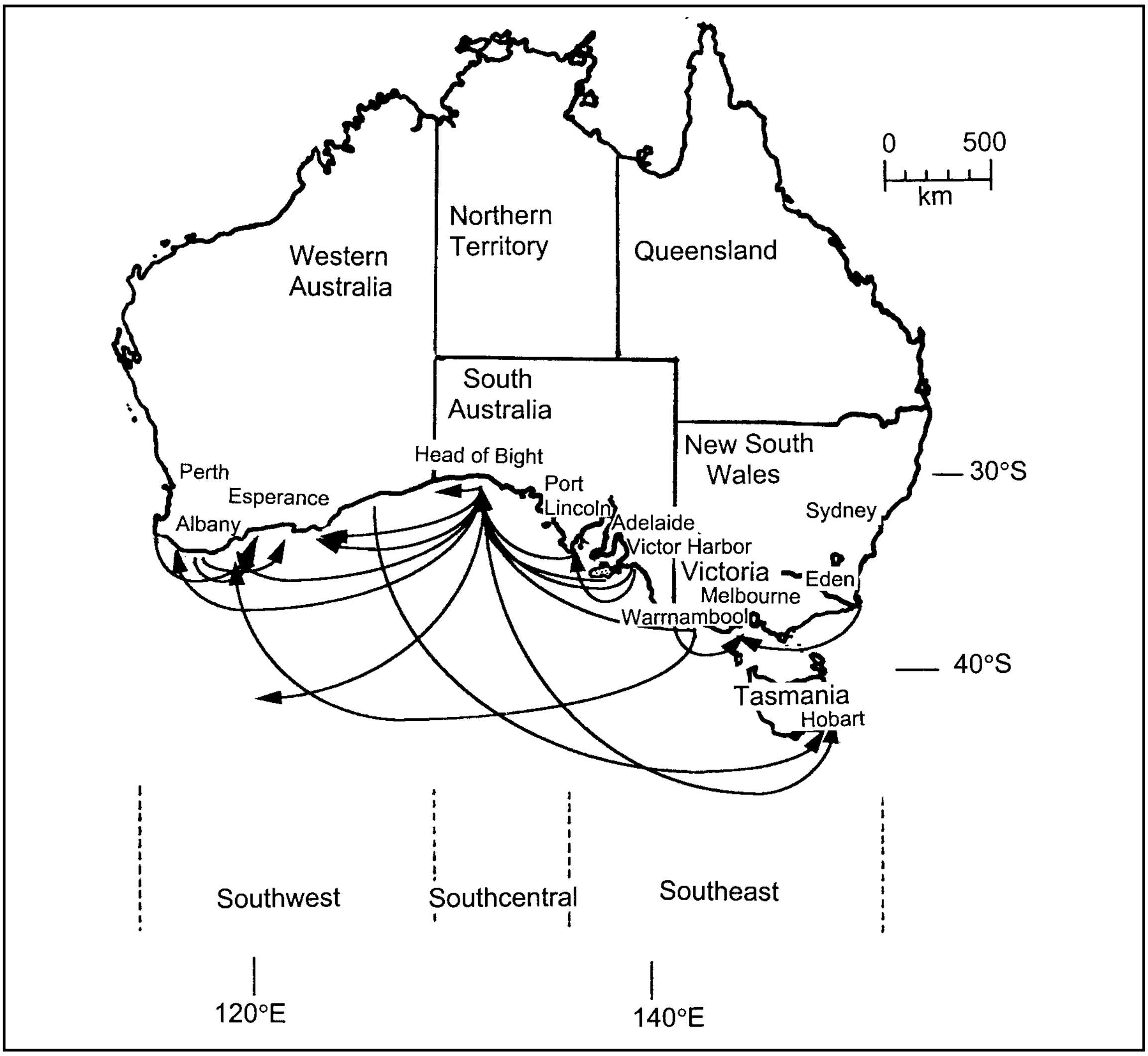

Fig. 1. Examples of movements made by individual right whales off southern Australia. Lines are representative only and are not intended to represent actual track. The positions of the 'southwest', 'southcentral' and 'southeast' zones are shown.

500m) of their yearling calf, suggesting that weaning was either taking place at the aggregation area or had occurred recently. Three of the remaining five returning yearlings were seen in the company of the cows initially and then subsequently were seen alone, indicating that some females do return to the aggregation area to wean their yearling calves. The final two yearlings were seen at the aggregation area with their cows (at ages of 344 and 334 days), although they were not subsequently seen alone, so it was not possible to determine where, or at what age, they were fully weaned.

Table 1 provides the sighting dates as both neonatal calves and independent yearlings for the 18 individuals, along with their calculated maximum age when observed to be fully weaned. The ages at which these yearlings were observed to be independent of the cow (fully weaned) ranged from 303 days to 419 days, with a mean of 364.6±7.8 days (±SE, *n* = 18) and median of 365.5 days, almost exactly 12 months.

Table 1

Sighting data for the 20 individuals identified as neonates at the Head of the Bight and resighted as yearlings the following season, including the age at which they were observed independent of the female (fully weaned).

ID cow	ID calf	Estimated birth date	Weaned by date	Age at which observed to be fully weaned (days)
9101	9125	11 Sep. 1991	16 Jul. 1992	309
9105	9129	31 Aug. 1991	3 Jul. 1992	307
9111	9135	27 Aug. 1991	23 Aug. 1992	362
9119	9143	21 Aug. 1991	26 Aug. 1992	371
9203	9236	4 Jul. 1992	2 Aug. 1993	394
9211	9244	22 Jul. 1992	13 Jul. 1993	356
9308	9377	16 Jul. 1993	13 Jul. 1994	362
9311	9380	14 Jul. 1993	23 Jun. 1994 (with cow)	>344*
9313	9382	27 Jul. 1993	13 Jul. 1994	351
9314	9383	25 Jul. 1993	24 Jun. 1994 (with cow)	>334*
9316	9385	9 Aug. 1993	1 Aug. 1994	357
9323	9392	24 Aug. 1993	23 Jun. 1994	303
9325	9394	3 Jul. 1993	31 Jul. 1994	393
9121	9395	17 Aug. 1993	2 Aug. 1994	350
9403	9462	27 Jun. 1994	15 Jul. 1995	383
9101	9471	23 Sep. 1994	27 Sep. 1995	369
9106	9474	21 Jul. 1994	26 Aug. 1995	401
9113	9478	27 Jun. 1994	20 Aug. 1995	419
9114	9479	29 Jun. 1994	8 Jul. 1995	374
9116	9480	24 Jul. 1994	30 Aug. 1995	402
			Mean (± SE) =	364.6 ± 7.8

* Values not included in calculation of the mean and median, because yearlings not sighted independently of cow.

Coastal movements

A total of 108 movements of greater than 200km were made by individual whales, 18 within a calendar year and 90 between years. For all of these movements combined, the mean distance travelled was 983±42 km (±SE, *n* = 108).

Due to the very different nature of movements made within and between years the two types of 'movements' are treated independently here.

Fig. 2 shows the frequency distributions of distance travelled and provides the mean distance of the two types of movements discussed here. Fig. 1 also shows representative examples of the movements of individual right whales detected off southern Australia during this study.

Appendix 1 contains two tables detailing the within- and between-year coastal movements recorded, and includes the date and location of the relevant sightings and the sex and status in 1995 of the individual if known.

Within-year movements

The 18 within-year movements ranged in length from 211-1,490km, and were made over time periods of 3-59 days. The mean within-year movement was 730±84km, and made over 34±4 days (±SE, *n* = 18). The longest within-year movement was made by a female (9228) that travelled from the Head of the Bight (31°28'S, 131°08'E) southwest to Point D'Entrecasteaux, Western Australia (34°50'S, 116°00'E), a distance of 1,490km in 41 days or less, at a minimum average travel speed of 1.51km/h. This small female was sighted in three consecutive study years at the Head of the Bight aggregation area, although never with a calf, and is likely to be immature. On 22 July 1994, a single adult (9452) was photographed at Portland, Victoria (38°20'S, 141°37'E) and was identified 49 days later at the Head of the Bight, on 9 September 1994, a distance of 1,297km northwest, where it remained for the next three

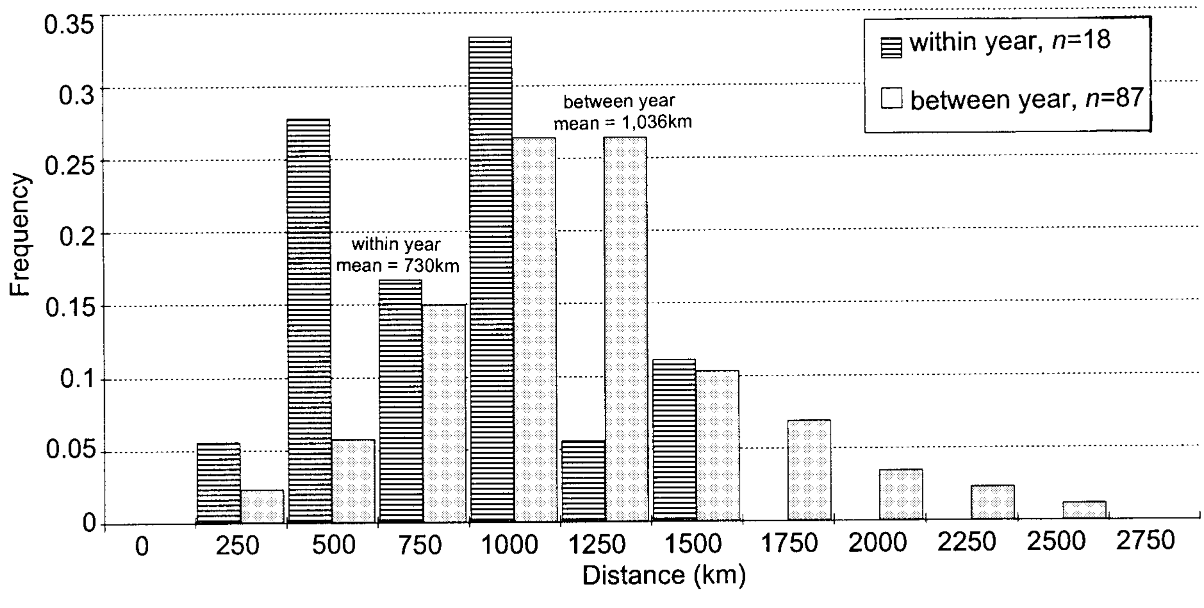

Fig. 2. Frequency distribution of the 18 within-year and 87 between-year (for which distance known) movements made by individual right whales during this study.

weeks. The minimum average travel speed was 1.10km/h. The fastest within-year movement recorded, with a minimum average speed of 3.66km/h, was made by a sub-adult (95N1) that travelled 351km east from Nelson, Victoria (38°06'S, 141°00'E) to Anglesea, Victoria (38°25'S, 144°12'E) in less than 4 days.

All of the movements described above were made by unaccompanied whales. Only one record of a within-year movement by a female accompanied by a calf was obtained. Female 9409 and calf, sighted at Port Lincoln, South Australia (34°40'S, 135°53'E) on 3 August 1994, was observed on 3 September at the Head of the Bight, 704km away, where they remained for five weeks.

Three of the 18 within-year movements (16.7%) were made in an easterly direction, two of them off the southern Western Australian coastline and one off the Victorian coast. All three were between 200km and 400km, being at the lower end of the range of within-year movements. Within-year movements made to the east were significantly shorter than those made to the west (Kruskall-Wallis ANOVA, $H_1 = 4.8$, $p < 0.05$). Also, as might be expected, there was a significant correlation between the distance travelled and the time period separating the two sightings (Spearman ranked correlation, $R = 0.627$, $p < 0.01$).

Between-year movements

The 90 between-year movements were made by 63 individual whales, and ranged from 210km-2,287km and over time periods between one and 18 years.

Due to three movements being from unknown localities on the Western Australian coastline, only 87 between-year movements are available for distance analysis. The mean between-year movement was 1,036±45km (±SE, $n = 87$), significantly greater than the mean within-year movement, (independent t-test, $t_{103} = -2.87$, $p < 0.05$), see Fig. 2.

The mean time interval separating between-year sightings was 3.3±0.3 years (±SE, $n = 90$). The longest single movement between consecutive sightings was between Point Culver, Western Australia (33°00'S, 124°45'E) and Swansea, Tasmania (42°07'S, 148°05'E), a great circle distance of 2,287km. These sightings were made in consecutive years. This same individual (94FN1) recorded the longest series of combined movements, travelling a minimum of 4,746km over a six-year period.

A female (9308), that calved at the Head of the Bight in 1993, and was resighted there in 1994, was photographed 1,505km southwest of there at 42°02'S, 120°30'E, on 14 December 1995. Observations made during the December sighting recorded dense swarms of crustacea in the region and several of the right whales sighted were observed feeding and defecating (see Bannister *et al.*, 1999).

Fifty of the 90 (55.6%) between-year movements were made by females, 24 (26.7%) by males and 16 (17.7%) by whales of unknown sex. There were no significant differences between the length, time or direction of the between-year movements made by these different sex-classes.

The 50 between-year movements of females were made by 35 individual whales, of which 26 were observed to be accompanied by calves on at least one occasion and thus sexually mature. Thirteen of these mature females have been observed to alter calving locations between subsequent births, with one individual (9205) altering calving location on two separate occasions. The longest distance between consecutive calving events was recorded for female 93F1, which calved and remained resident at Hassell Beach, Western Australia (34°50'S, 118°25'E) in 1990 and then in 1993 calved and remained resident at Fowlers Bay, South Australia, (31°57'S, 132°35'E), 1,353km to the northeast. This whale was not sighted in the intervening years.

Fidelity to the Head of the Bight aggregation area

Tables 2 and 3 summarise the number of times each of 61 calving females and 61 unaccompanied adults have been sighted at the Head of the Bight aggregation area along with the number of times they have been sighted at other localities on the Australian coast.

Table 2

The number of times each of 61 calving females have been sighted at the Head of the Bight aggregation area along with the number of times they have been sighted at other localities on the Australian coast. **Bold** values represent the number of individuals considered to be displaying some level of fidelity to the Head of the Bight (HOB).

Number of years sighted at HOB	Sighted nowhere else	Sighted 1x elsewhere	Sighted 2x elsewhere	Sighted 3x elsewhere
1	Not used	3	1	0
2	**28**	**2**	0	0
3	**10**	**6**	**3**	1
4	**3**	**2**	0	0
5	**1**	**1**	0	0
Total	42 (**42**)	14 (**11**)	4 (**3**)	1 (0)

Table 3

Sighting history of the 61 unaccompanied adults (14 females, 19 males, 20 calves and 8 of unknown sex) that satisfied the criteria for fidelity analysis. **Bold** values represent the number of individuals considered to be displaying some level of fidelity to the Head of the Bight (HOB).

Number of years sighted at HOB	Sighted nowhere else	Sighted 1x elsewhere	Sighted 2x elsewhere	Sighted 3x elsewhere
1	Not used	8	3	1
2	**19**	**8**	2	0
3	**8**	**5**	**1**	0
4	**3**	0	**2**	0
5	**1**	0	0	0
By sex/status	Sighted nowhere else	Sighted 1x elsewhere	Sighted 2x elsewhere	Sighted 3x elsewhere
Males, *n*=19	**8**	8 (**4**)	3 (**1**)	0
Non-calving females, *n*=14	**5**	5 (**5**)	3 (**2**)	1
Calves, *n*=20	**14**	6 (**3**)	0	0
Unsexed, *n*=8	**4**	2 (**1**)	2	0
Total	31 (**31**)	21 (**13**)	8 (**3**)	1 (**0**)

Of the 85 females which calved at the Head of the Bight aggregation area between 1991 and 1995, 61 have been included in this analysis of relative fidelity. Twenty-four females were excluded because they have only been seen once at the Head of the Bight aggregation area and nowhere else, making their relative fidelity indeterminable. Of these 61 females, 56 (92%) displayed some level of fidelity to the Head of the Bight aggregation area as defined by the criteria given in the methods.

Coincidentally, there also exist 61 identified unaccompanied whales in the Head of the Bight catalogue that have sightings histories suitable for this analysis. Of these, 46 (75%) show some level of fidelity to the Head of the Bight aggregation area. This is a significantly lower proportion than for the calving females (Yates corrected $\chi^2 = 9.29$, $p < 0.005$).

The unaccompanied whale category was further divided into known males, known females that have never been observed to calve at the Head of the Bight aggregation area, calves identified at the Head of the Bight and subsequently resighted, and whales of unknown sex.

Seventeen of the 20 calves (85%) displayed some level of fidelity to their birth site and 12 of the 14 (86%) females never observed to calve at the Head of the Bight showed fidelity to the aggregation area. Neither of these groups differed significantly in relative fidelity from females that had calved at the aggregation area (Yates corrected $\chi^2 = 1.77, 1.25, p > 0.25, 0.18$, respectively). However, of the 19 known males meeting the sighting criteria, only 13 (68%) displayed fidelity to the Head of the Bight, significantly fewer than for calving females, non-calving females or juveniles (Yates corrected $\chi^2 = 16.5, 8.2, 7.1$ respectively, all $p < 0.01$). The fidelity of whales of unknown sex to the Head of the Bight (63%) was not significantly different from that of known males (Yates corrected $\chi^2 = 0.35$, $p > 0.55$).

DISCUSSION

Reproductive biology

Klumov (1962) estimated a duration of gestation of 11-11.5 months for northern right whales in the North Pacific, back-calculated from estimates of the age of two immature whales at the time of their death and the growth rates of two foetuses. Donnelly (1969) estimated a gestation period of 10 months for southern right whales, based on behavioural observations of peaks in ‘courtship’ and calving off South Africa.

However, Best (1994) using a regression of foetal length measurements obtained from whaling data against their date of death, and an extrapolated estimate of the mean date of calving off South Africa, proposed a gestation period lasting between 357 and 396 days for southern right whales, and predicted that at least some conceptions occur within coastal waters. Burnell and Bryden (1997) suggest a gestation period in the order of 355 days at the Head of the Bight, Australia, based on behavioural observations of mating activity and the observed mean date of calving within that population. Both estimates are suggestive of an approximate 12 month gestation period for this species.

Although right whales off Australia and South Africa calve in the austral winter, the timing of calving may differ between these populations. Burnell and Bryden (1997) calculated a mean date of calving of 16 July at the Head of the Bight aggregation area, considerably earlier than Best’s (1994) estimate of 24 August at De Hoop, South Africa.

The only previous estimate of the mean calving interval within the Australian population of 3.14 years±0.84 years (±2SE, $n = 21$) is from aerial surveys of the Western Australian coastline (Bannister, 1990). However, an error exists in the presentation of these data with the actual interval being 3.48 years±0.52 years (±2SE, $n = 21$).

The mean calving intervals recorded during this study of 3.33±0.10 years (±SE, $n = 57$) at the Head of the Bight aggregation area and 3.64±0.13 years (±SE, $n = 117$) in the wider Australian population, are comparable with those recorded for other populations.

Best (1990a) reports an inter-calf interval, adjusted for biases between survey areas and against longer intervals, of 3.18 years (SD = 0.09 years, $n = 139$) off South Africa. Best *et al.* (2001) updated this estimate to 3.12 years (95%CI 3.07, 3.17). Cooke *et al.*’s (2001) finding of a mean calving interval of 3.35 years (SE = 0.05 years) at Peninsula Valdes, and Knowlton *et al.*’s (1994) estimate of the mean calving interval in the North Atlantic population of 3.67 years (SE = 0.11 years, $n = 86$) are both comparable with the 3.64±0.13 years (±SE, $n = 117$) recorded in the wider Australian population. Kraus *et al.* (2001) reported, however, that the calving interval for the North Atlantic has increased to over 5 years for the 1993-98 period.

It is clear that three-year inter-calf intervals are the most common for right whales off Australia with 72% of observed intervals at the Head of the Bight and 68% of the intervals in the wider Australian population being of three years duration. However, the proportion of four year inter-calf intervals observed at the Head of the Bight (14%) and in the wider population (15%) suggests that a noteworthy proportion of females do routinely calve on a four year cycle.

It is likely that most, if not all, of the six year inter-calf intervals recorded in this study are a result of a failure to detect an intervening calving at three years. Similarly, inter-calf intervals greater than six years are likely to be artefacts caused by a failure to observe one or more intervening calvings. If intervals of six or more years are excluded from the calculations, the mean inter-calf interval at the Head of the Bight becomes 3.28±0.09 years (±SE, $n = 56$) identical to the figure in the wider population, 3.28±0.06 years (±SE, $n = 107$).

The two- and five-year inter-calf intervals observed in this species are possibly anomalous, resulting from the abortion or early loss of a calf. Although infrequent, inter-calf intervals of two years have been observed off South Africa (Best, 1990a), Argentina (Payne *et al.*, 1990), Western Australia (Bannister, 1990) and the northeastern United States (Kraus *et al.*, 1986b; Knowlton *et al.*, 1994). Data presented in this study are suggestive of right whale calves being weaned close to 12 months of age meaning a two year inter-calf interval would require almost immediate post-lactation ovulation by the female if gestation is of the order of 12 months as discussed above.

It seems likely that such ‘early’ ovulation is only likely to occur in right whales following the premature loss of the previous calf, and the subsequent lessening of the physiological depletion of the female. Humpback whales appear to begin oestrous cycles immediately after the premature loss of a calf (Chittleborough, 1958), and Jones (1990) suggests that post-partum ovulation in the gray whale is only likely to occur after the abortion or early loss of a calf, allowing births in successive years rather than the normal two-year interval of that species.

If this is the case with female right whales, the frequency of two-year calving intervals in the population should provide some indication of the level of early neonatal mortality. However, the detection of such two-year intervals is severely hindered by the limited time that the female is available to be recorded in the company of a calf prior to its death, with monthly aerial survey regimes being unlikely to record these calvings. Further, stillborn or miscarried calves would be completely undetectable as would any additional mortality on the calves’ first southward migration. Under such conditions, five year inter-calf intervals may be indicative of the early loss or abortion of the intervening calf at three years going undetected, followed by a two-year interval. Cooke *et al.* (2001) also postulate this as the most likely explanation for the relatively large proportion of five year calving intervals in Argentina. It is relatively unusual to sight females at the Head of the Bight in non-calving years and it is noteworthy that of the five females which recorded five-year intervals at the Head of the Bight, four were sighted after three years, but were not recorded with calves. The likelihood seems strong that these females had failed calvings at three years which were not observed, before successfully calving at five years.

If this were the case, it could be expected that the frequency of two- and five-year inter-calf intervals combined may be more representative of the level of early infant mortality within the population. When combined, two- and five-year inter-calf intervals represented 9% of all intervals observed in the wider Australian population during this study. It should be noted that any such analysis will be biased by the apparent presence in the population of a small proportion of females whose reproductive cycle is four years. Such females may shorten their calving interval upon the early loss of a calf by reverting to the 'normal' three-year interval.

Knowlton *et al.* (1994) provide data on the frequency of occurrence of various calving intervals in the North Atlantic right whale population. The incidence of five-year inter-calf intervals in this population (16.3%) is exceeded only by three-year intervals and is substantially higher than the frequency of five-year intervals detected in this study (6.8%), or off South Africa (4.8%) by Best (1990a). Further, the combined incidence of two- and five-year inter-calf intervals in the western North Atlantic of 17.5% is almost twice as high as that recorded in this study (9.4%).

The failure of the North Atlantic right whale population to recover from exploitation has been cause for some concern (e.g. Knowlton *et al.*, 1994; IWC, 2001a). The high incidence of five-year inter-calf intervals observed within the North Atlantic population may be indicative of a higher proportion of unsuccessful calvings and the reduced fecundity of that population (National Marine Fisheries Service, 2000).

The mean age at which weaning had occurred for the 18 individuals recorded during this study is based on more substantial data than any previous published estimates for the species. The observation that some females will return with their year-old calves to their calving site supports similar observations made by Thomas and Taber (1984) at Peninsula Valdes. However, it is clear that in the present study this behaviour is perhaps the exception rather than the rule. Only a small number of females were resighted at the Head of Bight aggregation area in a weaning year, despite the substantial survey coverage and photo-identification effort that were achieved in this study. In addition, the resighting of three yearlings off the Australian coast, a considerable distance from their birth site, may mean that these individuals were left to navigate their return journey from the feeding grounds alone, or that their cows 'deposited' them at the coast at these other areas. Either way, it is clear that some juveniles become familiar with quite widely separated locations on the Australian coastline as early in life as their second winter.

Coastal movement

Despite the apparent over-representation of females in the coastal movements documented (53% *versus* 24%) it is unlikely that females make significantly more coastal movements than males. This discrepancy probably reflects the greater chance of photographically identifying females, and the greater ease with which identified individuals can be sexed as female. This identification bias is due to the longer residence periods within coastal aggregation areas of calving females than those of unaccompanied whales (Burnell and Bryden, 1997), with an associated increased likelihood of them being photographed, combined with the additional benefit of being able to determine the sex of a mature female on the basis of its continued accompaniment by a neonatal calf as well as via direct observation of the ano-genital configuration. In support of this explanation, the observed representations of the sex-classes in the movements recorded are not significantly different from the proportion at which each sex-class is represented in the Head of the Bight identification catalogue; viz. females 55%, males 21% and unknown sex 24%, ($\chi^2 = 3.35$, $p > 0.15$).

Due to differences in the effort applied to the collection of identifications within different regions and in different years, it is hard to draw any conclusions about trends or changes in coastal distribution from these data. Of the 14 changes of calving location made by the 13 females, eight were made in an easterly direction and six to the west. These data are more interesting in light of the strong fidelity to calving locations displayed by the species (Best, 1981; 1990b; Bannister, 1990; Payne *et al.*, 1990). It is clear that in this population some females do alter their calving location between subsequent calves, although the reasons are not known. Rarely, females show a lack of intra-year fidelity to a particular locality within a calving year, being observed to move considerable distances around the coastline with their calves during a single winter-spring season, for example individual 9409.

Movements of individually identified whales have been used in several areas to infer stock identity (e.g. Kraus *et al.*, 1986b; Donovan, 1991; IWC, 2001b). A total of 63 movements between the southwest region and the south central region have been documented in the present study ($n = 7$ within-years; $n = 56$ between-years). Given this degree of interchange, the likelihood of any meaningful population division between these regions appears remote. However, considerable fidelity was shown by mature females to specific aggregation sites during their calving years.

A further 25 movements between the southeastern Australian region and the south central region, and seven movements between the southeast region and southwest Australian regions have been documented. Although the number of movements detected to and from the southeast Australian region is substantially lower than for the other regions, it is worthy of note. The reduced level of interchange so far detected with the southeast region is more likely to be a factor of the limited research effort within that region compared with the other two regions than of any real population sub-division. This interpretation is supported by the fact that a concerted effort to obtain photo-identifications from southeastern Australia in 1995 nearly doubled the number of movements to and from that region in a single season (Burnell and McKenna, 1996).

A significant difference between the proportion of movements made in each direction existed between within- and between-year movements (Kruskall-Wallis ANOVA, $H = 16.9$, $p < 0.001$). Twenty-four percent of the between-year movements were made in a westerly direction, while 95% of the within-year movements were made in that direction. A migration pattern off southeastern Australia involving coastal movement being predominantly westerly was proposed as early as 1842 in written accounts of the 'black' whale fishery at that time, and was presumably based on the temporal and spatial distribution of coastal catches of right whales (Newland, 1921; Cumpston, 1970). Between-year resightings in coastal waters are likely to have been separated by an oceanic, latitudinal migration to the feeding grounds, meaning the only true coastal movements are likely made within years.

The results of this study, based on the movements of individually-identified whales, suggest that the great majority (95% in this study) of within-year movement on Australia's southern coastline takes place in a westerly direction. When combined with the high incidence of between-year movements that were made to the east (76%), the possibility of an almost circular, anti-clockwise migration for this species to the south of Australia is suggested. Fig. 3 shows the predicted seasonal migration of right whales to the south of Australia.

The movement patterns of right whales off the east coast of Australia, and in the Tasman Sea, are not known and may not relate to those presented here. However, the limited data available suggest that right whales using this region may follow a similar movement pattern to that proposed for the population as a whole. The only within-year movement that has been detected to date involving a whale sighted off the New South Wales coastline was made to the southwest, through Bass Strait to western Victoria (Burnell and McKenna, 1996). Similarly, a record exists of a within-year movement between the east coast of Tasmania and Western Victoria, presumably made in a northwesterly direction through Bass Strait (Burnell, 1997).

Mate *et al.* (1997), using satellite telemetry, showed that North Atlantic right whales can cover large distances (> 3,000km) visiting several different locations in between consecutive sightings at surveyed aggregation areas such as the Bay of Fundy. It is clear that many of the movements detected in this study would have involved travel over much longer distances than those reported and that unaccompanied whales that are consecutively sighted at the same location within a season may have left and returned to those sites between sightings.

However, these records of substantial amounts of coastal movement strongly suggest that the right whales utilising the Australian coastline represent a single stock, within which individuals may show strong fidelity to particular regions. Further, they emphasise the fact that regional conservation initiatives, such as the recent declaration of the Head of the Bight whale sanctuary and Marine Park, are of considerable importance to the entire Australian population.

Fidelity to the Head of Bight aggregation area

Despite being seen intermittently at widely separated locations, some individuals show strong fidelity to specific coastal aggregation areas, in particular mature females in their calving years. Fidelity to a geographic area, in the context being proposed, does in no way imply the exclusive use of that area by an individual whale. The large scale whale migrations, and the distribution of their prey, imply that the range of an individual right whale will be vast. However, the

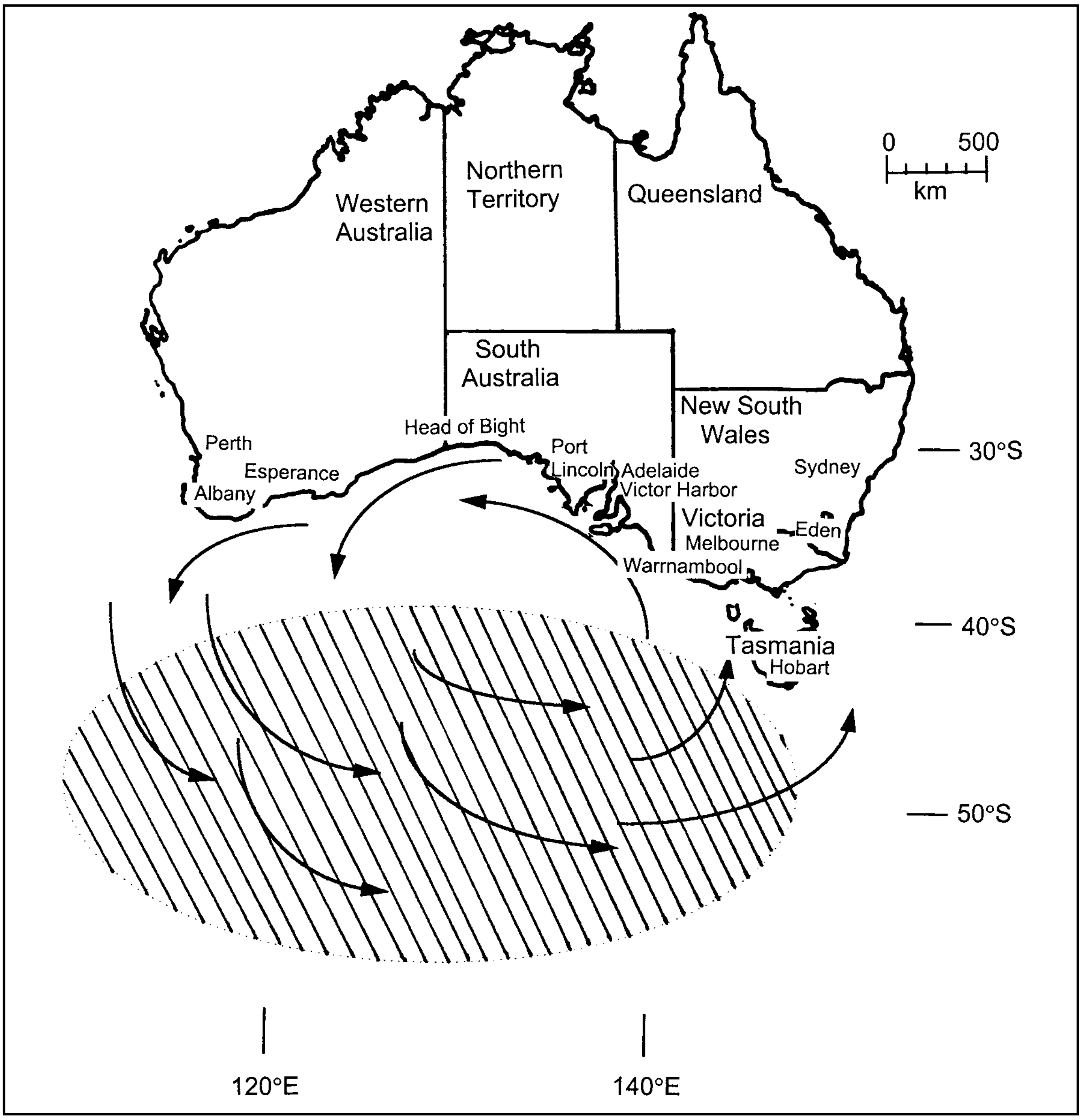

Fig. 3. The predicted seasonal migration of right whales to the south of the Australian continent, broadly based on movements of identified individual right whales. Hatched area likely feeding grounds.

consistent and repetitive (albeit intermittent) use of specific areas, often for a specific purpose such as breeding or feeding, can be considered a level of fidelity (e.g. Donovan, 1986). Whilst breeding females have been recorded returning repetitively to calve at locations on the coastlines of Argentina, South Africa and Western Australia (Payne, 1986; Bannister, 1990; Best, 1990a), almost nothing is known of the fidelity of non-calving whales to these coastal regions or of the geographic scale on which fidelity is displayed.

It was impossible to quantify the effort expended in the collection of photo-identification data used in this analysis of fidelity, meaning that comparisons between different regions and different years will be unavoidably biased and were therefore not attempted. However, a comparison between the relative fidelity of different age, sex and reproductive classes to the Head of the Bight is both meaningful and achievable since any bias between areas or years that does exist can be expected to impact relatively equally across these various classes. If a bias favouring detection of a particular age or sex class does exist, it would tend to act against the sighting of unaccompanied whales at locations other than the Head of the Bight, due to the infrequent survey regimes in those areas and the shorter coastal residence of unaccompanied whales (Bannister, 1997; Burnell and Bryden, 1997). Such a bias would have the effect of exaggerating the relative fidelity of unaccompanied whales to the Head of the Bight, thereby acting to reduce the differences in relative fidelity detected in this analysis.

Non-calving (unaccompanied) whales showed a significantly lower relative fidelity to the Head of the Bight than did mature females known to have calved at the site (Yates corrected $\chi^2 = 9.29$, $p < 0.005$). Further, males showed significantly lower relative fidelity to the Head of the Bight aggregation area than did females (both calving and non-calving) or juveniles. These data reinforce the possibility that males are indeed more transient in coastal waters, visiting a range of different localities and spending less time in particular aggregation areas. The predicted polygamous (in essence it is both polyandrous and polygynous) mating strategy (Brownell and Ralls, 1986; pers. obs.) and the documented fidelity of mature females to calving localities (possibly leading to matrilineal ‘sub-populations’) supports such a scenario, whereby the more transient males may provide the dispersal and genetic ‘mixing’ throughout the wider population. The very low fidelity of unsexed whales to the Head of the Bight is probably due to this group being predominantly male. This is suspected to be due to the increased difficulty in determining the gender of males and because the majority of gender determination during this study was achieved at the Head of the Bight, meaning whales showing the least fidelity to that site could be expected to have the least chance of having their gender determined.

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(Appendix 1 on following page)

Appendix 1

TABLES DETAILING THE WITHIN- AND BETWEEN-YEAR COASTAL MOVEMENTS RECORDED, INCLUDING DATE AND LOCATION OF RELEVANT SIGHTINGS AND THE SEX AND STATUS OF INDIVIDUALS IN 1995, IF KNOWN

Table 1

The 18 within-year movements of individual right whales recorded during this study. Key: A - Unaccompanied adult; C/Ca - Cow/calf pair; HOB - Head of Bight; WA - Western Australia; SA - South Australia; TAS - Tasmania; VIC - Victoria; NSW - New South Wales; W - West; E - East.

ID No.	Sex	Sighting locality 1, including date, photo number and status	Sighting locality 2, including date, photo number and status	Distance (km)	Days apart	Direction
9143	?	Victor Harbor, SA, 31 Jul. 1992, A	HOB, SA. 26 Aug. 1992, A	950	26	W
9203	F	Albany, WA. 22 Jul. 1985, ?, A	Stokes Inlet, WA. 2 Sep. 1985, ?, A	326	42	E
9228	F	HOB, SA 27 Aug. 1994, A	Pt D'Entrecasteaux, WA. 7 Oct. 1994, 1 8, A	1,490	41	W
9321	F	HOB, SA. 27 Sep. 1993, C/Ca	Eucla, WA. 30 Sep. 1993, C/Ca	211	3	W
9325	F	Mississippi Bay, WA. 17 Sep. 1983, ?, A	Cape Barren, WA. 30 Sep. 1983, 3-6 2a, A	280	13	E
9357	F	Kangaroo Island, SA. 16 Jun. 1993, SAM, A	HOB, SA. 30 Jul. 1993, A	788	44	W
9394	M	HOB, SA. 11 Aug. 1994, A	Yokinup Bay, WA. 29 Sep. 1994, A	840	49	W
9409	F	Port Lincoln, SA. 3 Aug. 1994, C/Ca	HOB, SA. 3 Sep. 1994, C/Ca	704	31	W
9420	M	Cape Barren, WA. 16 Aug. 1985, A	Augusta, WA. 1 Sep. 1985, A	495	16	W
9423	?	HOB, SA. 16 Jul. 1994, A	Rossiter Bay, WA. 8 Aug. 1994, R4 8, A	851	23	W
9425	?	HOB, SA. 18 Jul. 1994, A	Yokinup Bay, WA. 6 Sep. 1994, 10 3, A	840	59	W
9432	F	HOB, SA. 31 Jul. 1994, A	Yokinup Bay, WA. 25 Sep. 1994, A	840	56	W
9452	?	Portland, VIC. 22 Jul. 1994, A	HOB, SA. 18 Sep. 1994, A	1,297	58	W
9532	?	HOB, SA. 14 Jul. 1995, A	Bremer Bay, WA. 11 Sep. 1995, 4 10, A	1,148	59	W
95FN3	?	Nelson, VIC. 25 May 1995, A	Anglesea, VIC. 29 May 1995, A	351	4	E
95FN4	?	Eden, NSW. 28 Aug. 1995, Butt, A	Apollo Bay, VIC. 23 Sep. 1995, A	689	26	W
95FN5	?	Boston Bay, SA. 15 Aug. 1995, A	HOB, SA. 12 Sep. 1995, 25 1, A	704	28	W
95FN6	?	The Bluff, Victor Harbor, SA. 20 Jul. 1995, A	Boston Bay, SA. 15 Aug. 1995, A	327	26	W
			Mean (*n* = 18)	729.5	33.56	

Table 2

The 90 between-year movements made by individual right whales during this study. Key: A - Unaccompanied adult; C/Ca - Cow/calf pair; HOB - Head of Bight; WA - Western Australia; SA - South Australia; TAS - Tasmania; VIC - Victoria; NSW - New South Wales; W - West; E - East.

ID No.	Sex	Sighting locality 1, including date, photo number and status	Sighting locality 2, including date, photo number and status	Distance (km)	Years apart	Direction
9104	F	HOB, SA, 1988, C/Ca	Augusta, WA, 1990, ?	1,529	2	W
9104	F	Augusta, WA, 1990, ?	HOB, SA, 10 Oct. 1991, C/Ca	1,529	1	E
9105	F	Dillon Bay, WA, 16 Aug. 1986, 9-12 11, A	HOB, SA, Aug. 1988, DJN 88/7/9, C/Ca	1,149	2	E
9115	F	Pt Anne, WA, 6 Aug. 1983, 1-3 10, A	HOB, SA, 27 Sep. 1991, C/Ca	1,125	8	E
9115	F	HOB, SA, 27 Sep. 1991, C/Ca	Yokinup Bay, WA, 6 Sep. 1994, 11 3, C/Ca	808	3	W
9116	F	Kangaroo Island, SA, 1986, DJN, ?	HOB, SA, 26 Aug. 1991, C/Ca	780	5	W
91b	F	Cape Riche, WA, 1986, ?	HOB, SA, 21 Aug. 1991, C/Ca	1,207	5	E
9121	F	Augusta, WA, 15 Aug. 1985, 1-3, A	Pt Anne, WA, 2 Sep. 1988, 1-5 4, C/Ca	427	3	E
9121	F	Pt Anne, WA, 2 Sep. 1988, 1-5 4, C/Ca	HOB, SA, 1 Sep. 1991, A	1,103	3	E
9129	F	HOB, SA, 22 Jul. 1992, A	Albany, WA, 5 Sep. 1994,3 13, 4 8, A	1,294	2	W
9129	F	Albany, WA, 5 Sep. 1994,3 13, 4 8, A	HOB, SA, 10 Sep. 1995, A	1,294	1	E
9135	M	HOB, SA, 19 Jul. 1994, A	Tagon Bay, WA, 3 Aug. 1995, 10 5-7, A	810	1	W
9201	F	Pt Lincoln, SA, 1976, DJN, A	Pt Charles, WA, 24 Aug. 1984, 1 12, A	1,478	8	W
9201	F	Pt Charles, WA, 28 Sep. 1986, 5 3b, C/Ca	HOB, SA, 1989, DJN, C/Ca	1,103	3	E
9203	F	Albany, WA, 22 Jul. 1985, 1-2 3, ?	HOB, SA, 8 Jul. 1992, C/Ca	1,294	7	E
9205	F	?, WA, 1980, Sep 80 b 13-14	HOB, SA, 1986, DJN	?	6	E
9205	F	HOB, SA, 8 Sep. 1992, C/Ca	Israelite Bay, WA, 3 Aug. 1995, 12 1,C/Ca	717	3	E
9206	F	?, WA, 1983, ?	HOB, SA, 1984, ?	?	1	E
9209	F	Sleaford Bay, SA, 1979, DJN, ?	HOB, SA, 1986, DJN, ?	571	7	W
9210	F	HOB, SA, 1989, DJN, ?	Yokinup Bay, WA, 16 Aug. 1990, 6 12, A	808	1	W
9210	F	Yokinup Bay, WA, 16 Aug. 1990, 6 12, A	HOB, SA, 27 Aug. 1992, C/Ca	808	2	E
9220	F	Pt Lincoln, SA, 1970, DJN, ?	HOB, SA, 1988, DJN, A	567	18	W
9222	?	Hassel Beach, WA, 28 Sep. 1990, 3 13, A	HOB, SA, 7 Jul. 1992, A	1,241	2	E
9222	?	HOB, SA, 7 Jul. 1992, A	Trigelow Beach, WA, 6 Sep. 1994, 6 9, A	1,103	2	W
9227	?	HOB, SA, 26 Aug. 1992, A	Eden, NSW, 1 Sep. 1994, Butt, A	1,834	2	E
9236	M	HOB, SA, 27 Sep. 1992, Ca	Eden, NSW, 2 Aug. 1993, Butt, A	1,834	1	E
9302	F	Pt Charles, WA, 1 Oct. 1985, 10 8, C/Ca	HOB, SA, 25 Jun. 1993, C/Ca	1,103	8	E
9308	F	HOB, SA, 24 Jun. 1994, C/Y	42°02'S, 120°30'E. 14 Dec. 1995, JLB, A	1,505	1.5	SW
9310	F	Eucla, WA, 13 Aug. 1984, 1-2 12, C/Ca	HOB, SA, 1990, DJN	211	6	E
9314	F	Israelite Bay, WA, 7 Jul. 1990, 4 5-6, A	HOB, SA, 3 Sep. 1993, C/Ca	717	3	E
9316	F	Hopetoun, WA, 9 Sep. 1987, Y 4, A	HOB, SA, 23 Aug. 1993, C/Ca	1,073	6	E
9316	F	HOB, SA, 11 Jul. 1994, C/Y	Margaret Cove, WA, 3 Aug. 1995, 8 14-15, A	995	1	W
9321	F	Twilight Cove, WA, 17 Sep. 1989, JLB 3 36, ?	HOB, SA, 11 Aug. 1993, C/Ca	489	4	E
9325	F	Pt Charles, WA, 7 Aug. 1987, 5-16 2 3b, A	HOB, SA, 1989, SRB, ?	1,103	2	E
9330	F	HOB, SA, 27 Jul. 1993, A	Twilight Cove, WA, 11 Sep. 1995, 18 4, C/Ca	489	2	W
9331	M	HOB, SA, 12 Aug. 1994, A	Wylie Scarp, WA, 11 Sep. 1995, 14 4, A	540	1	W
9335	?	Israelite Bay, WA, 15 Aug. 1991, 5 7&11-12, A	HOB, SA, 4 Jul. 1993, A	717	2	E
9339	F	Tagon Bay, WA, 2 Sep. 1988, 1-11 11, A	HOB, SA, 11 Jul. 1993, A	810	5	E
93FB1	F	Hassel Beach, WA, 22 Oct. 1990, 1 10, C/Ca	Fowlers Bay, SA, 18 Aug. 1993, C/Ca	1,353	3	E
9341	M	Pt Charles, WA, 8 Aug. 1987, 4-8 10, A	Augusta, WA, 15 Aug. 1990, 1 7, A	427	3	W
9341	M	Augusta, WA, 15 Aug. 1990, 1 7, A	HOB, SA, 12 Jul. 1993, A	1,529	3	E
9344	F	HOB, SA, 18 Jul. 1993, A	Lucky Bay, WA, 4 Aug. 1995, 20 15, C/Ca	884	2	W
9346	M	HOB, SA, 1989, DJN, A	Cape Gantheaume, SA, 1992, SAM, A	780	3	E
9346	M	Cape Gantheaume, SA, 13 Jul. 1992, SAM, A	HOB, SA, 29 Jul. 1993, A	780	1	W
9349	F	Dillon Bay, WA, 16 Aug. 1986, 9-12 7, A	HOB, SA, 1990, DJN O/21/27, ?	1,152	4	E
9349	F	HOB, SA, 1990, DJN O/21/27, ?	Pt Charles, WA, 3 Oct. 1992, JLB s 7-9, C/Ca	1,103	2	W
9349	F	Pt Charles, WA, 3 Oct. 1992, JLB s 7-9, C/Ca	HOB, SA, 23 Jul. 1993, A	1,103	1	E
9351	M	Sellicks Bch, SA, 1988, DJN video, A	HOB, SA, 1990, DJN, A	775	2	W
9351	M	HOB, SA, 1990, DJN, A	Coorong, SA, 1991, DJN, A	888	1	E
9351	M	Coorong, SA, 1991, DJN, A	HOB, SA, 4 Aug. 1993, A	888	2	W
9355	M	HOB, SA, 25 Jul. 1994, A	Fishery Bay, SA, 6 Sep. 1995, A	575	1	E
9357	F	HOB, SA, 1990, DJN, A	Kangaroo Island, SA, 1993, SAM, A	780	3	E
9357	F	HOB, SA, 6 Jul. 1994, A	Anglesea, VIC, 31 May 1995, A	1,420	1	E
9358	M	Pt Ann, WA, 20 Sep. 1980, 6a, A	HOB, SA, 30 Jul. 1993, A	1,103	13	E
9360	M	HOB, SA, 15 Aug. 1994, A	Apollo Bay, VIC, 28 Jul. 1995, A	1,399	1	E
9366	F	HOB, SA, 1990, DJN, A	Victor Harbor, SA, 1992, ?, A	831	2	E
9366	F	Victor Harbor, SA, 1992, ?, A	HOB, SA, 25 Sep. 1993, A	831	1	W
9415	?	Hassel Beach, WA, 7 Sep. 1992, 3 8, A	HOB, SA, 11/7/94, A	1,241	2	E
9418	F	Wray Bay, WA, 20 Aug. 1993, 21 10-11, A	HOB, SA, 1 Aug. 1994, A	1,190	1	E
9420	M	Albany, WA, 19 Sep. 1985, 1-12, A	Israelite Bay, WA, 1988, ?, A	576	3	E
9420	M	Israelite Bay, WA, 1988, ?, A	Augusta, WA, 2 Sep. 1990, 1 5, A	814	2	W
9420	M	Augusta, WA, 2 Sep. 1990, 1 5, A	HOB, SA, 15 Jul. 1994, A	1,529	4	E
9424	?	Israelite Bay, WA, 28 Sep. 1990, 7 2, A	HOB, SA, 17 Jul. 1994, A	717	4	E
9428	M	Albany, WA, 22 Jul. 1985, 1-2 3 4, A	HOB, SA, 9 Aug. 1994, A	1,294	9	E
9434	M	Israelite Bay, WA, 3 Sep. 1990, 12 14, A	HOB, SA, 7 Aug. 1994, A	717	4	E
9434	M	HOB, SA, 7 Aug. 1994, A	Twilight Cove, WA, 3 Aug. 1995, 14 8, A	489	1	W
9441	M	Hassel Beach, WA, 7 Sep. 1992, 3 3&8, A	HOB, SA, 29 Aug. 1994, A	1,241	2	E
9443	F	Albany, WA, 20 Aug. 1992, 2 10, A	Israelite Bay, WA, 25 Sep. 1993, 6 9-10, A	576	1	E
9443	F	Israelite Bay, WA, 25 Sep. 1993, 6 9-10, A	HOB, SA, 15 Sep. 1994, A	717	1	E
9450	M	Dillon Bay, WA, 28 Sep. 1990, 5 1, A	HOB, SA, 20 Sep. 1994, A	1,152	4	E
9455	F	Pt Charles, WA, 3 Oct. 1992, JLB S 31-32, A	HOB, SA, 26 Sep. 1994, F	1,103	2	E
9456	?	Tagon Bay, WA, 1 Oct. 1985, 19-29 b3, A	HOB, SA, 2 Oct. 1994, A	810	9	E

cont...

Table 2 continued.

ID No.	Sex	Sighting locality 1including date, photo number and status	Sighting locality 2, including date, photo number and status	Distance (km)	Years apart	Direction
9458	?	Middleton, SA, 1991, DJN, A	HOB, SA,. 4 Oct. 1994, A	838	3	W
9458	?	HOB, SA, 4 Oct. 1994, A	Maria Island, TAS, 29 Aug. 1995, A	1,944	1	E
9471	M	HOB, SA, 25 Sep. 1994, Ca	Wanna, SA, 27 Sep. 1995, A	580	1	E
9480	M	HOB, SA, 28 Sep. 1994, Ca	Semaphore, SA, 30 Aug. 1995, A	780	1	E
94Y1	F	Sellicks Bch, SA, 1983, DJN video, C/CA	Yokinup Bay, WA, 19 Sep. 1994, C/Ca	1,423	11	W
94Y1	F	Yokinup Bay, WA, 19 Sep. 1994, C/Ca	HOB, SA, 6 Jul. 1995, A	808	1	E
94FN1	?	Tagon Bay, WA, 12 Sep. 1989, 7 18, Ca	Point Culver, WA, 17 Aug. 1993, 8 2-3, A	210	4	E
94FN1	?	Point Culver, WA, 17 Aug. 1993, 8 2-3, A	Swansea, TAS, 20 Jun. 1994, FN, A	2,307	1	E
94FN1	?	Swansea, TAS, 20 Jun. 1994, FN, A	Wylie Scarp, WA, 11 Sep. 1995, 14 7&12, A	2,249	1	W
9504	F	Tagon Bay, WA, 20 Oct. 1992, 4 11, C/Ca	HOB, SA, 24 Aug. 1995, C/Ca	810	3	E
9529	F	Cape Adieu, SA, 1986, DJN, ?	Pt Anne, WA, 7 Sep. 1992, 7 11&13, A	1,215	6	W
9529	F	Pt Anne, WA, 7 Sep. 1992, 7 11&13, A	HOB, SA, 9 Jul. 1995, A	1,103	3	E
9533	F	Logans Bch, VIC, Parer-Cook, DJN, C/CA	Pt Charles, WA, 3 Oct. 1992, JLB S 16, A	2,086	10	W
9533	F	Pt Charles, WA, 3 Oct. 1992, JLB S 16, A	HOB, SA, 14 Jul. 1995, A	1,103	3	E
9541	?	Esperance, WA, 16 Aug. 1990, 5 19, A	HOB, SA, 23 Aug. 1995, A	912	5	E
9545	M	?, WA, 12 Sep. 1989, 15 6-7, ?	HOB, SA, 10 Sep. 1995, A	?	6	E
95FN1	?	Albany, WA, 5 Sep. 1994, 5 8-9, A	Cape Tournefort, SA, 25/ Jul. 1995, A	1,639	1	E
95FN2	?	Yokinup Bay, WA, 6 Sep. 1994, 11 10, A	Cape Tournefort, SA, 25 Jul. 1995, A	1,187	1	E
			Mean (n = 90)	?	3.34	

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Status of southern right whales (*Eubalaena australis*) off Australia

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ABSTRACT

The history of Australian right whaling is briefly reviewed. Most catching took place in the first half of the 19th century, with a peak in the 1830s, involving bay whaling by locals and visiting whaleships in winter and whaling offshore in the summer. In the early 20th century, right whales were regarded as at least very rare, if not extinct. The first published scientific record for Australian waters in the 20th century was a sighting near Albany, Western Australia, in 1955. Increasing sightings close to the coast in winter and spring led to annual aerial surveys off southern Western Australia from 1976. To allow for possible effects of coastwise movements, coverage was extended into South Australian waters from 1993. Evidence from 19th century pelagic catch locations, recent sightings surveys, 1960s Soviet catch data and photographically-identified individuals is beginning to confirm earlier views about likely seasonal movements to and from warm water coastal breeding grounds and colder water feeding grounds. Increase rates of *ca* 7-13% have been observed since 1983. Some effects of different breeding female cohort strength are now beginning to appear. A minimum population size of *ca* 700 for the period 1995-97 is suggested for the bulk of the 'Australian' population, i.e. animals approaching the *ca* 2,000km of coast between Cape Leeuwin, Western Australia and Ceduna, South Australia.

KEYWORDS: SOUTHERN RIGHT WHALE; AUSTRALASIA; SURVEY-AERIAL; DISTRIBUTION; TRENDS; ABUNDANCE ESTIMATE

INTRODUCTION

As elsewhere in the Southern Hemisphere, right whales were considered very rare, if not virtually extinct, in Australian waters for at least the first half of the 20th century. More than 100 years earlier, people had been aware of their presence in some numbers in suitable coastal areas in winter: in 1804 they were regarded as such a danger to navigation in the Derwent River, Tasmania, that small boats had to keep close to the shore. Up to 50 or 60 animals could apparently be seen there in the shallows between May and November; in Hobart (42°55'S, 147°20'E) the Lieutenant-Governor is said to have been kept awake by their 'snorting' at night (Dakin, 1934).

The development of Australian shore-based whaling from 1805, particularly along the southeast coast of Tasmania, off western Victoria, South Australia and southern Western Australia, was accompanied by the operations of Tasmanian registered sailing vessels in bays as far afield as New South Wales and even New Zealand. In addition, the pelagic vessels from the USA, Britain and France that operated in the high seas in the summer were attracted to coastal areas in winter. By the late 1830s, as many as 50 shore stations were recorded from southeast Australia, although some may have been temporary sites used only for one season. Dawbin's (1986) estimate of the scale of killing from these combined sources – a minimum of 26,000 animals off New Zealand and southeast Australia between 1827 and 1899, with 75% taken in the ten years 1835-44 – is telling enough. It is even more so if, as Dawbin acknowledges, account is taken of losses of possibly up to 20% after harpooning and the lack of information on at least the British element of the fishery.

Clearly the stocks could not withstand such pressure. Off Western Australia, where right whaling began rather later than off southeast Australia, there were reports such as 'foreigners …. infest our bays from the beginning of May to the end of October [1839]', and 'every year now [1840] at the end of December, during January, February and March the [American] fleet could be expected' (Heppingstone, 1969, cited in Bannister, 1986). The scale of the pelagic operations can be gauged from the combined catch of 57 right whales by three American vessels in the summer of l840-41. In coastal waters, at Fowlers Bay, South Australia, one vessel alone, the *Amazon*, took 33 right whales in a little under three months from June-August 1840 (Bannister, 1986). No wonder that in late 1849, Nelson Cole Haley on the *Charles W Morgan* at Two Peoples Bay (34°57'S, 118°12'E) on the Western Australian south coast recorded: 'Some years ago whale ships came here in certain seasons to catch right whales, but it has been abandoned now for that purpose' (Haley, 1950).

The pelagic right whale fishery off Western Australia peaked in the late 1830s and rapidly declined. By about 1850, the offshore 'Coast of New Holland Ground' had ceased to be attractive to foreign right whaling vessels. The last shore-based Western Australian right whale catch was recorded in 1866, when an estimated seven animals were taken (Bannister, 1986). By 1900, interested Australians would have said right whales were virtually extinct, or at least exceedingly rare, anywhere in Australian waters.

When Chittleborough (1956) recorded the sighting of a cow and calf near Albany, WA, in 1955, he was unable to find any published scientific account of an Australian right whale sighting that century. The species' rarity in Australian waters was confirmed by others: Ling and Aitken (1981), commenting on the sighting of a cow and calf off South Australia in 1968, presumed they had been absent from there during the first half of the century. However, an increasing number of sightings off the south coast of Western Australia in the early 1970s led to annual aerial surveys along that coast from 1976. Other more recent survey work has been undertaken off South Australia and further east (Ling and Needham, 1991; Kemper *et al.*, 1997). Intensive biological studies have been undertaken at the Head of the Bight, South Australia since 1991 (Burnell and Bryden, 1997); since 1995 that work has included animals to the east and southeast, i.e. off Victoria, southern New South Wales and Tasmania (Burnell, 1997). This paper documents some of the main results recently obtained on distribution, numbers and increase rates, particularly those derived from the aerial surveys that began off the southern Western Australian coast and were later extended eastwards into South Australia.

DISTRIBUTION

Late 20th century sightings of Australian right whales have been concentrated in coastal waters of Western and South Australia, and to a lesser extent off Victoria, Tasmania and New South Wales (see Fig. 1). There have been records as far north as Exmouth, WA (22°23'S, 114°07'E), on the north west coast, and north of Sydney (33°53'S, 151°12'E) to Cape Byron, NSW (28°39'S, 153°37'E), on the east coast, but in general animals are concentrated along the south coast from west of Albany, WA to the Head of the Bight, SA. In some years there have been small concentrations at localities such as Port Lincoln (34°44'S, 135°52'E) and Victor Harbor, SA (35°34'S, 138°37'E) and Warrnambool, Vic (38°23'S, 142°29'E), while there are fairly regular sightings along the south east coast of Tasmania. The peak of abundance is in August-September, with animals commonly present from late June-early October.

The animals seen most regularly close to the coast are cows accompanied by calves of the year (Bannister, 1990; Burnell and Bryden, 1997). They are only present for long periods in the year of the calf's birth, when they may spend up to three months on the coast before heading south to colder waters, in their summer (presumed feeding) grounds. Other animals are also found close to the coast, relatively frequently but more irregularly, often in sub-adult or adult interactive groups and demonstrating courting and mating behaviour.

Information is now coming to light on the animals' probable summer distribution in colder waters south of the continent. 'Townsend's Charts' for the region[1] (Townsend, 1935) are consistent with indications from coastal sighting records, 1904-82 (Bannister, 1986), of northwards movement from the south, from Tasmania to Victoria or New South Wales in the early part of the (winter) season and later movement to the south. That was a strongly held view in the 19th century (see Dakin, 1934 and Aitken, 1981, cited in Bannister, 1986; also Dawbin, 1986, in particular citing Cumpston, 1970). An 1842 report (Aitken, 1981) described right whales approaching Tasmania from about the beginning of April, then moving towards western Victoria before continuing westwards to the Great Australian Bight. Additional animals are described as arriving along the whole southern coast direct from the south, then 'at Cape Le[eu]win [south west WA] the great body of whales seems to strike off southward, for in October and November they are again working towards the south east, by keeping two or three hundred miles from land'. Townsend's plots (summarised in Fig. 1) show a well-defined September catching ground close to the south coast of Western Australia, while plots representing October-December catching grounds appear further west and south, and to the

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[1] Townsend's charts show the positions of American whaling vessels on days when they caught whales (plotted by month).

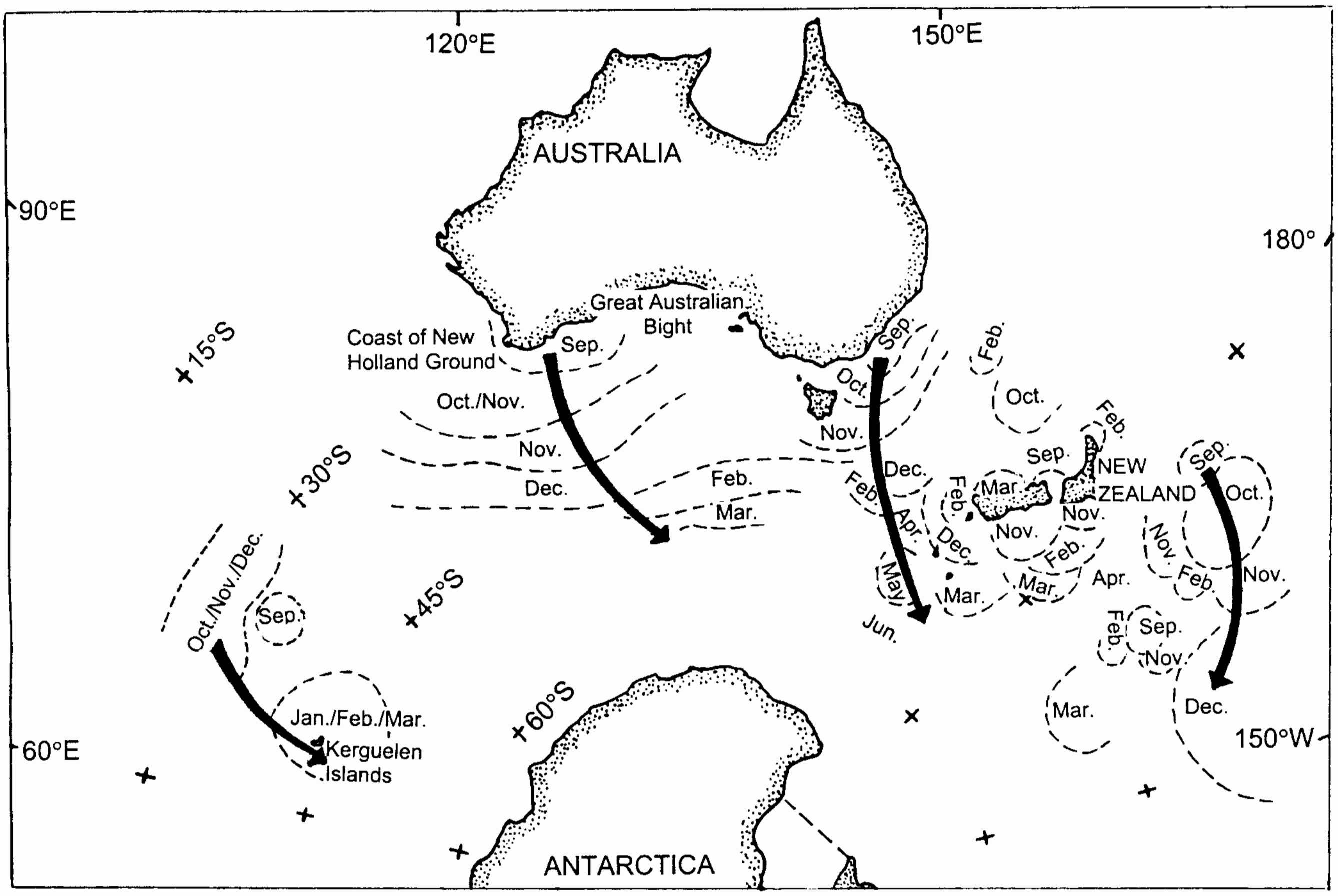

Fig. 1. Monthly positions of southern right whale catches, US 19th century whaling, Australasian region, summarised from Townsend's charts (1935). Inferred seasonal whale movements indicated.

east towards Tasmania. There are then a few February-March plots approaching Tasmania from the west, south of the Bight.

The expectation that right whales would be found well to the south of Western Australia in early summer is confirmed by Whitecar (1860) on the American whaleship *Pacific*, in 1856. Leaving Albany, WA, on 5 November, the ship steered south, to 40°S, '. . . where we expected to see right whales'. They did so, but by that date, the late 1850s, right whales had become increasingly hard to approach. '. . . [T]he moment the boat was lowered from the ship they absquatulated in as secret and shy a manner as a defaulting bank clerk . . . We could do nothing with these shy gentlemen . . . and steered northwest for Cape Le[eu]win . . . [for sperm whales]'.

Other well-defined spring-summer changes in catching positions are shown towards the south (Fig. 1). Examples are northeast of New Zealand, and in the southeast Indian Ocean near Kerguelen. There is also a well-marked southward change off southeastern Australia, from New South Wales through the Tasman Sea to the south of New Zealand, and over a wide range of months (September-June). The continuing southward change in early winter is anomalous, but consistent with recent records of winter concentrations at the Auckland Islands, south of New Zealand (Patenaude and Baker, 2001).

While there is no direct evidence that such changes in distribution of catching positions actually reflect whale movements, there are strong implications that they do. However, as usual with such data, they are limited in their coverage by the restrictions of wind, weather and current on sailing ship operations. In the Australasian region, there is no indication on Townsend's charts of right whale catches anywhere south of about 45°S. That seemed to be borne out by observations of a large concentration, of 75 animals, 41-44°S, 116-124°W, i.e. south of Cape Leeuwin WA, in December-January 1981-82 (Ohsumi and Kasamatsu, 1986). Nevertheless, a sightings cruise specifically for right whales found none in that area in February-March 1993, while 35 animals were encountered there in December-January 1995-96 (Bannister *et al.*, 1997). Following the lack of success of the 1993 cruise, those involved (including this author) assumed that at that time (February-March, i.e. late summer), right whales must have been further south. Such a possibility had already been demonstrated for right whales off South Africa: using Townsend's data, Best (1970) showed that in the southeast Atlantic and southwest Indian Ocean right whales in late summer can occur at least as far south as 55°S. The same was hypothesised by Best and Schell (1996) from stable isotope analyses.

The possibility that in late summer right whales in the southeast Indian Ocean may be found even further south, i.e. beyond 60°S, has been confirmed by sightings of animals at 64°S in February 1996 (Bannister *et al.*, 1999), and recent revelations of Soviet catches (of 14 animals) in the same area, i.e. south of 60°S between 92-106°E, in February-March 1963 (Tormosov *et al.*, 1998). The positions of the above sightings and catches are shown in Fig. 2.

Some direct evidence of a link between animals in colder waters in summer and on the Australian coast in winter is now available from photographically-identified individuals (Fig. 2). Two 'matches' have been made between animals identified off either Western Australia or South Australia in winter/spring and in the area at approximately 43°S where

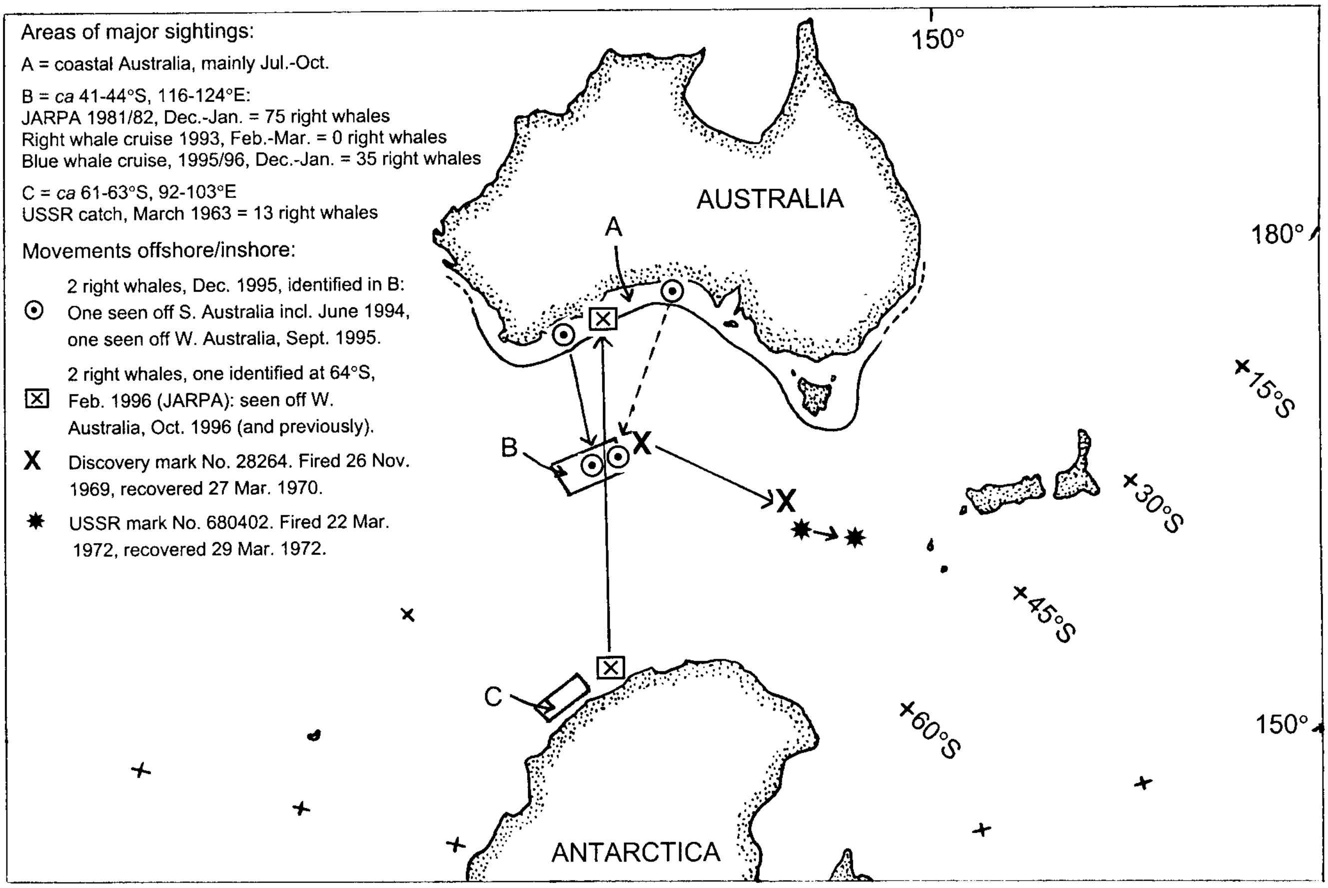

Fig. 2. Southern right whales off Australia: locations of sightings, catches and recorded movements (straight line routes), 1963-96.

the 35 animals were recorded in December-January 1995-96; the records involve straight line movement of 900 and 1,500 n.miles respectively (Bannister *et al.*, 1997). One animal photographed at 64°S in February 1996 had already been identified over a period of some 18 years on the coast of Western Australia, *ca* 1,700 n.miles due north (Bannister *et al.*, 1999).

Confirmation of likely eastward movement during summer to the south of the continent has come from two Soviet marking returns (Fig. 2), one involving movement of some 900 n.miles from 40°34'S, 124°02'E to 47°42'S, 148° 40'E in 122 days (*ca* 17 weeks) in late November 1969-March 1970, and another of some 200 n.miles from 47°20'S, 148°40'E to 48°00'S, 153°00'E over seven days in late March 1972 (Tormosov *et al.*, 1998).

Movements along the southern Australian coast, both within and between years, have been demonstrated by 'matches' of individuals identified in South Australia and Western Australia (Bannister, 1994) and between Tasmania, Victoria, New South Wales, South Australia and Western Australia (Burnell, 1997; 2001). The general coastwise trend seems to be towards the west, in line with earlier expectations; the extent of the reported movements is a strong indication that right whales found along the Australian coastline belong to a single stock.

INCREASE RATES

The aerial surveys off the south coast of Western Australian had two main aims, to provide: (1) information on relative numbers from year to year, and hence a rate of increase should it be occurring; and (2) a series of photographically identified individuals for information particularly on distribution, movement and other life history parameters. The remainder of this paper is concerned mainly with aim (1).

Survey strategy and area

The Western Australian aerial surveys have followed the same basic pattern since their inception in 1976. An attempt has been made each year to obtain a maximum count of animals on the coast in a narrow (*ca* 1 n.mile) band seawards of the beachline. Until 1993, a single engine, high wing monoplane (*Cessna* 172 or 185), with the same pilot each year, and a single observer/photographer, surveyed the coast along some 600 n.miles (1,100km) between Cape Leeuwin in the west and Twilight Cove in the east (Fig. 3). Flight tactics are described in Bannister (1990). Coverage varied over the period. The area was extended to the east from 1983 to accommodate reports of numbers of animals east of Israelite Bay, at the western limit of the Great Australian Bight, and towards Twilight Cove, relatively close to the South Australian border (Fig. 3).

In July-October each year, at least three flights were attempted, to ensure bracketing of the peak period of abundance (mid August - mid September) and provide information on residence times and within-season coastwise movements.

The area surveyed was again extended eastwards in 1993, to include the major calving ground at the Head of the Bight, SA. This followed a review of the programme, given increasing evidence of within- and between-season coastwise movements between South Australia and Western Australia, and to obviate if possible the effect upon the observed increase rate of animals migrating into the 'WA sector' from the east. The survey then covered some 1,100 n.miles (2,000km) between Cape Leeuwin, WA, and Ceduna, SA (Fig. 3). Initially the *Cessna* 185 was used on the extended flight but for fuel economy and safety it was

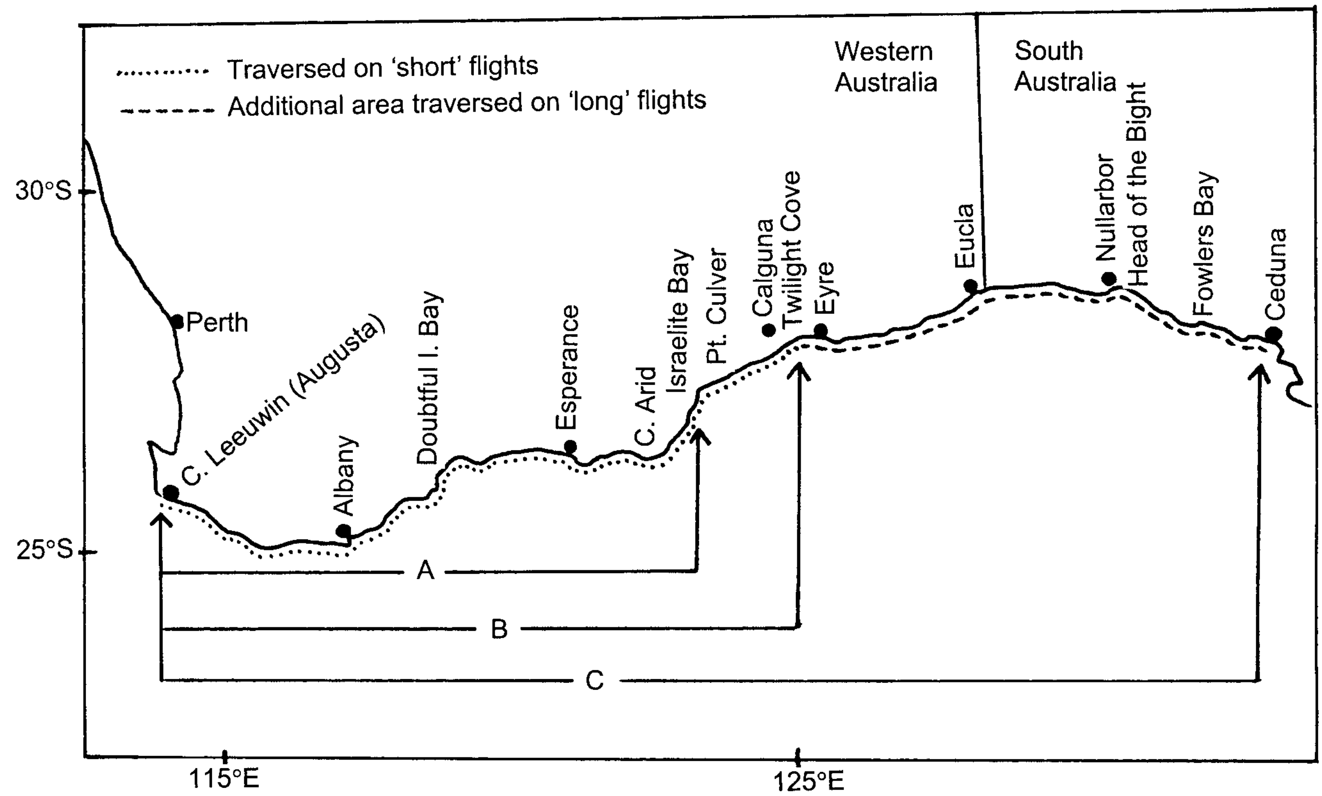

Fig. 3. Southern right whale aerial surveys, southern Australia 1976-97: approximate position of flight paths. A, B, C = limits of flight paths designated as in Tables 1-3

replaced by a twin-engined *Cessna* 337 from 1994. Three ‘long’ flights took place annually at first, but since 1994 they have been replaced by one ‘long’ flight covering the whole area (‘WA-SA sector’) at the season peak (mid August-mid September) and two ‘short’ flights covering the area Cape Leeuwin-Twilight Cove (the ‘WA sector’) in July/August and September/October.

A power analysis (by P.J. Corkeron, in Bannister, 1993) showed that at least five years’ consecutive annual surveys would be required from 1993 to obtain significant evidence of an increase rate. Given the three year calving interval, that was increased to six years to cover two full calving cycles. However, further analysis (Corkeron, in Bannister, 1997) showed that while that might be satisfactory for the population as a whole, including the non-calving element, a much longer period would be necessary to obtain a significant result for calving females (cow-calf pairs). Five cycles would be required, over fifteen years from 1993. While the first six-year cycle would be completed by a survey in 1998, to cover the five calving periods would require a further nine years after 1998, to 2007.

Table 1

Southern right whales, aerial survey, Western Australia: Numbers seen (Areas A, B : ‘short’ flights) 1983-97. a = all animals; b = ‘other’ animals, i.e. those unaccompanied by calves; c = cow-calf pairs.

	Area A			Area B		
	C. Leeuwin - East of Israelite Bay			C. Leeuwin - Twilight Cove		
Year	a	b	c	a	b	c
1983	27	5	11			
1984	54	26	14			
1985	47	29	9			
1986	50	12	19	63	24	24
1987	63	37	13	71	46	13
1988	75	39	18			
1989[1]	[64	22	21]			
1990	93	49	22			
1991[1]	[58	32	13]			
1992	84	44	20	91	45	23
1993	109	39	35	128	50	39
1994	112	66	28	132	96	28
1995	122	54	34	164	90	37
1996	143	71	36	171	95	38
1997	96	40	28	152	84	34

[1] Non-comparable data, see Bannister (1993).

Table 2

Southern right whales, aerial survey, Southern Australia, between C. Leeuwin, WA and Ceduna, SA: Numbers seen (Area C: ‘long’ flights) 1993-97. a = all animals; b = ‘other’ animals, i.e. those unaccompanied by calves; c = cow-calf pairs.

Year	a	b	c
1993	182	56	63
1994	199	101	49
1995	255	125	65
1996	233	123	55
1997	254	148	53

Datasets

For comparison of numbers with earlier results, two datasets have been used recently (Bannister, 1997):

(1) animals seen in the ‘WA sector’, Cape Leeuwin-East of Israelite Bay, WA;
(2) animals seen in the ‘WA-SA Sector’, Cape Leeuwin, WA-Ceduna, SA.

For (1), the greatest number recorded on any flight in one year where two or more flights have been completed has been used in past comparisons. Allowance has been made for resights between legs on each flight. Data are categorised into three classes: (a) ‘all’ animals; (b) ‘other’ animals, i.e. those not accompanied by calves of the year; and (c) ‘cow-calf pairs’. Counts have been made annually over the 22-year period 1976-97, but in the early years the coverage varied somewhat, either geographically or temporally; directly comparable data are available from 1983, apart from two years when bad weather prevented completion of the programme (Table 1: Area A). Dataset (2) allows comparison only from 1993 (Table 2). Because that survey regime was adopted to obviate the possible effect of between-year movement between the WA and SA sectors (Bannister, 1993), in due course the most valid comparison should involve that dataset.

For the ‘WA sector’, a geographically more extensive but temporally more restricted dataset can be used for year-to-year comparison, from 1986 but with no data for 1988-91 (Table 1: Area B). It includes a larger number of animals, particularly ‘other’ animals (non cow-calf pairs, (b)) now being found to the west of Twilight Cove, as well as those (often cow-calf pairs, (c)) congregating in the Cove itself.

The two ‘short’ flight datasets show a decrease in numbers in all classes for the WA sector in 1997 (Table 1: A, B). The same is true for the ‘long’ flight set for the WA-SA sector for cow-calf pairs (Table 2, c). Bad weather was encountered on much of the latter flight in 1997 (winds were greater than 30 knots on several occasions), and some undercounting may have resulted. The programme received a major setback with the sudden death in early 1996 of the pilot, John Bell, who had been responsible for all flights since their beginning in 1976. Excellent replacements have been found but on the ‘long’ flight, particularly, there have been difficulties in selecting the necessary period of four consecutive ‘good’ weather days. There is also the disadvantage that in 1996 and 1997 the ‘long’ flight aircraft was based at Port Lincoln, SA, to the east of the survey area, and had to fly into the prevailing weather systems on its first leg, westwards.

Trends

Table 3 (the results of the best-fit straight line regressions to the natural logarithms of the data, plotted in Fig. 4) shows highly significant regressions for all WA sector datasets, i.e. Areas A and B, classes (a), (b) and (c). The point estimates (range 7.1-13.5) are somewhat high by comparison with those (of *ca* 7%) from elsewhere, i.e. Argentina (7.1%, Payne *et al.*, 1990) and South Africa (7.2%, Best *et al.*, 2001). Nevertheless, the 95% confidence ranges for the WA sector all encompass, or are close to, the 7% value.

The increase rate for one of the three sets of WA-SA sector (‘long’ flight) results (‘other animals’, Table 3: Area C, (b)) is significant at the 95% level but with a very wide confidence interval, and for another set (‘all animals’, (a)) is approaching it, as expected from the power analysis. The rate for cow-calf pairs (c) does not yet show a positive increase.

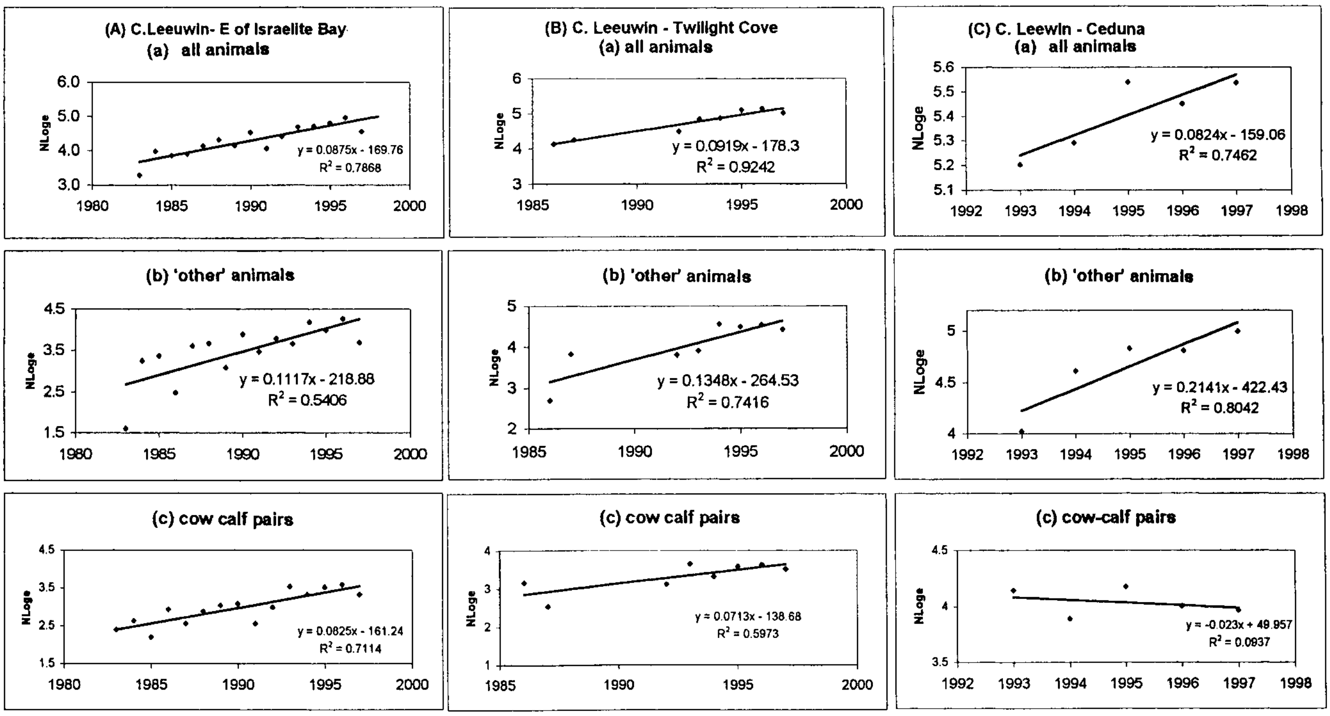

Fig. 4. Regressions for data of Tables 1-3.

Table 3

Best fit regressions to data (log *e*) of Tables 1 (Areas A, B) and 2 (Area C). a = all animals; b = 'other' animals, i.e. those unaccompanied by calves; c = cow-calf pairs.

	Area A			Area B			Area C		
	a	b	c	a	b	c	a	b	c
% rate of increase	8.7	11.2	8.3	9.2	13.5	7.1	8.2	21.4	-2.3
P-value	0. 0000	0.0018	0.0001	0.0001	0.0060	0.0245	0.0591	0.0392	0.6164
95% range of increase	6.0-11.5	5.0-17.3	5.1-11.4	6.6-11.8	5.5-21.5	1.3-12.9	-0.0-7.1	1.9-40.8	

The latter is to be expected given possible differences in cohort strength (see below) and the need, as demonstrated in the 1997 power analysis, for the surveys to cover five calving cycles.

The observed three-year calving cycle (as described for example in Bannister, 1990) could be expected to lead to differences in cohort strength. That is now becoming more readily apparent in the longer data series for the WA sector (Table 4, Areas A and B). The slopes of two regressions (Table 5, plotted in Fig. 5) are significant at the 95% level, and their increase rates (point estimates 7.7, 9.6%) are similar to those obtained for the cow-calf data as a whole in that sector (Table 3, A and B, (c)) but with much wider confidence intervals.

POPULATION SIZE

The survey methodology, originally adopted in 1976, has been deliberately continued over the years with as little change as possible to provide a comparable annual index of abundance; it was not developed at the outset to provide an absolute value. With only a very small number of additional animals recorded on survey 'return' legs, however, the counts obtained on the outward legs can be adjusted to represent a reasonably accurate estimate of the actual numbers close to the coast at that time, particularly the relatively sedentary and easily visible cow-calf pairs. On that basis it is appropriate to base an estimate of current population size on those figures, representing the maximum number of cow-calf pairs present at the peak of the season.

A naive model assumes that: (1) each female is recorded on the coast only once in three years; (2) there is no difference in the size of the adult female cohort each year; (3) the sex ratio is unity; (4) there are probably some unreproductive adult females present; and (5) in an expanding population there are at least as many immature animals as adults. Some of those assumptions are not likely to be met over a long period: calving female cohort size, for example, has varied over the five years 1993-97 from 49-65 (Table 2). That immature animals are likely to number at least as many as adults is conservative. Rice and Wolman (1971) for example, calculated that 61% of the eastern North Pacific gray whale population would have been immature at that time, when the population increase rate was averaging some 3% (Anon., 1993). Zeh *et al.* (1993) strongly suggested that in the slowly increasing Bering-Chukchi-Beaufort Seas bowhead population half or fewer than half of the animals were mature, although some of that might have been due to late sexual maturity[2]. Taking such considerations into account, the assumptions are appropriate for estimating at least a minimum current population size.

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[2] The Cape Town Assessment Meeting (item 10.3.2) recorded the ratio of juveniles and calves to adults in southern right whale populations as 1.4:1 as a consequence of the relatively high population growth rate.

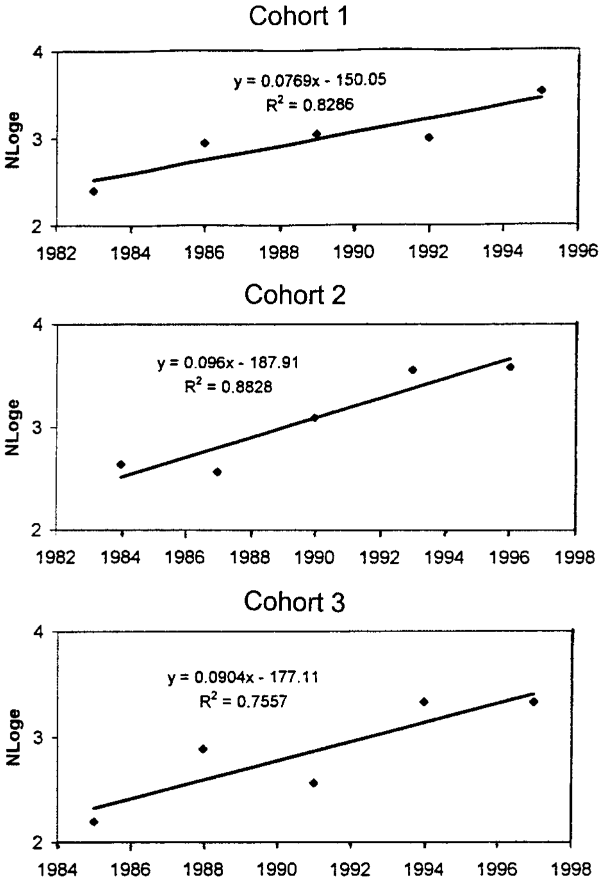

Fig. 5. Regressions for data of Table 4.

Table 4

Western Australia south coast, 1983-97.
Numbers of cow-calf pairs recorded at three year intervals.
Data from Table 1. 1, 2 ,3 = cohorts.

	Area A			Area B		
	1	2	3	1	2	3
1983	11					
1984		14				
1985			9			
1986	19			24		
1987		13			13	
1988			18			
1989	[21]			-		
1990		22			-	
1991			[13]			-
1992	20			23		
1993		35			39	
1994			28			28
1995	34			37		
1996		36			38	
1997			28			34

Table 5

Best fit regressions to data from Table 4 (Area A only).
1, 2, 3 = cohorts.

	1: 1983+	2: 1984+	3: 1985+
Increase (%)	7.7	9.6	9.0
p-value	0.0318	0.0177	0.0556
95% range of increase	1.3-14.1	3.2-16.0	-0.0-18.5

From the 'long flight' counts in 1995-97, the average number of reproductive females visiting the coast each year is 57. The minimum number of adult females in the population would then be 171, with a total adult population of more than 342. Allowing for immature animals, the size of the population visiting Australia's southern coast, i.e. between Cape Leeuwin, WA and Ceduna, SA over that period, 1995-97, would then be at least 684[3].

ACKNOWLEDGEMENTS

This paper is dedicated to the memory of John Bell, 1933-96, who up to 1995 piloted every flight from the beginning of the surveys in 1976, and without whose skills the data used here would not have been available. Over the years he was assisted first by Ray Smith and then by Alan Murdoch as observer/photographer. In 1996 and 1997, 'short' flights were piloted by Jenny Schmidt, with observer/photographer Andrew Halsall, and 'long' flights by John Rogers, accompanied by Ian Westhorpe. Many others have assisted over the years, including Gordon Anderson, Stuart Anstee, Scott Baker, John Bannister Jr., Paddy Berry, Peter Best, Lynne Broomhall, Stephen Burnell, Chris Burton, Nick Caputi, Graham Chittleborough, Peter Collins, Peter Corkeron, Doug Coughran, the late Bill Dawbin, Greg Donovan, Douglas Elford, Richard Holst, Hidehiro Kato, Cath Kemper, Geoff Kirkwood, Peter Lambert, John Ling, Astrida Mednis, Dave Mell, Pin Needham, Anne Nevin, Val Milne, Luis Pastene, Roger Payne, Deborah Thiele, Bob Warneke and the Trustees and staff of the Western Australian Museum. Dr Catherine Kemper (South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia) and Stephen Burnell (Department of Veterinary Anatomy and Pathology, University of Sydney, New South Wales 2600, Australia) commented on a draft typescript.

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[3] The Cape Town Assessment Meeting (Table 4), based on the 1995 reproductive female figure of 65 for the area Cape Leeuwin-Ceduna, allowing for additional animals off the remainder of the Australian coast, and using a more sophisticated analysis, estimated current (1997) population size for the 'Australian' population as 1,197; the *pro rata* figure for that part of the population visiting the area Cape Leeuwin-Ceduna is 848.

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Population status and habitat use of southern right whales in the sub-Antarctic Auckland Islands of New Zealand

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ABSTRACT

In the winters of 1995, 1996 and 1997, research was conducted in the Auckland Islands to evaluate the status of southern right whales in the New Zealand sub-Antarctic. Whales were present in high concentrations each year (maximum count of 146 whales) in a small area on the northeast side of the main island. Cow-calf pairs averaged 12% (range 9% to 14%) of the total population. Most cow-calf pairs were sighted resting at the surface (60%) or travelling (36%) and showed a strong preference for shallow (< 20m depth) nearshore waters. The ratio of females to males, as determined by molecular sexing using biopsy samples, varied from 54% to 39% over the three years but did not differ significantly from 1:1 in any year. Both males and females were found in varying group sizes, with the occurrence of social/sexual activity predominant (85%) in groups of three or more whales. Most single whales were found resting (59%) and occasionally approached the research vessel (19%). A total of 217 individual whales have been photo-identified over the three years of this study, 24% of which were resighted more than once in a season and approximately 15% of which were resighted in more than one year. The high density of whales in Port Ross during winter months, the presence of cow-calf pairs, including newborns, and the frequency of social and sexual activity indicates that the Auckland Islands are a primary wintering habitat for southern right whales in New Zealand waters. However, the low resighting rates within season and documented movement to nearby Campbell Island (290km) suggest that some whales are not resident in the Auckland Islands throughout the season. The rarity of right whales along the main islands of New Zealand and their apparent increase in numbers in the Auckland Islands suggests a major shift in habitat use from pre-exploitation times or the loss of a component of a historically sub-divided stock.

KEYWORDS: SOUTHERN RIGHT WHALE; SUB-ANTARCTIC; BREEDING GROUNDS; ABUNDANCE ESTIMATE; SEX RATIO; REPRODUCTION; BEHAVIOUR; HABITAT

INTRODUCTION

Prior to exploitation, southern right whales (*Eubalaena australis*) were widely distributed in New Zealand waters and the population is estimated to have included more than 10,000 individuals (Dawbin, 1986). Shore-based whaling was conducted along both the North and South Islands, with peak whaling involving at least 80 stations between 1843-1845 (Dawbin, 1986). In addition, considerable pelagic whaling by Americans occurred offshore near the Chatham Islands (Fig. 1), east of the Kermadec Islands and in the New Zealand sub-Antarctic Islands during the early 1800s (Townsend, 1935). There were also attempts at shore-based whaling in the sub-Antarctic islands with limited success. In 1849 a whaling station was established in Port Ross, Auckland Islands, that closed three years later, having caught only a single whale (Grady, 1986). Another station operated at Campbell Island (52°33’S, 169°08’E) from 1909-1913 and caught 63 right whales (Dawbin, 1986). By the end of the 19th century New Zealand southern right whales were considered commercially extinct (Dawbin, 1986).

Although protected from hunting by international agreement since 1935, recovery of southern right whales has been slow, and sightings along the coast of mainland New Zealand remain infrequent. More than 35 years elapsed between a sighting in 1963 (Gaskin, 1964) and the previous recorded sighting of a right whale along the New Zealand mainland in 1928. In the past 10 years there have been fewer than 30 reported sightings along the coast of New Zealand (N. Patenaude, unpub. data). Despite year-round occupation at the Kermadec Islands (Fig 1A) by the Department of Conservation, right whales have not been sighted there in the last 10 years (C. Roberts, pers. comm.).

In the sub-Antarctic islands, the pattern of recovery has differed. Although the high latitude of these islands is more consistent with known right whale feeding grounds worldwide, sightings of southern right whales in this area in winter months have increased during the last 50 years. Meteorological staff stationed at Campbell Island (Fig. 1A) from 1942 and 1990 consistently recorded sightings of southern right whales during this season. These sightings included social groups and the occasional presence of cow-calf pairs (Gaskin, 1968; Cawthorn, 1978; 1986; 1988; 1993). From 1995-1997, up to 44 whales were seen at one time at Campbell Island (Stewart and Todd, 2001). No calves were sighted during this period.

In comparison with Campbell Island, there have been few reports of right whales in the Auckland Islands until the last two decades. Whether this is because whales were absent or because the islands were rarely occupied by observers over the winter months is unclear. The New Zealand Coastguard occupied the islands year-round from 1942-1945 and did not report the presence of right whales (M. Cawthorn, pers. comm.). There is now little doubt that population growth around the Auckland Islands was slowed or even reversed by the illegal killing of 258 whales by Soviet factory ships from 1950-1970 (Tormosov *et al.*, 1998).

In the early 1980s, the crew of a private yacht reported sighting approximately 75 right whales at the northeast tip (Port Ross) of the Auckland Islands in winter (M. Cawthorn, pers. comm.). More recently, the Royal New Zealand Air Force (RNZAF) surveyed the Islands in July 1993, and reported 42 right whales including three cow-calf pairs in Port Ross (Donoghue, 1995). Following this survey, the University of Auckland and the New Zealand Department of Conservation jointly conducted the first winter scientific expedition to the Auckland Islands in 1995 to investigate the status of southern right whales in those waters (Patenaude *et al.*, 1998). This work has continued for two additional years. This paper reports on the current abundance and habitat use of southern right whales found in the Auckland Islands sub-Antarctic waters.

MATERIALS AND METHODS

Study area

The Auckland Islands are located 460km south of mainland New Zealand (50°33'S, 166°15'E; Fig. 1). The main island (Auckland) is approximately 40km long and 25km at its widest. The western coast of the main island is exposed and offers no sheltered areas while the eastern coastline is riddled with large embayments. The southern end of the main island forms a deep water harbour bordered by Adams Island. At the northeast end, Port Ross leads southwest into Laurie Harbour and is bordered by Enderby Island to the north.

Research was conducted in and around Port Ross from 17 July-9 August 1995, from 17 July-7 August 1996 and from 17 July-2 August 1997. In all three years, research was conducted from small vessels (4.6-5.2m) powered by outboard motors. Additionally in 1996 and 1997, a chartered motor-sailing vessel provided a second platform from which to conduct research. In 1995, small-boat surveys were conducted in nearby waters off the north and east shores of Auckland main island (Patenaude *et al.*, 1998). A film crew from the TVNZ Natural History Unit worked in parallel with the research team for two weeks in 1996 and collected underwater footage of whale behaviour. On 27 July 1996, a helicopter chartered by the film crew was used to survey the length of the Auckland Islands, including Carnley Harbour, for right whales (Fig. 1B).

Minimum abundance

To determine the minimum number of southern right whales in Port Ross each winter, combined shore- and boat-based surveys of Port Ross and adjoining areas were conducted, as described by Patenaude (1998). The areas were divided into sectors (Fig. 2A) and all sectors were simultaneously scanned by eye for a period of 10 minutes. The approximate locations of all whales observed at the surface were recorded. Given the short scanning time, and the minimum amount of travelling of the whales (see Results), duplicate sightings are unlikely. An animal was judged to be a calf when the portion of the animal visible at the surface was less than half of the length of an accompanying adult. A sighting was considered to include only one individual unless more than one individual could be counted at the surface within one and a half whale body lengths. Thus, these censuses represent a minimum estimate of the number of whales observed on each occasion.

Photo-identification

Photographs of callosity patterns, lip ridges and unusual skin pigmentation were collected for individual identification of the whales (Payne *et al.*, 1983; Kraus *et al.*, 1986; IWC, 1990). Photo-identification was conducted from small vessels and at times from the deck or mast of a larger chartered vessel. Photographs were taken with *Kodak* Tri-X or T-Max black and white film (ISO 400, pushed to 800 or 1600) using a 35mm SLR camera equipped with 200-300mm lenses. Effort was directed at photographing the left side of each whale although both sides were photographed when possible. Topside photographs were taken opportunistically from the mast of the larger vessel.

The analysis of photographs was based on the left side only and generally followed methods described by Payne *et al.* (1977; 1989), although in this case photographs were first sorted by the presence and extent of the lip callosity. All identification photographs were first cross-checked with other individually identified whales from within the same season and then with whales identified from previous seasons. When no match could be made, the whale was added to the catalogue as a new individual. All identified matches or new whales were confirmed by two experienced researchers. Calves were not included in the final photographic catalogue because the true callosity pattern on their heads are often obscured by ectoparasites inhabiting bare skin as well as callosity tissue (Payne *et al.*, 1983).

Biopsy sampling

Skin and blubber samples for genetic and pollutant analyses were collected using a compound bow with a small biopsy dart similar to that described by Brown *et al.* (1991). Biopsy

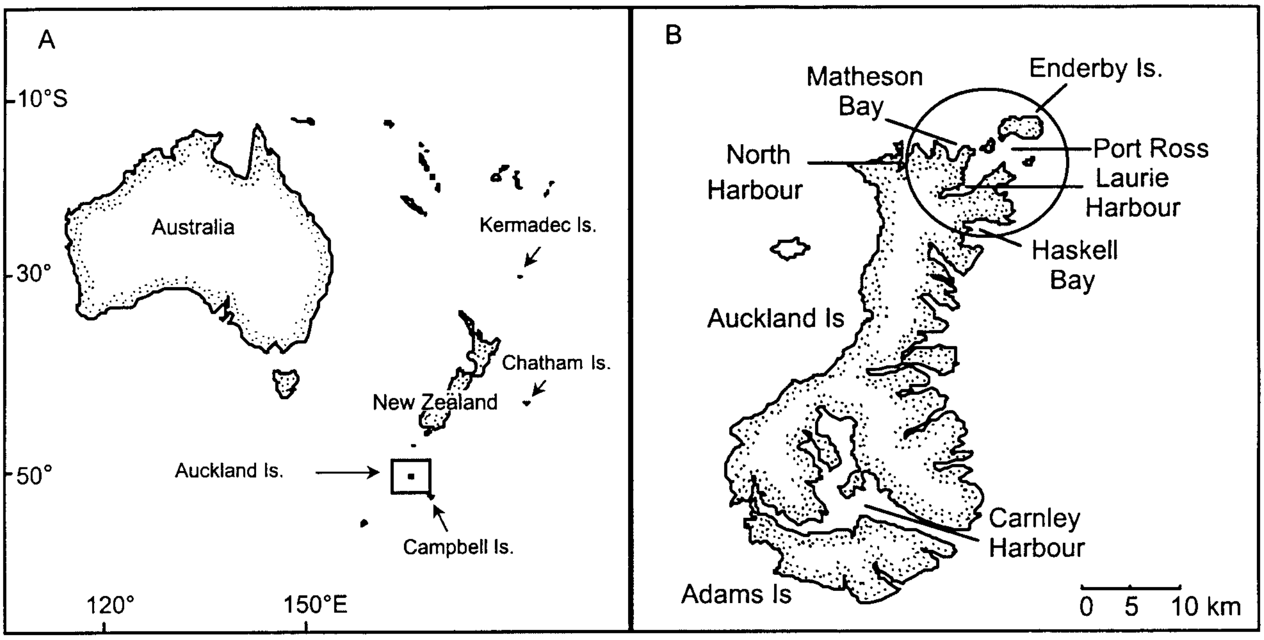

Fig. 1. Location of New Zealand islands (A) and map of the Auckland Islands with area of concentration of southern right whales encircled (B).

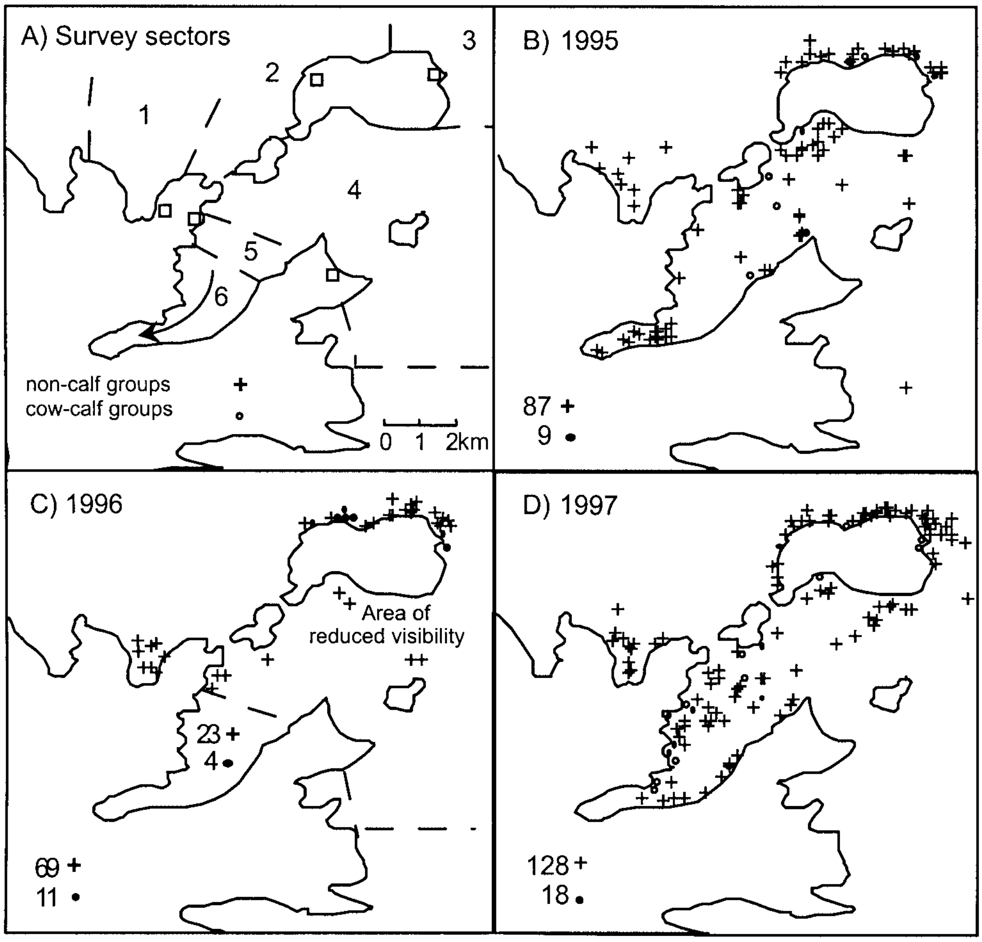

Fig. 2. (A) Map of study area divided into sectors showing shore-based observation points (squares) and path of boat survey (arrow) and location of whale sightings during simultaneous surveys of sector 1-6 in (B) 1995, (C) 1996 and (D) 1997. Location of whales was not recorded during the 1996 boat survey.

samples were collected non-systematically except on specific days when cow-calf pairs were targeted. Skin biopsy samples were stored in 70% ethanol or frozen in liquid nitrogen. In 1997, a midline slice of epidermis/blubber was stored in 10% neutral buffered formalin for immuno-histochemical analysis, and blubber samples were separately wrapped in acetone/hexane/methanol rinsed foil and frozen (-20°C) for organic chemical analysis (Moore *et al.*, 1998). Total DNA was extracted using standard methods (Sambrook *et al.*, 1989) as modified by Baker *et al.* (1991). The sex of individuals was identified by amplification and restriction fragment analysis of the ZFY/ZFX gene, as described by Palsbøll *et al.* (1992). Analysis of diversity and distribution of mitochondrial DNA (mtDNA) from samples collected in 1995 are reported by Baker *et al.* (1999).

Group size and behaviour

Prior to approaching a group of whales the group size and activity were recorded. Animals were considered to be part of a group if they were within one and a half whale lengths of each other and their activities were coordinated. Activities were placed into one of the following categories:

(1) *Rest*: whale remaining motionless, moving only slightly to breathe.
(2) *Travel*: directional forward movement that resulted in a change of location.
(3) *Social*: two or more non-calves interacting at the surface; no attempt was made to differentiate between social activity and sexual activity.
(4) *Approached boat*: whale altering its course to actively investigate the research vessel.
(5) *Play*: above surface activity not apparently linked to social activity. This included breaching, pectoral slaps, lobtailing and interactions with kelp.
(6) *Feeding*: whale travelling at the surface with mouth open.

Attempts were made to randomise sampling by regularly changing location of data collection, zig-zagging within the harbour and attempting to approach each group sighted. An exception was made in the case of cow-calf pairs. In most cases, encounters were terminated when whales showed signs of active avoidance. In 1996 and 1997, encounters with cow-calf pairs were minimised until directed surveys had been completed (see below) to reduce potential disturbance response to boat approaches.

Cow-calf abundance and habitat use

To estimate the total number of cow-calf pairs in Port Ross, directed surveys were conducted from aboard a motor/sailing vessel in 1996 and 1997. During each survey (two per year), the vessel moved around Enderby and criss-crossed Port Ross and Laurie Harbour (Fig. 1B, Fig. 3) in an attempt to approach every cow-calf pair in the area. Cow-calf pairs were located and photographed by an observer in the spreaders of the mast and a second photographer on deck and the location of all pairs encountered was noted on a map with 1km grids (Fig. 3).

Groups without calves were ignored. In both years the north coast of Enderby Island was not surveyed because of high sea states.

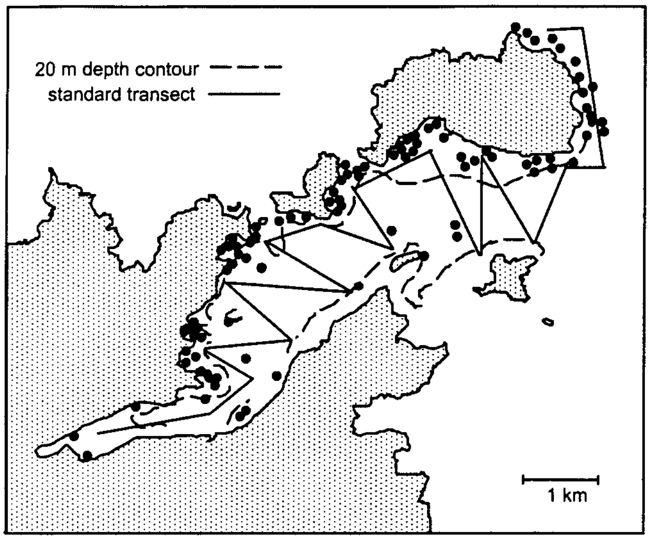

Fig. 3. Locations (filled circles) of all cow-calf pairs sighted during directed surveys conducted in winter, 1996 (3 and 5 August) and winter, 1997 (26 and 31 July).

RESULTS AND DISCUSSION

Distribution

During the winters of 1995, 1996 and 1997, whales congregated in Port Ross and nearby waters around Enderby Island and in Matheson Bay (Fig. 1). Observers on the helicopter that surveyed the length of the Auckland Islands in 1996 confirmed that the main aggregation of right whales was limited to Port Ross, despite what appears to be adequate habitat along the eastern coast of the main island. During a small boat survey in 1995, two whales were sighted outside Port Ross, along the northeast coast in Haskell Bay and one whale was sighted in North Harbour along the north coast (Fig 1B). This distribution is consistent with the location of whales reported from a RNZAF flight in 1993 (Donoghue, 1995).

Abundance and residency

Whales were present in Port Ross in high concentrations throughout the study period (mid-July until the first week in August) in all three years. Minimum abundance estimates from one-day shore- and boat-based counts were conducted in 1995, 1996 and 1997 as shown in Fig. 2. On 6 August 1995, observers counted a total of 71 groups including at least 87 adults (non-calves) and 9 calves. On 6 August 1996 the count was lower, in part due to poor sighting conditions. Only 50 groups were sighted, including 69 adults and 11 calves. On 28 July 1997, substantially more whales were sighted with 94 groups totalling 128 adults and 18 calves. The between-year variation may be real or may represent a within-season abundance variation, or variation in the ability of the observers to determine group sizes. In 1997, the density of whales was approximately five whales/km^2 in Port Ross.

A total of 217 individual whales have been photo-identified over three years of this study, almost half of which were identified in 1997 ($n = 92$; $n = 69$ in 1995; $n = 56$ in 1996). The larger proportion of whales identified in 1997 despite the shorter field season (16 days) corresponds to the increased photographic effort in that year. Of the sum total number of animals identified each year ($n = 236$), only 24% were resighted on subsequent days within a season. When whales were resighted within the 16-23 day field seasons, the average interval between first and last sighting was 6.4 days (SD = 4.0). The longest resighting interval within season extended to the entire 20 day period in 1995. This single adult was photo-identified on 20 July and resighted on the 9 August. About 15% of whales were identified in two years of the study years and only one whale was identified in all three years.

Although the resightings rate and interval between first and last sightings were constrained by the duration of the field season and photo effort, these seem lower than reported for some other wintering grounds (Bannister, 1990; Burnell and Bryden, 1997). It suggests that some whales are not resident throughout the field season.

Reproduction

Cow-calf pairs were present throughout the three winter field seasons. The small size of calves, some with the presence of foetal folds and wrinkly skin suggests they were newborn. Based on the three one-day censuses conducted, the number of calves averaged 12% (range 9-14%) of the total population. In an attempt to estimate the total number of cow-calf pairs in the area, directed surveys were conducted from aboard a motor/sailing vessel in 1996 and 1997. On 3 August 1996, 20 cow-calf pairs were approached. Two days later, 22 cow-calf pairs were encountered. On 26 July 1997, 24 cow-calf pairs were sighted and approached. Five days later, 26 cow-calf pairs were encountered.

In total, 43 cows have been photo-identified over three years of this study (12 in 1995, 11 in 1996 and 20 in 1997). This represents a minimum count of the number of mature females in this population. No cow sighted with a calf was resighted in a subsequent year or in the year preceding the birth of its calf. One female sighted in a social group of three in 1995 was resighted in 1997 with a calf.

Group size and activity

The size and pre-approach activity of groups were recorded on 358 occasions (Table 1). Most groups approached (29%) were composed of three or more (non-calf) individuals ($n = 103$). About 25% of non cow-calf groups encountered were single ($n = 90$), and 23% were in pairs ($n = 82$). Groups containing cow-calf pairs were encountered 23% of the time ($n = 83$). The largest group observed was a surface-active group of at least 10 individuals.

Most single individuals were found resting at the surface (59%). On 19% of encounters single individuals approached the research vessel and appeared attracted by the sound of the outboard motor in neutral. Travel by non-calf groups was rarely observed (3-10%). Activity of groups with a calf are considered separately below. Social activity was predominant with groups of three or more (non-calf) whales encountered (83%). Apparent mating activity was observed on most of these occasions as evidenced by abundant whitewater, erect penises and females exposing their bellies to the surface. Intromission between males and females was observed and documented on film once.

Presumed feeding was rarely observed despite the presence of swarms of *munidea sp.* On 30 July 1997 a single whale repeatedly surfaced with its mouth open. The film crew also documented a whale travelling underwater with mouth open, apparently pumping water with its tongue. Defecation was never observed.

Table 1

Frequency of activity of southern right whales in relation to group size and composition. N = Total observations.

	% Activity					
Group size	Rest*	Travel	Play	Social	Approach boat	N
Single	60	10**	11	-	19	90
Pair (excluding cow-calf pairs)	29	12	5	45	9	82
Group 3-10 (excluding cow-calf pairs)	14	3	0	83	<1	103
Cow-calf pairs	64	36	0	0	0	67
Cow-calf pairs and other(s)	50	13	0	38	0	16

* For cow-calf pairs, rest referred to the cow, regardless of the activity of the calf.

** One whale was observed swimming back and forth in a rip, presumably feeding.

Sex ratio

A total of 182 whales were sexed by molecular method. Of these, 96 were males and 86 were females (Table 2). Adults assumed to be cows because of their association with a calf were confirmed to be female ($n = 26$). The percent of females varied from 54% to 39% over the three years but the sex ratio did not differ significantly from 1:1 in any year. However, the collection of samples was not random with respect to cow-calf pairs and the ratios could be biased towards cows in some years. It is unknown how many whales are duplicate samples because biopsy samples were not always associated with photo-identification. However, attempts were made to minimise duplicate sampling by biopsying each whale in the same body area and scanning each whale approached for the small biopsy mark prior to sampling. Further analysis at nuclear loci should resolve this.

Table 2

Sex of southern right whales at the Auckland Islands as identified by molecular analysis of skin biopsy samples, 1995-97.

	1995		1996		1997		Total	
	Males	Females	Males	Females	Males	Females	Males	Females
Calves	2	2	2	2	1	1	5	5
Non-calves*	30	26	22	10	39	19	91	55
Cows	0	7	0	13	0	6	-	26
Total	32	35	24	25	40	26	96	86

* Excluding cows.

Cow-calf habitat use

The majority of sightings of cow-calf pairs during directed surveys were found on the western shore of Laurie Harbour and Port Ross and on the northeast shore of Enderby Island (Figs. 1B and 3). Weather conditions prevented a full survey of the north coast of Enderby Island but several cow-calf pairs were sighted along its northern coast during shore-based observations.

Of the 78 cow-calf pair sightings made in charted depths, 90% were located in waters less than 20m deep and all but three sightings were made within 500m of shore. Most groups including a calf (61%) were sighted resting at the surface and only 31% of groups including a calf were observed travelling (Table 1). Several episodes of riding above the mother's back were also observed. When cow-calf pairs were sighted with other whales (19% of the time), cows spent less time resting (38%) and spent an increased amount of time socialising at the surface (38%). During these occasions, the calf was more often found playing at the surface (13%).

On the Peninsula Valdés wintering grounds, Thomas and Taber (1984) reported that travel was the predominant activity for cows and calves during the entire infant period, and specifically characterised the behaviour of newborn calves while play did not begin until calves were one or two months old. We have not made any attempt to categorise the age of calves and, because of the limited duration of the field seasons, made no attempt to characterise the change in cow-calf behaviour over time.

CONCLUSIONS

The observations collected during the past three field seasons confirm that the Auckland Islands are an important habitat for wintering southern right whales. The total number of photo-identified animals is evidence that the current stock includes at least 217 whales including 43 reproductive females. Whales are concentrated almost exclusively in Port Ross, despite what appears to be adequate habitat to the east and further south. Whales are clearly engaged in behaviour typical of a breeding ground, with most groups engaged in social and sexual activity. Cows give birth in or near Port Ross and seek out shallow nearshore waters for calf rearing.

Re-identification of individual right whales from the Auckland Islands and Campbell Island within and between seasons demonstrates interchange between the two areas, suggesting that the two aggregations are part of a single sub-Antarctic wintering population (Cawthorn, 1990; Patenaude *et al.*, 2001). The low resightings rate within a season and length of residency at the Auckland Islands suggest the possibility of broader movement outside the New Zealand sub-Antarctic. However, significant differences in the distribution of mtDNA lineages indicates that whales wintering in the Auckland Islands are demographically distinct from those wintering along the southwest coast of Australia (Baker *et al.*, 1999). Further research should be directed at determining the genetic relationship between the New Zealand sub-Antarctic population and whales along eastern Australia and Tasmania.

The consistent presence of whales in the sub-Antarctic islands is in marked contrast to the very low levels of sightings along the New Zealand mainland and Kermadec Islands. This suggests that there has been a major shift in habitat use of a single stock or loss of a component of a historically sub-divided stock.

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A note on observations of southern right whales at Campbell Island, New Zealand

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ABSTRACT

Southern right whales were observed at Campbell Island, in New Zealand's sub-Antarctic ocean, over four field seasons (1983, 1994, 1995 and 1997). Whales were present in both the winter and autumn of 1994. An average of 7-21 whales were seen each season, with a maximum of 44 whales per day in July 1995. Individual whales were resighted in the area over periods of several days to two months. A change to shorter residence periods occurred between the early 1980s and 1990s. Some interchange occurs between Campbell Island and the Auckland Islands, with a recent decrease in number at the former and an increase at the latter.

KEYWORDS: SOUTHERN RIGHT WHALE; SUB-ANTARCTIC; CENSUS; PHOTO-IDENTIFICATION; BEHAVIOUR

INTRODUCTION

Southern right whales (*Eubalaena australis*) were once widely distributed around New Zealand's mainland and sub-Antarctic islands. Pre-European Maori chants and narratives identified right whales as 'Tohora'. Richards (1993) estimated that before exploitation there were at least 10,000 animals in these waters. In 1829, shore-based whaling from New Zealand began at Cook Strait and Preservation Inlet, and by the 1840s, approximately 80 shore-based whaling stations had been established. In addition, bay whaling from pelagic vessels began in the early 1830s and these operations also expanded quickly (McNab, 1913). This pressure was too great and by the mid-1840s southern right whales were considered to be commercially extinct (Dawbin, 1986). Although international protection for all right whales came into effect in 1935, the New Zealand 'population' has shown little sign of recovery in mainland coastal waters (IWC, 2001).

Historic whaling records confirm the occurrence of southern right whales in Northwest Bay, Campbell Island, during the winter months (e.g. Townsend, 1935), and between 1909 and 1916, two small whaling stations operated there (Kerr and Judd, 1978). Isolation, extreme weather conditions and poor catches caused the early closure of these operations. A New Zealand meteorological base operated at Campbell Island from the early 1940s until 1995 and opportunistic whale sightings were reported periodically by staff members between 1942 and 1964 (Gaskin, 1968). In 1973, the Fisheries Research Division of the New Zealand Ministry of Agriculture and Fisheries set up a New Zealand marine mammals sighting programme. Sporadic observations of southern right whales at Campbell Island included reports of numbers and signs of highly active social groups, and the occasional presence of cow/calf pairs (Cawthorn, 1978; 1982; 1988; 1993). From the mid-1980s until 1995, information from Campbell Island was largely based on opportunistic sightings. However, in 1988, a Department of Conservation team worked with meteorological staff to monitor the number of whales visiting Campbell Island throughout that year (Moore and Moffat, 1990).

In 1982-1983, one of us (RS) made detailed observations and obtained photographs for individual identification of whales at Campbell Island as one of the meteorological staff. In 1994-1995 an expedition was based at Northwest Bay and sightings of right whales were recorded from February to March 1994 and in July 1995. These records led to a dedicated programme of observations under the aegis of the especially established Project Tohora Trust. The Project's first three-month winter investigation was at Northwest Bay from June to September 1997. It's objectives are to:

(1) estimate winter residency by photo-identification of individual right whales at Campbell Island;
(2) determine winter abundance and minimal population estimate by daily census counts;
(3) record behaviour and habitat use of southern right whales at Campbell Island;
(4) develop educational material on the southern right whale for teaching purposes;
(5) bring an indigenous perspective to the science of the sea.

This report summarises Project Tohora's 1997 observations, as well as those made in 1983, 1994 and 1995.

METHODS

In 1983, 1994, 1995 and 1997, observations of southern right whales were made at Northwest Bay, Campbell Island (52°33'S, 169°09'E, Fig. 1). Shore-based observations were recorded and photographs of callosity patterns and unique markings of whales were obtained from shore-based stations or from small boats. In all seasons, observers used 35mm SLR cameras equipped with a range of 80-200mm, 440mm or 500mm lenses. *Fuji Neopan* 400 and 1600, *Fujichrome* 400, *Ektachrome* 400 and *Ilford* 400 film was used.

Prior to 1997

In 1983, shore-based counts of whales at Northwest Bay and Perseverence Harbour were conducted opportunistically by a single observer. Watch periods were also devoted to behavioural observations of whales. During February-March 1994, onshore observers conducted opportunistic counts of

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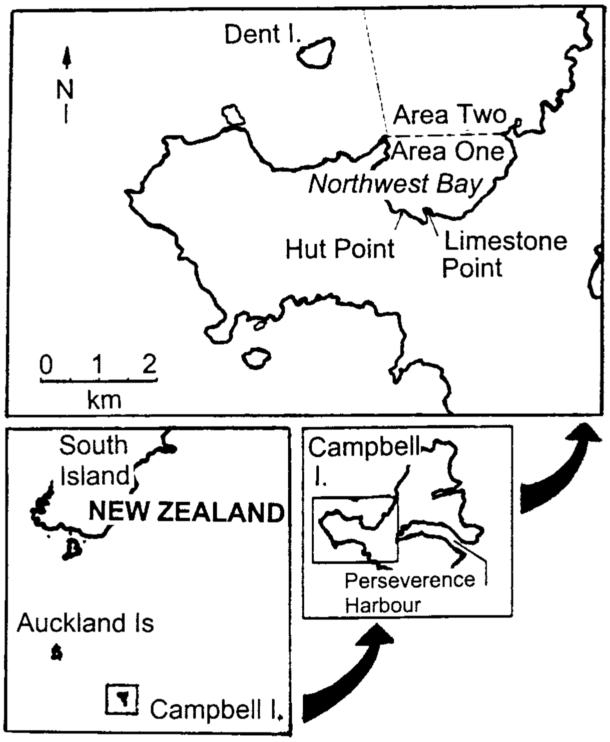

Fig. 1. The Northwest Bay (52°33'S, 169°09'E) area of concentration of southern right whales at Campbell Island.

whales at Northwest Bay. Boat and shore-based observations were made from 1-24 July 1995. Counts were obtained on days during periods of high social activity when whales were more visible. Sea-based operations were conducted from two 3.8m *Naiad* rigid-hull inflatables with 25hp *Yamaha* outboards.

1997

In 1997, a team of six people worked at Northwest Bay from 21 June to 1 September. From 24 June to 26 August, two systematic whale counts were made daily at 0900 and 1400hrs. Weather, seastate and visibility were noted for each count. Additional behavioural observations and opportunistic counts were conducted throughout the day. The 0900hr count was made from Hut Point (Fig. 1). Two areas (Areas One and Two, see Fig. 1) were divided into segments and observers scanned their assigned segment for a period of ten minutes. Observers communicated when whales entered or departed from their segment to ensure that no whales were double-counted. The number of whales and their positions were entered onto a grid map. Group size and whale activity was also recorded. The 1400hrs count was conducted either from Hut Point or from Hut Point and Limestone Point (Fig. 1). Simultaneous counts from more than one location were coordinated through the use of VHF radios.

In addition, two *Naiad* rigid-hull inflatables, as in 1995, were deployed with a crew of two on nine days, with the priority to photograph whales. Socially active whales were given precedence over single 'resting' individuals. If the whales showed signs of disturbance, i.e. dramatic behaviour changes, observers either approached a different group or re-approached the same group after a 'rest' period of 20-30 minutes. Boat days were limited by either unfavourable sea conditions or lack of whales.

RESULTS

A summary of whale sightings at Campbell Island is given by year in Table 1. In the 1980s, 58 days of observations from shore were made. In the 1990s, 91 days of observations from shore and 17 days of boat observations were made.

11 June-26 September 1983

A number of individually identifiable whales were resident in Northwest Bay during 1983 (Table 2): one cow with a new-born calf (83-05); one cow with a new-born albino calf (83-11); one whale with a saddle blaze (SB-01); and one sub-adult (83-13). The sub-adult was resighted interacting with New Zealand sea lion pups at Perseverance Harbour on 20 November. There were seven previous sightings of the same whale interacting with sea lion pups in Northwest Bay (10 July-21 August). Similar accounts of such behaviour had been noted in previous seasons (D. Harris, pers. comm.).

Whales were seen resting and travelling slowly within Northwest Bay until late June. Socially active groups of between 2-9 individuals were observed from July-September. Whales were observed engaging in sexual activity. Single whales were occasionally seen with open mouths but feeding behaviour was not observed.

11 February-18 March 1994

Whales were seen feeding on most days; breaching was occasionally observed and no whales were seen resting. A cow and her calf were resident for 28 days between 19 February and 18 March.

1-24 July 1995

Whales were observed in socially active groups of 2-9 individuals. No calves were observed. The highest concentration of socially active groups occurred on the eastern side of Northwest Bay. Courting and sexual activity were evident. On nine days there were between 3-5 socially active groups present in the Northwest Bay study area.

22 June-29 August 1997

During this time, whales were generally observed resting or cruising slowly within the bay. No calves were seen. Breaching, lobtailing and social activity intensified in late August. Whales were observed feeding on two occasions.

Table 1

Records of southern right whales at Campbell Island, 1983-97.

Year	Period	Locality	Total days observed	No. of whales per day			Mean residency period of recognised individuals	Total no. identified animals
				Maximum	Minimum	Average		
1983	11 Jun.-26 Sep.	Northwest Bay	56	30	2	14.4 (n=56)	75 days, n=4, range 60-85	34
1983	19 Jun.-25 Jun.	Perseverence Harbour	2	2	1	1.5 (n=2)	Non-resident whales	0
1994	11 Feb.-18 Mar.	Northwest Bay	13	5	1	2.3 (n=13)	22.3 days, n=3, range 3-36	3
1995	1 Jul. -24 Jul.	Northwest Bay	24	44	5	20.6 (n=12)	0 (not recorded)	7
1997	22 Jun.-29 Aug.	Northwest Bay	54	28	1	7.2 (n=67)	13.8 days, n=5, range 2-27	31

Table 2

Northwest Bay residency periods of recognised individuals, 1983, 1994 and 1997[1].

ID no.	First and last sightings	No. days
1983[2]		
83-05	19 Jun. - 28 Aug.	71
83-11	29 Jul. - 26 Sep.	60
SB-01	5 Jun. - 28 Aug.	85
83-13	3 Jul. - 25 Sep.	84
1994		
94-01	11 Feb. - 18 Mar.	36
94-02	19 Feb. - 18 Mar.	28
94-03	3 Mar. - 5 Mar.	3
1997		
SB-02	24 Jul. - 19 Aug.	27
14	27 Jul. - 9 Aug.	14
08	2 Aug. - 8 Aug.	7
31	6 Aug. - 24 Aug.	19
25	8 Aug. - 9 Aug.	2

[1] 1995 residency periods were not recorded. [2] 1983 Perseverence Harbour, no residency (i.e. whales did not remain).

Repeated sightings of five photo-identified right whales revealed that some animals remain resident in the area for several weeks, the longest known period being 27 days (Table 2).

DISCUSSION

Southern right whales were observed at Campbell Island during February to March and June to September, with peaks in abundance between July and September. These observations are consistent with earlier records that show whales to be present here between March and October, with peaks between June and August (Cawthorn, 1978; 1982; 1988; 1993; Moore and Moffat, 1990).

At least some animals remain in the Bay in the winter and early spring (June-September). In the one late summer observation period, one cow-calf pair was resident over a 28 day period. Individual whales remained in Northwest Bay for 8-12 weeks in 1983, including two cow-calf pairs (Table 2). Shorter residency periods of recognised individuals and the absence of cow-calf pairs in the 1990s may reflect a change in habitat use since the early 1980s.

In 1983 in Northwest Bay, the average number of whales seen daily was 14.4 and most whales arrived in mid-winter (9 July). The average number was smaller (7.2) in 1997 and most whales arrived later (20 August). It is possible that the expedition left the Island before the peak in occupancy. It is clear that Campbell Island is an important habitat for right whales in this part of the Southern Ocean but it seems likely that relatively large annual variations occur in numbers visiting the island. Photo-identification work carried out with the University of Auckland revealed that some interchange between Campbell Island and the Auckland Islands occurs (Patenaude *et al.*, 2001).

Patenaude *et al.* (1998) and Patenaude and Baker (2001) found concentrations of right whales in Port Ross and nearby Enderby Island in the Auckland Island Group between 1995 and 1997. The population increased there during the 1997 season, whereas the Campbell Island sightings decreased. Further observations and individual identifications will be necessary to examine the relationship between the occupancy of these two habitats. [It is unclear whether these animals represent a remnant of the New Zealand mainland population or a distinct stock that never migrated to the mainland's coastline (Gaskin, 1968).]

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A note on movements of southern right whales between the sub-Antarctic Auckland and Campbell Islands, New Zealand

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ABSTRACT

To investigate the interchange of southern right whales between wintering grounds of the New Zealand sub-Antarctic, photographs of 31 individuals from Campbell Island were compared to 217 individuals from the Auckland Islands. Three whales first identified at the Auckland Islands in 1995 or 1996 were found at Campbell Island in 1997. One whale identified at Campbell Island in 1995 was seen later that same winter at the Auckland Islands. This provides the first evidence of both within- and between-year movements of whales between the two New Zealand sub-Antarctic aggregations, suggesting that they are part of one intermingling population.

KEYWORDS: SOUTHERN RIGHT WHALE; BREEDING GROUNDS; SUB-ANTARCTIC; MOVEMENTS; PHOTO-IDENTIFICATION

INTRODUCTION

Although once abundant throughout New Zealand waters, there are now only two winter concentrations of southern right whales (*Eubalaena australis*) in New Zealand waters. Whales have primarily been observed at the Auckland Islands (50°33’S, 166°15’E; Patenaude *et al.*, 1998; Patenaude and Baker, 2001) with a smaller aggregation found 160 n.miles further south at Campbell Island (52°33’S, 169°09’E; Stewart and Todd, 2001); see Fig. 1. The relationship between these two habitats is unclear. The only previously reported resighting between islands was of a presumed female sighted in May 1988 at Campbell Island and thought to be resighted at Auckland Islands 1.5 months later (Cawthorn, 1990).

Here we report on a collaborative effort to compare regional photo-identification catalogues collected during field expeditions in 1995 and 1997 at Campbell Island (BT and RS) and in 1995, 1996 and 1997 at the Auckland Islands (NP).

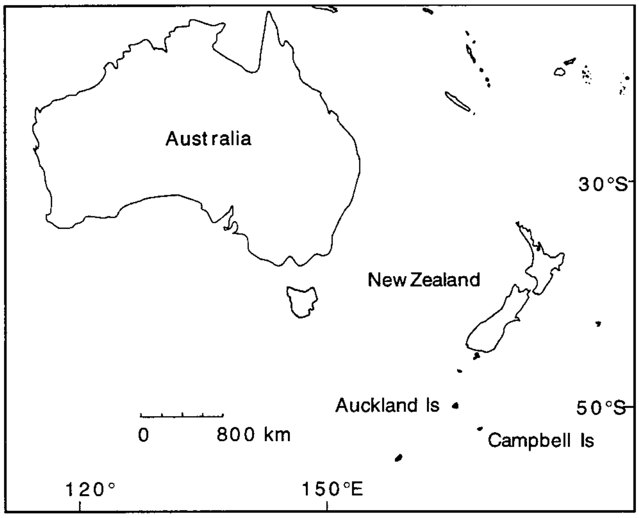

Fig. 1. Location of New Zealand’s sub-Antarctic Auckland and Campbell Islands.

METHODS

Identification photographs were collected in the Auckland Islands during winter field expeditions from mid-July to the first week of August 1995, 1996 and 1997 and in Campbell Island in July 1995 and from late June to late August 1997. Callosity patterns, lip ridges or unusual colour patches were used for individual identification (Payne *et al.*, 1983; Kraus *et al.*, 1986). Photo-identification was conducted from small vessels (3.8-4.7m) at both locations, and at times from the deck or mast of a larger motor/sailing vessel (Auckland Islands) or from cliff-tops along Northwest Bay at Campbell Island. Photographs were taken at the Auckland Islands with *Kodak* Tri-X or T-Max black and white film (ISO 400, pushed to 800 or 1600) or *Fuji* film (ISO 400 and 1600) and at Campbell Island using 35mm SLR cameras equipped with a range of lenses from 80-500mm.

Identification photographs at the Auckland Islands were collected non-systematically, except in cases when efforts were directed at capturing cow-calf pairs (Patenaude and Baker, 2001). At Campbell Island, photographs were selectively targeted towards socially active groups. The comparison of photographs between the two regions was limited to the whales’ left side. A total of 31 individually identified whales from Campbell Island in 1995 ($n = 5$) and 1997 ($n = 26$) were compared to the Auckland Islands catalogue of 217 individually identified whales collected in 1995 ($n = 69$), 1996 ($n = 56$) and 1997 ($n = 92$). Individually identified whales were compared by two people experienced with photo-identification, and matches were confirmed by a third person experienced with right whale photo-identification. The sex of some photo-identified animals was identified using molecular methods from skin biopsy samples (Patenaude and Baker, 2001).

RESULTS

Four matches were made between the two regional catalogues (Fig. 2). Of the five whales identified at Campbell Island in 1995, one was sighted at the Auckland Islands later that winter. This whale (ID22, Fig. 2) was first photographed

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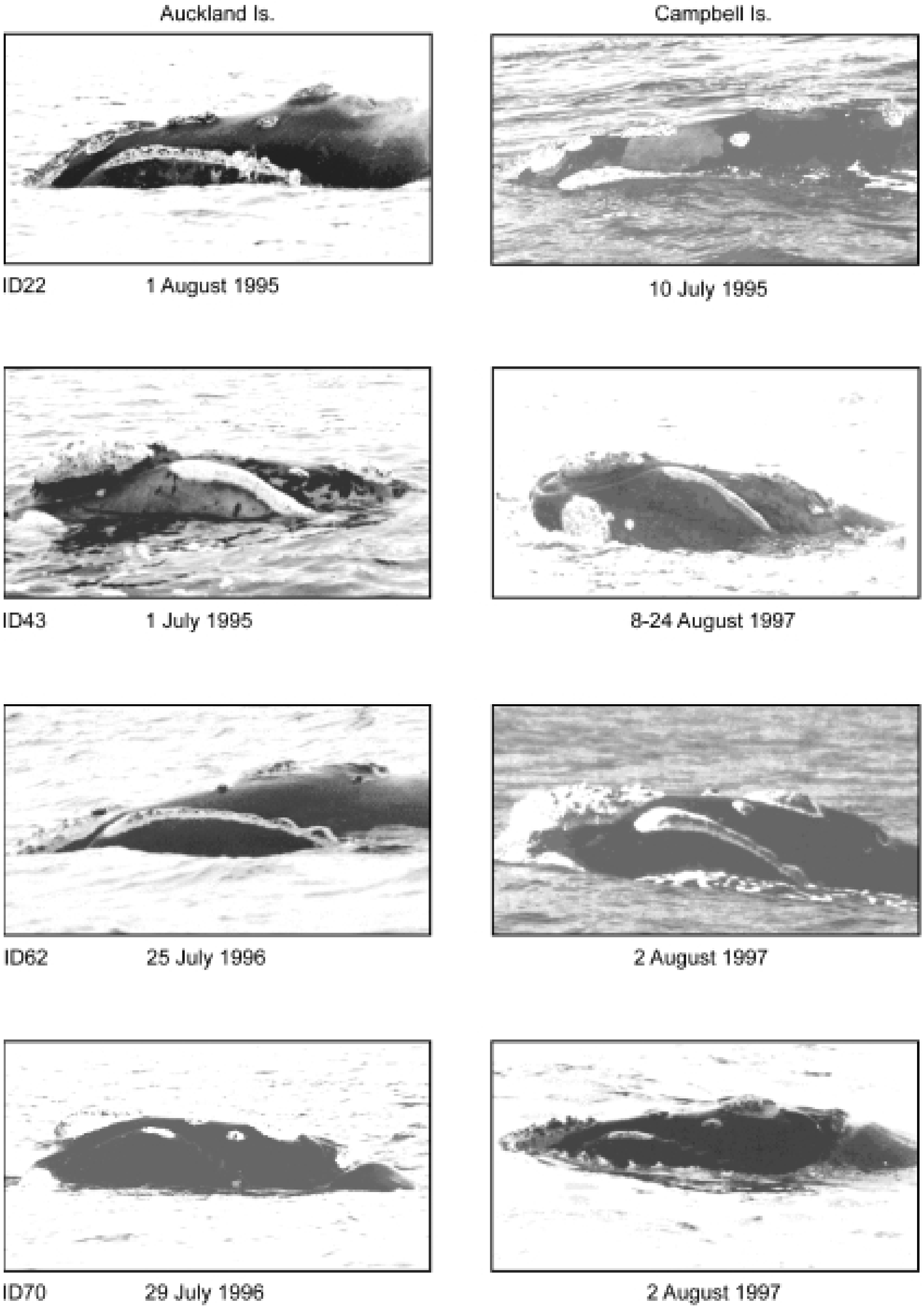

Fig. 2 Photo-identified southern right whales matched between Auckland Islands (left) and Campbell Island (right).

at Campbell Island on 10 July 1995. It was then photographed at the Auckland Islands 22 days later, in a socially active group.

Of the 26 whales photo-identified at Campbell Island in 1997, three were matched to photographs collected at the Auckland Islands. One whale (ID 43, Fig. 2), identified as a male, was sighted in July 1995 at the Auckland Islands and resighted two years later at Campbell Island on 8, 9 and 24 August 1997. These last three sightings represent the longest within-season residency period recorded for Campbell Island (Stewart and Todd, 2001).

One whale sighted at the Auckland Islands on 25 July 1996 (ID 62, Fig. 2) was resighted on 2 August 1997 at Campbell Island. Another whale sighted on 29 July 1996 at the Auckland Islands (ID 70, Fig. 2) was also resighted 2 August 1997 at Campbell Island.

CONCLUSIONS

The photographic evidence provides documented evidence of both within- and between-year movements of whales between the two New Zealand sub-Antarctic aggregations and suggests that the two aggregations are part of one intermingling population. There is insufficient information to conclude if there is age or sex class sub-division between the two regions. However, while almost 12% of whales sighted at the Auckland Islands in 1995-1997 were calves (Patenaude and Baker, 2001), no cow-calf pairs were sighted at Campbell Island in 1995 or in 1997, although three cow-calf pairs were sighted there in 1983 (Stewart and Todd, 2001).

ACKNOWLEDGEMENTS

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Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Península Valdés, Argentina

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ABSTRACT

Photographs of the right whales which occur between June and December in the waters surrounding Península Valdés, Argentina, have been obtained from aerial surveys conducted each year from 1971 to the present. Resightings of previously catalogued individuals enable various demographic parameters to be estimated. From analyses of multiple resightings of females accompanied by calves, estimates of the following demographic parameters were obtained, based on the data collected during 1971-90: mean calving interval 3.35 yrs (SE = 0.05 yrs); mean age at first calving 9.1 yr (SE = 0.3 yr); adult female annual mortality rate 0.019 (SE = 0.005); annual percentage rate of population increase 6.9% (SE = 0.7%); reproductive female population size in 1990: 328 animals (SE = 21). No evidence of any trend with time in mean calving interval, mortality rate or rate of population increase was found.

KEYWORDS: SOUTHERN RIGHT WHALES; PHOTO-IDENTIFICATION; INDIVIDUAL RECOGNITION; BIOLOGICAL PARAMETERS

INTRODUCTION

Photo-identifications of individual whales based on natural markings have been obtained from aerial surveys each year since 1971 to study a population of southern right whales (*Eubalaena australis*) on their winter assembly grounds around Península Valdés, Argentina. The methods used to record natural markings and to identify resightings of individual whales, and the characteristics of the study season and area, are described by Payne (1986) and Payne *et al.* (1983).

An analysis of the data to estimate population size and demographic parameters was conducted by Payne *et al.* (1990) using data from 1971-1986. For the present analysis, the data for the period 1971-1990 were available. The study is ongoing and photographs have continued to be taken each year, however, photographs after 1990 have not yet been catalogued.

A total of 1,223 distinct individuals was catalogued up to 1990, and each individual was seen in an average of 2.4 different years. Some 339 individually identified whales were observed at least once in definite association with a calf, and each of these were recorded in an average of 2.15 different years with a calf, giving a total of 728 observed calvings, where an 'observed calving' means that the mother was individually identified and recorded as having a calf, even if the calf was not individually photo-identifiable (Fig. 1).

Survey effort varied from year to year, and therefore the numbers identified in each year do not necessarily reflect the numbers of whales present.

For the reasons discussed by Payne *et al.* (1990), only the sightings of females accompanied by calves are used to estimate population parameters. The reasons for not using the other components include:

(1) animals not previously seen with a calf are of unknown sex and maturity status, whereas the probability of a whale entering the study area during the study period may well depend on sex and maturity status;

(2) although some females were seen in the study area in years in which they apparently had no calf, the absence of an accompanying calf in an observation does not necessarily imply that no calf is present, hence it is not possible to divide observations of females into those with and without calves.

Conventional mark release models are not suitable for these data because of the periodic nature of the calving process. Breeding females calve at intervals of 2-5 years, mainly 3 years (Fig. 2). Although females are sometimes observed in the study area in years in which they do not calve, the probability of them being in the area and being observed appears to be less than in years in which they calve. Of whales which had been previously observed to calve, there were a total of 389 resightings with calves, but only 242 resightings without calves. Since the average calving interval is at least three years (see below), these figures imply that a whale is much more likely to be seen in the study area when it has a calf than when it does not. Hence, the assumptions of independence of sightings probabilities from year to year that are required for most mark release models are not fulfilled.

The birth interval model of Barlow and Clapham (1997) is also not applicable to these data, since it relies on the assumption that the probability of sighting a whale is independent of whether or not it has a calf.

The distribution of observed calving intervals (Fig. 3) does not directly reflect the true calving interval distribution because not all calvings are observed. Not all calvings that occur in the study area are necessarily recorded because not all whales in the study area are recorded each year and not all calves have yet been born when the mother is sighted. The calf, even if present, is not always seen when the mother is sighted, nor is it always in sufficiently close or unique association with an adult for the latter to be definitely identified as the parent (for example when there are two or more adults in close proximity to the calf). Furthermore, some calvings in the population may occur outside the study area. Two females that had been recorded with calves off

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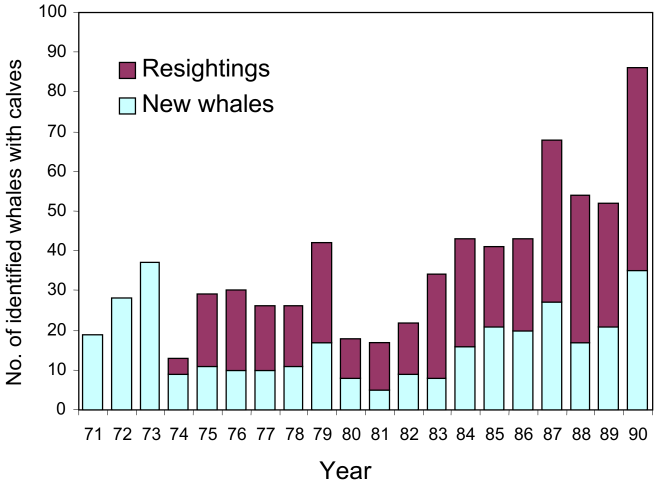

Fig. 1. Number of whales individually identified with calves, divided into those observed to calve for the first time, and those observed to calve for a second or subsequent time.

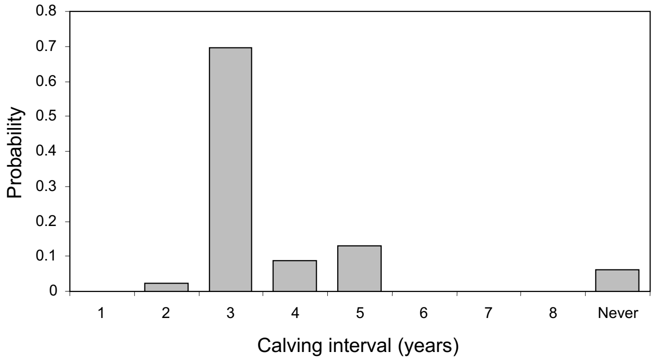

Fig. 2. Estimated distribution of calving intervals in the breeding population.

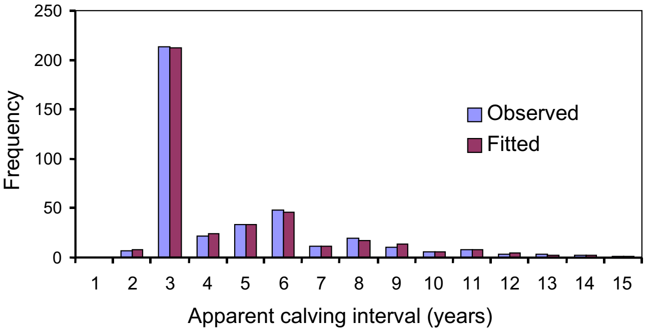

Fig. 3. Observed and fitted distributions of intervals between observed calvings of individually identified whales.

Península Valdés were resighted with calves in later years in a different nursery area off Laguna, southern Brazil (Best *et al.*, 1993).

In this paper an amended version of the model developed by Payne *et al.* (1990) is applied to the 1971-90 data to estimate the pattern of calving intervals and other demographic parameters.

MATERIAL AND METHODS

As noted above, the observation of a female in a given year without a calf does not necessarily imply that it did not calve in that year. Hence, only positive identifications of females with calves are used in this analysis. A female is recorded as calving in a given year if it is seen at least once in exclusive close association with a calf in that year, using the criteria given by Payne and Dorsey (1983).

The data consist of sequences of observed calvings of whales. There is one sequence for each of the 339 whales that was observed to calve at least once in the study period (1971-90 for this analysis). Each sequence is of the form: (t_{ij}, $j = 1, ..., k_i$) where t_{ij} is the year of the jth observed calving of whale i and k_i is the number of observed calvings of whale i. For example, a typical sequence might be: (1973, 1976, 1983, 1989).

Although relatively few calves were observed with distinctive markings that enabled them to be re-identified subsequently as adults, those few provide potentially valuable information on the age at first calving. Of 246 calves entered into the catalogue, 25 were subsequently re-identified with calves of their own.

We first outline a method for interpreting the calving sequence data and then develop an extension to make use of the identifications of whales as calves. To interpret the calving sequence data, two models are required:

(1) a model of the population which includes a model of the calving sequences occurring in the population;
(2) a model of the sampling process which enables determination of the likelihood or goodness-of-fit of the population model to the observed data.

The parameters of the population model are estimated by finding the parameter values that maximise the likelihood of the observed data.

Population model

The model is of the female breeding population. An individual is considered a member of the breeding population from the year of its first calf to the year of its last calf, both years inclusive.

Generic population model

We first define a generic model which involves minimal assumptions but many potential parameters, and then consider special cases of the generic model involving fewer unknown parameters. The most parsimonious model giving acceptable fit to the data will be selected.

The model contains the following parameters:

C_t	expected number of calvings in year t. It is convenient to define t so that $t = 0$ refers to the first year for which there are data. The actual number of calvings in year t is assumed to have a Poisson distribution with expectation C_t.
R_t	expected recruitment to the breeding population in year t (expected number of animals calving in year t for the first time). The actual number of first calvings in year t is assumed to have a Poisson distribution with expectation R_t.
N_t	expected size of the female breeding population in year t.
m	maximum interval between successive calvings of an individual.
$h_{t,i}$ ($i = 1, ..., m$)	probability that a whale calving in year t will next calve in year $t+i$ ($i = 1, ..., m$). The probability that a whale calving in year t never calves again is $1-\sum_i h_{t,i}$.

As will become apparent, it is necessary to model the population parameters from m years prior to the start of the data series, up until the end of the data series ($t = -m, \ldots, T$, where T is the last year with data).

The C_t satisfy the recurrence relation:

$$C_t = R_t + \sum_{i=1}^{m} h_{t-i,t} C_{t-i} \tag{1}$$

The expected breeding population in year t,N_t, is given by:

$$N_t = C_t + \sum_{i=1}^{m-1} C_{t-i} \sum_{j=i+1}^{m} h_{t-i,j} \tag{2}$$

The first term on the right hand side of this expression is the expected number of individuals calving in year t; the second term is the expected number of individuals which do not calve in year t but which have two adjacent calvings that straddle year t. The expression reflects the definition of the breeding population as being females between the year of their first calf and the year of their last calf, both end points inclusive.

Mortality is not featured explicitly in the model. It is implicitly included in the probability that a whale will never calve in the study area again, if ‘mortality’ is defined to include reproductive senescence and/or permanent emigration as well as actual death.

ASSUMPTIONS

The probability that a whale calving in year t will next calve in year $t+i$ is assumed to be independent of its calving history prior to year t. Under this assumption, the parameters $h_{t,t+i}$ determine the calving sequence process in the breeding population.

Minimal population model

The minimal model is the simplest meaningful special case of the generic model. The minimal model includes the following additional assumptions:

(a) the calving interval probabilities are constant over time: $h_{t,i} = h_i$

(b) the expected recruitment (number of first calvings) increases exponentially at a constant annual rate, r:

$$R_{t+1} = R_t(1+r) \tag{3}$$

Under these assumptions, the expected number of calvings, C_t, and the breeding population size, N_t, also increase at the same annual rate, r.

The minimal model contains (m+2) independent biological parameters to be estimated: h_i ($i = 1, \ldots, m$), r, and C_0, the expected number of calvings in the initial year. When the values of these parameters are specified, the full sequence of C_t ($t = -m, \ldots, T$) and N_t can be derived using equations (1) and (2). The procedure for determining the choice of m, the maximum calving interval, is described below.

For computational purposes it is convenient to work with the following transformation of the h_{it}:

$$\lambda_{it} = \log(h_{it} / (1 - \sum_{j=1}^{i} h_{jt})) \tag{4}$$

There is a 1:1 relationship between the λ_{it} and the h_{it}, but each of the λ_{it} can take any value in the range $(-\infty, +\infty)$. Some derived parameters of interest are defined in the following sections.

Implied survival/mortality rates

The *equivalent annual survival rate, S,* corresponding to a given set of calving interval probabilities, h_i, is the level of annual survival that would give the specified probability of a given calving being the last calving if the survival probability were independent of the calving history. S is the value which satisfies the following equation:

$$\sum_{i=1}^{m} h_i S^{-i} = 1 \tag{5}$$

If survival rate is affected by calving history, then the equivalent survival rate is a form of weighted average of the history-specific rates. The *equivalent instantaneous mortality rate* is given by:

$$M = \ln S \tag{6}$$

The quantities, $h_i^* = h_i S^{-i}$, can be regarded as conditional calving interval probabilities, conditional on survival to the next calving.

Mean calving interval

The mean calving interval is given by:

$$\bar{h} = \sum_{i=1}^{m} i h_i / \sum_{i=1}^{m} h_i \tag{7}$$

Mean calving rate

We define the ‘mean’ calving rate to be the ratio of the expected number of calves produced in a year to the expected breeding population size in that year: C_t / N_t. Because we have defined an individual’s membership of the breeding population to begin and end with a calving, our definition of calving rate may yield slightly higher values than some other definitions in use.

Deviations from the minimal model

After fitting the minimal model, we investigated whether an improved fit to the data could be obtained by allowing additional parameters. The following extensions to the minimal model were considered, each involving one extra parameter.

(1) time trend in mortality rate: $M_t = M_0 + t\mu$ (μ constant);

(2) time trend in rate of increase: $r_t = r_0 + t\rho$ (ρ constant);

(3) time trend in calving interval probabilities: $\lambda_{t,i} = \lambda_i + \gamma t$ (γ constant).

Positive values of γ correspond to a tendency for calving intervals to decrease with time.

When investigating a possible time trend in mortality rate, the conditional calving interval probabilities, h_i, are assumed constant over time. When looking for a time trend in the calving interval probabilities, these are rescaled so that the equivalent mortality rate remains constant over time. Initially, one is looking only for evidence of specific *directions* of departure from the minimal model. Only when such evidence is found is it worthwhile considering in more detail the nature of such departures.

Modelling the sampling process

For the model of the sampling process, the following additional notation is required:

n_t	number of distinct calvings observed in year t;
$n_{t,i}$	number of individuals that were observed to calve in year t and were next observed to calve in year $t+i$ $(i > 0)$;
$n_{t,0}$	number of individuals that were observed to calve in year t but not subsequently;
$n_{-,t}$	number of individuals that were first observed to calve in year t;
T	last year of data ($T = 0$ is the first year of data, hence there are T+1 years of data in total unless some years were missed);
U_t	expected number of calvings (not necessarily observed) in year t by individuals who have not previously been observed to calve;
p_t	probability that a calving occurring in year t will be observed: $p_t = 0$ for $t < 0$;
$g_{t,i}$	probability that an individual that calves (but is not necessarily observed) in year t will next be observed to calve i years later $(i > 0)$;
$g_{t,0}$	probability that an individual that calves (but is not necessarily observed) in year t will not be observed to calve again within the period of the current dataset.

ASSUMPTIONS

The probability that a random calving in a given year will be recorded is assumed to be independent of its previous calving record. Under this assumption, the expected frequency of a calving sequence (t_1, t_2 ,...) is the product of the expected frequency of the initial observation in the sequence (the expected number of first observed calvings in year t_1) times the product of the probabilities of each subsequent step in the sequence given the sequence to date.

Following Cormack (1981), the frequencies of each possible calving sequence are treated as independent random variables each with a Poisson distribution. To evaluate the likelihood of the data, we require an expression for the expected frequency of a given calving sequence.

The following equations yield the values of U_t in terms of C_t:

$$U_t = C_t \ (t \leq 0)$$

$$U_t = R_t + \sum_{i=1}^{m} h_{t-i,t} U_{t-i}(1 - p_{t-i}) \ (t > 0) \qquad (8)$$

The expected number of whales first observed to calve in year t is p_t U_t.

The probability that a whale observed to calve in year t is next observed to calve in year $t+i$ is given by:

$$g_{t,1} = h_{t,1} p_{t+1}$$

$$g_{t,i} = h_{t,i} p_{t+i} + \sum_{j=1}^{i-1} h_{t,j}(1 - p_{t+j}) g_{t+j,i-j} \qquad (i = 2,...,m) \qquad (9)$$

$$g_{t,i} = \sum_{j=1}^{m} h_{t,j}(1 - p_{t+j}) g_{t+j,i-j} \qquad (i > m)$$

The probabilities $g_{t,i}$ are calculated recursively: first for $i = 1$, then for $i = 2$, and so on.

The probability of the terminal step in a sequence (the probability that a whale observed to calve in year t is not observed to calve again) is given by:

$$g_{t,0} = 1 - \sum_{i=1}^{T-t} g_{t,i} \qquad (t = 0,\dots, T-1)$$
$$g_{T,0} = 1 \qquad (10)$$

The expected frequency of a given observed calving sequence (t_1, t_2,..., t_n) is thus:

$$p_t U_t \Big(\prod_{j=1}^{n-1} g_{t_j,t_{j+1}}\Big) g_{t_n,0} \qquad (11)$$

Hence, the log-likelihood of the entire dataset, ignoring constant terms, is given by:

$$L = \sum_{t=0}^{T} \left[n_{-,t} \ln(p_t U_t) - p_t U_t + \sum_{i=0}^{\min(m,T-t)} n_{t,i} \ln g_{t,i} \right] \qquad (12)$$

The parameters are estimated by maximising the log-likelihood over the free parameters. There are (m+2) + (T+1) free parameters to estimate in the minimal model: C_0, r, h_i ($i = 1$,..., m), and p_t ($t = 0$,..., T). In each of the three alternative models listed above there is one extra parameter. The values of all other parameters are calculated from these basic parameters using the above equations.

The expression n_t/p_t provides an estimator for the actual (as opposed to the expected) number of calvings occurring in year t.

The variances of each parameter estimate are estimated from the curvature of the log-likelihood. Using vector notation, let **x** be the vector of free parameters and **z** be the vector of calculated parameters. Then:

$$\mathrm{var}(\mathbf{x}) \cong (\delta^2 L/\delta x^2)^{-1} \qquad (13)$$

$$\mathrm{var}(\mathbf{z}) \cong (\delta z/\delta x) \ \mathrm{var}(\mathbf{x}) \ (\delta z/\delta x)^{\mathrm{T}} \qquad (14)$$

where the superscript $^{\mathrm{T}}$ denotes transpose.

There remains the question of how to choose the value of m, the maximum length of calving interval. Because a model with a low value of m is a special case of a model with a higher value of m, the likelihood increases with increasing m. We therefore choose, as a conservative estimate of m, the lowest value of m that is consistent with the data in the sense of not being rejected in favour of a higher value of m in a likelihood ratio test. This is not necessarily the best criterion for general use, but, as noted below, the results in this case indicate $m = 5$ so clearly that a detailed consideration of the selection criteria for m is not necessary for this particular dataset.

Age at first calving

Some of the calves observed had distinctive markings that enabled them to be re-identified subsequently as adults. Since these animals are of known age, they provide information on the age at first reproduction. The distribution of ages at first observed calving of known-age animals is shown in Fig. 4. These do not necessarily correspond to the true age at first calving because not all calvings are seen.

Although the sample of known-age animals that have themselves been seen to calve is still small, a method of analysis is outlined here with a view to re-applying it when the data for more years become available.

The true distribution of age at first calving can be investigated by extending the above model to include the observations of identified individuals as calves. The following additional parameters are required:

l	maximum age at first calving;
$f_{t,i}$ $(i = 1, ..., l)$	probability that a calf in year t will first calve itself at age i;

α	probability that a calf in the catalogue has sufficiently distinctive marks to be re-identifiable as an adult;
$q_{t,i}$	probability that a calf observed with distinctive markings in its year of birth t will be first observed to calve at age i ($i = 1, ..., l$);
$q_{t,0}$	probability that a calf observed with distinctive markings in year t will not be observed to calve again within the period of data.

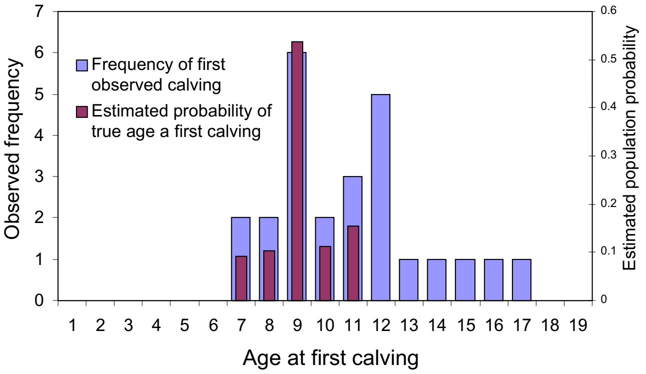

Fig. 4. Distribution of age at first observed calving of known-age individuals, and estimated probability distribution of true age at first calving in the population.

The following additional data are used:

$a_{t,i}$ ($i = 1, ..., l$)	number of calves observed with distinct markings in year t which are subsequently first observed to calve at age i;
$a_{t,0}$	number of calves observed with distinct markings in year t which have not subsequently been observed to calve.

The $q_{t,i}$ are given by the following expressions:

$$q_{t,i} = \alpha\left[f_{t,i} p_{t+i} + \sum_{j=1}^{i-1} f_{t,j}(1 - p_{t+j}) g_{t+j,i-j} \right] \qquad (i = 1, \ \dots, l)$$

$$q_{t,i} = \alpha\left[\sum_{j=1}^{l} f_{t,j}(1 - p_{t+j}) g_{t+j,\, i-j} \right] \qquad (i > l) \qquad (15)$$

$$q_{t,0} = 1 - \sum_{j=1}^{T-t} q_{t,j}$$

For each t, the $f_{t,i}$ will sum to less than unity; many calves will never themselves have a calf, for example because they are male or die before attaining maturity. The parameter α is a nuisance parameter, which can be discarded and subsumed into the $f_{t,i}$, if the latter are interpreted as relative rather than absolute proportions.

The mean age at first calving for females born in year t is given by:

$$\sum_{i=1}^{l} i f_{t,i} \Bigg/ \sum_{i=1}^{l} f_{t,i} \qquad (16)$$

The age at which a whale identified as a calf is first observed to have its own calf can be treated as a multinomial random variable, taking values $\{0,\dots, l\}$ with probabilities $q_{t,j}$ ($j = 0, ..., l$) where the value zero means 'never or not yet'. Hence, the log-likelihood of these data, ignoring constant terms, is given by:

$$L_2 = \sum_{t=0}^{T-1} \sum_{j=0}^{\min(l,T-t)} a_{t,j} \ln q_{t,j} \qquad (17)$$

This log-likelihood is added to the calving-sequence log-likelihood given in expression (10), to yield a total log-likelihood. Since the sample size of known-age animals is currently too small to permit examination of possible changes in the age at first calving over time, we assume for this analysis that the $f_{t,i}$ are time-invariant, i.e. $f_{t,i} = f_i$. The f_i are estimated along with the parameters of the calving-sequence model by maximising the total log-likelihood.

The maximum age at first calving, l, is chosen by finding the minimum value of l which is consistent with the data in terms of not being rejected in favour of a higher value of l. This procedure yields a conservative estimate of the mean age at first calving.

Survival rate of calves to first reproduction

Since not all calves have sufficiently distinctive marks to be re-identifiable as adults, a direct estimate of survival from birth to maturity based on the proportion of calves subsequently identified as adults would be liable to be negatively biased. We can, however, estimate the survival rate of calves to first reproduction that would be needed to yield the estimated recruitment to the breeding population, on the assumption that all recruits were born within the population.

Assuming a 50:50 sex ratio at birth, the required survival probability of female calves to first reproduction is given by:

$$S_t^* = 2R_t \Bigg/ \sum_{i=1}^{l} C_{t-i} f_i \qquad (18)$$

This quantity is time-invariant for the minimal model. Strictly speaking, it represents the probability that an observed female calf will survive to produce a calf: mortality between birth and the time of the initial observation of the calf is not included.

RESULTS

Calving intervals

Values less than five years for the maximum calving interval (m) are clearly rejected on a likelihood test ($P \approx 0$), whereas values of 5, 6, 7 or 8 fit the data virtually equally well (Table 1). This is reflected both in the virtually constant likelihood for $m \geq 5$, and in the estimated probabilities of 6-8 year intervals being close to zero. Thus, the data are consistent with a maximum interval of five years, and indicate that longer intervals, if they do occur, are rare in the population.

The fit between the observed and predicted distributions of observed calving intervals from the model with $m = 5$ is clearly acceptable ($\chi^2 = 2.5$, d.f. = 11, $P > 0.5$; Fig. 3). Hence the value $m = 5$ is selected for all the results that follow. The model adequately explains all observed calving intervals of six years or more as combinations of shorter intervals with one or more intermediate missed calvings. Because intervals shorter than three years are rare, virtually all observed intervals up to and including five years will be genuine calving intervals, without intervening missed calvings.

Table 1

Selection of the maximum calving interval.

	Maximum calving interval (yr) in model					
	3	4	5	6	7	8
Interval	Estimated interval probabilities					
1	0.000	0.000	0.000	0.000	0.000	0.000
2	0.215	0.110	0.023	0.023	0.022	0.021
3	0.741	0.751	0.692	0.692	0.689	0.649
4		0.089	0.089	0.089	0.084	0.079
5			0.131	0.131	0.131	0.118
6				0.000	0.000	0.025
7					0.008	0.015
8						0.022
Never	0.045	0.050	0.065	0.065	0.066	0.070
Mean interval	2.774	2.977	3.351	3.351	3.381	3.584
Log-likelihood	-920.3	-886.1	-862.1	-862.1	-862.0	-861.9
verdict	reject	reject	select			

The estimated distribution of calving interval probabilities is bimodal, with three years as the most common interval, but with five-year intervals more common than four-year intervals (Fig. 2). To assess whether the bimodal pattern was a significant result or merely a chance effect, the likelihood was re-calculated with the probabilities of four- and five-year intervals interchanged. The deterioration in goodness of fit was significant ($P < 0.01$), which suggests that the observed bimodal pattern is unlikely to be due to chance.

We conjecture that five-year intervals are more common than four-year intervals because they are caused by a specific event, such as a pre- or perinatal loss of a calf around the end of the usual three year interval, followed by a reduced interval of two rather than the usual three years to the next birth because of the skipped lactation.

Population parameters and trends

Precise estimates were obtained of the annual mortality rate in the breeding population, the mean calving interval, the mean calving rate, the R_{II} recruitment rate, and the annual rate of population increase (Table 2). The increase in the population is highly significant (estimated annual rate 6.9%, SE = 0.7%).

Table 2

Estimates of various demographic parameters.

Parameter		Estimate	S.E.
Annual rate of increase		0.069	0.007
Equivalent annual mortality rate		0.019	0.005
Equivalent annual survival rate		0.981	0.005
Mean calving interval		3.35	0.05
Mean calving rate		0.338	0.005
Probability of interval length	1 year	0.000	
	2 years	0.023	0.009
	3 years	0.695	0.023
	4 years	0.089	0.014
	5 years	0.131	0.019
R_{II} recruitment rate (R_t / N_t)		0.085	0.007
Mean age at first calving		9.1	0.3
Mean survival to first reproduction		0.92	0.11

The breeding population is estimated to have increased from 92 individuals (SE = 9) in 1971 to 328 in 1990 (SE = 21) (Table 3). The estimated annual sampling probability ranged from a low of 0.29 in 1981 to a high of 0.90 in 1973 (Table 3). Since the survey effort varied substantially from year to year, the variation in sampling probability does not necessarily reflect any variation in the presence of whales in the study area.

Table 3

Estimated numbers of calvings, female breeding population, and sampling probability by year.

Year	Calvings	S.E.	Population	S.E.	Sampling probability	S.E.
1971	30	3	92	9	0.63	0.05
1972	35	2	98	9	0.80	0.04
1973	41	1	105	9	0.90	0.02
1974	37	3	112	9	0.35	0.03
1975	41	2	120	9	0.71	0.04
1976	44	3	128	9	0.69	0.04
1977	46	3	137	9	0.56	0.03
1978	50	3	147	9	0.52	0.03
1979	54	2	157	9	0.78	0.03
1980	56	3	168	9	0.32	0.02
1981	60	3	179	9	0.29	0.01
1982	65	3	192	10	0.34	0.01
1983	69	3	205	10	0.49	0.02
1984	74	3	219	11	0.58	0.03
1985	79	4	234	12	0.52	0.02
1986	85	4	251	13	0.51	0.02
1987	91	4	268	15	0.75	0.04
1988	97	5	287	16	0.56	0.03
1989	104	6	306	19	0.50	0.03
1990	111	7	328	21	0.77	0.05

There is some indication of a three-year cyclic fluctuation in the estimated annual numbers of calvings, relative to the expected numbers, which is not predicted by the model (Fig. 5). The initial variation in numbers of calvings by year is predicted by the model to even out over time because the average calving interval is not exactly three years. The mechanism which causes such fluctuations to persist merits further investigation.

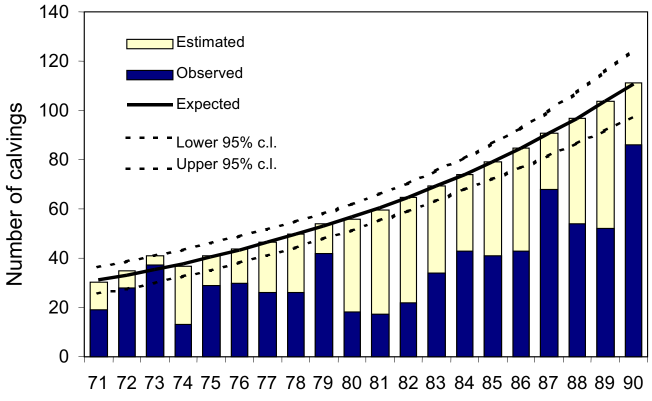

Fig. 5. Observed and estimated numbers of calvings by year, and expected numbers (fitted exponential trend) with 95% confidence limits.

Deviations from the minimal model and additional diagnostics

None of the three one-parameter extensions to the minimal model yielded a significant improvement in fit ($P > 0.1$; Table 4). We conclude that there is as yet no evidence for any change over time in the mean calving interval, the adult mortality rate or the rate of population increase. These conclusions should be re-examined when the data for a longer series of years have become available.

Table 4

Tests for extensions to the minimal population model.

Nature of extension to model	Estimate	S.E.	ΔL[1]	Significance
Annual trend in mortality rate	0.0022	0.0016	0.9	$P > 0.1$
Annual trend in rate of increase	0.00038	0.0035	0.6	$P > 0.1$
Annual trend in mean calving interval	–0.0047	0.0042	0.8	$P > 0.1$

[1] Increase in log-likelihood when parameter is included in model.

Age at first calving

The minimum observed age at first calving is seven years (Fig. 4). Models with maximum ages of first calving of eight years or less are clearly rejected ($P \approx 0$; Table 5). On a one-tailed test, which seems appropriate in this case, a maximum age at first calving of 9 years is just rejected in favour of 10 years, which is itself just rejected in favour of 11 years ($P < 0.05$ in each case). The value of 11 years is not rejected in favour of higher values ($P > 0.1$).

Table 5

Selection of the maximum age at first calving.

Age at first calving	Maximum age at first calving (yr) in model: 7	8	9	10	11	12
	Estimated probabilities					
7	1.00	0.69	0.18	0.10	0.09	0.09
8		0.31	0.21	0.20	0.10	0.10
9			0.62	0.58	0.54	0.39
10				0.12	0.11	0.11
11					0.16	0.15
12						0.18
Mean interval	7.00	7.31	8.44	8.72	9.14	9.67
Log-likelihood	-inf	-1004.6	-974.9	-973.5	-971.6	-970.9
verdict	reject	reject	just reject	just reject	select	

The results for the maximum age at first calving are not as clear-cut as the results for the maximum calving interval, because the number of known-age animals that have themselves been observed to calve was still very few in 1990. The mean age at first calving, assuming a maximum age at first calving of 11 years, is 9.1 years (SE = 0.3 years). It is possible that this is still an underestimate and that more data might indicate yet higher ages at first calving. The estimated modal age at first calving is nine years, with about 50% of first calvings estimated to occur at this age (Fig. 4).

The corresponding survival probability of female calves to their first calving, which would be required to account for the increase rate of the population in the absence of immigration, is estimated using formula (18) to be 0.92 (SE = 0.11). This implies an average annual mortality rate of calves and juveniles of about 0.01 (SE = 0.01).

DISCUSSION

The results of this paper demonstrate that precise estimates of important demographic parameters, including the survival/mortality rate, the rate of population increase and the mean calving rate or calving interval, can be obtained from individual recognition data of this kind, provided that the data are collected over a long enough period.

Cataloguing and matching of the photographs obtained since 1990 should enable refinement of the estimate of the mean age at first calving and the opportunity to test whether the demographic rates are changing over time. As the data series lengthens, the labour involved in cataloguing new photographs by hand increases substantially, because each new photograph has to be checked against a larger catalogue. However, recent computer-based methods to aid matching (Hiby, 1999; Burnell *et al.*, 2001) promise to considerably ease the task.

The estimates of biological parameters for this population obtained in this analysis are similar to but more precise than those obtained for the same population by Payne *et al.* (1990). This is partly due to the longer data series (1971-90 as opposed to 1971-86 in the earlier analysis), and partly due to the additional assumption in this analysis of a simple exponential trend in the expected numbers of calvings. The estimates of demographic parameters obtained for this population are similar to those obtained by Best *et al.* (2001) for the southeast Atlantic population of this species using virtually the same methods.

The sensitivity of our demographic parameter estimates to possible immigration or emigration is of interest in the light of evidence of possible interchange between populations (Best *et al.*, 1993). In terms of the model used, permanent emigration is indistinguishable from mortality; if it occurs, the rate is subsumed into the estimated mortality rate. Temporary emigration spanning a calving, if it occurs, is indistinguishable from missed calvings; it will be reflected in the estimates of the recording probability but not in the demographic parameters. Temporary emigration between calvings has no effect on the data or estimates.

Since the model makes no assumptions about the extent of immigration, if any, estimates of demographic parameters remain valid in the presence of immigration. The estimate of the survival rate of female calves to first reproduction that would be required to account for the population increase rate in the absence of immigration, is high but not implausible (0.92, SE = 0.11). Hence, the analysis provides no evidence that significant immigration has occurred.

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Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements

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ABSTRACT

Southern right whales (*Eubalaena australis*) have been studied on their nursery ground at Península Valdés, Argentina, every year since 1970. Since 1990, 1,208 individuals have been identified from photographs taken during annual aerial surveys; 618 whales were seen in two or more years. Patterns of habitat use have changed during the study in ways which suggest that right whales may be capable of substantial behavioral and ecological flexibility. One male and three females from Península Valdés have been sighted on other nursery grounds (Tristan da Cunha and southern Brazil). Three individuals from Península Valdés were sighted on feeding grounds off Shag Rocks and South Georgia. Some right whales from Península Valdés showed carbon and nitrogen isotope ratios very similar to those seen in right whales off South Africa, while others showed distinctive isotope ratios indicating that they fed in a different area. Whales of all ages and both sexes moved frequently between three major regions of concentration on the Península Valdés nursery ground. Subadults and adult females with calves were resighted at higher rates than adult males and females in non-calf years. Changes in the geographic distribution of whales at the Península include: (1) abandonment of a major region of concentration; (2) establishment of a nursery area adjacent to the centre of a growing whalewatching industry; and (3) small-scale shifts in distribution, possibly in response to natural and human disturbances.

KEYWORDS: SOUTHERN RIGHT WHALE; BREEDING GROUNDS; FEEDING GROUNDS; SURVEY-AERIAL; DISTRIBUTION; MIGRATION; MOVEMENTS; SITE FIDELITY; SOUTH ATLANTIC

INTRODUCTION

Migratory species have large ranges that typically include several different habitat types. Individuals may vary in their use of these habitats. Such variations may be idiosyncratic or systematically related to age, sex or other characteristics of individuals. Average patterns of use may change over time for the populations as a whole. Such variations in habitat use are of interest because they influence the behavioural flexibility of the species and the interpretations of population data used in management of the species.

Southern right whales (*Eubalaena australis*) are distributed between 20°S and 60°S latitude and make annual migrations between higher latitudes where they feed in summer and coastal regions in lower latitudes where females calve and raise their young in the winter and spring. These migrations were documented in the previous century by whaling records (e.g. Townsend, 1935), but recent knowledge of current populations comes primarily from long-term studies of the whales on their coastal nursery grounds (e.g. Payne, 1986; Best, 1990b; Bannister *et al.*, 1999; Bannister, 2001; Burnell, 2001; Palazzo and Flores, 1998; Patenaude and Baker, 2001). When an individual leaves the nursery ground, its probable destination is a feeding ground, but the location of current feeding grounds and the links between nursery and feeding grounds are not well understood (IWC, 2001) and are based largely on sporadic sightings of individually identified whales on feeding grounds (Goodall and Galeazzi, 1986; Ohsumi and Kasamatsu, 1986; Hamner *et al.*, 1988; Best *et al.*, 1993; Best, 1997; Bannister *et al.*, 1999; Moore *et al.*, 1999), and genetic and isotope ratio analyses of tissue samples (Best and Schell, 1996; Portway *et al.*, 1998; Baker *et al.*, 1999; Schaeff *et al.*, 1999).

This paper presents evidence that right whales can be flexible in several aspects of their habitat use. The data come from a 27-year study of a population of right whales in the waters off Península Valdés, Argentina, which they use as a nursery ground. This is examined first at a large scale and then at the level of the nursery ground. Descriptions include: (1) long-range movements of individuals; (2) variation in use of the Península as individuals age or change reproductive status; and (3) changes in the overall distribution of whales at the Península, and their possible relationship to natural and human disturbances.

Right whales can be individually identified by the number, shape and location of callosities (raised patches of roughened skin) on their heads (e.g. Payne *et al.*, 1983; Kraus *et al.*, 1986; Best, 1990a). These callosities are covered by dense colonies of 'whale lice' (amphipod crustaceans of the family Cyamidae) whose white bodies clearly distinguish callosity tissue from intervening areas of smooth black skin (Payne *et al.*, 1983). Since 1970, Roger Payne and his associates have used these distinctive patterns to follow the lives of known individuals on the nursery ground at Península Valdés (Payne, 1986).

Payne's study is the first systematic investigation of the right whale population at Península Valdés. During its first decade (1970s), the study documented basic features of the species' life history, such as age-at-first-reproduction and calving interval (Whitehead and Payne, 1981; Whitehead *et al.*, 1986), and patterns of temporal and spatial distribution at the Península were noted (Payne, 1986). Although stragglers may be present throughout the year, the main group of whales begins to arrive in May or June, reaches peak numbers by the end of September or early October and most depart for the feeding grounds by December (Payne, 1986). It is not known exactly where the whales feed but three

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individuals identified off Península Valdés have been resighted in waters near South Georgia (Best *et al.*, 1993; Moore *et al.*, 1999). While at the Península, the whales concentrate in distinct regions (see Fig. 1). Calves spend the first three months of their lives on the nursery ground, during which time they develop critical motor and social skills (Taber and Thomas, 1982; Thomas and Taber, 1984).

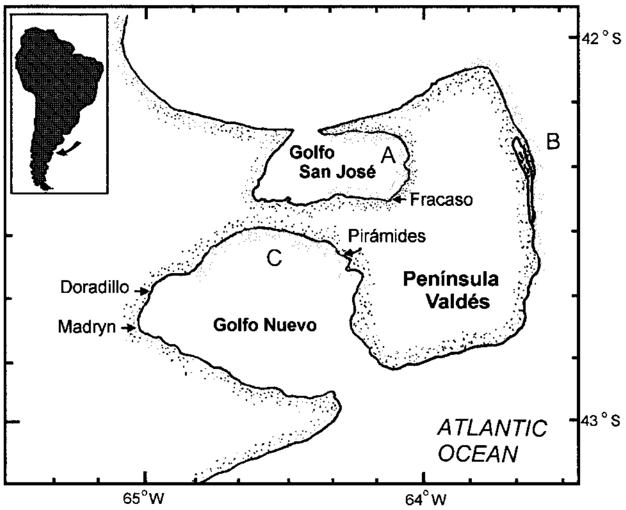

Fig. 1. Map of the southern right whale nursery grounds at Península Valdés, Argentina. Stippling indicates regions (A, B and C) where the whales concentrated between 1971-90.

In the study's second decade (1980s), the rapidly increasing number of repeat sightings was used to make improved estimates of population size and growth rate (Payne *et al.*, 1990; Cooke *et al.*, 2001). During this period changes in the population's spatial distribution were also noted, and Thomas (1988) documented harassment of nursing mothers by kelp gulls (*Larus dominicanus*). These and other developments have continued during the third decade (1990s). In several respects the population's status and behaviour have changed significantly from what seemed to be a stable pattern at the start of the study. For example, gull harassment has become much more intense and geographically widespread (Rowntree *et al.*, 1998).

METHODS

Aerial surveys

The population of right whales at Península Valdés has been surveyed annually since 1970, by flying along the 495km perimeter of the Península in a light plane (usually a single-engine *Cessna 182*). From 1971 onwards, survey observers have photographed the callosity pattern of any whale encountered, noting its location, behaviour and whether it was accompanied by a calf. Survey techniques and analysis procedures are described by Payne (1986), Payne and Dorsey (1983), Payne and Rowntree (1984) and Payne *et al.* (1983). Survey effort has varied considerably from year to year, and was generally greater during the early years of the study (see Fig. 2), when flight time was less expensive. In those years, the same regions were surveyed repeatedly. Surveys of the entire perimeter of the Península were undertaken periodically to identify any changes in the regions where the whales concentrated. Effort varied in the number of flights per year, the timing of surveys and the specific regions of coastline surveyed. However, the purpose of each survey was to photograph as many individuals as possible so flights were consistently directed to regions where the whales were known or suspected to occur. In years with more surveys, a larger proportion of the whales present were undoubtedly photographed. In principle, such variations in effort might create spurious trends. The major quantitative changes described here are too large and too well documented to be artifacts of this kind, but variable survey effort has undobutedly caused minor systematic biases in our estimates of some parameters.

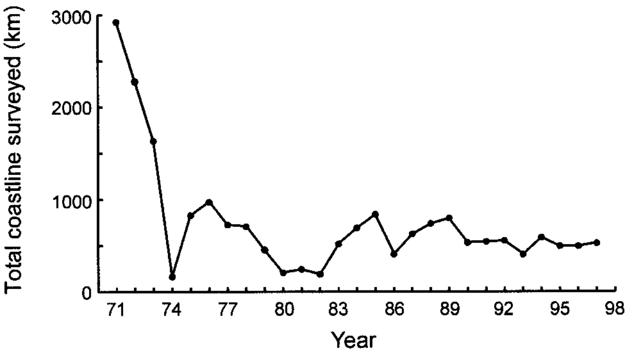

Fig. 2. Total number of kilometers of coast flown each year at Península Valdés during annual surveys of right whales.

The three regions where the whales concentrate (Fig. 1) have been surveyed each year since the study began. Surveys of the regions of concentration occurred between 15 September and 2 November with the exception of six years (1975-1977, 1982 and 1993) when these regions were surveyed either before or after those dates. Within each decade of the study there have been five or more years where surveys of the regions of concentration were conducted during the time of peak whale abundance, 15 September-15 October. This relatively complete coverage of the regions of concentration would seem to guarantee that the large-scale changes observed in these areas are real and not the result of variation in timing or the number of surveys in a region. The study is on-going and since 1991 the entire 495km perimeter of the Península has been surveyed at least once each year during the time of peak whale abundance. The population has increased throughout the course of the study (Cooke *et al.*, 2001) and the regions in which the whales concentrate have expanded. The increase in the number of whales has required more circling to photograph individuals and resulted in longer surveys. In 1971, it was possible to survey the entire Península in a day; by the 1990s, a complete survey took two to three days.

The following definitions of different age/sex categories are used in this paper: (1) subadults are whales of one to four years old that were individually identified in their calf year; (2) females are considered adults from the first year they were sighted with a calf, and are further grouped into years when they were seen with a calf and years when they were not seen with a calf (non-calf years); (3) adult males are individuals that have been morphologically sexed and do not include known-aged whales that are younger than five years. Adulthood is designated at five years of age so as to restrict the subadult category to individuals that are almost certainly immature. The mean age at first calving for southern right whales is between 8.5 and 9.1 years of age and the youngest female seen with a calf was six years old (Best *et al.*, 2001a; IWC, 2001). A female right whale in the North Atlantic (*Eubalaena glacialis*) was observed with a calf when she was five years old (Knowlton *et al.*, 1994). Assuming a one-year gestation period (Best, 1994), that female would have reached sexual maturity when she was four.

Length of stay

The length of time different categories of whales stay at Península Valdés was estimated by counting the number of days between a whale's first and last sightings in 1973, the year with the greatest time span between the first and last surveys (6 June to 9 December). The last surveys of the season (in December in four different years) were examined to see which age/sex categories of whales stayed the latest on the nursery ground.

Long-range distribution

Photographs of right whales from a variety of locations in the Southern Hemisphere have been examined. Whales with callosity patterns photographed in sufficient detail to determine individual identity were searched for in the catalogue of whales identified at Península Valdés. The results of these searches are described in Table 1, along with other published matches.

Isotope ratio analyses

Baleen plates were collected from seven adult and subadult whales that stranded at Península Valdés. Plates were sampled with an engraving tool at 2cm intervals along their length from base to tip. Zooplankton samples were obtained from six stations using ring nets (505µm) on the continental shelf between 50-55°S. Euphausiids and calanoid copepods were separated and dried for storage. Zooplankton were powdered prior to analysis and the carbon and nitrogen isotope ratios for all samples were then determined with a *Europa* 20/20 automated continuous flow isotope ratio mass spectrometry system. Average values for all samples for each baleen plate are reported in standard del notation relative to PDB (Pee Dee Belemnite) standard (carbon) and atmospheric nitrogen (nitrogen). The zooplankton and baleen data were compared with published data on Antarctic zooplankton to make the best match of the observed data with those anticipated for whales feeding in the region.

Yearly resighting patterns on the nursery ground

Use of the nursery ground by different categories of whales was examined by calculating resighting frequencies of whales seen in at least two different years at Península Valdés. Sighting frequencies were calculated for adult males, subadults and females in calf and non-calf years. A whale's first and last sightings were used to indicate that the animal was alive during the intervening years, but these were excluded from the resighting calculations. For females, this involved discarding the first and last years that they were seen with calves, to ensure that the females were reproductively active during the period being examined. Sighting frequencies for subadults were calculated for years one through four, excluding the calf year and last year the whale was seen regardless of age. For each year a whale was known to be alive, it was recorded as either having been seen or not seen.

Given that female right whales from Península Valdés usually calve once every three years (see Cooke *et al.*, 2001), and that female right whales have never been observed to calve at a one-year interval, females could not possibly be resighted with calves in each of the 1,609 opportunities that

Table 1

Individual right whales from the Southern Hemisphere with identifying photographs that have been compared to the catalogue of right whales identified at Península Valdés (42°S, 64°W) between 1971-90. Numbers in parentheses indicate whales yet to be compared to the catalogue.

Location	Latitude/longitude	Date	Whales photographed	Whales ID'd	Not enough information	No. matches with Valdés whales	Reference/photographer
Nursery grounds							
South Africa	33-35°S,19-21°E	Sep. 1974	47	24	23	0	Best *et al.* 1993
Gough Island	40°S,10°W	1974	1	0	1		P. Best
Tristan da Cunha	37°S,12°W	Oct. 1989	2	2	0	1	Best *et al.* 1993
Brazil	28°S,49°W	Sep. 1987	9	8	1	2	Best *et al.* 1993
Brazil	28°S,49°W	Aug., Sep. 1988	5	5	0	1	Best *et al.* 1993
Brazil	28°S,49°W	Aug. 1992	8	(7)	1	?	J.T. Palazzo
Brazil	28°S,48°W	1994	10	(10)	0	?	J.T. Palazzo
Brazil	27°S,48°W	Sep. 1981	2	2	0	0	I. Camara
Brazil	32°S,52°W	Aug. 1977	1	1	0	0	I. Camara
Brazil	32°S,52°W	Sep. 1994	1	0	1	0	L. Barcellos
Brazil	32°S,52°W	Oct. 1991	1	1	0	0	Dantas and Siciliano
Brazil	23°S,43°W	Sep. 1991	1	0	1	0	S. Siciliano
Brazil	23°S,52°W	Dec. 1992	1	1	0	0	S. Siciliano
Chile	23°S,70°W	Jun. 1984	1	0	1	0	J.C. Cardenas
Argentina	41°S,65°W	Aug. 1972	1	1	0	0	J. Jehl
Australian Bight	31°S,131°E	1993	1	1	0	0	S. Burnell
New Zealand	40-47°S, 165-175°E	1981	1	1	0	0	W. Doak
New Zealand	39°S,174°E	Aug. 1982	1	1	0	0	M. Cawthorn
New Zealand	47°S,168°E	1990	1	1	0	0	A. Cox
Feeding grounds							
South Georgia	54°S,38°W	Dec. 1972	1	0	1	0	M. Payne
South Georgia	54°S,38°W	Apr. 1977	1	1	0	0	F. Todd, J. Jehl
South Georgia	54°S,38°W	Mar. 1984	1	1	0	1	Best *et al.* 1993
South Georgia	54°S,38°W	Aug. 1989	1	0	1	0	T. Barton
Shag Rocks	53°S,41°W	Jan., Feb. 1997	20	12	8	2	Moore *et al.* 1999
Antarctic	63-64°S,61-63°W	Apr. 1986	4	3	1	0	G. Stone
Antarctic	60-63°S,47-62°W	Jan. 1983 + 1984	3	2	1	0	Ohsumi and Kasamatsu 1986
Antarctic	?	Mar. 1995	2	1	1	0	M. Foucard
Total			128	86	42	7	

occurred to see them between their first and last calf years. To derive a meaningful estimate of resighting frequencies of adult females, the number of times females with calves could have been seen with calves if they always calved at three-year intervals were counted. It was assumed that a female could not calve in the two years following her first sighting with a calf, nor in the two years preceding her last sighting with a calf.

Frequencies were calculated by dividing the number of years a whale was seen by the total number of years between its first and last sighting. Year-to-year sighting frequency is affected by the sightability of individuals. For example, females in calf years remain on the nursery ground for a long time and spend much of that time in shallow water resting at the surface. As a consequence they are easier to photograph than females in non-calf years and so are expected to have a higher resighting frequency, other things being equal.

It should be emphasised that the resighting frequencies presented here can be viewed only as relative measures and do not represent the actual return frequencies of the different categories of whales. However, because all categories received approximately the same survey effort in a year, differences among categories should reflect real differences in their behaviour such as amount of time spent at the surface, frequency of return to the nursery ground or the length of stay on the nursery ground.

Movements between regions of concentration

When the whales are at Península Valdés, they regularly occupy specific stretches of coast which are described here as ‘regions of concentration’. These regions are indicated with stippling in Fig. 1. To determine whether individuals returned repeatedly to the same region of concentration on the nursery ground or moved between regions of concentration from one year to the next, the number of ‘moves’ and ‘stays’ for successive sightings of identified individuals were counted. For example, if a whale was seen in region A in year one and region A and then B in year two, it was scored as a ‘stay’ between years one and two and a ‘move’ within year two. ‘Moves’ within and between years were given equal weight. The frequency of moves between regions of concentration was calculated as the total number of moves divided by the total number of moves plus stays for different age/sex categories of individuals. Unlike the analysis of resightings, no sightings were excluded in the analyses of moves. Sightings of subadults were recorded between the calf year through age four. Sightings of adult females were recorded from the first year they were seen with a calf. Movement patterns for females were divided into two groups: movements between years that they were seen with calves and movements between years that they were not seen with calves.

In the 1980s, the whales abandoned their region of concentration along the Outer Coast of the Península and an increasing number joined the concentration in Golfo Nuevo. To gain a better understanding of this change in the whales’ distribution, a year-by-year analysis of the frequency and direction of the moves of known individuals was undertaken. Analyses were undertaken to identify the year when the whales started to abandon the Outer Coast and to see whether the whales that began moving into Golfo Nuevo were the same individuals that left the Outer Coast. Only the moves of females in calf years were examined because they were the predominant category of whale seen along the Outer Coast in the 1970s and because they were the category with the most resightings. The population of right whales at Península Valdés is growing (see Cooke *et al.*, 2001). If the tendency for females to move remains the same but the number of calving females increases as a result of population growth, then the number of moves observed would be expected to increase. To adjust for population growth, the proportion of moves among all resightings for each year of the study was examined.

RESULTS

General results 1971-1990

Between 1971 and 1990, 1,208 individual right whales were identified from photographs taken during 104 aerial surveys of Península Valdés. Among the identified whales, 340 were females, 33 were males and 252 were known-age individuals (whales identified in their calf year). Of the 1,208 identified whales, 58% were sighted on more than one aerial survey and seven were sighted on 20-23 different surveys. Half of the whales were seen in two or more years and 21 whales were seen in 9-12 different years.

Length of stay on the nursery ground

Females with calves remain significantly longer on the nursery ground than other whales ($t = 3.34$, d.f. = 91, $p = 0.001$). In 1973, females with calves stayed a mean of 77 days (SD = 36.4, $n = 36$, range 15-170 days) while other whales stayed 52 days (SD = 34.4, $n = 57$, range 8-145 days). Of the 45 individually identified whales seen late in the season (December), 15 (33%) were females with calves, 9 (27%) were subadults, one (2%) was an adult male and 16 (36%) were whales of unknown age and sex.

Long-range distribution of Península Valdés right whales

The Península Valdés catalogue was examined for 69 whales photographed in other regions of the Southern Hemisphere (Table 1). Seven matches were found and are described below.

Nursery grounds

Four whales that were identified off Península Valdés have been photographed on other nursery grounds in the Southern Hemisphere (Table 1). A male that was seen at Península Valdés in six different years between 1971-78 was photographed 4,424km away off Tristan da Cunha in 1989 (Best *et al.*, 1993). Three females that were photographed off Península Valdés, two with calves, were photographed in other years with calves off southern Brazil, 2,051km away (Best *et al.*, 1993). No further matches were found for the other 45 right whales from Southern Hemisphere nursery grounds (Table 1) that were compared with the Península Valdés catalogue.

Feeding grounds

Three right whales photographed off Península Valdés (a female and two adults of unknown sex) were photographed on feeding grounds near South Georgia 2,272km to the southeast of the Península. Two of the whales were near Shag Rocks (Moore *et al.*, 1999) and the other was off Bird Island (Best *et al.*, 1993). None of the 17 other right whales photographically identified on Southern Hemisphere feeding grounds were found in the Península Valdés catalogue.

The average isotope ratios from seven baleen plates collected from whales that stranded at Península Valdés are shown in Fig. 3 and compared with right whale data from South Africa (Best and Schell, 1996). Four of the whales cluster within the range of isotope ratios found for whales off South Africa (–22 to –26‰ δ^{13}C, 5 to 7‰ δ^{15}N). However,

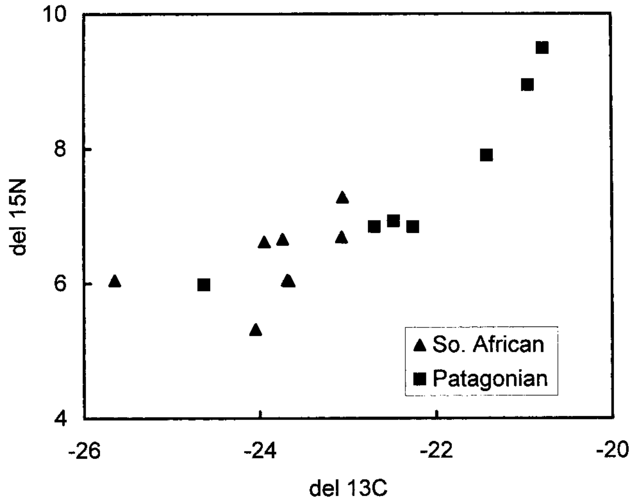

Fig. 3. Average $\delta^{13}C$ and $\delta^{15}N$ values from Patagonian right whale baleen (squares) sampled at 2cm intervals along the lengths. Baleen plate lengths ranged from 65-245cm. South African whale data (triangles) are from Best and Schell (1996).

three whales had higher $\delta^{15}N$ and $\delta^{13}C$ values (–20.5 to –21.5‰ $\delta^{13}C$, 7.8 to 10‰ $\delta^{15}N$), indicating that their food sources were more enriched for heavy isotopes than the food of the other whales. Zooplankton samples from the continental shelf along the southern Argentine coast had copepod $\delta^{13}C$ values of –23.0, –19.1, –20.2 and –20.5‰ and $\delta^{15}N$ values of 8.4, 8.8, 14.6 and 10.7‰. Two samples of euphausiids collected near 54-55° S had $\delta^{13}C$ values of –18.1 and –18.0‰ and $\delta^{15}N$ values of 10.5 and 12.3‰. The more elevated isotope ratios in these zooplankton may account for the elevated values observed in the baleen and imply that these whales consumed significant amounts of food from higher latitudes.

Table 2

Year to year resighting frequencies of different categories of right whales on the nursery ground at Península Valdés between 1971-90.

	Resightings		
Category of whale	Possible	Actual	Frequency
Adult males	234	52	0.22
Whales 1-4 years	257	87	0.34
Adult females	1,609	368	0.23
Assuming 3-year calving interval			
in calf years	367	197	0.53
in non-calf years	1,242	171	0.14
year before calf	389	23	0.06
year after calf	386	41	0.11

Resightings and distribution on the Península Valdés nursery ground

Resighting patterns

Resighting frequencies between years were significantly different for different categories of whales (Table 2). Subadults had the highest resighting frequency (0.34). Adult males were resighted as often as adult females (0.22 *versus* 0.23) when female sightings in calf and non-calf years were combined. However, adult females were seen more in calf years than in non-calf years. If females always calved at three-year intervals, then they could have been seen 367 times in calf years and 1,242 times in non-calf years. They were actually seen with calves 197/367 times for an adjusted resighting frequency of 0.53 in calf years, and without calves 171/1,242 times for an adjusted frequency of 0.14 in non-calf years; this difference is highly significant ($\chi^2 = 255$, $p = 0$). In years when they calved, females had the highest resighting frequency (0.53) of all categories of whales. The non-calf resightings occurred significantly more often in the year *after* a female was seen with a calf than in the year *before* ($\chi^2 = 5.67$, $p = 0.018$).

The resighting frequency of subadults decreased with age from a high of 0.51 at age one to 0.22 at age four (Fig. 4). These known-aged whales were not dying at the rate implied by this rapid decline in their resighting frequency. Of the 92 whales that were first identified at Península Valdés in their calf year between 1971 and 1989, and that were seen in at least one other year, 59% were resighted when they were older than four years. Seventeen of the 54 known-aged whales that were resighted when they were older than four were not seen between the ages of one and four.

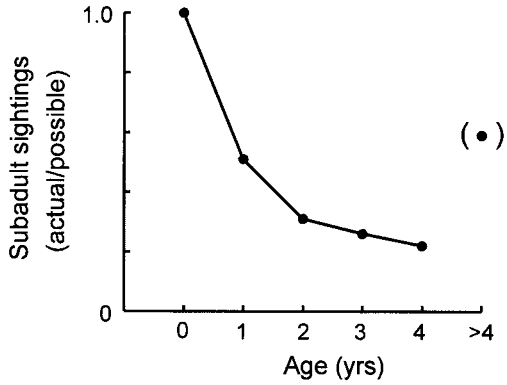

Fig. 4. Resighting frequencies of 92 subadult right whales between the ages of one and four years. Number of subadults in each year class that were sighted divided by the number of subadults in that year class known to be alive. The dot in parentheses indicates the 59% of the subadults that were seen when they were older than four.

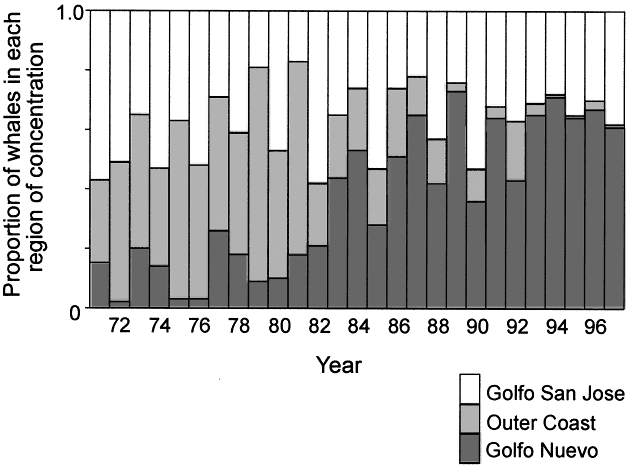

Fig. 5. Yearly distribution of right whales between the three regions of concentration at Península Valdés. Years 1971-90 are based on total number of whales individually identified. Years 1991-97 are based on total number of whales sighted.

Changes in distribution on the nursery ground

The geographical distribution of whales at Península Valdés has changed considerably between 1971 and 1997. Fig. 5 shows the yearly distribution of whales between the three regions of concentration: Golfo San Jose; the Outer Coast of the Península; and Golfo Nuevo. Data from 1971-90 are based on the number of whales individually identified in each region and data from 1991-97 are based on the number of whales sighted. In the early years of the study most of the whales were seen in the northern bay, Golfo San Jose, and along the Outer Coast. At that time the Outer Coast was the region of concentration with the highest proportion of females with calves (0.68) followed by Golfo San Jose (0.36) and Golfo Nuevo (0.09) (Payne, 1986). In the 1980s, the whales began abandoning the Outer Coast and establishing a new nursery ground in the southern bay, Golfo Nuevo. By the 1990s, the highest proportion of females with calves (0.63) occurred in Golfo Nuevo and few whales were seen along the Outer Coast.

The changes in use of the different regions are shown in greater geographic detail in Fig. 6, which depicts the overall sighting rate per kilometer of survey coverage for each 5km segment of coastline, separately for each of the three decades of the study. Few whales were sighted along the Outer Coast in the 1990s despite complete surveys of the coast each year and the greatest number of whales was recorded in Golfo Nuevo. Within the regions of concentration, the particular segments of coast with the most whales have also changed. In the 1970s in Golfo San Jose, the 5km strip with the most whales was between kilometers 65-70 (Fracaso), but in the 1990s it was between kilometers 85-90. In Golfo Nuevo, the 5km strip with the most whales has remained between kilometers 340-350, but the number of whales in Golfo Nuevo has increased in the 1990s and the area in which they are concentrating has extended to include kilometers 370-425.

A subgroup of females that calved in Golfo Nuevo in 1994 and 1997 has shifted its region of concentration. In 1994, the concentration of these females with calves was near Playa Doradillo (kms 405-410), 50 kilometers to the west of the usual concentration of mother-calf pairs and the centre of the whalewatching industry in Piramides (see Figs 1 and 6). Three years later, in 1997, the females returned with their calves to the same area near Playa Doradillo.

Movements between regions of concentration

All age/sex categories of whales were seen to move between the regions of concentration at the Península (0.53 of all adult resightings involved moves). Only a small proportion of resightings (53/787 or 7%) were within-year moves, so most moves came from individuals returning to different regions of concentration in subsequent years. Some age/sex categories of whales moved significantly more than others (Table 3). Females in calf years and subadults were indistinguishable in their frequency of moves between successive sightings (0.48 and 0.45 respectively, $\chi^2 = 0.52$, $p = 0.47$). Likewise, females in non-calf years and males were indistinguishable in their frequency of moves (0.56 and 0.60 respectively, $\chi^2 = 0.52$, $p = 0.47$). But females in non-calf years and males moved significantly more than females in calf years and subadults ($\chi^2 = 4.02$-5.30, $p = 0.04$-0.02 for all possible comparisons). The differences in frequency of moves for different categories of adult whales was the same in the 1970s and 1980s, but all categories of adult whales moved significantly more in the 1980s (Table 3). There were too few sightings of subadults in the 1980s to include them in the analyses and the results from the 1990s are still being analysed.

Table 3

Movement frequencies of right whales between the regions of concentration on the nursery ground at Península Valdés. The frequency of moves = the number of moves in successive sightings divided by the total number of successive sightings for that category (in parentheses).

	Frequency of moves			
	All data	1970s	1980s	Significance 1970s *vs* 1980s
All adults	0.53 (785)	0.48 (377)	0.57 (408)	p=0.009
Females in calf years	0.48 (409)	0.36 (122)	0.54 (287)	p=0.001
Whales 1-4 years	0.45 (135)			
Females in non-calf years	0.56 (285)	0.53 (195)	0.62 (90)	NS p=0.160
Adult males	0.60 (91)	0.53 (60)	0.74 (31)	p=0.054

Fig. 7 shows the proportion of moves in the resightings of females with calves from 1971 through 1990. There were fewer moves between successive sightings in the 1970s than in the 1980s (Fig. 7d). There may have been a peak in moves

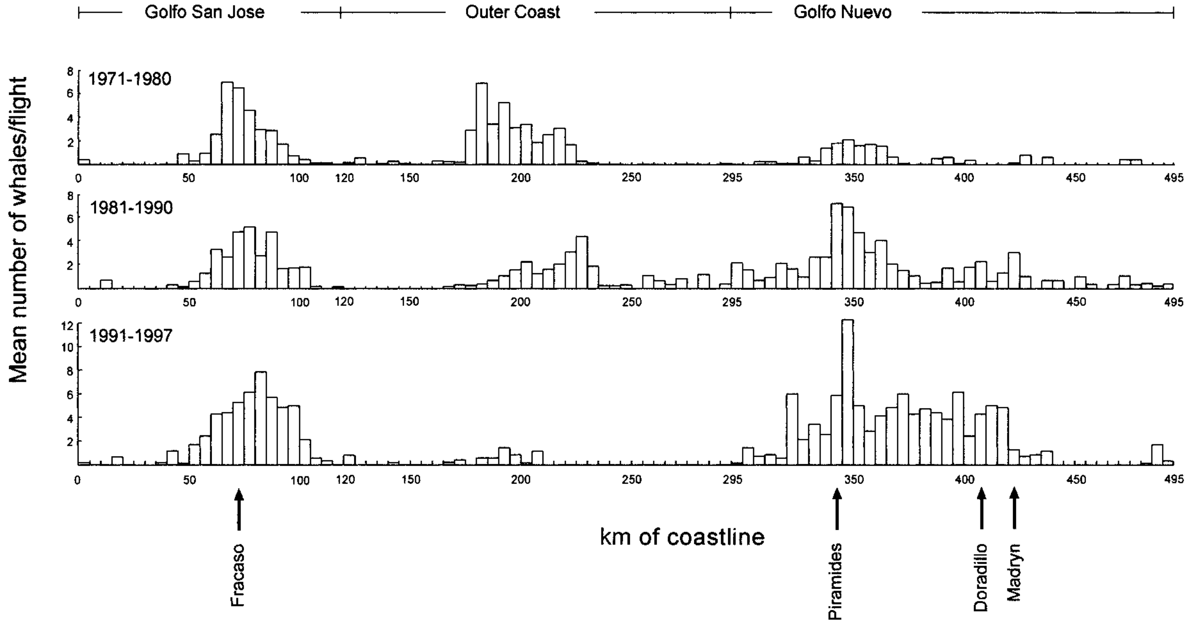

Fig. 6. Changes in the distribution of right whales by decades between 1971-97. The numbers of whales seen in each 5km segment of coast is the number of whales sighted divided by the number of surveys over that segment of coastline in each decade. Kilometre 0 occurs at the western mouth of Golfo San Jose and km 495 occurs at the western mouth of Golfo Nuevo.

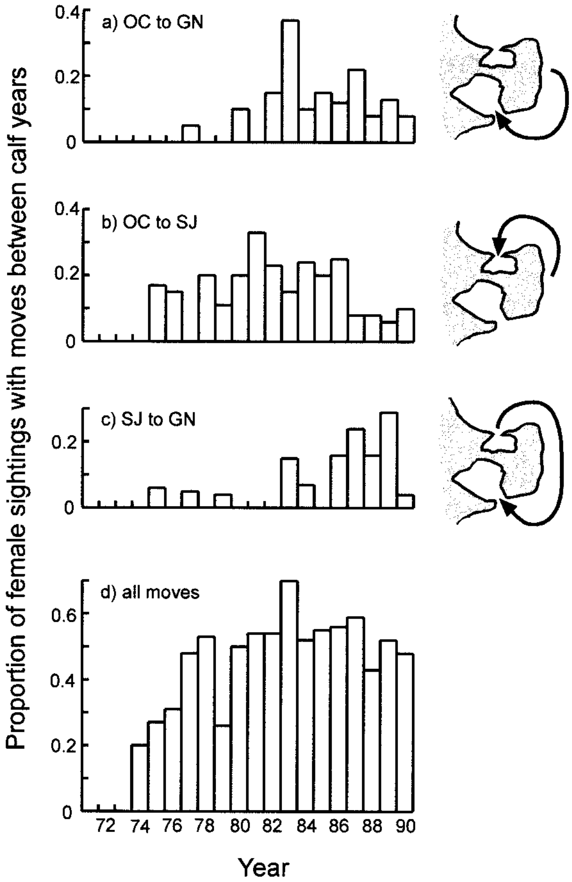

Fig. 7. Movement between the regions of concentration at Península Valdés by females in years that they calved. The proportion of moves in each year is the number of moves divided by the total number of resightings of females with calves in that year. The direction of the most frequently seen moves are shown in 7(a) Outer Coast to Golfo Nuevo, 7(b) Outer Coast to Golfo San Jose, and 7(c) Golfo San Jose to Golfo Nuevo.

in 1983, indicating that an event around that time may have caused the whales to abandon the area. Unfortunately, 1980, 1981 and 1982 were years with poor survey coverage so we cannot be sure that the moves in those years are representative.

There were six possible moves that females could have made between the regions of concentration. Figs 7a, 7b and 7c show the distribution of the most frequently seen moves (22% from the Outer Coast into Golfo Nuevo, 26% from the Outer Coast into Golfo San Jose and 20% from Golfo San Jose into Golfo Nuevo). Fig. 7a shows a peak in movement from the Outer Coast into Golfo Nuevo in 1983 and a steady movement in that direction in the years that followed. Fig. 7b shows a steady movement from the Outer Coast into Golfo San Jose across all years of the study but with a peak in moves in 1981 which again could be an artifact of the poor survey coverage in that year. There is a steady increase in moves from the Outer Coast into Golfo San Jose from 1975-86 and then a sharp decline in moves in this direction. Fig. 7c shows that females in calf years began increasing their moves from Golfo San Jose into Golfo Nuevo in the late 1980s. These data indicate that females in their calf years do not appear to be faithful to a particular region of concentration on the nursery ground and that something caused the majority of the moves in the 1980s to be either from the Outer Coast into Golfo San Jose (25%), or from the Outer Coast into Golfo Nuevo (27%). From 1986-90 there appeared to be a movement of females from Golfo San Jose into Golfo Nuevo such that 76% of all moves in that direction (during the 20 years between 1971-90) occurred during that period of five years.

Problems that could affect the recovery of the Península Valdés right whales

Scars provide evidence of previous injuries. The most prevalent scars on the right whales at Península Valdés are 5-20cm lesions caused by kelp gulls which have learned to feed on skin and blubber that they gouge from the whales' backs (Rowntree *et al.*, 1998). Kelp gulls were first observed feeding in this manner around 1979 (R. Payne and R. Bastida, pers. obs.). In 1990, 32% of the whales had lesions on their backs that could be attributed to gull attacks (Rowntree *et al.*, 1998). The gull attack problem continues to escalate. In 1984, gulls rarely attacked calves (Thomas, 1988) but by 1997, most of the calves in the Golfo San Jose study area had a series of gull-induced lesions along their spines. The frequency of gull attacks in the study area almost doubled between 1995 and 1997, from 12% to 20% of the intervals the whales were under observation (Rowntree *et al.*, 1998; VJR, M. Lanfiutti, M. Failla and G. Ruiz unpublished data).

The frequency of gull attacks is not the same in all regions of the Península. In 1995, data were collected from three different sites around the Península. The number of gull attacks in Fracaso (kilometers 70-80) was three times higher than at the two other sites (Rowntree *et al.*, 1998). Research by Thomas (1988) indicates that the kelp gull attack behaviour may have originated in Fracaso. In the 1970s this broad, gradually sloping, sandy bottomed beach was a preferred area for whales; but by the 1980s the segment of coast with the highest number of whales shifted several headlands away from Fracaso, and this shift continued into the 1990s (Fig. 6). It is not known whether this movement was driven by gull attacks, but it was a movement away from the site with the highest frequency of gull attacks. However, whales with lesions do not appear to be more likely to move than whales without lesions. In the 1980s, 47% of 91 whales with lesions moved between successive sightings, compared to 57% of 137 whales without lesions ($\chi^2 = 2.06, p = 0.15$). In 1997, gull harassment was so widespread at Península Valdés that there appeared to be no area in which the whales were free from attacks.

Thirty-two whales were photographed at Península Valdés (2.6% of identified whales) with scars from injuries not caused by gulls. Ten whales had large, long-lasting wounds, ranging from round openings to long open gashes. One calf survived for at least one year with most of its fluke-tips cut off. Eight whales have regularly spaced slash marks that appear to be propeller scars from small boats. These scars were first seen in 1982. Seven whales have long, thin gashes generally oriented along the length of the whale's body. Five whales have smaller wounds on their bodies or nicks along their tailstocks. Two whales have white jagged wounds on the surfaces of their flukes, from which hang loose flaps of skin. While observing whales from shore parallel scars have been seen which by their placement, spacing and number must have resulted from bites by killer whales (*Orcinus orca*). Stranded calves with killer whale tooth scars have also been found. However, these bite marks are small and difficult to document in photographs taken from an airplane. One female with a rope threaded through her baleen has also been seen.

DISCUSSION

Long-range distribution

Genetic analyses of mitochondrial control region sequences from right whales off South Africa and Península Valdés found 32 polymorphic sites that yielded 23 haplotypes (Portway *et al.*, 1998). Three of these haplotypes were found on both nursery grounds (South Africa and Península Valdés), while the remaining 20 haplotypes were unique to one nursery ground or the other. The distribution of haplotype frequencies for the two nursery grounds differed significantly and quantitative estimates of genetic differentiation suggest that for purposes of management and conservation, the right whales off Península Valdés and South Africa should be considered to represent genetically distinct populations (Portway *et al.*, 1998). Different levels of expression of white and gray skin pigmentation in the two nursery grounds (Best, 1981; 1990a; Payne *et al.*, 1983; Schaeff *et al.*, 1999) provide additional evidence that the whales using the two nursery grounds are genetically differentiated. Sightings data also indicate a separation of the nursery grounds. Twenty-four whales identified off South Africa in 1974 had not appeared in the Península Valdés catalogue as of 1990 (Table 1).

However, low levels of gene flow could occur between nursery grounds. A male that was seen over an eight year period at Península Valdés was photographed later off Tristan da Cunha in the central South Atlantic (Best *et al.*, 1993), a region that appears to be a nursery ground (Best, 1988). A female right whale photographed off nearby Gough Island (40°S, 9°W) was photographed five years later off South Africa with a calf (Best *et al.*, 1993), suggesting a link between Gough Island and South Africa.

Right whale females show flexibility in their use of nursery grounds. Two females that had calves at Península Valdés were seen in other years with calves off southern Brazil, 2,051km away (Best *et al.*, 1993). These sightings indicate either that females may move between nursery grounds in the year their calves are born, or they may use different nursery grounds in different years.

Resightings of three whales from Península Valdés on the feeding grounds near South Georgia indicate that these waters are one migratory destination for the whales calving at Península Valdés. Genetic analyses of tissue samples collected from whales on the feeding grounds near South Georgia revealed 10 haplotypes but the sample size was too small to permit a test of population differentiation (Schaeff, pers. comm.).

Isotope ratio data suggest that at least a portion of the whales from Península Valdés feed south of the Polar Front and in regions where the bulk of the prey species have carbon and nitrogen isotope ratios similar to the prey consumed by South African whales (Best and Schell, 1996). Baleen from three of the Península Valdés whales indicated that they fed in another region where their prey were more enriched for heavy isotopes. Six samples of copepods and euphausiids collected from continental shelf waters between 50-55°S had δ^{13}C and δ^{15}N values that averaged –19.9% and 10.9% respectively. Schell *et al.* (1989) found that bowhead whales (*Balaena mysticetus*) had baleen carbon isotope ratios that averaged 1.1% more enriched than muscle tissue which closely approximated diet. The δ^{15}N values for bowheads were enriched by approximately 3% relative to diet. If right whales have similar isotopic fractionation, then the zooplankton diet would be expected to have δ^{13}C values near –23% and δ^{15}N values near 4-6% instead of the –19.9% and 10.9% reported above for the continental shelf. These expected values are more enriched in the heavy isotopes than the values reported by Rau *et al.* (1991a) for copepods and euphausiids from the Weddell Sea (–28% δ^{13}C, 2.6% δ^{15}N) but consistent with Drake Passage data (–25.5 to –30.3% δ^{13}C for particulate organic matter) also reported by Rau *et al.* (1991b). The average isotopic difference between copepods and euphausiids is only about 1.5% in the same environment (Schell, 1992) and cannot account for the observations assuming different whales ate solely euphausiids or copepods. Similarly, Schell (1992) found no significant isotope ratio differences in the various life stages of both copepods and euphausiids at a location. In contrast, the invertebrate samples from the Argentine coast (–18.0 to –23.0% δ^{13}C, 8.4-14.6% δ^{15}N) were more enriched than the whales, also indicating that the primary source of food was located south of 55°S. This conclusion should be regarded as tentative, however, owing to the small number of samples analysed to date.

More sighting, genetic and isotope data are needed to determine the primary feeding grounds of the different Southern Hemisphere right whale populations, and to determine whether different populations share the feeding grounds. It is also important that a comparison be made between the 1,208 whales photographed off Península Valdés and other individual right whales in the catalogues of other Southern Hemisphere researchers. Newly developed software for computer-assisted matching of right whale callosity patterns will greatly facilitate these comparisons (Burnell and Shanahan, 2001; Hiby and Lovell, 2001).

Patterns of use of the nursery ground by different categories of whales

The name ‘nursery ground’ indicates the importance of such a region for females with young calves. Similarities in the resighting patterns at Península Valdés of females in their calf years and subadults (one to four years old) suggest that the nursery ground may be as important to subadults as it is to calving females or at least that both categories of whales have similar residency times. Female right whales with calves stay significantly longer on the nursery ground at the Península (77 days) than other categories of whales, and along with subadults are among the last animals to leave the area. Females in calf years and subadults have significantly higher resighting frequencies than females in non-calf years and males (Table 2). For subadults to have resighting frequencies similar to females with calves, they must spend a long time at the Península (indicated by their sightings late in the season) and they must spend much of their time in places and activities that make them easy to photograph, i.e. close to shore and/or at the surface. Males may have a low resighting frequency compared to subadults and females in calf years (Table 2) but they are, nevertheless, regularly sighted on Southern Hemisphere nursery grounds (Table 2; Burnell and Bryden, 1997; Schaeff and Best, 1998), unlike male right whales in the North Atlantic where only one adult male was identified among 96 adults (91 females, 4 whales of unknown sex) over a thirteen year period on the right whale calving/nursery ground off the southeastern United States (Kraus *et al.*, 1993).

One-year-old calves were resighted at the Península as often as females in their calf years (0.51 and 0.53 of possible resightings, respectively) indicating that many subadults return to the nursery grounds at one year of age. Thomas and Taber (1984) observed females abandoning their yearling calves on the Valdés nursery ground. Studies of mother-calf pairs show that weaning can take place when whales are eight months old, but more typically occurs when they are about a year old (range 8-17 months; Hamilton *et al.*, 1995; Burnell, 2001). Although mothers may bring their yearling calves back to the nursery ground, two to four year old subadults have not been observed in close proximity to their mothers, which suggests that older subadults return independently of their mothers. While the subadults are on the nursery ground their comparatively high resighting frequency indicates that they spend time in ways that give them a similar sightability to females with calves and a different sightability to females in non-calf years.

Although all categories of whales moved between the regions of concentration, females in calf years and subadults were indistinguishable in their frequency of moves and moved significantly less than males and females in non-calf years (Table 3). Female right whales with calves on the nursery ground off the Head of the Bight in Australia also show a greater fidelity to the aggregation area than unaccompanied whales, while males showed significantly less site fidelity than calving females, non-calving females or juveniles (Burnell, 2001). Calving right whales off South Africa show variable sight fidelity (ranging from 0-74%) with the highest fidelity in the area with the most whales (Best, 1990b).

Similarities in the frequency of resightings and frequency of moves of different categories of whales at Península Valdés may indicate similar ways of using the nursery ground. If this is true our results suggest that subadults and females with calves use the nursery ground in a similar but different way from males and females in non-calf years.

Changes in distribution at Península Valdés

The change in the distribution of whales at Península Valdés between the 1970s and 1980s was not simply a movement of calving females from the Outer Coast into Golfo Nuevo. When the calving females abandoned the Outer Coast they appeared to move with equal frequencies into the northern (Golfo San Jose) and southern (Golfo Nuevo) bays of the Península. In addition, calving females appeared to begin moving from the northern gulf into the southern gulf in the late 1980s. This is a surprising result since during the same period human activities (shipping, recreational boating, fishing and whalewatching) were developing far faster in the southern gulf than in the northern gulf where all of these activities, with the exception of fishing, were inhibited in their expansion by laws declaring Golfo San Jose a sanctuary.

Changes in distribution have been noted in other right whale nursery grounds. Between the 1970s and 1980s, right whales off South Africa appeared to expand their range up the west coast and to shift the location of some regions of peak density (Best, 1990b). These shifts in regions of peak density are similar to shifts observed at Península Valdés (Fig. 6).

Problems that could affect the recovery of the Península Valdés right whales

The wounds caused by kelp gulls do not appear to be life-threatening, but the whales' responses to gull attacks may seriously deplete the energy reserves of females and their young calves (Rowntree *et al.*, 1998). In 1995, mother-calf pairs that were attacked increased the amount of time spent travelling at medium to fast speeds by almost four times that of mother-calf pairs that were undisturbed. Approximately 24% of a typical mother's day was spent in states of gull-induced disturbance (Rowntree *et al.*, 1998). The increase in energy expenditure due to gull harassment comes at a time when the mothers are largely fasting. Blubber reserves accumulated to feed calves are being spent fleeing gull attacks. The movement of the whales away from the site with the highest level of gull harassment in Golfo San Jose may indicate that the gulls are driving the whales from this prime calving area.

Gull harassment probably arose when the rapidly growing gull population began to outstrip its more traditional food supply. Kelp gulls are innovative feeders (Murphy, 1936; Pierotti and Annett, 1990) and their attack behaviour appears to be learned. Juveniles take part in almost one-third of the attacks and the behaviour is spreading through the population as is indicated by the observation that attack frequencies have grown at a faster rate than the gull populations (Rowntree *et al.*, 1998). Reducing the number of gulls by restricting their access to food resources at waste disposal sites might bring some relief to the whales.

A thriving whalewatching industry has developed around the whales that return to Golfo Nuevo each year. Despite the industry, the number of whales in the Golfo Nuevo concentration has continued to increase (Fig. 6). Studies in the late 1980s showed that the activities of the boats did not affect the swimming speeds of mother-calf pairs (Alvarez Colombo *et al.*, 1990). Since then, the growth of the industry and interactions between the whales and boats have been studied by Rivarola *et al.* (2001). They found that some types of boat manoeuvers caused right whales to move away from whalewatching boats, and that when whales were scarce, the same mother-calf pairs were often subjected to repeated approaches by boats. They note that the 1994 shift of the mother-calf concentration from the centre of the whalewatching industry could be a response to disturbance. However, they also note that the right whales began using the Golfo Nuevo nursery ground in increasing numbers at the same time that the industry began its expansion and the whales centred their concentration only 5km from the industry's base in Piramides (see Figs 1 and 6).

Aside from the gull-induced lesions, only 2.6% of the 1,208 right whales identified at Península Valdés have obvious scars. This is a lower incidence of scarring than the 3-4% of mature female right whales with fishing gear entanglement scars off South Africa (Best *et al.*, 2001b) and a much lower incidence than is observed for right whales in the western North Atlantic; from 1970-1988, 50 animals were documented to fit serious injury/mortality criteria, 26 (52%) from entanglement and 24 (48%) from ship strikes (Knowlton and Kraus, 2001). Boat-propeller scars were first seen at Valdés in 1982, indicating that some boats may be maneuvering too close to the whales. Rivarola *et al.* (2001) describe particular approaches by whalewatching that cause the whales to move away from them. The low incidence of scars in the Península Valdés right whales (aside from those caused by gulls), indicates that the whales are suffering a much lower level of disturbance from boats, ships and ropes than is reported for right whales in the western North Atlantic (Knowlton and Kraus, 2001).

However, off southern Brazil four right whales have recently stranded as a result of colliding with ships (two whales cut in two and two whales with long gashes from propeller blades) and nine right whales have been reported entangled in fishing gear (Lodi *et al.*, 1996; Greig *et al.*, 2001). Females sighted off both Península Valdés and southern Brazil indicate that some portion of the Valdés population is likely to encounter problems with fishing gear.

Flexibility in distribution

Our 28 years of observation of individual right whales off Península Valdés show that right whales can be flexible in their choice of habitat. On a large scale, a male was seen on two different nursery grounds (off Península Valdés and off Tristan da Cunha). Two females were seen in different years with calves on two different nursery grounds (off Península Valdés and off southern Brazil). Flexibility is also apparent in use of the different regions within the nursery ground at Península Valdés. Although the whales concentrate in distinct regions of the Península, individuals moved between these regions in over half (53%) of their successive sightings (Table 3). Females abandoned an important nursery area and established a new one with no apparent negative effect on the continued growth of the population. In 1994 and 1997, a group of females using one of the regions of concentration shifted their preferred area 50km to the west.

It is unclear whether any of the observed changes in distribution can be attributed to disturbance. Whales that were scarred by gull attacks returned in subsequent years to regions where they were initially scarred. The site with the highest frequency of gull attacks is no longer a preferred area but females with calves do continue to use it. Females in the 1994/1997 calving cohort in Golfo Nuevo moved away from the centre of the whalewatching industry into bays with a high incidence of gull harassment, near Madryn, a region of the Península with the highest boat and ship traffic. The fact that females in other calving years have not moved to this area suggests that social cohesion and individual preference might be influencing the moves reported here more than disturbance.

It has been difficult to determine why the whales abandoned the Outer Coast of the Península. Major changes may have occurred in bottom topography, owing to storms that destroyed protection from the strong ocean currents that run parallel to shore. In the early 1970s, there was a slight bulge in the coastline which created an eddy that was often occupied by right whales. The bulge eroded somewhat after 1975 and the whales shifted further south. But ultimately, it is not clear why the whales are changing their distribution on the nursery ground. A better understanding of the characteristics the whales search for in a preferred nursery ground is needed.

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Demand-driven commercial whalewatching in Península Valdés (Patagonia): conservation implications for right whales

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ABSTRACT

One of the largest remaining populations of the southern right whale, *Eubalaena australis*, breeds along the coast of Península Valdés, in Argentine Patagonia. The area offers excellent opportunities for whalewatching because it is possible, with predictability, to have close-up views of animals of all ages. During 11 years, from 1987 to 1997, more than 337,000 tourists took part in boat excursions to watch right whales. The demand increased during this period over 14 times from 5,214 tourists in 1987 to 73,726 in 1997. From 1991 to 1994, more than 8,000 boat trips were required to satisfy a demand of 125,000 people. Most whalewatching involved pregnant animals or mothers and calves that often attempted to avoid the boats. In 1997, whalewatching generated direct revenues of at least $US 1 million in boat fees, and direct plus indirect revenues of over $US 15 million (not including travel costs to Patagonia). The rapid growth of tourism in relation to whales has undisputed economic and public-awareness benefits but it is also raising concern about potentially detrimental effects on the animals. The lack of a management plan and of estimates of a tourist ‘carrying capacity’ allows customer demand to be the main driving force behind a commercial activity based on this vulnerable species.

KEYWORDS: RIGHT WHALE; WHALEWATCHING; SOUTHERN HEMISPHERE; SOUTH AMERICA; BEHAVIOUR; SUSTAINABILITY; BREEDING GROUNDS

INTRODUCTION

Whalewatching is one of the most rapidly growing and economically attractive tourist activities worldwide (Hoyt, 1992). It is also an incentive for the conservation of whales. If properly managed, whalewatching can benefit local economies, scientific research, educational purposes, public awareness, recreational activities and, ultimately, the whales themselves (IFAW Tethys and Europe Conservation, 1995).

Argentine Patagonia is one of the best places in the world to watch the depleted southern right whale (*Eubalaena australis*) with predictability and at close range (Payne, 1972a; b; 1976; 1986; Bastida and Lichtschein, 1981; Harris and García, 1986; Rivarola *et al.*, 1995a; b; Campagna and Lichter, 1996). Individuals from one of the largest remaining populations of this species (*ca* 2,600 whales; IWC, 2001b) breed, from May to December, along the coast of Península Valdés (Whitehead *et al.*, 1986; Payne *et al.*, 1990). Until the 1970s, the existence of whales breeding in the waters around Península Valdés was known by few apart from the residents of the nearby coastal towns (Gilmore, 1969; Cummings *et al.*, 1971; Garciarena, 1988). Today, whalewatching based on southern right whales has become the most important tourist attraction in Patagonia (Campagna *et al.*, 1995; Rivarola *et al.*, 1995a; b). The rapid growth of whalewatching has raised concerns about its effects on the animals almost from its beginning (Lichtschein and Bastida, 1983; Bastida, 1987; Rivarola *et al.*, 1995a; b). While whalewatching is known to induce short-term behavioural changes in the target species (Watkins, 1986; Garciarena, 1988; Alverez Colombo *et al.*, 1990; Arias *et al.*, 1992), it is unknown whether this activity can adversely affect the long-term viability of such species (IFAW Tethys and Europe Conservation, 1995).

The aims of this study are to describe the trend in the demand for whalewatching, evaluate the ability of the industry to satisfy that demand, estimate the economic value of the activity and evaluate the short-term effects of whalewatching on the behaviour of whales. The paper expands and updates the information provided by Rivarola *et al.* (1995a; b) and summarises an unpublished technical report requested by the United Nations Environment Programme (UNEP) on whalewatching in Argentina (Campagna *et al.*, 1995). The 11 year period covered by this report (1987-1997) represents virtually the entire history of whalewatching in Patagonia. This study shows that whalewatching has not only important economic effects for Patagonia but also largely unknown potential effects upon the conservation of the southern right whale in the southwest Atlantic Ocean.

BACKGROUND INFORMATION

Biological aspects

The world population of southern right whales had been estimated at 4,000 individuals, divided into 3-4 sub-populations (Klinowska, 1991). More recent theoretical estimates of abundance levels yield 7,571 individuals, divided into 11 breeding units (IWC, 2001b). Coastal Patagonia is one of the most important places for right whale reproduction in the southwest Atlantic (Payne, 1972a; b; 1976; 1986; 1994; Bastida and Lichtschein, 1981; 1984; Harris and García, 1986; Payne *et al.*, 1990). In 1986, there were an estimated 1,200 southern right whales in the population that breeds off the coast of Península Valdés (Whitehead *et al.*, 1986; Payne *et al.*, 1990). This population was growing at a rate of approximately 7.1% per year (Payne *et al.*, 1990). Current estimates for the Argentine breeding unit are of 2,577 animals (IWC, 2001b).

Right whales breed during the Southern Hemisphere winter and spring in two protected Patagonian bays, Golfo Nuevo and Golfo San José, and along the outer coast of Península Valdés (Fig. 1; Payne, 1972a; b; 1976; 1986; 1994; Payne and Rowntree, 1984). The first adults arrive in

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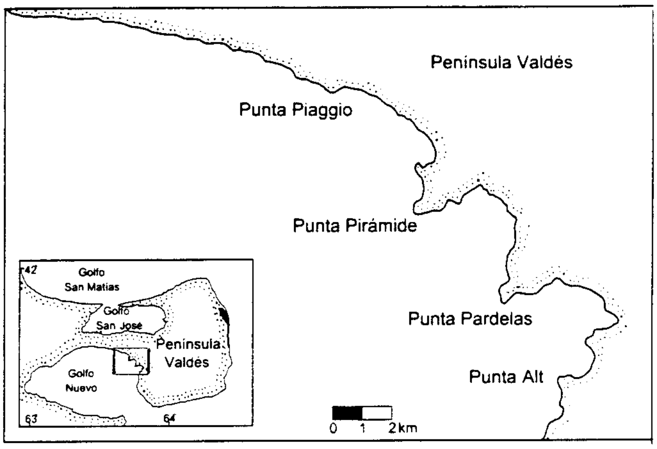

Fig. 1. Map of the study area.

April and May and increase in number until the height of the season, between September and October. Only a few whales remain in the area until December (Payne, 1986).

A long-term demographic and behavioural study conducted in Patagonia had resulted in the identification of 1,223 individuals by 1990, based on natural markings (Payne *et al.*, 1983; 1990; Cooke *et al.*, 2001). These records, compiled over almost three decades, show that only a fraction of the population is found each breeding season off the coast of Península Valdés. Adult females tend to return to the area only during the years that they give birth, and most females calve every three years. About 50 calves are born each year in the area (Payne *et al.*, 1983; Whitehead *et al.*, 1986).

Whalewatching in Argentina

Whalewatching is a prominent economic activity in Argentina but only in Patagonia (Garciarena, 1988). The waters surrounding Península Valdés offer whalewatchers close-up views of mothers and calves, and individuals of various ages and reproductive status (Payne, 1972b; 1976; 1994; Bastida and Lichtschein, 1981; 1984; Harris and García, 1986). Right whales are found throughout the year, except for the period January-March. Animals tend to stay within 100m of the coast and are often seen as close as 5-10m from the shore.

This situation has promoted a rapidly growing whalewatching industry based in the small town of Puerto Pirámide, on the shores of Golfo Nuevo (Fig. 1). Whalewatching began commercially in the early 1970s, when local boat operators took small groups of people, mostly foreigners, in small inflatable boats with outboard engines, to watch whales (Lichtschein and Bastida, 1983; Bastida, 1987). There are no data regarding the number of people that bought boat tickets to watch whales until 1987. Estimated numbers of tourists range from a few hundred in the 1970s and early 1980s to nearly 5,000 people per year in the mid-1980s.

Legal protection of whales

At a national level, the Argentine Congress has declared southern right whales a ‘Natural Monument’ (law 23094 of 1988). This status applies in territorial waters and does not apply to whales in international waters or even in waters under the jurisdiction of local Provincial governments. None of the Patagonian coastal provinces has ratified this law for their respective territories.

At a Provincial level, the Government of the Province of Chubut declared Golfo San José a ‘Provincial Marine Park’ (law 1238 of 1975) to protect one of the most important breeding areas of the right whale in South Atlantic waters. This law was later modified (Decree 1713 of 1979) changing the protected status of the Gulf to one of management for multiple use. Whalewatching takes place within the jurisdiction of Chubut Province; therefore, regulations to manage the activity and protect the whales are the responsibility of the Provincial rather than national Government. The first regulations to protect whales encountered during whalewatching trips date from 1984 (law 2381). This law defines:

(1) some protected areas along the coast where whalewatching is not allowed (since then, new areas have been added by law 4098 of 1995);
(2) minimum permitted distance of boats to whales (100m with engines on, 50m with engines off);
(3) minimum permitted distance of divers to whales (100m);
(4) restriction of number of boats around a whale (only one at a time); and
(5) some manoeuvres to be considered as harassment (e.g. driving the boat in circles around the whale, chasing whales).

The enforcement of restrictions on whalewatching activities is the responsibility of two agencies: the Organismo Provincial de Turismo of Chubut (for the protection of the whales), and the Prefectura Naval Argentina (for safety on board). However, regulations are difficult to enforce and manoeuvres that may qualify as harassment according to Provincial regulations are a regular component of whalewatching trips. Despite this, no serious boat accidents have been formally reported or documented since the activity began and no strong evidence exists of whale injuries caused during whalewatching trips conducted by licensed professionals. Boat drivers are all local residents and experienced navigators.

General setting

Besides tourism related to whales, the area is facing increasing development of many kinds. Puerto Madryn, on the shores of Golfo Nuevo, is one of the fastest growing cities in coastal Patagonia, with a population of about 45,000 inhabitants by the mid-1980s. It lies along the western coast of the Gulf and releases large quantities of sewage into its waters. An aluminium factory and several fish processing plants generate a considerable amount of shipping traffic and an unknown level of pollution.

Golfo San José was previously the only place set aside as a refuge for right whales (see above). However, the present legal status of the Gulf allows for the development of economic initiatives. For example, in 1992, aquaculture began on a small scale in the Gulf, involving ropes suspended from buoys in prime right whale habitat. This has occurred despite the fact that studies of northern right whales show that they have difficulty avoiding ropes; for example Knowlton and Kraus (2001) report that of 50 animals either severely injured or killed, 26 had suffered injuries from entanglements.

METHODOLOGY

Estimating demand

Demand was defined as the number of people that purchase whalewatching tickets. Whalewatching was defined as the observation of whales from boats. Information on the number of tourists buying whalewatching tickets, the numbers of whalewatching trips and the revenue derived from this commercial activity were obtained from several different sources: the Organismo Provincial de Turismo de Chubut (Tourism Agency of Chubut Province), Prefectura Naval Argentina (Coastguards) and the private companies that provide the services. Whalewatching records are kept by the Prefectura Naval Argentina but are reported by the companies that provide the service. Records list boat departure times, number of passengers, names of the companies and skippers of the boats for every excursion leaving Puerto Pirámide.

Calculating the income for the 1994 season

The economic aspects of whalewatching in Península Valdés were calculated based on the 1994 season, a year when the activity was strictly controlled and the economic data were most reliable. Income from boat fees was estimated based on an average cost of $US20 per person for a whalewatching trip. The upper limit of the cost per trip is fixed by contract between the companies that provide the services and the Provincial Government that regulates the activity. A 10% deduction from boat fees is paid as tax to the Provincial Government. Boat fees have remained more or less constant during the last five years (from $US15-25 in 1998).

Direct and indirect revenues included income from boat fees plus room and board for two full days ($US40 per day per person), souvenirs (10% of total receipts), the cost of travelling to Península Valdés from Puerto Madryn and entrance fees to Península Valdés. The calculation of revenue does not include travel costs to Puerto Madryn.

For comparative purposes, an estimate of direct and indirect income was calculated for the 1997 season. Numbers were based on the taxes paid by the companies providing the whalewatching services.

Whale behaviour in response to boats

General observations of the interaction between whales and boats were conducted from vantage points on the cliff tops at Puerto Pirámide, Península Valdés, during the 1993-1994 whalewatching season. Observations covered the coastal area between Punta Piaggio (42°32’S, 64°28’W) and Punta Alt (42°41’S, 64°16’W) (Fig. 1). Most boats operated within 1-2km of Puerto Pirámide and were easily observed from the cliffs.

Animal counts

An estimate of the number of whales present in the study area was obtained by counts made twice a day throughout the season, from the highest point at Puerto Pirámide Wildlife Reserve (located about 3km from the port of departure of the whalewatching boats). Each count took about 30 minutes and differentiated mothers and calves from adults (solitary or in groups).

Boat activity

Interactions between boats and whales were described for 116 trips. The following boat manoeuvres were recorded.

1. Direct approach: the boat moved from the port or some point at sea in a straight line towards a whale.
2. Encircling: the boat moved around the whale or group of whales within a distance of 10-100m.
3. Chasing: the boat moved behind a whale or parallel to it, increasing its speed when the whale increased its distance.

These three boat manoeuvres are forbidden by the law that regulates whalewatching in Argentina (see above). We refer to them as high impact manoeuvres and compared the response of whales during trips in which none of the manoeuvres were used ($n = 20$) to others in which all three were used in the same trip ($n = 45$).

Whale activity

The following behaviours were recorded.

1. Approach: the whale approached a boat and remained at less than one body length from it for several minutes.
2. Moving away: the whale moved away from a boat, swimming either at the surface or underwater.

Target of whalewatching

A total of 565 scan samples were recorded daily every 30 minutes for seven hours during the 1993 season. This enabled us to assess the proportion of whalewatching trips in the study area made either on mother-calf pairs or on individuals without calves. Boats typically approached more than one whale during trips that lasted from about 45-100min. Most boats usually remained with the same whale for less than 30 minutes. Therefore, the 30 minute period between each successive scan sample allowed for some changes to take place (e.g. beginning/end of some trips, change of whalewatching site). This avoided the same event being recorded several times.

Interactions between boats and whales

Scan samples were also used to estimate the proportion of time during which one or more boats were watching whales. Information on the manoeuvres of boats and the behavioural response of whales to such manoeuvres was recorded as a serial record for 116 whalewatching trips during 1993. A ‘whalewatching trip’ was defined as the period between the time the target boat left port until the time it returned. Each serial record consisted of a detailed chronological description of the main events that occurred from boat departure to its return about one hour later. When more than one whale was approached by a boat during a trip, records of interactions were differentiated for each individual whale or mother-calf pair.

RESULTS

Demand and efficiency of the commercial activities

At least 337,685 tourists engaged in whalewatching trips during the 11 years considered in this study (June-December 1987-97, Fig. 2). The demand for boat trips to watch whales increased immensely for that period. In 1997, at least 73,726 tourists watched whales from boats (versus 5,214 for 1987).

The monthly distribution of the demand varied during the season, reaching a maximum in October (Fig. 3). Between 27 and 33% of the annual demand was concentrated in this month. The peak number of tourists coincided with the maximum number of whales in the calving area (Figs 3 and 4). The number of boat trips per month was correlated with the demand for the same period (Fig. 5; Kendall’s T for the 1994 season chosen as an example = 3.15, $P < 0.05$, $n = 7$).

The number of boat trips per season, and thus the exposure of whales to disturbance and potential accidents, was higher during most seasons than an optimum number that could have satisfied the same demand (Table 1). The mean number of tourists per trip in the early 1990s was 12-13, considerably

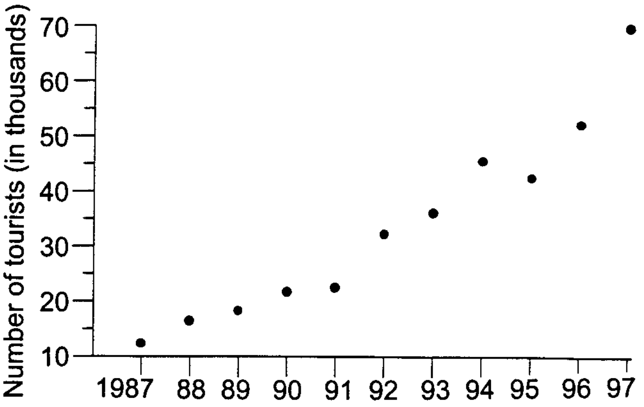

Fig. 2. Trends in the demand for whalewatching at Península Valdés for the period 1987-97.

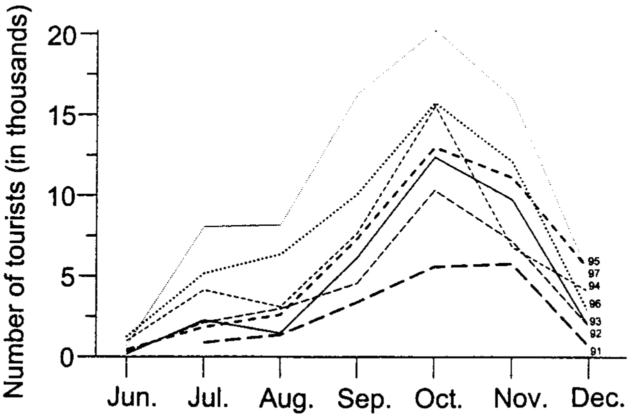

Fig. 3. Number of tourists per month for seven whalewatching seasons.

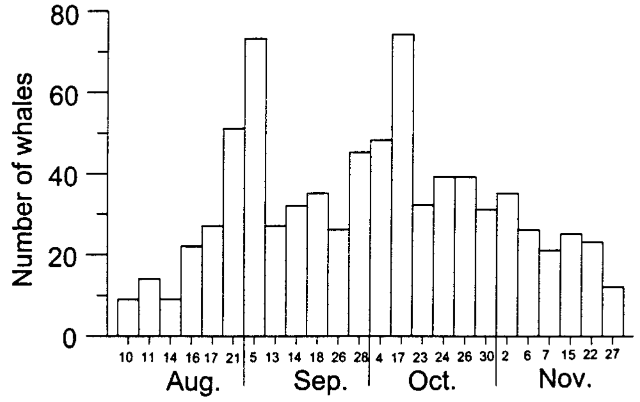

Fig. 4. Maximum number of whales counted in the study area.

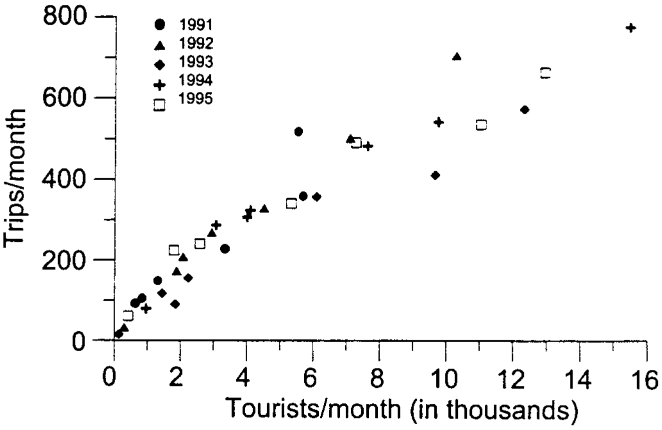

Fig. 5. Whalewatching trips per month as a function of the number of tourists.

less than the average boat capacity for those years of 20 passengers per boat. In 1991, 43% of trips carried half the vessel's capacity; in 1992, this figure was 35%. This means that there were *ca* 1,400 trips in which boats took 10 or fewer passengers. In only 22% of 2,209 trips for 1992 were the boats filled to capacity. In 1993, a restructuring of the companies reduced the total number of boat trips, despite an increase in demand by approximately 5,000 compared with the previous year. However, an increase in the number of whalewatching companies in 1994 from three to six reduced efficiency to 61% of the optimum, the same as in 1991. In 1994, operating at maximum efficiency, the companies could have serviced about 5,000 people per day in tours that lasted about one hour. More than 600 tourists could have been engaged in whalewatching trips at any given time. However, efficiency during that year was only 80% of that for 1993 (Tables 1 and 2).

Target of whalewatching

Mothers and calves were the selected target for whalewatching in 49% of 565 scan samples recorded in 1993. At the beginning of the season, when most births had yet to occur, single whales were approached more frequently than later in the season. Towards the end of the season, all approaches were targeted at the few mothers and calves that still remained in the area (Fig. 6).

Table 1

Progression of tourist demand and whalewatching trips for the period 1991-94 (data not available for other seasons). In 1993 whalewatching companies worked cooperatively and most boats filled their capacity before leaving port.

Variable	1991	1992	1993	1994	Total (1991-94)
No. of tourists	17,446	29,121	33,772	44,987	125,326
No. of whalewatching trips	1,435	2,208	1,706	2,774	8,123
Maximum number of tourists allowed per boat per trip	20	20	20[2]	see Table 2	20–80 (see Table 2)
Mean ± 1 SD number of tourists per trip	12.0 ± 5.8	13.2 ± 5.8	19.8 ± 8.4	16.0 ± 3.4	15.3 ± 3.5
Range	1–20	1-20	1-20 1-40[2]	1-80	1–80
Efficiency of industry measured against the 1993 season[1]	60%	66%	100%	80%	77%
Number of expected trips if boats had been filled to capacity	869	1,453	1,346	1,693	5,361
Observed efficiency as a percent of optimum efficiency[3]	60%	66%	79%	61%	66%

[1] Calculated as a rate of the mean number of tourists per boat trip relative to 1993 (e.g. 12.0/19.8 = 60 %).

[2] A larger boat for 40 passengers was used during the last months of the 1993 season.

[3] Calculated by dividing the optimum number of trips (i.e. trips that would have occurred if boats were filled to capacity) by the observed number of trips per season.

Table 2

Number of boats and boat capacity (in brackets) during the 1991-1994 seasons. In 1994 only six companies were authorised for whalewatching activities, two companies ran tours that were not aimed at whalewatching but that approached whales on an opportunistic basis.

Type of vessel	1991	1992	1993	1994
Number of companies	5-6	6	3	8
Boats (≥ 20)	11	12	5	7
Boats (≥ 40)	0	0	1	2
Boats (≥ 90)	0	0	0	1
Catamarans (*ca* 80)	0	0	0	3
Sail boats	0	0	0	1
Catamarans (*ca* 120)	0	0	0	1
Total vessels	11	12	6	15

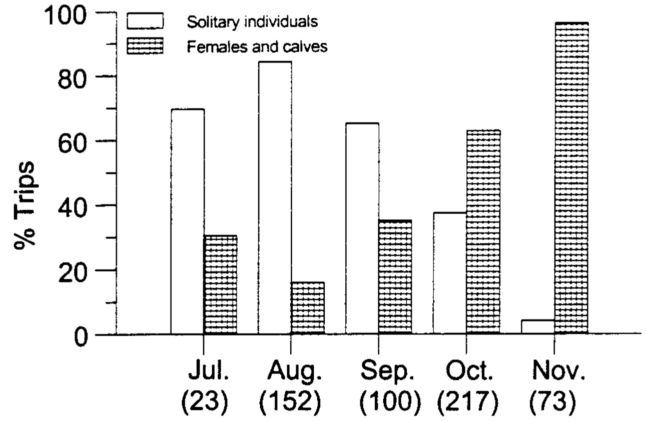

Fig. 6. Proportion of solitary individuals and mother-calf pairs exposed to whalewatching per month. Number of trips is given in parentheses.

Economic aspects

Total direct and indirect revenues for 1994 were $US 10.3 million. This revenue includes boat fees, travel costs, room and board, souvenirs and entrance fees to the Península. In 1997, the total income from boat fees was estimated at more than $US 1 million and total direct and indirect revenues over $US 15 million (not including travel costs to Patagonia).

Short-term effects of whalewatching on whale behaviour

For 81% of the time that an animal or a group of whales were exposed to whalewatching, only one boat at a time approached the target (based on 565 scan samples taken every 30 mins). For 19% of the whalewatching time, the animal or group was approached by two or more boats simultaneously.

From 116 observed whalewatching trips, boats intercepted (direct approach: 49% of the trips), encircled (49%) or chased (54%) whales at least once during the trip. These manoeuvres occurred up to nine times during the 45-100 minutes that a trip lasted. In only 17% of the 116 trips one of the high impact manoeuvres occurred during the approach; however, in 39% all three manoeuvres took place within one trip.

These manoeuvres affected the behaviour of the whales, although the response of the animals was not consistent. Some whales approached the boats even when all three high impact manoeuvres occurred during the interactions (Table 3). However, when direct approach, encircling and chasing occurred during the same whalewatching trip, whales moved away from the boats significantly more frequently than: (a) approaching boats (Mann-Whitney $U = -3.98$; $P < 0.05$; Table 3); and (b) when those manoeuvres were absent (Mann-Whitney $U = -4.39$, $P < 0.05$).

Table 3

Mean (± standard error) number of times per trip when one or more whales approached or moved away from a whalewatching boat as a function of the occurrence of high impact (HP) manoeuvres (i.e. direct approach, encircling and chasing). Data are for observations in which all three manoeuvres occurred during the same trip. Total number of trips is in parentheses.

	Approach	Move away
With HP manoeuvres	1.95 ± 0.45 ($n = 20$)	4.76 ± 0.42 ($n = 25$)
Without HP manoeuvres	2.35 ± 0.40 ($n = 20$)	1.85 ± 0.27 ($n = 20$)

DISCUSSION

Almost 30 years since the first whalewatchers pioneered the activity, southern right whales have become the most important tourist attraction along *ca* 3,000km of coastal Patagonia (Campagna *et al.*, 1995; Rivarola *et al.*, 1995a; b). Placed in an international perspective, whalewatching in Argentina has grown to levels similar to those in Japan, Mexico, Australia and the United Kingdom (Campagna *et al.*, 1995).

Due to the local, national and international interest that whales generate, whalewatching in this area is likely to continue to increase. A prediction that, by the end of this century, over 150,000 tourists per year will be buying boat tickets to watch whales in this area, may even be an underestimate. The activity is a multi-million dollar industry and our figures are a conservative estimate of its economic importance. Virtually all (91%) of the 82,000 or more tourists that visited Península Valdés during the period June-December 1997 were involved in whalewatching. It is clear that there is an expanding demand, focused on the whales, which did not exist a decade ago. 'Ecological' tourism is today one of the fastest growing sources of income and employment for the Province of Chubut (Rivarola *et al.*, 1995a).

Since its beginning as an organised commercial activity, whalewatching has been driven by demand. Management decisions have not taken into account the possibility of adverse changes in the behaviour and distribution of whales. The tourist 'carrying capacity' of whalewatching has not been estimated but, as stated by Hoyt (1992), it may already have been reached.[1] There have been several attempts to improve management which ended in statements of good intent but no serious commitment from any of the involved parties. In 1997, the Provincial Government officially requested a management plan for Península Valdés that would include updated regulations for whalewatching. It is not known if this initiative will be the starting point of a new approach.

Short-term effects on whale behaviour and distribution

Perhaps the best way to evaluate the impact of whalewatching may be to show the effect of the activity on the survival, breeding success and distribution of individual whales (IFAW Tethys and Europe Conservation, 1995). To date, however, there are no such comprehensive data for the

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[1] Numbers of visitors in 1998 and 1999 were 79,481 and 74,512, respectively.

southern right whales of Patagonia. An important change in distribution that involved a traditional whalewatching area was noted in 1994. The number of whales around Puerto Pirámide peaked in early September ($n = 73$ animals on 5 September 1994). At the same time, about 50 mothers and calves were found at El Doradillo, 30-40km west of Puerto Pirámide, towards the city of Puerto Madryn. El Doradillo had not previously been recorded as such an important calving location. An average for 1991-1997 reveals that fewer than half the number of animals seen at Puerto Pirámide concentrated at peak season at El Doradillo (Rowntree *et al.*, 2001). The 1994 whalewatching activity was consequently targeted at the few animals that remained around Puerto Pirámide, with sometimes up to six boats around the same mother-calf pairs. However, changes in calving areas have been previously recorded for the waters around Península Valdés with no apparent connection to human activities (Payne *et al.*, 1990). However, the occupation of this 'new' coastal area still persists at a level of about ten mother-calf pairs for 1997 (Carribero, 1998; Carribero, pers. comm.).

At present, our knowledge of the impact of whalewatching on the behaviour of right whales is limited to a description of general indicators of potential negative effects. The short-term response of southern right whales to the proximity of boats in Patagonia has been described several times during the last decade. In the early 1980s, it was observed that some whales avoided boats with outboard engines, but some whales seemed to be attracted to them (G. Harris and C. García, unpublished report to the Government of the Province of Chubut). The first study to quantify the effects of whalewatching on whale behaviour was conducted in the mid-1980s based on theodolite readings. This work consisted of descriptions of changes in the behaviour and speed of whales that could be attributed to the presence of boats (Garciarena, 1988; Alverez Colombo *et al.*, 1990; Arias *et al.*, 1992, results summarised by the authors in Campagna *et al.*, 1995; IWC, 2001b). It was found that the mean swimming speed of solitary individuals and groups other than mother-calf pairs was faster within the whalewatching area of Golfo Nuevo than at Golfo San José. However, the speed of mother-calf groups did not vary significantly between the two, perhaps because young calves limit the mothers' swimming speed; if a mother increases her speed to avoid a boat, the calf could be left behind. Swimming behaviour was also less erratic at Golfo Nuevo and whale reaction to the presence of boats varied as a function of the stopping distance of the boat. Our data on the reaction of whales to approaching boats reinforces these results, and also shows that whales move away from boats that are encircling or following them as well as from boats that approach them directly.

Since the right whale is a long-lived species with a very low reproductive rate, it will be difficult to obtain information over a short time on the effects of whalewatching on survival and breeding. In the meantime, when considering whether whalewatching is harmless to whales, results from pilot impact studies should encourage a more cautious attitude. Whalewatching trips in this area are aimed at individuals that are in the most important stages of their biological cycles (pregnant females, mothers with calves, newly born calves, mating animals). Policy-makers must rely on the precautionary principle and management decisions must be based on the available circumstantial evidence. A step-wise introduction of permits, with regular feedback from population monitoring, would seem a viable approach to sustainable management.

Changing attitudes

The attitude of government officials and entrepreneurs responsible for promoting and conducting whalewatching activities must be shifted towards a more conservative approach. Efforts to sell dramatic whalewatching experiences, for example, with whales breaching a few metres away from boats (a sign that the boat may be disturbing the whale) and people touching whales (against the law), should be changed to the promotion of whalewatching as a peaceful, respectful and fascinating activity.

Attitudes towards whalewatching are often based on the assumption that clients will only be satisfied by being close to the animal. As companies compete to attract tourists, if one boat closely approaches a whale, the others are obliged to do so as well. Therefore, the experience is often limited to seeing whales in close proximity. The need to satisfy an uninformed demand is indirectly conveyed, rather than the need to respect the animal.

Regulations

Most regulations issued by the Province of Chubut are similar in essence and content to those affecting whalewatching in other parts of the world (Campagna *et al.*, 1995). If properly enforced, some of these regulations would improve the quality of management in relation to conservation. Priority should be given to maintaining current reserves and setting aside new marine reserves in critical right whale habitat, such as the entire area of Golfo San José and the main calving areas of Golfo Nuevo.

More precisely, present regulations could be improved as follows.

(1) Whalewatching boats should take a qualified guide on board to improve the educational experience.
(2) Protected calving areas should incorporate new areas that have not previously been safeguarded from disturbance.
(3) Navigation should not be allowed in calving areas early and late in the season. The length of the whalewatching season may have to be shortened to decrease potential harassment of the first females arriving at the calving area and the last leaving it.
(4) Consideration should be given to redefining the legal status of Golfo San José, currently a multi-purpose area, as a Marine Park devoted to, among other things, the protection of whales.

Long-term study of the basic biology of the species, data from well-designed studies of the impact of human activities on the whales, and the commitment of Patagonian coastal communities to prevent further degradation of prime right whale habitat should give the southern right whale an opportunity to continue its recovery. It will also ensure the continuity of an industry that has a strong educational potential and that may protect right whales against commercial activities. However, unregulated, unlimited numbers of people approaching a few whales hundreds of times, in what would otherwise be a calm, peaceful environment for calving and breeding, is a clear recipe for unsuccessful management.

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Occurrence of southern right whales (*Eubalaena australis*) along southeastern Brazil

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ABSTRACT

This paper reports on the occurrence of southern right whales (*Eubalaena australis*) in southeastern Brazilian waters (18°S-25°S), with evidence of their use of the region as an important calving area. Only in recent years have right whale sightings and strandings been reported regularly within the surveyed area. Of 71 distinct sightings reported since 1936, 39 (54.9%) were mother-calf pairs observed close to the shore. Most of these sightings (91.5%) were reported from early July to late October. Eight confirmed strandings of this species were observed within the surveyed area, six of which were between July and October. Stranded calves represented 62.5% of these records. Two calves showed evidence of incidental capture. The increasing number of sightings, and recent reports of stranded calves and one adult female could be indicative of an increase in cetacean research efforts in the region. However, it also suggests use of the southeastern Brazilian coast as an important right whale calving area.

KEYWORDS: SOUTHERN RIGHT WHALE; SOUTH ATLANTIC; INCIDENTAL SIGHTINGS; STRANDINGS

INTRODUCTION

Southern right whales (*Eubalaena australis*) have typically been observed in every ocean from about 20°S to 50°S (Cummings, 1985). Along the western South Atlantic, wintering southern right whales have been reported in Argentina (Omura, 1986; Whitehead *et al.*, 1986; Payne *et al.*, 1990), Uruguay (Townsend, 1935) and southern, southeastern and northeastern Brazilian coastal waters (Carvalho, 1938; Castello and Pinedo, 1979; Câmara and Palazzo Jr., 1986; Secchi, 1990; Simões-Lopes *et al.*, 1992; Greig *et al.*, 1994; Lodi *et al.*, 1996).

Historical documents provide some information on this species' distribution and exploitation along the Brazilian coast (e.g. Townsend, 1935; Ellis, 1969). Despite being protected by an international agreement since 1935, direct captures occurred along the coast of Santa Catarina state (27°S) until 1973 (Palazzo and Carter, 1983).

Little is known about this species in Brazilian waters. Systematic surveys to study right whales are lacking in most parts of their range. Most of the available data were obtained through occasional sightings and strandings along the southern Brazilian coast (25°S-34°S). In the last 20 years, right whales have occasionally been reported in southeastern Brazil (18°S-25°S).

This paper reviews the occurrence of southern right whales along the southeastern Brazilian coast in recent decades and presents evidence that this region is an important calving area for right whales.

MATERIAL AND METHODS

The study area in southeastern Brazil includes São Paulo (SP), Rio de Janeiro (RJ) and Espírito Santo (ES) states (Fig. 1). This area is characterised by a great number of shallow bays and inlets with calm waters along *ca* 1,940km of coastline (Diretoria de Hidrografia e Navegação, 1966).

Data have been compiled from scientific literature (Carvalho, 1938; Sawaya, 1938; Ellis, 1969; Moreira *et al.*, 1994; Capistrano *et al.*, 1996; Lodi *et al.*, 1996; Zampirolli *et al.*, 1998; Azevedo *et al.*, 1999; Di Beneditto and Ramos, 1999), media files (Folha de São Paulo and A Tribuna de Santos) and visits to museums and other institutions (Museu de Zoologia da Universidade de São Paulo, Museu Nacional do Rio de Janeiro, Museu do Mar de Santos and Museu do Instituto de Pesca de Santos) that keep osteological material and/or photographs, to ensure species identification. Unpublished data from occasional sightings and dedicated observation surveys have also been included. Dedicated surveys have been carried out in Atafona (RJ) since 1993, in Campos Basin (RJ) since August 1998 and in Arraial do Cabo (RJ) since July 1999.

A 'sighting' refers to an observation of a right whale individual or group at a known position within the surveyed area.

RESULTS

Sightings

Right whale sightings presented here cover the period between 1936 and 1999. Some of these sightings may be duplicates. The compiled data comprises 71 sightings ($n = 135$ whales) made in the coastal waters of São Paulo ($n = 17$), Rio de Janeiro ($n = 51$) and Espírito Santo ($n = 3$). The majority of the reported sightings (91.5%) were concentrated in the four-month period between July and October (Table 1). Since 1981, right whale sightings have been reported within the study area in every year except 1987, 1990, 1994 and 1997. Mother-calf pair observations represent 57.1% of all sightings.

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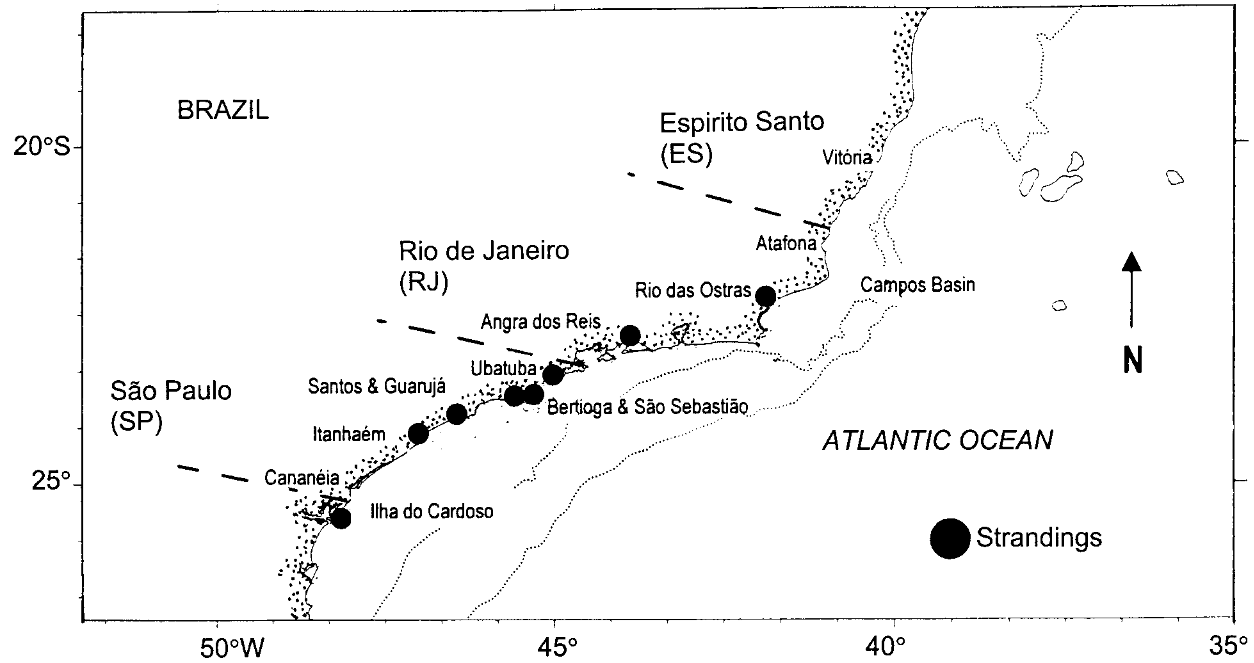

Fig. 1. Brazilian southeastern coast in detail showing the exact points where southern right whales strandings were reported from 1936-1998. A total of 71 confirmed sightings have been reported since 1936 from Cananéia (SP) to Vitória (ES). The majority of sightings were observed in coastal waters between Ubatuba (SP) and Atafona (RJ).

Table 1

Monthly sightings of southern right whales, *Eubalaena australis*, in each state along the southeastern Brazilian coast. Sightings (n=71) occurred between 1938 and 1999.

State	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
São Paulo	-	6	3	1	7	-	-	17
Rio de Janeiro	1	9	22	9	5	4	1	51
Espírito Santo	-	-	2	-	1	-	-	3
Total	1	15	27	10	13	4	1	71

Table 2

Southern right whales, *Eubalaena australis*, strandings (n=8) reported along the southeastern Brazilian coast from 1936 until 2000. L = Body length.

Date	Location	L (cm)	Sex	Source
Oct. 1936	Guarujá, SP (23°59'S, 46°15'W)	calf/L?		Sawaya (1938)
27 Jan. 1955	Itanhaém, SP (24°10'S, 46°45'W)	*ca* 800		Present study
19 Sep. 1984	Bertioga, SP (23°50'S, 46°08'W)	*ca* 1,300		Lodi *et al.* (1996)
17 Aug. 1995	Angra dos Reis, RJ (23°10'S, 44°20'W)	*ca* 590	F	Capistrano *et al.* (1996)
19 Sep. 1995	Ubatuba, SP (23°10'S, 45°04'W)	*ca* 400	M	Present study
6 Jul. 1996	São Sebastião, SP (23°49'S, 45°24'W)	420	M	Present study
8 Sep. 1998	Rio das Ostras, RJ (22°26'S, 42°49'W)	1,740	F	Azevedo *et al.* (1999)
14 Jan. 2000	Ilha do Cardoso, SP (25°00'S, 48°55'W)	750		Present study

Strandings

Only eight strandings have been reported from the southeastern Brazilian coast: six in São Paulo and two in Rio de Janeiro (Table 2). Five of the stranded right whales were calves, one was a juvenile (Fig. 2) and the other two were adults. The two stranded whales examined from Rio de Janeiro showed evidence of net entrapment; however, for the other specimens the cause of death remains unknown. Umbilical cord remains were observed with a dead calf stranded at São Sebastião.

DISCUSSION AND RECOMMENDATIONS

The relatively high percentage of mother-calf pair sightings (54.9%) and strandings of calves (including one dead calf with umbilical cord remains), provide evidence of the possible use of southeastern Brazilian coastal waters by right whales as a calving area. Ellis (1969) described whales, mainly mother-calf pairs, using shallow bays and inlets during rough sea conditions. Females with calves may come closer to the shore in higher proportions than single individuals or multiple adult groups. If so, this would mean that mother-calf pairs might be over-represented in our sample. Sightings effort must be expanded to include offshore waters to determine if this is the case.

Historical documents and published literature reveal that right whales were found along the southeastern Brazilian coast in the past. Depletion of the species is known to have occurred in Brazilian waters over the last four centuries (IWC, 2001). Scientific studies of right whales in Brazil only began in the 1980s and sighting effort in coastal waters has not been uniform. Dedicated surveys have only been conducted in Santa Catarina in the last decade and in Rio de Janeiro in recent years. Data collected since then suggest that the population is increasing (Pinedo, 1984; Câmara and Palazzo Jr., 1986). The data presented here suggest that right whales are reoccupying areas along the southeastern Brazilian coast which they inhabited prior to their exploitation. It is clear that interpretation of possible trends is confounded by the increase in research effort. Further systematic research is required before firm conclusions on movement, distribution and population parameters can be drawn.

As in other areas of the world, right whales face several potential threats along the southeastern Brazilian coast. Gillnets are used in coastal areas and may be an important cause of mortality, as suggested by some of the strandings

Fig. 2. A juvenile southern right whale stranded at Itanhaém (24°10'S, 46°45'S), São Paulo, on 27 January 1955. (Folha de São Paulo Files).

and reports by Capistrano *et al.* (1996) and Lodi *et al.* (1996). In addition, there are several major ports (e.g. Santos, São Sebastião, Angra dos Reis, Rio de Janeiro and Vitória) within this area and vessel traffic is intense. Thus, as the right whale population grows and reoccupies its historic range, collisions with ships (and incidental catches) may increase and threaten recovery. A further potential threat arises out of uncontrolled approaches by bathers, divers and whalewatching vessels. These concerns reinforce the need for adequate educational programmes in southeastern Brazil, directed towards fishermen, tourists and public institutions such as lifeguard offices and environmental organisations.

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Stranding events of southern right whales, *Eubalaena australis*, in southern Brazil

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ABSTRACT

Although international protection has been granted since 1935, southern right whales have only recently shown signs of recovery, possibly due to anthropogenic factors. Off Brazil, illegal hunting of right whales occurred until 1973. This paper reports on surveys conducted along the southern Brazilian coast and the information recovered on right whale strandings for this area from 1977-1995. In the first 10 years of this period only four cases were registered. However, in contrast, 20 cases were counted during the last nine years. These results are discussed in relation to marine traffic and the fisheries in the area that produce risks of collision and entanglement. Further, the possibility of storm surges being a preponderant factor in the mortalities in this area is presented. These yearly rates are compared with neighbouring areas that are also inhabited by the right whales. Both possibilities fit the hypothesis that the right whales using the Brazilian coast for breeding may finally be showing signs of recovery.

KEYWORDS: SOUTHERN RIGHT WHALE; ATLANTIC OCEAN; STRANDINGS; SURVEY–SHORE-BASED; SOUTHERN HEMISPHERE; SOUTH AMERICA

INTRODUCTION

When North Atlantic right whales (*Eubalaena glacialis*) were showing first signs of depletion, whalers turned their attention to the southern right whales (*Eubalaena australis*). They were intensively hunted throughout the Southern Hemisphere to near commercial extinction (e.g. see the summary in IWC, 2001).

In 1935, right whales received their first international protection and this was continued after the signing of the International Convention for the Regulation of Whaling in 1946 (Donovan, 1992). Recently, there has been evidence of recovery in several Southern Hemisphere populations; however, the same is not true for the North Atlantic or North Pacific right whales (IWC, 2001).

Intensive studies of southern right whales off the eastern coast of South America began in 1971, at the Península Valdéz nursery area off the Argentinian coast. Photo-identification methods have proved particularly successful for examining behaviour as well as estimating population parameters (e.g. Payne *et al.*, 1990). Similar studies have been carried out off South Africa (e.g. Best, 1981), Tristan da Cunha (Best, 1988) and, to a lesser extent off the southern Brazilian coast (Simões-Lopes *et al.*, 1992; Best *et al.*, 1993). These studies have provided an insight into the major migration routes of the species in the South Atlantic (Best *et al.*, 1993). The population that breeds off Argentina also uses Tristan da Cunha and the Brazilian coast as breeding grounds, as well as an area off South Georgia for feeding (IWC, 2001).

In Brazil, whaling began in the 17th century in the state of Bahia and had expanded along the coast to Santa Catarina by the 19th century (Ellis, 1969). Even after international protection, it appears that some right whales were hunted illegally in Brazil until 1973 (Palazzo and Carter, 1983; Tormosov *et al.*, 1998).

Strandings of South Atlantic right whales in their major breeding grounds appear to be rare and are usually reported when they are the result of interactions with vessels or fishing gear (e.g. Best, 1984). Since 1977, southern right whale strandings off the Brazilian coast have been reported in the literature or recorded in log books, irrespective of their cause. Such data are relatively easy to obtain and do not involve great costs or major research programmes.

This paper reports on right whale stranding events along the southern coast of Brazil between 1977 and 1995.

MATERIALS AND METHODS

This study was carried out along the state of Rio Grande do Sul, Brazil, which shares borders with Uruguay to the south and with the Brazilian state of Santa Catarina to the north (Fig. 1). Its 618km coastline extends from Chuí (33°45'S) to Torres (29°19'S). Beach surveys by car along the 400km stretch between Chuí and Mostardas (31°10'S) to record stranded animals were carried out from 1989-1995. Further information on strandings was obtained from media files, researchers from other laboratories that surveyed the complete Rio Grande do Sul State coastline during their studies and from marine mammal researchers who had previously covered the same area. Records of sightings of mother-calf pairs along the study area were also obtained in the same way.

Survey effort varied over the total period of this study. Information from 1977-1986 was collected during surveys undertaken by a number of researchers. These surveys covered 100km every two weeks or alternately, 400km to the north in one month and 220km to the south in the other. Effort was not constant throughout the ten year period, being less intense at the beginning and at the end. From 1987-1990, surveys were carried out opportunistically. In 1991, a regular programme was established and surveys were carried out every two weeks, covering alternately 220km to the south and 200km to the north.

Any animals found dead were photographed and sexed and measured according to Leatherwood *et al.* (1982). Some individuals found were too decomposed to determine sex and there were other cases where the recorded information provided little detail. Some parts of the skeletons were recovered and deposited in the collection at the Museu Oceanográfico 'Prof. Eliézer de C. Rios' in Rio Grande.

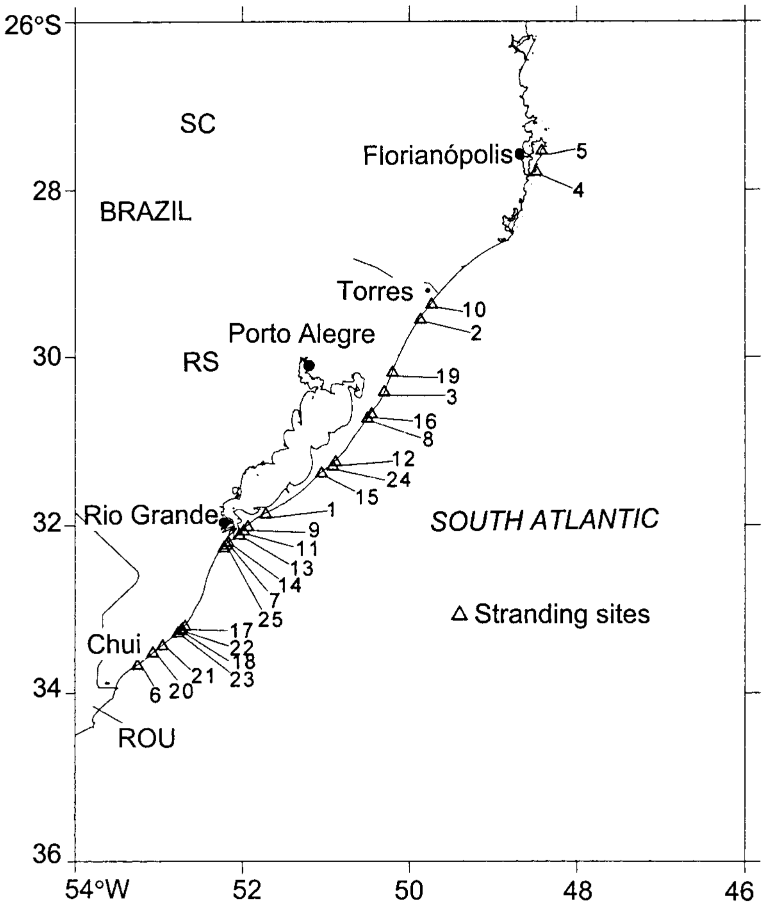

Fig. 1. Southern right whale stranding sites on the southern Brazilian coast between 1977 and 1995. ROU = Oriental Republic of Uruguay; RS = Rio Grande do Sul State in Brazil; SC = Santa Catarina State in Brazil. The numbers are related to those of Table 1.

RESULTS

A total of 12 mother-calf sightings from shore were recorded between 1983 and 1994 (1 in 1983, 1985, 1988 and 1989, 3 in 1991, 4 in 1992 and 2 in 1994) showing a slight increase over time. Photographs of the pairs showed that they were not resightings. Twenty-three strandings/beachings were recorded between 1977 and 1995 along the Rio Grande do Sul State coast (Table 1). Four occurred from 1977-1986 and the other 19 from 1987-1995. The highest numbers occurred during the month of October but strandings also occurred in late winter (August and September). Nine individuals were calves, while 14 were sub-adults or adults.

In 1989, a young right whale was found washed ashore with propeller cuts on its head; it had been sighted several times with two other adult whales during the two previous weeks (Secchi, 1994). In 1991, two halves of a right whale were found about half a mile apart from each other. In the same year, an adult male that had been reported by the Navy as floating dead two days before was found on the beach. In 1992, a fisherman reported having collided with a right whale during trawling but no dead whale was later found. In October 1993, a right whale was found beached 16km south of Rio Grande (32°08'S) with four propeller cuts on its caudal stock.

On 14 October 1987, a 5m male was found stranded on Cassino beach (32°10'S; F. Rosas, pers. comm.). On 5 August 1992, a 6m female still with vestiges of the umbilical cord was found stranded at Cidreira (30°10'S) (L. Susin, pers. comm.). On 9 October 1993, a 5.5m female was found stranded close to the Mostardas lighthouse (31°13'S); another whale measuring 4.6m was also found stranded close to the Albardão lighthouse (33°12'S). These four individuals were probably neonates.

Table 1

Southern right whale stranding events on the southern coast of Brazil, between 1977 and 1995. Cases 4 and 5 were in the state of Santa Catarina.

Case	Date	Length (m)	Sex	Source
1	26 Aug. 1977	14.00	F	Castello and Pinedo, 1979
2	1 Aug. 1979	Calf	Ind.	Palazzo and Carter, 1983
3	1 Sep. 1982	Calf	Ind.	Palazzo and Carter, 1983
4	25 Aug. 1983	Calf	Ind.	Lodi *et al.*, 1996
5	28 Sep. 1983	Calf	Ind.	Lodi *et al.*, 1996
6	1 Nov. 1984	12.00	Ind.	Lodi *et al.*, 1996
7	31 Aug. 1987	17.50	M	F.W. Rosas, pers. comm.
8	17 Sep. 1987	13.00	Ind.	CEBECLIM
9	14 Oct. 1987	5.00	M	F.W. Rosas, pers. comm.
10	8 Sep. 1988	6.00	Ind.	CEBECLIM
11	25 Aug. 1989	7.50	M	Secchi, 1994
12	26 Sep. 1990	15.00	F	NEMA
13	30 Sep. 1990	14.50	F	-
14	8 Oct. 1991	13.50	M	-
15	12 Oct. 1991	14.00	M	L. Calliari, pers. comm.
16	12 Oct. 1991	Adult	Ind.	L. Calliari, pers. comm.
17	14 Feb. 1992	xx	Ind.	-
18	14 Feb. 1992	Calf	Ind.	-
19	5 Aug. 1992	6.00	F	L. Susin, pers. comm.
20	2 Oct. 1992	14.30	Ind.	-
21	16 Aug. 1993	Ind.	Ind.	-
22	9 Oct. 1993	10.50	M	-
23	9 Oct. 1993	4.58	Ind.	-
24	9 Oct. 1993	5.54	F	-
25	25 Oct. 1993	12.50	M	-

DISCUSSION

The number of strandings found during the second period of this study (19 in nine years) is high when compared to the four cases that occurred during the first period (10 years) of our study. It is important to note that in the neighbouring state of Santa Catarina, which is the main breeding ground for the species in Brazil (Simões-Lopes *et al.*, 1992) and where the search effort was also high, only two strandings were registered during the total period (19 years) (J.T. Palazzo Jr., pers. comm.).

This increase in sightings and strandings in the study area might imply that the species is returning to its historical breeding grounds, as has also been suggested by Castello and Pinedo (1979), Lodi and Bergallo (1984), Câmara and Palazzo Jr. (1986) and Simões-Lopes *et al.* (1992). If there has been a real increase in the number of individuals using the Brazilian coast, it might be reasonable to expect that strandings would also be more frequent. An increase in the number of individuals in this general area would also increase the likelihood of collisions with marine traffic. This would be similar to the problem reported by Wiley *et al.* (1995), who described a notable increase in the number of humpback whale strandings between two similar periods on the southeastern coast of the USA. They noted that this might be attributed at least in part to an increase in the number of juveniles using that coastal habitat with the associated increase in the probability of collisions.

Anthropogenic activities are one cause of right whale mortality off the Rio Grande do Sul coast. Three of the 23 stranding cases showed evidence of anthropogenic interaction, whilst the other cases were not sufficiently investigated to determine the cause of death. Marine traffic in the area is extensive due to the presence of the Port of Rio Grande, which is the only fishing facility on the state coast and therefore attracts most of the fishing fleet of southern Brazil. Approximately 535 fishing boats operate in the area all year round (IBAMA, unpublished data).

Sciaenids represent an important fishing resource for the local fleet (approximately 81% in weight of the region's bony fish; Haimovici *et al.*, 1996) as well as for boats from neighbouring Santa Catarina (Haimovici *et al.*, 1989; Reis, 1992). The operating range of most vessels in these fleets is up to the 80m isobath, an area that corresponds with the coastal migration route of right whales to and from their wintering grounds. This overlap between fishing and migration areas causes potential risk of collisions and entanglements. In addition, the port of Rio Grande receives an average of 1,435 (n = eight years of data) cargo ships per year, although most of this traffic occurs during the first months of winter (5th Naval District, unpublished data) and is therefore before the months in which most of the strandings were observed. In this context, however, it is interesting to note that while Santa Catarina has more than one port (including the Port of Itajaí, a large fisheries port) and its coastline is the major breeding ground for right whales in Brazil, few strandings have been reported here. The survey effort in the region was as extensive as that further south in Rio Grande do Sul.

Despite the extensive fishing effort off the coast of Rio Grande do Sul, to date no cases of entanglement in fishing gear have been recorded. This may reflect the fact that most of the fisheries target bottom-dwelling species using either bottom-set or trawl gear (right whales spend most of their time near the surface during migration making it unlikely that they would become entangled in bottom gear). Along the coasts of Santa Catarina and Rio de Janeiro, six and three entanglements have been reported respectively (Lodi *et al.*, 1996). Here, by contrast, although coastal fisheries are not as common as off Rio Grande do Sul, they use surface-set gear in the shallow waters where right whales breed.

That right whales are vulnerable to ship strikes and entanglements has been shown in other areas (IWC, 2001). Kraus (1990) and Knowlton and Kraus (2001) reported that collisions with vessels and entanglements in fishing nets were significant causes of mortality in the northwest Atlantic. Best *et al.* (2001) summarises ship strikes and entanglements of right whales off the South African coast. The lack of stranding records of southern right whales connected with shipping accidents in Australian waters is thought to be due to the fact that, at present, the species is rarely found in the major ports and shipping channels of Southern Australia and New Zealand; prior to the 1850s these areas were part of their range and were used as nursery/calving grounds (F. Michaellis, pers. comm.).

The continental shelf off Rio Grande do Sul is extensive, has a gentle slope and the coastline is open and sandy, compared to that of Santa Catarina which has several bays and opportunities for shelter (Fig. 1). These features make stranding events more likely here when compared with Santa Catarina. Storms usually hit the coast from the south or southeast, pushing water up against the shore and producing a storm surge; this can result in an elevation of sometimes more then two meters above the normal sea level (Calliari *et al.*, 1997). Right whales using this coast as a migration route, calving or nursing ground, may try to seek shelter closer to the shore during strong storms and thus end up stranded. This situation would be unlikely in Santa Catarina due to the greater number of shelter opportunities and this could account for its low number of stranding events (only two during the study period). It is interesting to note that Ellis (1969) deduced from whaling accounts that southern winds were favourable for whaling off the Brazilian coast because the whales came closer to the shore.

Little is known about the migration route of southern right whales off the Brazilian coast. The period in which most strandings occurred is consistent with the May-December period reported by Lodi and Bergallo (1984). Sightings of mother-calf pairs close to the shore (e.g. Secchi, 1994) as well as the stranding of neonates on the Rio Grande do Sul coast indicate that the groups seen are either returning from calving areas further north or that the Rio Grande do Sul coast is used as a calving and nursery area (although to a lesser extent than the Santa Catarina coast). However, Simões-Lopes *et al.* (1992) had affirmed that while the Santa Catarina coast is used for mating, calving and nursing, the Rio Grande do Sul coast is used mostly as a migration path. Thomas and Taber (1984) suggest that nursing in southern right whales at Península Valdés can last up to 14 months after birth. The sightings and strandings of newborns and mother/calf pairs reported here provide evidence that the Rio Grande do Sul coast may represent a calving/nursing area for the species.

In conclusion, there are several factors that may explain the relatively high number of stranding events in this area compared with the major breeding ground in Santa Catarina. These include: (1) increase use by whales, possibly as a breeding ground; (2) exposed open coast that favours stranding events; and (3) greater probability of collisions with fishing and cargo vessels. It is strongly recommended that directed studies to establish the importance of this coast as a breeding ground and migration route be carried out.

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Demographic parameters of southern right whales off South Africa

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ABSTRACT

Aerial counts of right whale cow-calf pairs on the south coast of South Africa between 1971 and 1998 indicate an annual instantaneous population increase rate of 0.068 per year (SE = 0.004) over this period. Annual photographic surveys since 1979 have resulted in 901 resightings of 550 individual cows. Observed calving intervals ranged from 2-15 years, with a principal mode at 3 years and secondary modes at 6, 9 and 12 years, but these make no allowance for missed calvings. Using the model of Payne *et al.* (1990), a maximum calving interval of 5 years produces the best fit to the data giving a mean calving interval of 3.12 years (95% confidence interval: 3.07, 3.17). The same model produces an estimate for adult female survival rate of 0.983 (95% CI: 0.972, 0.994). The Payne *et al.* (1990) model is extended to incorporate information on the observed ages of first reproduction of grey-blazed calves, which are known to be female. This allows the estimation of age at first parturition (median 7.88 years 95% CI 7.17, 9.29). Updates of estimates and confidence intervals for the other demographic parameters are: adult female survival rate 0.986 (0.976, 0.999); first year survival rate 0.913 (0.601, 0.994) and instantaneous population increase rate 0.071 (0.059, 0.082). These biological parameter estimates are shown to be compatible with the observed increase rate of the population without the need to postulate immigration.

KEYWORDS: RIGHT WHALE; SOUTHERN HEMISPHERE; POPULATION PARAMETERS; SURVIVORSHIP; REPRODUCTION; MATURATION; SURVEY-AERIAL; TRENDS; MODELLING

INTRODUCTION

Counts made on fixed-wing aerial surveys of the population of right whales (*Eubalaena australis*) that over-winters on the southern coast of South Africa indicate an instantaneous increase rate of 0.068 per year between 1971 and 1987 (Best, 1990b). Butterworth and Best (1990) have shown that this rate of increase is compatible only with a relatively restricted range of values for calving rate, age at first parturition and survival rate. Between 1979 and 1998, aerial photographs of right whales have been taken annually on separate helicopter surveys, and used for photo-identification of individuals from their callosity patterns and/or dorsal pigmentation (Best, 1990a). In this paper, the results of the photo-identification project are analysed to provide estimates of calving interval, survival rate and age at first parturition, and to investigate their compatibility with the observed rate of population increase in the context of Butterworth and Best's (1990) results.

MATERIAL AND METHODS

Between 1969 and 1987, fixed-wing surveys were flown off the south coast of South Africa from Woody Cape, Algoa Bay, to Muizenberg, False Bay, in late September/early October each year, and counts of all right whales seen were made. The techniques used and results obtained have already been published (Best, 1990b). From 1979 to 1998, annual photographic surveys of the right whale population on the southern coast of South Africa have been carried out by helicopter. Details of the survey techniques have already been published (Best, 1990a), but in the context of this paper the important point is that the surveys were carried out in as standard a manner as possible. To this end they were flown at the same time of year each year (earliest flight 6 October, latest flight 25 October, with 77% of animals being photographed between 11 and 21 October), using the same strategy on each flight. The same stretch of coastline, Nature's Valley to Muizenberg, was searched once each year, usually from east to west so that the pilot and photographer were on the coastward side of the aircraft. Where possible, flights were confined to days of good visibility and when surface winds were less than 15 knots. Searching was undertaken at a height of 1,000ft (305m); any whale encountered was inspected for the presence of a calf, and if one was detected, the aircraft would descend to 300ft (95m) for photography. Unless supplies were running low, usually one film (12 exposures) was taken of each cow-calf pair. Animals without calves were normally not photographed.

For all animals except calves, the photographs from each year's survey were compared with the existing catalogue of known individuals. Each animal was compared in turn with the entire catalogue, and potential matches noted. The original photographs of any potential matches were then compared with those of the survey animal. If a match was established, the animal was incorporated in the catalogue as a 'synonym'. If no match was found, photographs of the survey animal were then compared again with the entire catalogue before it was accepted as a new individual. In total, 1,451 cow-calf pairs were photographed between 1979 and 1998, with a final catalogue of 550 individual cows. Intervals between calves were established on 901 occasions.

Calving interval and survival rates

Observed calving intervals are biased representations of the true calving frequency, because *inter alia* cows on longer intervals are under-represented in the sample (having a greater proportion of incomplete calving intervals) and no allowance is made for missed calvings. In reality, a cow

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calving in a particular year might not be photographed because (a) the calf died before the survey, or was born after the survey, or (b) the cow plus calf were outside the survey area at the time of the survey, or were in the survey area but were overflown. To estimate the true calving interval, the maximum likelihood approach adopted in Payne *et al.* (1990) and developed further by Cooke *et al.* (1993) has been used. Their models are summarised below, mainly because some of the equations involved were printed incorrectly in Payne *et al.* (1990). For a more detailed discussion of these models the reader is referred to the above references.

The same notation as Payne *et al.* (1990) is adopted:

p_j	the probability that a calving in year j is recorded;
h_j	probability that a female calving in year m has her next calf in year $m+j$, given that she has survived to year $m+j$;
q_j	the probability that a female calving in year m has a calf in year $m+j$, given that she has survived to year $m+j$;
n_i	number of calvings recorded in year i;
n_{ij}	number of females recorded to calve both in year i and in year j, where $i<j$;
j_{max}	the maximum calving interval, where possible values considered are $j_{\max} = 4, 5, 6$ and 7;
s_j	the probability that a female that calved in year m survives to year $m+j$;
n	total number of years in which calvings have been recorded.

The probabilities q_j are related to the probabilities h_j by the following equation:

$$q_j = \sum_{i=1}^{j} h_i q_{j-i} \tag{1}$$

where $q_0 = 1$ and the h_i satisfy the condition:

$$\sum_{i=1}^{j_{\max}} h_i = 1 \tag{2}$$

The n_{ij} are assumed to follow a Poisson distribution with expected value given by:

$$\mu_{ij} = n_i s_{j-i} q_{j-i} p_j \quad (i<j) \tag{3}$$

so that the likelihood function is then given by:

$$L(n_{ij}; p_j, h_i, S) = \prod_{j=1}^{n} \prod_{i=0}^{j-1} \frac{e^{-\mu_{ij}} \mu_{ij}^{n_{ij}}}{n_{ij}!} \tag{4}$$

where S is the annual survival rate of females (assumed constant), so that $s_j = S^j$.

The mean calving interval is given by:

$$\sum_{j=1}^{j\max} j h_j s_j \Big/ \sum_{j=1}^{j\max} h_j s_j \tag{5}$$

This model also provides estimates for p_j given by:

$$\hat{p}_j = \sum_{i=0}^{j-1} n_{ij} \Big/ \sum_{i=0}^{j-1} n_i q_{j-i} s_{j-i} \tag{6}$$

and these in turn yield estimates of the number of calvings in each year ($\hat{N}_j$ where $\hat{N}_j = n_j/\hat{p}_j$). The model proposed by Payne *et al.* (1990) to estimate the annual rate of increase expressed as an instantaneous rate is also applied to these data. If N_0 is the number of calvings in the first year of the study, δ is the annual instantaneous growth rate, and the trend in the calving population size is modelled as:

$$N_j = N_0 e^{\delta . j} \tag{7}$$

then Equation (3) can be rewritten by replacing p_j in terms of N_j as:

$$\mu_{ij} = n_i n_j s_{j-i} q_{j-i} e^{-\delta . j} / N_0 \quad (i<j) \tag{8}$$

and the likelihood function given by Equation (4) can be maximised to give an estimate for the annual instantaneous growth rate. Confidence intervals for the parameter estimates are obtained using the likelihood profile method (Schnute and Groot, 1992).

Age at first parturition

Photographs of any previously un-photographed adults taken on a survey were compared with those of calves taken four or more years earlier. This analysis was confined to matching calves and adults that carried grey blazes (see Best, 1990a), as these animals are known to be female (Schaeff *et al.*, 1999). Restriction of the analysis to known females allows the estimation of the juvenile survival rate in addition to the age at first parturition. In the catalogue of adult females from 1979 to 1998 there was a total of 63 such 'grey-blazed' individuals, and from 1979 to 1992 a total of 64 grey-blazed calves was photographed. A total of 31 matches was found, all for cows photographed from 1987 onwards (see Table 4). The analysis that follows makes the tacit assumption that all calves with visible grey blazes retain them. This seems plausible because while the blazes tend to darken with age, their shapes remain unchanged over time (Payne *et al.*, 1983; Best, 1990a).

The observed ages at first parturition are subject to the same types of bias as the observed calving intervals, in that later maturing individuals will be relatively under-represented, and some first calvings will go undetected. Hence, a modelling approach has been adopted to estimate the true median age at first parturition.

Let m_i be the number of female calves seen in year i, where $i = 1979, \ldots, 1992$, and t_k be the number of such females seen to first reproduce at age k, where $k = 6, \ldots, 13$.

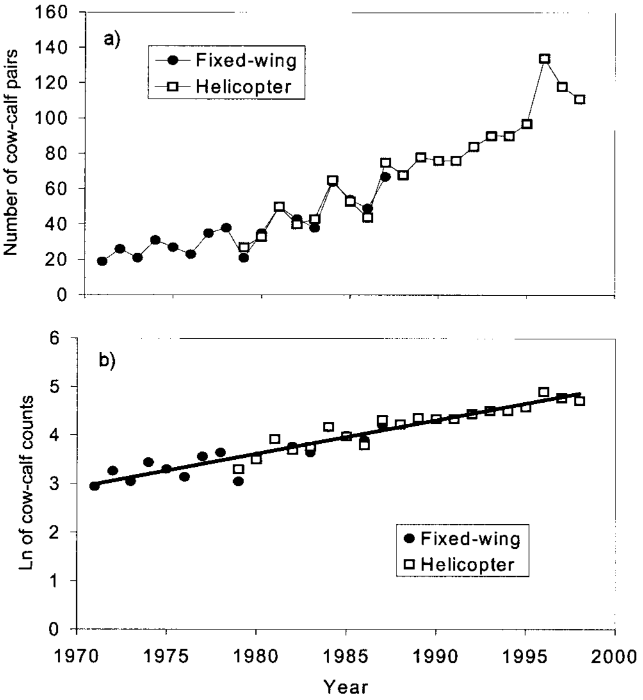

Fig. 1. Numbers of right whales with calves seen on surveys by fixed wing aircraft, 1971 to 1987, and by helicopters 1979 to 1998 expressed as (a) raw counts, (b) natural logarithms of counts.

Table 1

Observed right whale cow-calf pairs on the south coast of South Africa between 1979 and 1998. Number of calvings recorded in each year as well as the number of females that have been resighted with a calf in later years are shown.

a) The number of females recorded to calve both in year i and in year j (n_{ij}), where $i < j$

Year i	Year j ($i < j$)																		
($i < j$)	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
1979	0	1	17	2	4	14	2	2	10	3	5	8	4	4	6	5	3	4	4
1980		0	0	22	2	2	15	4	3	17	5	3	15	3	3	15	6	3	10
1981			0	2	31	0	4	27	3	5	15	8	6	12	5	4	16	6	5
1982				0	1	28	3	2	24	4	3	18	5	4	14	4	4	12	3
1983					0	2	21	5	4	23	8	4	17	6	5	17	4	3	15
1984						0	1	42	6	4	30	8	6	25	7	6	25	10	7
1985							0	2	34	4	3	27	4	5	27	5	6	19	6
1986								0	1	31	2	4	22	3	3	19	5	4	13
1987									0	3	43	5	4	34	4	6	34	8	9
1988										0	1	37	3	4	34	5	7	28	4
1989											0	2	47	7	4	38	8	10	31
1990												0	0	39	1	4	35	4	5
1991													0	2	46	5	6	37	7
1992														0	1	50	13	4	38
1993															0	1	48	6	6
1994																0	1	55	3
1995																	0	1	54
1996																		0	3
1997																			0

b) Number of calvings recorded in each year i (n_i)

Year	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
n_i	27	33	50	40	43	65	53	44	76	69	78	76	76	85	90	90	97	134	118	111

Define λ_k to be the proportion of animals of age k which have reached first parturition (either at that age or earlier). This is re-parameterised as:

$$\lambda_k = \begin{cases} 1/\left[1 + e^{-(k-a_m)/\Delta}\right] & k \geq 6 \\ 0 & k < 6 \end{cases} \tag{9}$$

where a_m is the age at which 50% of the population reach first parturition and Δ measures the spread of this ogive. Define $\tilde{S}$ as the survival rate for the first year of life (S is assumed to apply for each year thereafter); then for each k the expected value of t_k ($\hat{t}_k$) can be represented in terms of m_i, $\tilde{S}$, S, p_j and λ_k. For example, when $k = 6$, $\hat{t}_k$ is given by:

$$\hat{t}_6 = \sum_i m_i \tilde{S} S^5 p_{i+6} \lambda_6 \tag{10a}$$

and for $k = 7$, $\hat{t}_k$ is given by:

$$\hat{t}_7 = \sum_i m_i \tilde{S} S^6 p_{i+7} (\lambda_7 - \lambda_6) + \sum_i m_i \tilde{S} S^6 (1 - p_{i+6}) \lambda_6 h_1 p_{i+7} \tag{10b}$$

and so on for other values of k.

The observed t_k are assumed to follow Poisson distributions with expected value $\hat{t}_k$ so that the likelihood function is given by[1]:

$$L(t_k; a_m, \Delta, S, p_j, h_i, \tilde{S}, \delta, N_0) = \prod_{k=6}^{13} \frac{e^{-\hat{t}_k} (\hat{t}_k)^{t_k}}{t_k!} \tag{11}$$

Incorporating the information available on matched calves and adults as well as the adult resighting information, one can obtain estimates for the calving interval and the age at first parturition concurrently. This was achieved by maximising the likelihood obtained from the product of the two individual likelihood functions given by Equations (4) and (11). Penalty functions were used to ensure that h_i values were not negative and that the juvenile survival rate ($\tilde{S}$) did not exceed the adult survival rate (S). This last constraint is imposed because it seems likely that if the mother dies during a calf's first year of life, the calf would die too.

RESULTS

Counts on annual surveys

Fig. 1a shows the counts of right whales with calves seen on fixed-wing surveys from 1971-1987, and helicopter surveys from 1979-1998. The counts for the helicopter surveys are based on the actual numbers photographed, as obtained after the photographs have been matched and any inadvertent duplicates omitted. For the period of overlap between surveys (1979-1987), correlation between counts on the two surveys is excellent ($r^2 = 0.914$), indicating that survey efficiencies using fixed-wing and helicopter aircraft were similar. If the counts are expressed as natural logarithms and plotted against time (Fig. 1b), then annual instantaneous increase rates (i.e. δ of Equation (7)) of 0.0679 (SE = 0.0102) are obtained for the fixed-wing surveys from 1971-1987, and 0.0692 (SE = 0.0058) for helicopter surveys from 1979-1998. These rates of increase are not significantly different ($t = 0.11$, two-tailed $p > 0.90$), and a common regression line indicates that the population has been increasing at an instantaneous rate of 0.068 (SE = 0.004) per year for the last 28 years.

Calving interval

Table 1 gives the observed values for the number of right whale calvings recorded each year and the number of females that were observed to calve in both year i and year j. Fig. 2 shows the distributions of observed calving intervals

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[1] Strictly this product should be extended to values of $k > 13$, for which expectations are non-zero even though there are no actual recordings. However, for the parameter values estimated, the expectation for $k = 14$ is already very small (about 0.2), so that this complication was ignored for simplicity.

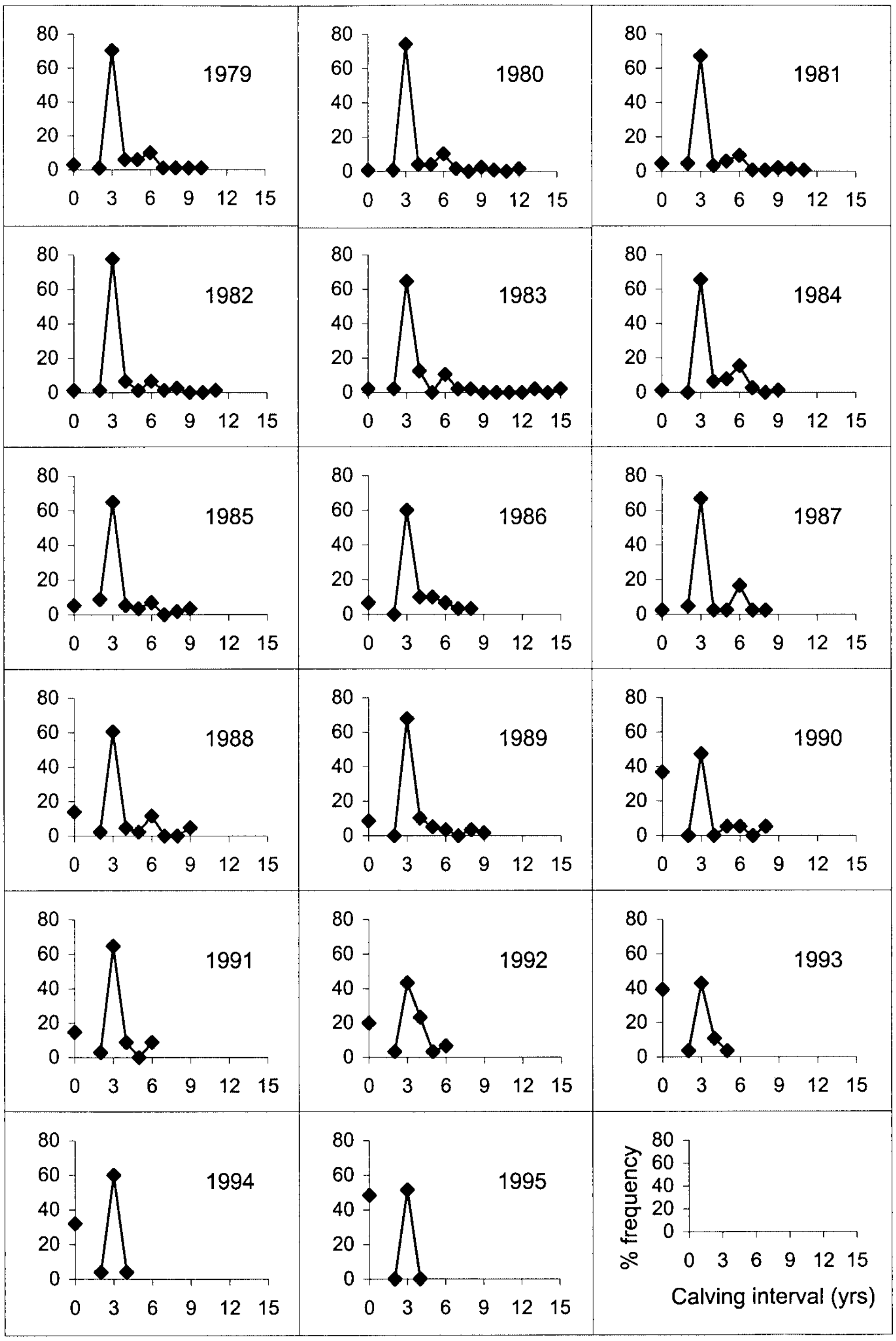

Fig. 2. The distribution of observed calving intervals by annual cohort (◆ = incomplete calving intervals).

for each cohort of females from 1979 to 1995 (the data for the 1996 and subsequent cohorts are not included because the time for which they have been at large is only two years or less). The distribution has an obvious mode for each cohort at three years, and for most cohorts a much smaller mode around six years. Some early cohorts also have a few intervals around nine years, and very few at about 12 years: the longest observed interval is 15 years. Arithmetic means of the observed intervals range from 3.00-4.09 years, with four of the five lowest (3.00-3.57) occurring in the years 1991-1995, clearly indicating the effect of the exclusion of longer intervals due to the brief period that these animals have been 'at large'.

Table 2 gives the estimated probability distributions of calving intervals from the Payne *et al.* (1990) model, for different choices of the maximum calving interval (j_{max}). The log-likelihood values, together with considerations of parsimony, indicate that the distribution with a maximum calving interval of five years produces the best fit (although a maximum value of six years is not discounted). This distribution has a mean calving interval of 3.12 years with a (likelihood-profile-based) 95% CI of 3.07, 3.17. Fig. 3 compares the distribution of observed and model predicted (Equation (3) summed over i) frequencies of subsequent calvings in relation to the period (j-i) elapsed since the first sighting of an animal with a calf, on the assumption of a maximum interval of five years; the overall fit is good ($\chi^2 = 8.89$, $p = 0.632$).

The model also provides estimates of the probability that a calving which occurs in a particular year is recorded (Table 3); from this, the 'true' number of calvings occurring in that year can be estimated (Fig. 4). Recording probabilities are

Table 2

Estimates of the probability distribution of calving intervals (h_j), mean calving interval (yr) and annual survival rate (S) for right whales off South Africa for different choices of maximum calving interval (j_{max}), based on the Payne *et al.* (1990) model of Equations (1) to (4). Results in brackets represent 95% confidence intervals obtained by the likelihood profile method.

Parameter	Assumed maximum calving interval (years)			
	4	5	6	7
h_1	0.00	0.00	0.00	0.00
h_2	0.05	0.03	0.02	0.02
h_3	0.87	0.85	0.71	0.71
h_4	0.08	0.08	0.08	0.08
h_5	-	0.04	0.05	0.05
h_6	-	-	0.14	0.14
h_7	-	-	-	0.00
S	0.985	0.983 (0.972,0.994)	0.979	0.979
Mean calving interval	3.03	3.12 (3.07,3.17)	3.54	3.55
Log-likelihood	3,758	3,764	3,766	3,766
Decision	reject	accept and select	accept	reject

Table 3

The recorded number and expected 'true' number of calvings for the years 1979 to 1998. The estimated probability that a calving in year j is recorded is also given. The available data preclude the model providing estimates for the first three years: 1979 to 1981.

Year i	Recorded number	Expected number	Estimated probability of recording ($\hat{p}_j$)
1979	27	-	-
1980	33	-	-
1981	50	-	-
1982	40	52	0.76
1983	43	53	0.82
1984	65	79	0.82
1985	53	65	0.81
1986	44	57	0.77
1987	76	97	0.79
1988	69	87	0.80
1989	78	96	0.81
1990	76	96	0.79
1991	76	97	0.78
1992	85	109	0.78
1993	90	118	0.76
1994	90	119	0.75
1995	97	129	0.75
1996	134	177	0.76
1997	118	157	0.75
1998	111	150	0.74

generally high (> 70%), but seem to have declined slightly in recent years.

The true number of calvings annually (provided the reproductive rate remains constant) can be used as an index of the abundance of mature females. The model of Payne *et al.* (1990) for estimating a trend in the number of calvings (Equations (7) and (8)) produces an instantaneous rate of increase from 1982-1998 of 0.071 per annum (Fig. 5), with a 95% CI 0.059, 0.082. This is very similar to the rate estimated from counts on the same helicopter surveys from 1979-1998 (0.0692).

Incorporating age at first parturition

Table 4 shows the number of grey-blazed female calves seen in year *i* and the number of such females seen to calve for the first time at age *k*. These apparent[2] ages at first parturition

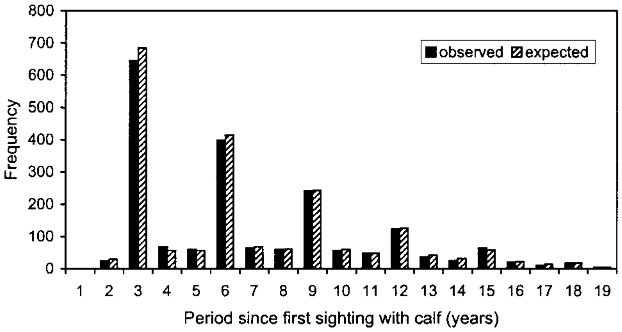

Fig. 3. The distribution of observed and expected subsequent calving intervals in relation to the period elapsed since an animal was first sighted with a calf.

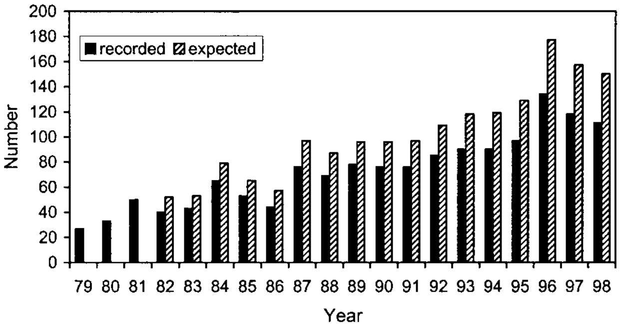

Fig. 4. The distribution of recorded number and expected 'true' number of calvings for the years 1979-1998. The available data preclude the model providing expected numbers for the first three years: 1979-1981.

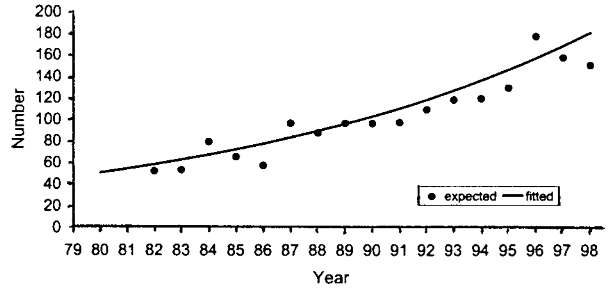

Fig. 5. Trend in the expected number (from Fig. 4) of total calvings by year off South Africa, 1982-1998. The fitted line is estimated using Equations (7) and (8).

Table 4

Observed numbers of grey-blazed right whale calves (known to be female) on the south coast of South Africa between 1979 and 1992, and the number of such females seen to first reproduce at age *k*.

(a) The number of female calves seen in year *i* (m_i).

Year i	1979	1980	1981	1982	1983	1984	1985
m_i	3	3	5	1	2	4	10
Year i	1986	1987	1988	1989	1990	1991	1992
m_i	1	5	2	5	6	7	10

(b) Number of female calves seen in some year *i* that are later seen to first reproduce in year *j* at age $k = j - i$ (t_k).

Age (k)	6	7	8	9	10	11	12	13
t_k	6	3	8	7	2	2	1	2

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[2] The word 'apparent' is used to signify that the actual first calving of the animal might not have been detected.

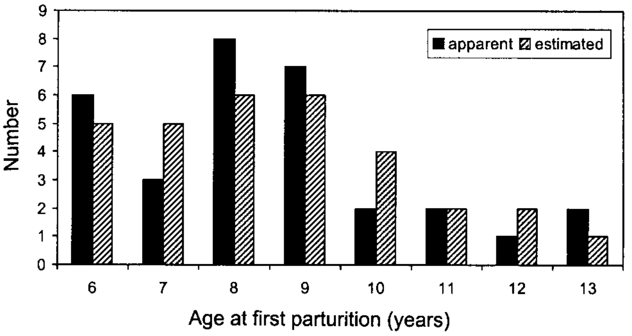

Fig. 6. The distribution of apparent and corresponding model-estimated (Equations (9) to (11)) ages at first parturition in right whales off South Africa. Note: the word 'apparent' is used because missed calvings mean that some observations above reflect subsequent rather than true first parturition.

Table 5

Estimates of various demographic parameters (see text for definitions) for right whales off South Africa for different choices of maximum calving interval based upon the model of Equations (9) to (11) which incorporates data on observations of apparent first parturition. Results in brackets represent 95% confidence intervals obtained by the bootstrap procedure of Appendix 2.

	Assumed maximum calving interval (years)			
Parameter	4	5	6	7
h_1	0.00	0.00	0.00	0.00
h_2	0.05	0.03 (0.02, 0.04)	0.03	0.03
h_3	0.87	0.85 (0.84, 0.87)	0.78	0.78
h_4	0.08	0.08 (0.07, 0.09)	0.08	0.08
h_5	-	0.04 (0.01, 0.06)	0.04	0.04
h_6	-	-	0.07	0.07
h_7	-	-	-	0.00
S	0.987	0.986 (0.976, 0.999)	0.986	0.986
L	0.076	0.071 (0.059, 0.082)	0.067	0.068
N_0	45	47 (40, 56)	46	46
	0.888	0.913 (0.601, 0.994)	0.908	0.865
a_m	8.01	7.88 (7.17, 9.29)	8.02	8.09
$\varnothing$	1.13	1.03 (0.60, 2.09)	1.06	1.12
Mean calving interval	3.03	3.12 (3.07, 3.17)	3.35	3.33
Log-likelihood	3,770	3,776	3,777	3,777
Decision	Reject	Accept	Reject	Reject

range from 6-13 years (mean 8.5 years, SD 2.0 years; Fig. 6). Table 5 gives the estimated parameters when the model of Payne *et al.* (1990) for calving intervals is updated to include information available on matched female calves and adults to estimate the age at first parturition and improve survival rate estimates. Percentile bootstrap confidence intervals (Efron, 1981; 1982) are given for the parameter estimates[3]. The log-likelihood values indicate that a maximum calving interval of 5 years should be chosen. The point estimates for the probabilities of different calving intervals do not change from those obtained from the Payne *et al.* (1990) model in isolation (Table 2). Fig. 6 also shows the distribution of apparent age at first parturition predicted by the model of Equation (9) to (11). The overall fit to the observed distribution is good ($\chi^2 = 4.13$, $p = 0.127$).

From the first parturition ogive fitted by the model (Fig. 7), the age at which 50% of females have their first calf is estimated as 7.88 years (95% CI 7.17, 9.29).

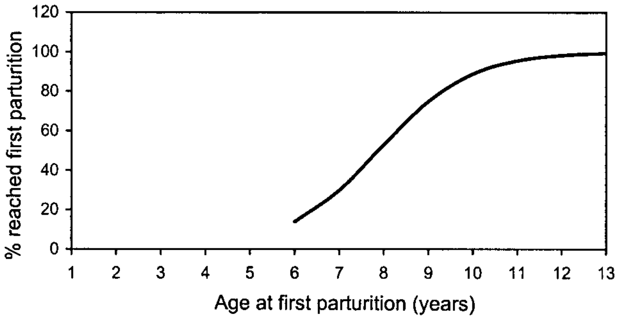

Fig. 7. Ogive of estimated proportion of females at each age that have calved at least once.

Survival rates

The model used for estimating calving intervals can also produce estimates of adult female survival rate. The best estimate for the South African right whale data is 0.983 (95% CI 0.972, 0.994) when the model proposed by Payne *et al.* (1990) is applied. This estimate increases to 0.986 (95% CI 0.976, 0.999) when the combined model of Equations (9) to (11) is used.

There is also the potential for estimating the juvenile survival mortality rate, given the restriction of the reproduction data used (Table 4) to animals known to be female. This results in a juvenile (to age 1) survival rate estimate of 0.913 (95% CI 0.601, 0.994).

DISCUSSION

The average calving interval in South African right whales was estimated previously as 3.18 (SE = 0.09) years (Best, 1990a). This estimate included an attempted correction for missed calving intervals by stratifying the data to exclude animals calving on the periphery of the survey area, but did not specifically incorporate resighting probabilities. As such, it is less reliable than the estimate made in this paper (3.12 years, 95% CI 3.07, 3.17).

The adult female mortality rate in South African right whales was also estimated previously as 0.0227-0.0260 (equivalent to a survival rate of 0.974-0.977), although this estimate assumed that detection (= sighting) probability had remained constant at around 77% (Best and Kishino, 1998). Estimates in Table 3 suggest that the probability of recording calvings has actually declined slightly over the time period (from about 0.80 in 1982-4 to 0.75 in 1996-8); such a decline would have effectively caused the mortality rate in Best and Kishino (1998) to be over-estimated. Hence the survival rate estimate produced in this paper is likely to be more reliable (0.986, 95% CI 0.976, 0.999).

Juvenile survival (to age 1) was estimated as 0.88 in North Atlantic right whales (Kraus, 1990). This figure excluded neonatal mortality, estimated as 0.05 by Kraus (1990). Best

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[3] Likelihood-profile-based confidence interval estimates were also computed for a number of the quantities estimated; the results were near identical to those obtained from this bootstrap approach.

et al. (2001) document mortalities of 31 ‘calves of the year’ in South African right whales between 1963 and 1998. Thirty of these calves were recorded between 1969 and 1998, during which time a total of 1,701 calves was counted on annual surveys. As 86% of observed neonatal mortality occurred prior to the timing of the annual surveys (Best *et al.*, 2001), the neonatal mortality rate would amount to $30 \times 0.86/1{,}701 = 0.015$. This estimate makes no allowance for missed calvings, but neither does it attempt to estimate missed mortalities, so the direction of any likely bias is unknown. This neonatal mortality is additional to the juvenile mortality of 0.087 estimated from the photo-identification data; in effect, it may be ‘hidden’ in the model, either as a greater age at first parturition or an extended mean calving interval. Given that the majority of stranded calves are believed to be the offspring of primiparous females (Best and Rüther, 1992), the former is the more probable.

The process of comparing photographs from the different surveys to establish ‘synonyms’ has the potential to produce both false positives and false negatives. The latter, which can arise as a result of minor changes in callosity patterns or of poor quality photographs, are considered to be relatively more likely than the former, and would lead to negatively biased estimates of the adult female survival rate. However, given the very low number of cases subsequently identified as false negatives when photographs from later surveys became available, any such bias is probably small.

In an earlier analysis of biological and other data from this population, Butterworth and Best (1990) concluded that the observed rate of increase was compatible only with a fairly small region of ‘biologically realistic’ parameter space. Given an annual reproductive rate of 0.314, the best estimate of annual instantaneous increase rate at that time (0.068) could be generated only if the age at first parturition was between seven and nine years and the adult female mortality rate between 0.01 and 0.02, unless the population was open to immigration (the lower limit of each of these two sets of bounds was based upon argued biological realism and observations off Argentina in Payne *et al.*, 1990). As concluded by Butterworth and Best (1990), a powerful way to test whether the observed increase rate contained an element of immigration would be to obtain estimates of the age at first parturition (and possibly adult mortality rate) from longitudinal studies of individually identified animals: if these estimates should lie outside the feasible region of parameter space, it could be concluded that immigration was occurring.

The new or updated estimates for mean calving interval, age at first parturition and adult (plus juvenile) survival rate obtained in this paper now provide the opportunity to test their compatibility with observed population increase rates. Using the ‘balance equation’ for a growing population with a steady age structure (Butterworth and Best, 1990):

$$(1+r)^{a_m} = (1+r)^{a_m-1} S + q\rho\tilde{S} S^{a_m-1} \tag{12}$$

where:
r is the annual rate of population increase;
q is the proportion of births that are female; and
ρ is the calving rate,

the parameter r can be calculated. It is assumed that the proportion of births that are female is 0.5 (Tormosov *et al.*, 1998). The calving rate is larger than the reciprocal of the mean calving interval because an adult whale has a calf immediately it enters the breeding population, as pointed out by Cooke *et al.* (1993). The method to compute the calving rate is given in Appendix 1. From Equation (12), the distribution of r can be computed using bootstrap methods (Appendix 2). Fig. 8 gives the distribution of r computed from biological parameters using Equation (12) and that obtained from the estimate of annual instantaneous growth rate parameter δ of Equation (7) (i.e. solving for r in the equation $1+r = e^{\delta}$). Since these distributions reflect near complete overlap, there is no indication that immigration is needed to account for the annual instantaneous growth rate of 0.071.

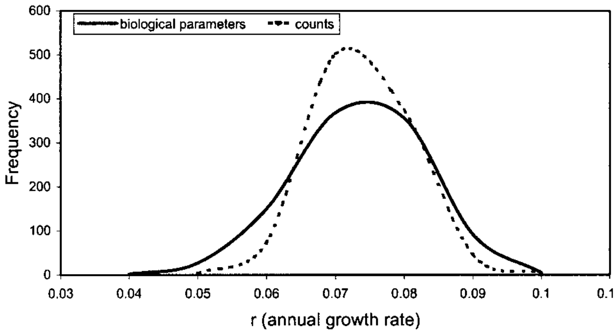

Fig. 8. Comparison of distributions of annual growth rate (r) computed from biological parameters (Equation (12)) and estimated directly from annual calvings (Equation (7)).

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Appendix 1

COMPUTING PREGNANCY RATE

Assume that adult natural survival rate is S and that the population is increasing at a steady annual rate, e^{δ}. Set $z = Se^{-\delta}$. Then if a_m is the age at first parturition (assumed to be fixed) and there are N_0 females of this age at present, the total number of adult females in the population is:

$$N_{tot} = N_0 + N_0 z + N_0 z^2 + \cdots = \frac{N_0}{(1-z)} \qquad \text{(A1.1)}$$

since $S < 1$ and $\delta > 0$ so that $z < 1$.

Note that the proportions-at-age in this population are identical to those of a population in equilibrium with annual survival rate of z. Thus, the numbers of calves produced annually at present is equal to the number of calves produced by a single cohort of such a population over its lifespan.

Let O_k be the number of calves produced that are the kth offspring of their respective mothers. From the assumption of a fixed age at first parturition, the number of first offspring is:

$$O_1 = N_0 \qquad \text{(A1.2)}$$

The number of second offspring is made up as:

O_2 = Proportion of N_0 females which survive one year and then reproduce +
Proportion of N_0 females which survive two years and reproduce for the first time since producing their offspring +…

$$= N_0 z h_1 + N_0 z^2 h_2 + \dots$$

$$= \quad N_0 \sum_{j=1}^{j_{\max}} z^j h_j \qquad \text{(A1.3)}$$

Now since calving and survival probabilities are assumed to be independent, the proportion (w) of the N_0 whales that survive to produce their second offspring is the same as the proportion of those which produce a second offspring that survive to produce their third, and so on, i.e.:

$$O_{k+1} w O_k \qquad \text{(A1.4)}$$

where from (A1.3):

$$w = \sum_{j=1}^{j_{\max}} z^j h_j$$

where $w < 1$ as $z < 1$ and $h_j \leq 1$, so that:

$$O_k = \left[\sum_{j=1}^{j_{\max}} z^j h_j \right]^k O_1 \qquad \text{(A1.5)}$$

Now the total number of calves born is the sum of those that are their mothers' first, second, third…offspring, i.e.:

$$O_{tot} = O_1 + O_2 + O_3 + \cdots$$

$$= \sum_{k=0}^{\infty} O_1 \left[\sum_{j=1}^{j_{\max}} z^j h_j \right]^k$$

$$= \frac{N_0}{\left\{ 1 - \sum_{j=1}^{j_{\max}} z^j h_j \right\}} \quad \left(\text{as } w = \sum_{j=1}^{j_{\max}} z^j h_j < 1 \right) \qquad \text{(A1.6)}$$

Thus, the calving rate ρ is given by:

$$\rho = \frac{\text{number of births}}{\text{number of adult females}} = \frac{O_{tot}}{N_{tot}}$$

$$= \frac{(1-z)}{\left\{ 1 - \sum_{j=1}^{j_{\max}} z^j h_j \right\}} \qquad \text{(A1.7)}$$

Appendix 2

COMPUTATION OF THE PARAMETRIC BOOTSTRAP DISTRIBUTION OF *r* AND OTHER DEMOGRAPHIC PARAMETERS

The following algorithm was used to estimate the distribution of the annual growth rate (r) (the same procedure also yields the distributions for other parameters).

(1) The number of calvings recorded in year i (n_i) and the number of female calves seen in year j (m_j) are assumed to be known and taken to be the number observed.
(2) The number of females recorded to calve both in year i and in year j, where $i < j$ (n_{ij}) are generated as a Poisson random variable with expected value given by Equation (3).
(3) The number of female calves seen in year j that are seen to first reproduce at age k, where $k = 6, ..., 13$ (t_k) are generated as a Poisson random variable with expected value given by equations such as Equations (9a) and (9b).
(4) The bootstrap sample consists of the observed samples n_i and m_j together with the generated Poisson samples n^*_{ij} and t^*_k.
(5) Calculate the bootstrap replication $L^*(n^*_{ij}, t^*_k; \delta^*, N^*_0, h^*_i, S^*, a^*_m, \Delta^*, \tilde{S}^*)$, i.e. maximise the combined likelihood function to obtain model parameter estimates using the bootstrap sample.
(6) Calculate the bootstrap replication r^*, the annual growth rate of the above bootstrap replication, using Equation (12).
(7) Repeat steps 1-6 B times (where B is in the range of 500-1,000), obtaining B independent realisations of r^*, say $r^*(b)$, $b = 1, 2, ... B$.

Note: The residuals of the fit of the original models to the data were checked for consistency with the Poisson distributions assumed, with no significant evidence of either over- or under-dispersion forthcoming, so that the procedures of steps 2 and 3 above would seem defensible.

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Mortalities of right whales and related anthropogenic factors in South African waters, 1963-1998

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ABSTRACT

Between 1963 and 1998, 55 mortalities of southern right whales and a further three 'possible right whale' mortalities were recorded on the South African coastline. Of the known right whale mortalities, 31 could be classified as 'calves of the year', 8 as juveniles and 14 as adults. Relatively few (6.5-16.1%) of the calf mortalities could be attributed to anthropogenic factors, compared to juveniles (25-50%) and adults (35.7-57.1%). Apparent causes of death included ship strikes (4 definite, 7 possible) and entanglement (4 definite, 1 possible), with one harpooning incident. Five non-fatal ship strikes and 16 instances of non-fatal entanglement were also recorded. Whilst the gear most commonly involved in non-fatal entanglement was crayfish trap lines, three of the four entanglement fatalities involved longline gear. The incidence of scars attributable to previous entanglement remained constant amongst mature females from 1979-1997, at 3-4%. Recorded mortalities increased over the period 1963-1997 at a rate no different from that of population growth over the same period. The current level of anthropogenic mortality does not seem to be affecting population recovery.

KEYWORDS: RIGHT WHALE; FISHERIES; INCIDENTAL CAPTURE; STRANDINGS; SHIP STRIKES; SOUTHERN HEMISPHERE

INTRODUCTION

The population of southern right whales (*Eubalaena australis*) that visits the coast of southern Africa in winter was severely overexploited in the first half of the nineteenth century, received official international protection in 1935, and since 1969 has been staging a recovery on the South African coast (Best, 1990b; Best *et al.*, 2001). The current population, however, is still almost an order of magnitude smaller than some estimates of its unexploited size (Richards and du Pasquier, 1989).

While on the coast, right whales are usually found within 10km (and most often within 2km) of the shore (Best, 1990b) and tend to congregate in sheltered bays with flat, sandy bottoms. These habitat preferences bring them into juxtaposition with human activities, including commercial and recreational fishing and boating. Right whales are slow moving, do not show strong boat-avoidance behaviour and appear attracted to drifting or anchored objects (including naturally occurring components of the ecosystem such as kelp), possibly for the tactile experience. These behavioural traits make the species vulnerable to collisions with vessels ('ship strikes') and entanglement in a variety of floating and fixed gear. Some such interactions can prove fatal for the whale.

In the North Atlantic, anthropogenic sources of mortality such as ship strikes and entanglement have been suggested as a significant factor inhibiting the growth of the right whale population (Kraus, 1990; IWC, 2001). This paper attempts to document existing levels of right whale mortality, both natural and anthropogenic, off South Africa, both as a baseline against which to evaluate future trends and as an indication of where potential problems may arise.

MATERIALS AND METHODS

From 1963, the senior author kept records of all cetaceans stranded (or killed as a result of fishing activities, etc.) that came to his attention in the Western Cape (roughly from Lamberts Bay on the west coast to Mossel Bay on the south coast). Most of these have been inspected, and measurements, photographs and samples have been taken and deposited in the South African Museum. Up to and including 1998, this represented some 776 mortalities. In addition, there have been some 165 strandings not visited by the senior author but for which supporting data (photographs, measurements, etc.) were available; these have been termed 'unattended strandings'. Within this total database of 941 mortalities there are records of 51 right whales. An additional four right whale mortalities from the Eastern Cape have also been recorded (Table 1).

Some of the unattended strandings have involved instances where species identification was uncertain, although the descriptions of three suggest they were right whales. These have, therefore, been listed separately as 'possible right whale' mortalities (Table 2).

From 1981-1998, all incidents of non-fatal entanglement and ship strikes involving right whales on the South African coast that came to the authors' notice, either through the media or from members of the public, were recorded; these amounted to some 21 incidents over 17 years (Tables 3 and 4). Seven instances where the species identity was uncertain have been recorded as 'possible right whales' (Table 5).

From 1979-1997, annual aerial surveys of the right whale population along the southern coast of South Africa have been flown by helicopter, in which all cow-calf pairs seen were photographed for individual identification purposes.

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Table 1

Known mortalities of right whales in South African waters, 1963-98.

Field no.	Date	Length (m)	Sex	Locality	Comments
63/6	14 Aug. 1963	13.11	M	30°25'S,31°50'E	Harpooned in error
68/16	24 Aug. 1968	15.19	F	Plettenberg Bay	Stranded live, after calf
-	24 Aug. 1968	Calf	-	Plettenberg Bay	Stranded live
71/8	24 Oct. 1971	7.09	M	Springmount, Algoa Bay	Stranded live
77/6	12 Aug. 1977	4.01	M	Die Mond, Bredasdorp	Found dead
78/39	14 Sep. 1978	10.06	M	Mossel River, Hermanus	Stranded live
82/17	6 Aug. 1982	4.78	M	Blythesdale, KwaZulu-Natal	Caught in anti-shark nets
82/22	28 Sep. 1982	>11.97	-	Arniston	Blubber and appendages
82/31	3 Nov. 1982	5.17	-	Arniston	Stranded dead
82/32	22 Oct. 1982	5.82+	F	5.6km E of Skipskop	Found dead, tail eaten by sharks
	2 Dec. 1982	-	-	Thysbaai, Cape St Francis	Decomposed, fragments of skeleton
	27 Jul. 1983	14.3	F	Beachview, Port Elizabeth	Died at sea - shark bites. Five apparent propeller marks
84/2	8 Feb. 1984	Adult	-	Jakkalsfontein	Seen from air - ship strike?
84/27	8 Sep. 1984	9.25	M	Voorsteklip, Walker Bay	Found dead, entangled in longline
UA69	16 Oct. 1984	~7.2	-	East London harbour	Struck by dredger
86/29	16 Aug. 1986	~4.60	F	De Kelders, Walker Bay	Found dead
86/32	~1 Sep. 1986	4.85	M	Skipskop, De Hoop	Found dead
87/16	22 Aug. 1987	5.36	M	Silverstroomstrand	Stranded live
87/27	27 Aug. 1987	13.76	F	Sedgefield	Washed ashore dead, entangled in longline
87/31	15 Oct. 1987	5.76	M	Die Plaat, Walker Bay	Found dead
88/30	~10 Sep. 1988	14.1	M	25km E of Sundays River	Washed ashore dead - ship strike
88/31	~10 Sep. 1988	14.0	M	25km E of Sundays River	Washed ashore dead - ship strike
89/23	31 Jul. 1989	4.63	M	7.3km N of Dwarskersbos	Found dead
89/30	5 Dec. 1989	14.7	M	Romans Bay, Gansbaai	Found dead
UA133	7 Oct. 1989	12-15	-	20km N of Hondeklip Bay	Washed ashore dead
UA134	30 Oct. 1989	14.8	M	Kings Beach, Algoa Bay	Stranded dead
90/28	8 Aug. 1990	10.31	M	De Kelders, Gansbaai	Washed ashore dead - entangled in line with float
90/29	14 Aug. 1990	4.80	F	Grotto Beach, Hermanus	Stranded live
91/15	29 Aug 1991	4.85	F	4km E of Koppie Alleen	Found dead
91/18	12 Sep. 1991	6.65	M	1km W of Koppie Alleen	Found dead
91/22	<20 Sep. 1991	~5.50	-	1.4km N of Dwarskersbos	Found decomposed
92/13	<9 Aug. 1992	5.32	M	5km W of Koppie Alleen	Found dead, not fresh
92/16	<5 Nov. 1992	~6.42	M	1km E of lagoon, Hermanus	Washed ashore decomposed
93/13	<16 Aug. 1993	3.9+	-	Between Long Beach and Koppie Alleen	Blubber and appendages, tail missing
93/17	10 Sep. 1993	5.89	F	Infanta, St Sebastian Bay	Found dead
93/18	<10 Oct. 1993	4.7+	F	Lekkerwater, De Hoop	Found decomposing, tail cut off
94/5	8 Mar. 1994	11.76	M	Matroosklip, Cape Point	Found dead
94/12	22 Sep. 1994	11.23	F	Kabeljoubank, Breede River	Found dead, possible ship strike?
	23 Sep. 1994	4.7	-	Kabeljou River mouth, Jeffrey's Bay	
	28 Oct. 1994	~11.0	-	Plettenberg Bay	Washed ashore dead
94/16	10 Nov. 1994	10.66	M	Shell Bay, St Helena Bay	Found dead - possible ship strike
95/12	8 Oct. 1995	~15.5	F	Moonlight Bay, Hangklip	Washed ashore dead - possible entanglement
UA157	25 Jul. 1996	~5.5	-	Witsand, St Sebastian Bay	Found dead
UA158	30 Aug. 1996	Calf	-	Voelklip, Hermanus	Tail only washed ashore
UA159	1 Sep. 1996	4.9	-	Glentana, Mossel Bay	Found dead
96/21	28 Jul. 1996	14.61	F	Scarborough, Cape Peninsula	Washed ashore dead - possible ship strike
96/25	23 Sep. 1996	~14.0	F	Witsand, St Sebastian Bay	Found dead
	- Jun. 1997	Adult	-	Mpekweni River mouth	Washed ashore decomposed
97/07	11 Jul. 1997	5.5	M?	St Sebastian Point	Found dead
UA166	25 Sep. 1997	Adult	F	Vaalkrans-Hamerkop	Washed ashore decomposing
97/11	16 Oct. 1997	~5-6	-	Stoney Point, Betty's Bay	Washed ashore dead
98/08	<30 Jul. 1998	~7.1	?	Boggemsbaai, Mossel Bay	Found decomposing
98/10	18 Aug. 1998	4.95	?	Rhyspunt, De Hoop	Died at sea
98/09	19 Aug. 1998	3.9	F	Koppie Alleen, De Hoop	Found dead, fresh
UA165	<7 Oct. 1998	5.4+	?	Die Dam, Quoin Point	Found decomposing, tail cut off

Table 2

Mortalities of 'possible right whales' on the South African coast, 1963-98.

Field no.	Date	Length (m)	Sex	Locality	Comments
UA49	19 Jul. 1983	~4.6	-	5km S of Elands Bay	Found dead
UA?	26 Oct. 1996	15-20	-	Vermont	Found dead in kelp - towed out to sea
UA160	18 Nov. 1996	~6	-	Pearly Beach	Found dead

Details of the survey techniques and subsequent photographic matching procedures used are given in Best (1990a). The survey was timed each year to occur around 15 October, by which date most calves have been born (Best, 1994). After the 1997 survey, the photographic catalogue contained some 521 adult females (unadjusted for natural mortality). Photographs of each female sighted were assessed for the presence of entanglement scars (recognising that the ease of detecting such scars from the air is less than from vessels; A. Knowlton, pers. comm.).

Table 3

Reported instances of ship strikes on right whales in South African waters that did not result in known mortality.

Date	Locality	Vessel involved	Outcome
21 Nov. 1986	False Bay	Fisheries protection vessel *Protector I*	Damage to screw and bracket - vessel abandoned but later towed in – whale cut but apparently OK
6 Jan. 1995	Table Bay	Launch *Condor*	Propeller and shaft damaged
6 Sep. 1997	Hout Bay	[Launch]	Damage to prop and bracket estimated at R20,000, whale apparently survived
28 Aug. 1998	St Sebastian Bay	6m inflatable *Balaena*	Submerged whale hit by skeg on outboard motor - no apparent damage to boat or whale
14 Oct. 1998	False Bay	Catamaran *Cape of Good Hope Ferry*	Whale hit pontoons, not propeller - no apparent damage to boat or whale

Table 4

Reported instances of non-fatal gear entanglement of southern right whales on the South African coast.

Date	Locality	Gear involved	Outcome
18 Oct.1981	Kommetjie	Orange rope round tail stock snared on sea floor, then around middle of body when whale broke free	Whale free-swimming
17 Nov. 1990	3 n.miles S of Vondeling Island	Crayfish trap line	Whale (large adult) cut free
21 Feb. 1991	Off Yserfontein	Yellow and blue ropes plus float – crayfish trap line?	Whale (adult) free-swimming
6 Nov. 1991	Off Olifantsbos	Crayfish trap line	Whale (12-15m) cut free
17 Nov. 1992	Between Stoney Head and Vondeling Island	Crayfish trap line	Whale (4-4.5m) cut free
29 Aug. 1994	Durban, KwaZulu-Natal	Anti-shark net	~6m - free-swimming
15 Sep. 1994	Zinkwazi, KwaZulu-Natal	Anti-shark net	~15m - cut free
26 Sep. 1994	Blythesdale, KwaZulu-Natal	Anti-shark net	~6.5m - free-swimming
22 Dec. 1994	Yserfontein	Rope plus 2 buoys round tail – crayfish trap line?	Whale free-swimming
20 Sep. 1995	False Bay	Fishing net	Whale free-swimming - later died? See Table 1
18 May 1996	Lamberts Bay	Yellow rope round tail stock and rear half of body	Whale free-swimming
4 Dec. 1997	5-6km N of Dassen Island	Rope and floats - crayfish trap line, possibly through mouth	Whale free-swimming
14 Aug. 1998	Rhyspunt, De Hoop	3 loops of green rope and red buoy	Whale free-swimming
23 Aug. 1998	Kalk Bay, False Bay	Rope and buoy behind head	Whale free-swimming
Undated	Smitswinkel Bay	Diver's float line	Whale swam off with line plus speargun
Undated	False Bay	Diver's float line	Line removed from one flipper but whale swam off still attached to gear

Table 5

Recorded instances of non-fatal gear entanglement on the South African coast possibly involving southern right whales.

Date	Locality	Gear involved	Outcome
7 Aug. 1990	Hermanus	Anchor line of ski-boat	Rope cut, whale swam off
24 Nov. 1990	Jutten Island/South Head	Entangled in rope	Small adult, free-swimming
7 Dec. 1990	3km N of Vondeling Is.	Crayfish nets, ropes and buoys	Adult (15-18m), cut free except for one small buoy and some rope round tail
10 Dec. 1991	1 n.mile off Stompneus Light	Crayfish trap line plus buoy	Free-swimming
13 Jan. 1995	12 n.miles SW of Dassen Is.	Crayfish trap lines plus a number of buoys	About 14m long, cut free[1]
2 Nov. 1996	Brighton Beach, KwaZulu-Natal	Anti-shark net	Calf, freed itself
15 Sep. 1997	Betty's Bay	Anchor line of inflatable	Rope cut, whale later freed of line

[1] Whale identified as a humpback but described as lacking a dorsal fin.

RESULTS

Recorded mortalities

Size and sex composition

The 33 dead whales that were accurately measured fell into three groups, the first from 3.90-7.09m ($n = 18$), the second from 9.25-11.76m ($n = 6$) and the third from 13.11-15.19m ($n = 9$) according to length (Fig. 1). The first group consisted entirely of calves of the year, judging from the short baleen and (in most cases) unhealed or healing navel regions. Given that 12.37m was the size of the smallest mature female measured photogrammetrically by Best and Rüther (1992), the other two groups are assumed to represent juvenile (i.e. sexually immature) and adult (i.e. sexually mature) animals, respectively. The ages of the six juveniles were adjudged to be between one and four years, based on stable isotope patterns in their baleen (Best and Schell, 1996). If the inaccurately measured animals are assigned to these groupings, there were 31 calves of the year, 8 juveniles and 14 adults amongst the 55 known mortalities (the remaining two animals were unmeasured and could not be assigned).

In a review of Soviet catch data, the sex ratio amongst 213 southern right whale foetuses was 1.03 male to 1 female (Tormosov *et al.*, 1998). Of the sexed calves in this study, 11 were male and 7 female, while of the sexed juveniles, 5 were male and 1 female. The apparent predominance of males amongst stranded calves and juveniles combined (16 males to 8 females) is not, however, statistically significant (chi-square = 2.67, $0.25 < p < 0.10$). Amongst the sexed adults there were 5 males and 7 females.

Seasonality

All but two of the mortalities occurred over the five-month period from early July to early December, matching the seasonality of right whales in South African coastal waters.

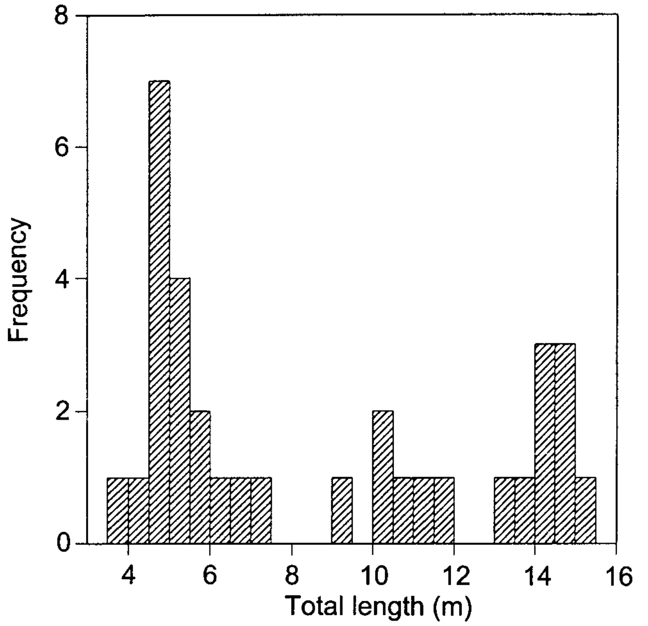

Fig. 1. Size composition of southern right whale mortalities in South African waters, 1963-1998.

The two exceptions were an adult from early February and a juvenile from early March. The seasonal occurrence of non-anthropogenic mortalities amongst 21 calves of the year (that were not decomposed when found) indicated that most (~86%) occurred by 15 October, or the mean date of the annual photographic surveys (Fig. 2).

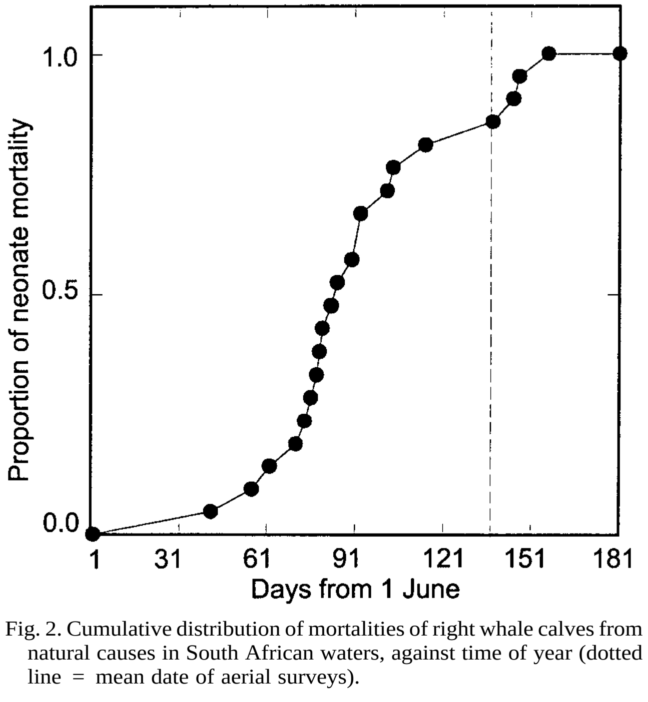

Fig. 2. Cumulative distribution of mortalities of right whale calves from natural causes in South African waters, against time of year (dotted line = mean date of aerial surveys).

Causes of death

CALVES

The deaths of only two of the 31 calves could definitely be attributed to anthropogenic factors, one being entangled in anti-shark nets at a bathing beach off Natal, and the other being struck by a dredger in East London harbour (Best, 1984). A press report of the latter incident stated that the strike occurred at about 0730hrs as the 4,541 ton suction dredger *D E Paterson* was making its way towards the river-mouth entrance of East London harbour. Crew of a cargo ship had earlier reported to port staff the presence of a cow-calf pair at the harbour entrance, so the *D E Paterson* had been warned to be on the lookout. Despite this, the captain reported that as the dredger was coming up to pass the breakwall the pair suddenly surfaced directly in front of the ship's bow. The calf took the full brunt of the impact and had the full length of the vessel pass over it before the propeller caught it. After attempts by the mother to support the bleeding calf, it made its way across the river to a small sandy beach in front of the East London yacht club where it stranded and died shortly afterwards. Photographs of the dead calf show at least three separate curved incisions through the dorsal blubber, one just anterior to the coaming, one mid-dorsally and one in the lower back at about the level of the genital aperture. No photographs of the ventral region were available. The mother stayed in the area for several hours, and a large crowd of workers had to 'shout and do everything they could' to stop the cow from beaching herself (*Daily Dispatch*, 17 October 1984).

A further three strandings of calves in which the tails were cut off may represent ship strikes; three such instances involving northern right whales are reported by Kraus (1990).

JUVENILES

Two of the eight juveniles came ashore dead with longline entangled around their caudal peduncle and tail. One of these (84/27) carried 182m of longline, comprising 121m of brown braided nylon, 18m of green cable-lay rope and 43m of monofilament nylon tracer: metal quick-release clips were also present (Best, 1984). The opinion of fishing experts consulted was that this gear originated from the local longline fishery for hake (*Merluccius* spp.). When first seen, the second juvenile (90/28) was floating dead with longline and a red plastic buoy wrapped around its peduncle. By the time the senior author reached the stranding, however, all the gear had been removed; a sample of the line examined later showed that it was identical to the brown braided nylon in which the first juvenile had been entangled.

Two other juveniles may have been the victims of ship strikes. In the case of one of these (94/16), there was a diagonal slash through the blubber near the genital aperture, through which the viscera protruded: this might indicate that the whale was floating dead when struck (Kraus, 1990), although the animal was not heavily decomposed (skin still intact). In the other instance (94/12), bystanders claimed that there had been a boat strike in the adjoining bay two to three days previously, and that the animal bore cuts across the back (however these cuts were not seen by the senior author on the side of the animal that was visible). A fifth animal (78/39) was noticeably emaciated, with the back hollowed so much that the dorsal ridge of the scapula could be clearly seen; on dissection, 189 cestodes weighing 3,475g were collected from the intestines. This was the only mortality for which a possible natural cause of death could be established.

ADULTS

Two adult females died possibly as a result of entanglement. The first (87/27) came ashore dead and was beginning to decompose, with longline entangled around the base of the left flipper and the body at about the level of the anus. The base of the right flipper was also badly scarred, and the body surface bore numerous weals that were most prominent where the epidermis was missing. A portion of the line recovered weighed 7kg, and consisted mainly of the same 8mm braided nylon line described previously. This was accompanied by some 5mm braided line, 4mm cable-lay line, 2mm monofilament nylon tracer, 4 metal quick-release clips, 1 plastic squid lure, 3 small aluminium reflectors and a conical lead weight. This description most closely resembled gear from a pelagic longline fishery for tuna or swordfish (B. Rose, pers. comm.).

The second adult (95/12) may also have been the victim of entanglement; four days after it washed ashore (clearly having died at sea some time previously), 12m of chain and a buoy were recovered *ca* 200m from the carcass. The links of the chain were covered with buttery whale fat, despite the surrounding rocks having no oil on them. Eighteen days previously a right whale had been seen and photographed entangled in a fishing net about 18 n.miles from the site of the stranding.

A total of five adult whales appear to have died as a result of ship strikes, two of which (the adult males 88/30, 88/31) were linked to an actual incident. The roll-on, roll-off ferry MV *Barrier* (11,000 tons) was getting up speed on leaving Port Elizabeth harbour at 16:53hrs on 7 September 1988, when nine whales were spotted ahead of the vessel, crossing the bows. Although not stated, it seems possible that the whales were engaged in courtship activity. They failed to dive to avoid the vessel, which was travelling at 12-13 knots, about 4.4 n.miles from the harbour entrance. No avoidance action was taken because it was anticipated that the animals would dive. Impact with at least one animal was felt. On looking aft into the setting sun all that could be seen was blood in the water (Capt I.D. Chown, pers. comm.). Three days later, the two whales were found on the beach 5km apart and about 15 n.miles from the site of impact. The damage to one whale was described as ‘propeller shaved off flipper, cut flipper bone, cut through gape below eye and above eye, taking off rostrum (some of which came up on beach nearby)’. The other whale appeared superficially undamaged.

The other three mortalities attributed to ship strikes all bore evidence of contact with motorised vessels. One of these (84/2) was originally seen on the beach from the air, and although quite fresh appeared to have suffered major damage at its mid-length, the whale being ‘bent’ at an unnatural angle. Two days later all that could be found on the beach was a section of intestine 25m long, although the body later washed ashore further to the south. The second whale (96/21) washed ashore dead and was starting to decompose. Although no external marks could be seen, when the skeleton was later prepared for display it was found that the rostrum was broken right across and some of the skull bones were missing. It cannot be discounted that this damage was inflicted post-mortem. The third whale came ashore dead bearing five apparent propeller marks, plus several shark bites, suggesting that it had died at sea some time before. The whole body was twisted as it lay, as if it had been crushed, and there was a vertical split in the body across the thorax; it was assumed that the damage was due to a ship striking it (G.J.B. Ross, pers. comm.).

One adult male (63/6) was harpooned in error by a catcher-boat from the Durban whaling station. At the time the right whale was swimming with a group of sperm whales, of which four (all males) were also shot by the same catcher-boat, three 39ft (11.9m) and one 40ft (12.2m) in length.

Ship strike and entanglement incidents that did not result in a recorded death

Only five non-fatal ship strikes on right whales were recorded (Table 3), all involving relatively ‘high-profile’ ships (a Government fisheries patrol vessel, a whalewatching catamaran, the senior author’s own inflatable and two launches carrying tourists). In three of these collisions considerable damage was inflicted to the vessel. Other incidents that may have occurred with less public vessels and/or in which relatively minor damage was incurred most probably went unreported.

There were 16 instances of non-fatal entanglements involving right whales (Table 4) and a further seven that may have involved right whales (Table 5). Apart from five animals entangled in nets (one in a fishing net and the others in beach protection nets against sharks), all the incidents reported involved entanglement in ropes. Nine of these were associated with crayfish trap lines (6 positively and 3 tentatively), 2 involved anchor ropes of small boats, 2 involved float lines of spearfishermen, while 5 could not be attributed to a particular source. Five of the animals entangled in crayfish trap lines, one entanglement in anti-shark nets and both animals entangled in anchor lines, were cut free and all or part of the gear removed. Both animals entangled in diver’s floatlines escaped with the line still attached. The remaining 13 whales were all free-swimming when first seen, and were not disentangled.

Incidence of scarring in the population attributable to entanglement and ship strikes

Within the photographic catalogue of identified mature females, there are 15 individuals with scarring that is attributable to entanglement. In 14 of these cases the scarring appears as white lines on the peduncle at the base of the flukes, while in the 15th instance the scars appear as raised ridges (weals) that run irregularly over the back and head of the animal. No animals have lost such scars during the periods they have been monitored (up to 16 years). After being smoothed by threes, it can be seen that the incidence of such individuals, expressed as a proportion of the number photographed on annual surveys, has remained more or less constant throughout the time series at between 3-4% (Fig. 3). Only one animal has been photographed both with and without scars, suggesting that whales usually acquire the scars before they are first photographed, i.e. while they are young, sexually immature animals.

Only one animal in the photographic catalogue (or 0.2% of the total) exhibits scars that could be reasonably attributed to ship strikes. These appear as a set of four parallel lines an estimated 15-50cm in length and about 25cm apart, situated diagonally across the right flank, and so presumably inflicted by a relatively small vessel. They were present when the cow was first photographed (in 1995), and so far have persisted for three years.

DISCUSSION

Most (56.4%) of the 55 recorded right whale mortalities in South African waters involved calves of the year. Relatively few (6.5-16.1%) of these mortalities could be attributed to anthropogenic factors. Although recorded mortalities of juveniles and adults were fewer, the proportions that could be attributed to anthropogenic factors were much higher, 25-50% and 35.7-57.1% respectively. Causes of mortality were divided between entanglement or possible entanglement (5 cases) and ship strikes or possible ship strikes (11 cases), with one harpooning incident.

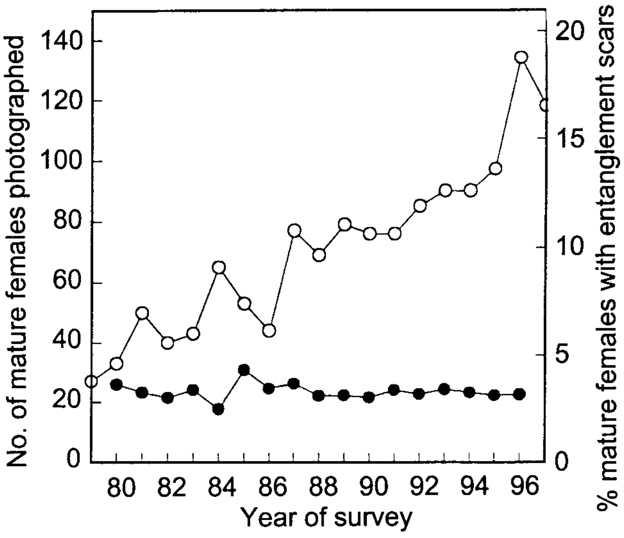

Fig. 3. Number of mature female right whales photographed annually on the South African coast, 1979-1997 (open circles), and the proportion of these carrying entanglement scars, after smoothing by threes (solid circles).

The incidence of recorded mortalities by five-year period in the senior author's dataset has shown a steady increase, from 1 in 1963-67 to 3, 1, 5, 8, 12 and 16 in succeeding five-year periods. This rate of increase (on average an exponential value of 9.4±2.0% per year) is compatible with the estimated rate of population increase between 1982 and 1998 (7.1%, 95% CI = 5.9, 8.2%, Best *et al.*, 2001). This suggests that there has not been a marked increase in the recorded *per capita* mortality rate over the 30-year time span. Such a conclusion depends, of course, on there being a constant efficiency of reporting of mortalities over the time period, an assumption that is difficult to prove.

There is also an interesting contrast between the apparently frequent observation of live animals entangled in crayfish trap lines, and the finding that the three recorded right whale mortalities in which entanglement was a factor involved gear from a longline, not crayfish operation. Crayfish traplines are usually constructed of cable-laid polypropylene rope with a minimum diameter of 12-14mm, whereas the longline gear has mainly been a braided nylon rope with a maximum diameter of 8mm (and including monofilament line as thin as 2mm in diameter in at least two cases). It is possible that the thinner the line, the deeper it cuts into the whale's integument and the more it tends to bind in on itself. These factors would, firstly, make it more difficult for the gear to come off naturally, and, secondly, increase the degree to which the whale might become physically disabled through the destruction of underlying muscles or tendons. Alternatively, the relative degree of mortality inflicted may be associated with the weight of gear involved.

The finding that the incidence of entanglement scars in the photographic catalogue of mature females has remained constant over the period 1979-1996 is somewhat surprising, given that these scars presumably remain throughout life. If the population was constantly exposed to the risk of entanglement, one would expect the incidence of scarred animals to increase naturally over time. The failure to do so suggests that the animals pass through a 'window of exposure' to entanglement, possibly when they are young (as indicated by the rarity with which mature females pick up such scars). The closure of this window could be related to changes in the distribution/migration of the animals with age, or to a behavioural change (increased gear avoidance) as the animals get older.

The scarcity of scars attributable to boat strikes in the photographic catalogue suggests either that such strikes occur less frequently than entanglement amongst adult females, or that when they do, they are more likely to be fatal.

As the South African right whale population is increasing at a rate that must be close to the maximum biologically possible (Best *et al.*, 2001), the current degree of anthropogenic mortality does not seem to pose a major conservation concern for this population. This is not to say that the situation could not change; an increasing whale population and an increasing human use of coastal waters for commercial and recreational pursuits, would seem to make an acceleration of interactions between them inevitable.

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A note on recent sightings of southern right whales (*Eubalaena australis*) along the east coast of Madagascar

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ABSTRACT

Southern right whales (*Eubalaena australis)* are distributed throughout the Southern Hemisphere, where they seasonally migrate between high latitude feeding grounds and low latitude breeding grounds. While there are detailed records of historical and recent whaling off the southern, southwestern and southeastern African coasts, historical catches in Madagascar's waters are poorly documented. There have also been no recent, documented sightings of southern right whales off the east coast of Madagascar. Here we report two sightings, one of a single individual in Antongil Bay in northeastern Madagascar and the other of a mother and calf pair near Fort Dauphin on the southeastern coast. DNA obtained from a biopsy sample of the single animal showed it was a male possessing one of the common South Atlantic right whale mitochondrial haplotypes. The available DNA data provide limited suggestive evidence that the individuals documented off Madagascar represent long-distance migrants from the well-documented South African population. However, the possibility that these southern right whales are members of a small or remnant population from the historical whaling grounds of Delagoa Bay, Sofala Bay or the Crozet Island feeding grounds cannot be excluded. Regardless of population assignment for these individuals, it appears that some southern right whales may be using different parts of Madagascar's east coast during the wintering season.

KEYWORDS: SOUTHERN RIGHT WHALE; INDIAN OCEAN; BREEDING GROUNDS; GENETICS

INTRODUCTION

Southern right whales (*Eubalaena australis)* are thought to comprise several populations distributed throughout the Southern Ocean (IWC, 2001). Whaling records have shown that right whales formerly occupied ranges that they no longer do today (Wray and Martin, 1983; IWC, 1986a; Richards and du Pasquier, 1989). Commercial whaling operations over the last two centuries brought southern right whales to near extinction. Despite legal protection in 1935, exploitation of right whales in the Southern Hemisphere continued to occur as late as 1971 (Tormosov *et al.*, 1998).

During the austral winter, southern right whales migrate north to the more temperate and tropical waters of the sheltered bays and inlets along the coasts of South America, southern Africa and Australia, where they breed and calve (Brownell *et al.*, 1986; IWC, 2001). In general, one or two months after calving, the cows begin their migration to higher latitudes for the remainder of the year (Townsend, 1935; IWC, 2001). Recent evidence suggests the gestation period may be one year or more (Best, 1994; Burnell and Bryden, 1997). This seasonal migration is so predictable that whalers stationed along these coasts were consistently able to catch right whales (Richards and du Pasquier, 1989).

Records of whaling off southern Africa (1785-1805 and 1792-1912) identify the historical presence of large stocks of right whales around the Cape of Good Hope (34°S), as well as at lower latitudes (*ca* 23°S) such as Walvis Bay, Namibia (Townsend, 1935; Best and Ross, 1986). These records also show right whale concentrations and movements of individual animals further north into the Mozambique Channel, Maputo Bay (25°S, historically known as Delagoa Bay) and the Bay of Tigres in Angola, West Africa (17°S) (Townsend, 1935; Richards and du Pasquier, 1989). While the historical estimate of stock size is likely to be inaccurate, Richards and du Pasquier (1989) speculate that the stock size of right whales around the southern coasts of Africa before 1785 would have numbered approximately 20,000. In the 120 years (1792-1912) of shore-based open boat whaling only, Best and Ross (1986) estimate that the catch of right whales was 1,580 individuals. For the entire Indian Ocean between 1830-1909, Best (1987) estimated a total Indian Ocean catch of about 12,500 right whales, with total catches for all stocks estimated between 70,325-74,693.

There was comparatively little whaling (or at least analysed records) for right whales in the waters around Madagascar (Wray and Martin, 1983; IWC, 1986b). Records show that shore-based whaling began in the 1750s, but no other details are known (IWC, 1986b). Some records point to the presence of right whales between Delagoa Bay and Madagascar (presumably the west coast) in the months of May-September (Richards and du Pasquier, 1989). However, while sightings of right whales around Madagascar are mentioned in the literature, no published accounts of historical right whale catches from the east coast of Madagascar have been identified. Furthermore, there are no documented recent sightings of right whales along the eastern coast of Madagascar. The sheltered bays and inlets along this coast were possibly once a migratory destination for right whales from a smaller whaling ground in the Crozet Islands (46°S, 50°E) in the southern Indian Ocean.

Antongil Bay (16°00'S, 49°55'E) in the Masoala Peninsula region of northeastern Madagascar has recently been documented as a major calving area for humpback whales, *Megaptera novaeangliae* (Rosenbaum *et al.*, 1997b). The bay itself is large, occupying 2,800km^2, and is nearly 80km in length from the mouth to the northern end. Historically, the area attracted considerable attention from American whalers looking for humpback whales (Nordhoff,

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1856), with more recent hunting during the 20th century (Angot, 1951; Best *et al.*, 1998). The areas in the southern region of Madagascar are passed by humpback whales on both their southern and northern migrations. This note reports on two confirmed southern right whale sightings from Madagascar, one of a single individual in Antongil Bay in the northeast, and the other of two individuals near Fort Dauphin on the southeast coast.

METHODS

Daily field surveys were conducted for humpback whales and other marine mammals from two 6m fibreglass boats between July and September 1996-1999. Randomised transects were conducted by each boat in equally divided eastern and western portions of Antongil Bay to minimise sampling bias and to examine possible trends associated with spatial and temporal distribution. When whales were encountered, the initial and terminal positions of a group were recorded using a *Trimble GeoExplorer* II. Photographic identification and video recording typically occurred with each group sighting. Boat surveys were carried out using a single vessel in a similar manner to that described above for the southeast coast between October and December 1999.

Skin tissue samples were collected by biopsy darting whenever possible and these were stored in 95% Ethanol. Methods for DNA extraction, PCR amplification and mitochondrial DNA control region sequencing are detailed in Rosenbaum *et al.* (1997a). The obtained sequence was aligned and compared to other available sequences from southern right whales (Baker *et al.*, 1999; Portway *et al.*, Submitted). Sex was determined using molecular methods (Palsbøll *et al.*, 1992).

RESULTS

On 29 July 1997 at 11:32hrs, a southern right whale was encountered in the northern portion of Antongil Bay (15°31’S, 49°56’E) (Fig. 1). The individual alternated between flippering and lobtailing behaviour. Upon cessation of the lobtailing, three humpback whales approached the right whale to within 800m at the surface. On the following surfacing, the right whale and humpback groups were clearly separated. The right whale maintained consistent 15-17 minute dive times, with 2-3 minute surfacing intervals, for approximately four hours.

From the tissue biopsy sample, the individual was determined to be a male with one of the most common maternal lineages found among right whales in the South Atlantic (Portway *et al.*, Submitted). This lineage is the same as one of two mitochondrial haplotypes found in all three sampled populations from South Africa, South Georgia and Argentina in that study.

The second sighting occurred on 20 November 1999 (25°12’S, 46°38’E), approximately 40km southwest of Fort Dauphin (Fig. 1). During surveys for humpback whales, a mother and calf right whale pair was encountered at 07:45hrs. The calf was observed to repeatedly breach. Deteriorating weather conditions (Beaufort Sea State >4) prohibited additional work with this group, and the surveys were terminated at 08:30hrs with the last position of the right whale recorded as 25°12’S, 46°40’E.

DISCUSSION

While sightings records or historical data offer no link between right whales sighted off Madagascar and the closest locations where concentrations of this species have been

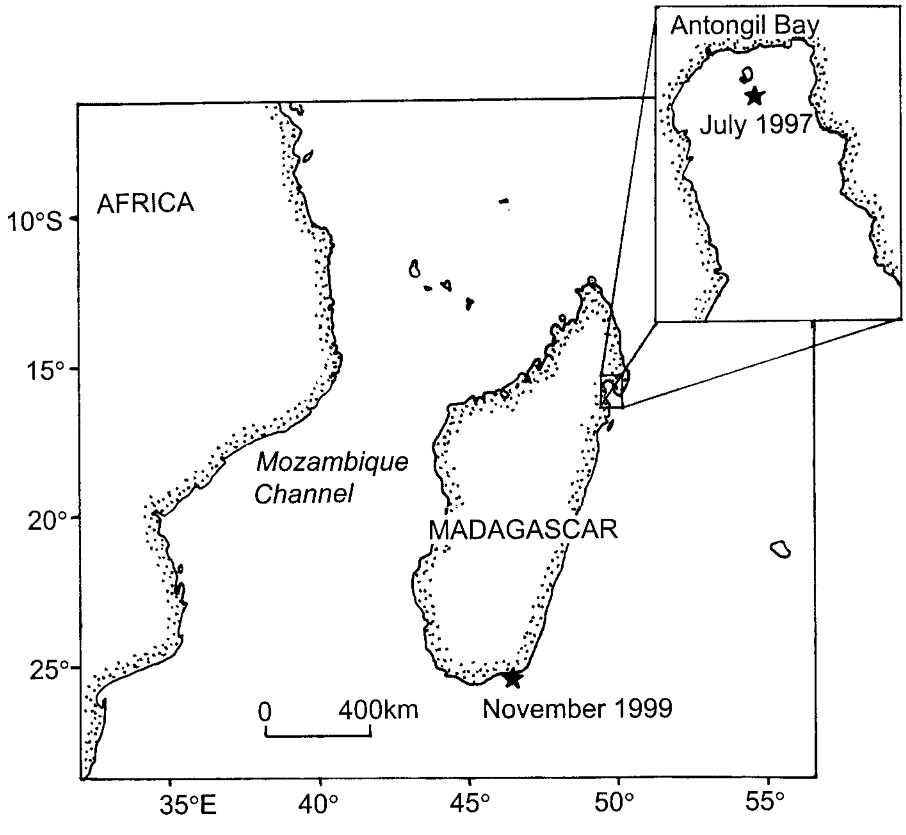

Fig. 1. Dates and locations of sightings of southern right whales (★) off Madagascar, western Indian Ocean. Inset shows Antongil Bay.

well-documented, such as the southern coast of South Africa or the Crozet Islands, it is interesting to consider the possibilities for population affinity. One possible explanation for the sighting of right whales in Madagascar's waters is that the individuals are migrants from the population off southern South Africa at the extremes of their range. As reported by Best *et al.* (1993), animals identified in southern South Africa have shown long-range movements. The most compelling evidence for the animals' South African origin exists from the one individual whose maternal lineage haplotype matched one of the two most common haplotypes found only in the South Atlantic Ocean. However, an analysis of differences or similarities in haplotype composition or frequency alone is unlikely to uncover significant population affinity within an ocean basin. Additional analytical approaches with finer resolution, such as multiple-locus genotyping, and more exhaustive sampling from other locations would be necessary for assigning population affinity for these whales. If these right whales are in fact animals from the South African population, the minimum distances travelled to southeastern Madagascar and Antongil Bay would be 2,782 and 3,995km respectively. Those distances are within the range of distances reported for long-range movements of southern right whales from the South African population and consistent with movements within the South Atlantic (Best *et al.*, 1993).

Alternatively, the right whales seen off Madagascar's coast may be individuals from a remnant or slowly recovering population from the historical whaling grounds of Delagoa Bay, Sofala Bay or the Crozet Islands. The mother and calf pair sighted off southern Madagascar were approximately at the same latitude as Delagoa Bay. Richards and du Pasquier (1989) state that two ships took 29 right whales while cruising off Madagascar (most likely the west coast, but no indication is provided) and at anchor in Delagoa Bay, although no indication is given as to how many whales were taken at each site. To our knowledge, there are no other historical records showing calving of right whales in bays along the coast of Madagascar, as there have been for Delagoa or Sofala Bays. Furthermore, no historical whaling records suggest northern calving areas for animals found in the austral summer on the Crozet whaling grounds. The Crozet grounds (40-52°E) lie nearly 2,300km directly south of southern Madagascar and 3,400km south of Antongil Bay, and may serve or have once served as wintering grounds for this population.

In the western Indian Ocean, the majority of historical whaling catch data show concentrated hunting from Delagoa Bay to Sofala Bay along the African coast or on the Crozet grounds (Wray and Martin, 1983). Another possibility is that the population that once used Delagoa and Sofala Bay as calving grounds is now using Madagascar's coast, following extirpation or reduction in numbers due to intense periods of whaling. Based on historical records, Richards and du Pasquier (1989) suggest that there appeared to be several different migrations by potentially different stocks for the calving seasons from late May to early September. However, these data were mostly concentrated on the coasts of continental Africa. The timing of the migratory cycle from historical records was consistent with the northernmost sighting of the right whale in Antongil Bay reported here. The sighting of right whales in southern Madagascar in late November might be explained by different groups of animals that travelled to more northerly latitudes (around 23-25°S) than others which calved at more southern latitudes. Such an occurrence was thought to cause an extension of the whaling season off South Africa because of the greater distances (and time required) by right whales travelling further north to other calving grounds (Richards and du Pasquier, 1989).

The only detailed historical dataset from the western Indian Ocean other than the pelagic or coastal African whaling records comes from the offshore Crozet grounds. During two different periods of exploitation, large takes of right whales occurred: at least 1,000 in 1841-45 (Richards, 1990) and about 300 in 1962-1968 during the illegal Soviet expeditions (Tormosov *et al.*, 1998). Whales from the Crozet grounds were so intensely exploited that the population was considered depleted or scarce by the 1870s (Wray and Martin, 1983). Intensive exploitation in the Crozets prior to the 1850s may have reduced the numbers of right whales to the point that whaling ships subsequently operating along the east and west coasts of Madagascar would not encounter right whales with great frequency during the late 19th century. The more recent Soviet exploitation would have had a similar effect. In the austral summers of 1962 and 1963 alone, Soviet pelagic whalers took 115 females from the Crozet Islands, possibly impacting the number of pregnant females observed following that first reported year of hunting (Tormosov *et al.*, 1998). Such periods of intense exploitation, coupled with a general lack of dedicated survey effort along Madagascar's coastline, could have contributed to the scarcity of right whale sightings off Madagascar. The current status of the Crozet Island population of right whales remains largely unknown.

For the western Indian Ocean, there are few reports of right whales as far north as 16°S. A newspaper article reports a sighting of a right whale in the waters of Mauritius at 20°S, 57°E (Best, pers. comm.). With the documented takes of right whales at Delagoa Bay and the current sighting of a mother and calf at 25°S, the sighting of a southern right whale in Antongil Bay may be the northernmost sighting in the western Indian Ocean. In the eastern Indian Ocean, Maury's charts show right whales off the western Australia coast at 15-20°S, though the most recent northern record has occurred at approximately 22°S (Bannister, 1986; IWC, 2001). Richards and du Pasquier (1989) note that some right whales may have calved during July and August at latitudes as high as 17°S in the South Atlantic, with the occasional whale being found in equatorial waters. The latter is supported by recent observations of a right whale, presumed to be a southern right whale, sighted off Gabon at 1°S of the Equator (Darling, pers. comm.). Interestingly, a rare North Pacific right whale sighting in Hawaiian waters occurred at 20°N in 1979 (Rowntree *et al.*, 1980). This lone right whale was observed amidst a group of humpback whales for nearly three hours. Similar interactions between humpback and right whales have occurred where right whale sightings are more common (M. Engel, pers. comm.). However, for the right whale sighting at Antongil Bay, any interaction with humpback whales did not last long, although there were a number of humpbacks in the general vicinity.

The overall population affinity of right whales in Madagascar remains uncertain. Because the sampled individual was of the maternal lineage most common among whales from the South Atlantic, the genetic results at this level of resolution are inconclusive. It is difficult to determine whether this individual was from a remnant local population or maybe a migrant from a well-documented population (Best, 1990). Additional information on the lineage types and frequencies from other historical populations would be necessary to differentiate between the two hypotheses. Despite over 650 hours of boat-based surveys in Antongil Bay and 2,500km of aerial surveys in the northeast region, no additional right whales have been sighted. The sightings reported here provide some evidence that members of a remnant/small population, or possibly individuals with exceedingly long-distance movements, are now frequenting the coast of eastern Madagascar.

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Sightings of southern right whales (*Eubalaena australis*) in Namibian waters, 1971-1999

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ABSTRACT

Southern right whales were originally abundant in Namibian waters in winter and spring. They were either eradicated from the region or driven to extremely low numbers more than a century ago. Since 1971, 36 incidental sightings and three aerial surveys confirm the regular presence of the species within its historical calving range, between June and December. Calving has been recorded in four successive years and at least 10 calves were born in the area between 1996 and 1999, confirming the existence of a small established breeding population. This represents a northward extension of the hitherto known modern regular calving range in the South East Atlantic Ocean by more than 1,000km.

KEYWORDS: SOUTHERN RIGHT WHALE; INCIDENTAL SIGHTINGS; AERIAL SURVEY; DISTRIBUTION; REPRODUCTION

INTRODUCTION

The southern right whale (*Eubalaena australis*) was originally widely distributed in all oceans of the Southern Hemisphere between approximately 20°S and 55°S. The main calving areas were concentrated at mid-latitude in coastal waters of South America, southern Africa, southern Australia and New Zealand (IWC, 2001).

In the eastern South Atlantic Ocean, some bays along the southwestern African coastline south of 20°S have historically been visited each spring by female right whales to give birth and raise their young, and possibly to mate with accompanying males (Best and Ross, 1986).

Exploitation of southern right whales in the region started during the 18th century. The peak of right whale catches in the area was between 1785 and 1805 (Best, 1981; Best and Ross, 1989; Richards and du Pasquier, 1989; Dekker and de Jong, 1998). Along the Namibian coast (Fig. 1), whalers operated principally from June to September and found right whales inshore, mainly in bays, one near 27°30'S (possibly Bakers Bay), Elizabeth Bay, Angra Pequena or Lüderitz Bay, Angra de Conceicao, possibly Spencer Bay (25°40'S), Walvis Bay, and several other smaller bays to the north including Angra Fria, and up to Baia dos Tigres in southern Angola (Lacroix, 1968).

By the beginning of the 19th century, catches along the Namibian coast already seemed to be declining (Richards and du Pasquier, 1989). The region of Walvis Bay became a centre for the exploitation of humpback whales (*Megaptera novaeangliae*) in the mid 19th century and, despite the scarcity of records, it can be assumed that the remaining right whales would also have been targeted during this period. At the time of the beginning of modern whaling, several shore-based whaling stations operated along the Namibian coast between 1912 and 1914, and again between 1923 and 1930, and also along the Angolan coast from 1909 to 1930. Although details of the catch composition are very incomplete, there is no evidence of southern right whales in the catches (with the exception of one right whale taken in southern Angola in 1913), possibly an indication that the local breeding population had been eradicated long before the species was granted international protection in 1935 (Best and Ross, 1986; Best, 1994a).

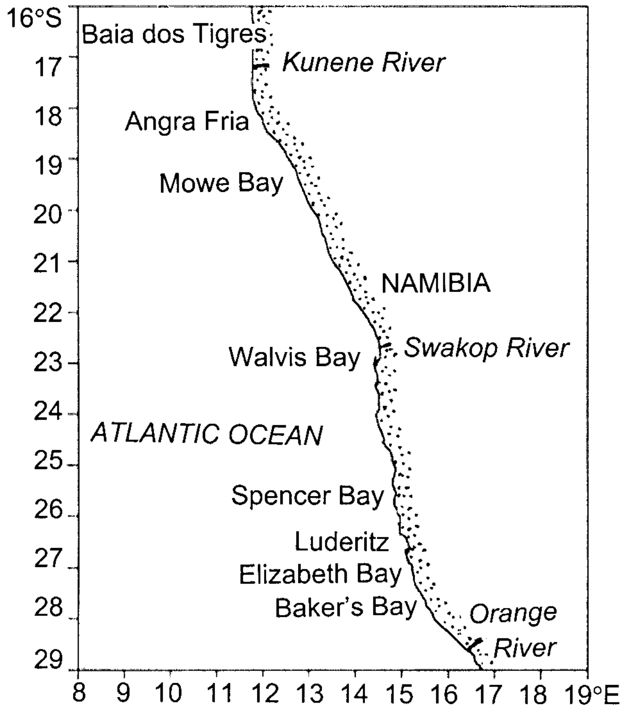

Fig. 1. Map of the Namibian coast.

Along the south coast of South Africa, a small remnant population has been reported during the first half of the 20th century and has been increasing since (Best, 1970; 1981; 1990b), but no record of the species in Namibian waters could be found until the early 1970s. Best (1981) reported four confirmed incidental sightings between 1971 and 1981 (including a mother and calf pair) and an additional two sightings (including another mother and calf pair) during an aerial survey in 1978. These were the first indications that

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breeding adults frequented the area, at least occasionally, since the beginning of the 19th century. However, the take of a 49ft female off Gabon in 1951 as reported by Budker and Collignon (1952), implies that right whales may still have been at least transiting through Namibian waters at this time.

This study reviews recent incidental sightings and the results of aerial surveys along the Namibian coast in order to update the status of the species in the region.

MATERIALS AND METHODS

Since 1987, skippers and crew of fishing and mining vessels as well as coastal mining contractors have been encouraged to document and report cetacean sightings; species identification guides and reporting forms were distributed. Each report was critically evaluated and classified as doubtful, possible, probable or confirmed according to the experience of the observers, the conditions of the sighting (distance, visibility) and the supporting evidence provided (notes, sketches, photographs and video footage). Sightings were classified as confirmed if they were supported by photographic or video material with some of the species-specific characteristics clearly visible, or if they were made by observers whose experience in identification was known. A sighting was classified as probable if it was reported by an observer whose experience in identification was not known to the authors, provided it was accompanied by detailed notes and/or sketches of body size and colouration, presence of callosities, shape of the flippers and flukes and the absence of a dorsal fin. Animals were termed calves only when observed in close association with an adult and with an estimated size less than half that of the adult. Only the probable and confirmed sightings of southern right whales are discussed here. Other species of baleen whales regularly reported were humpback and minke whales (*Balaenoptera acutorostrata*) while the bulk of the reports consisted of small odontocetes. When not provided, geographical coordinates of the sightings were estimated from topographical and nautical maps. Only known duplicate sightings were excluded, so it is possible that the data include some sightings of the same individuals on different days.

As most of the Namibian coast is uninhabited and very remote or with restricted access, there is a probable geographical bias in the sighting effort in favour of the few permanent coastal settlements. On the other hand, there appear to be no reasons to suggest a seasonal bias.

In 1998 (29-30 September) and 1999 (7-8 October), aerial surveys were conducted along the coast between the southern Namibian border at the Orange River mouth and the Swakop River mouth. Each survey was divided into two legs, flown on successive days starting in Lüderitz, each leg being flown twice on the same day and returning to Lüderitz in the evening. The northern leg encompassed 512km of coastline and the southern leg 310km. The basic survey methodology followed that of studies of other southern right whale populations in South Africa (Best, 1981), Argentina (Payne *et al.*, 1983) and Australia (Bannister, 1985; 1986). High-winged aeroplanes were used, a *Cessna* 206 with four observers (including the pilot) in 1998 and a *Cessna* 172 with two observers (including the pilot) in 1999. The survey track followed the coastline within 1.5km offshore and about 500m offshore and parallel to the line of breakers. Observers continuously scanned the sea surface on both sides of the aircraft. When searching, the speed of the aircraft was maintained between 182 and 222km per hour. The survey altitude was maintained at 1,000ft (305m) except when visibility conditions were not optimal when the altitude was lowered to between 500 and 700ft (152-183m). Areas under coastal fog were not surveyed. When whales were sighted, the aircraft circled the animals at an altitude of 300ft (91m) to confirm identification and determine the position using GPS equipment. Photographs were taken out of an open window with a hand-held 35mm camera equipped with a motor-drive and a telephoto lens (180mm *f* 2,8).

RESULTS

Incidental sightings

Out of 36 probable and confirmed incidental sightings recorded in Namibian waters since 1971, 28 have been reported since 1990 (Table 1). This apparent increase in reporting rate can, in great part, be attributed to the large increase in 'observer effort' since the late 1980s and in particular with the development of coastal diamond mining operations in the Lüderitz region. All these sightings were made close to shore (within 3km from the coast), probably a reflection of both whale distribution and observer effort.

Right whales have been sighted only during the second half of the year, between the beginning of June and the beginning of December (Fig. 2). The average date of those sightings is 4 September ($SD = 45$ days, $n = 36$). The majority (25 out of 36) of the sightings was concentrated in a three-month period (July-September). With the exception of 8 sightings involving between 1 and 3 cow-calf pairs, most sightings were of single animals ($n = 19$) and the rest of pairs of large whales, assumed to be adults ($n = 9$).

The pair of large whales observed in Lüderitz Bay on 1 September 1993 included a male. For more than four hours the whales were observed (with binoculars and spotting scope) from the shore at distances ranging from 50-300m, involved in what appeared to be mating activity. The two whales remained together, most of the time in body contact, striking the surface repetitively with flukes and flippers. The erect penis of one of them was clearly visible several times.

Survey results

Table 2 summarises the coverage achieved by the two surveys of 1998 and 1999. Coastal fog is common along the Namib Desert coast and is the cause of the low coverage achieved in 1998. The southern right whale sightings during the surveys are also summarised in Table 2.

Occurrence of calving

Combining incidental sightings and survey data (Tables 1 and 2), 12 cow-calf pairs have been recorded since 1990. Between 1996 and 1999, mother and calf pairs were sighted every year: 2 in 1996; 4 in 1997; 3 in 1998; and 1 in 1999. From the observed size of the calves (between one third and half the length of the accompanying adult) it was deduced that they were calves-of-the-year. Cow-calf pairs were sighted between mid-July and the beginning of December (Table 1).

Observations at Elizabeth Bay in 1996 provided some details of the residence period of a mother and calf pair. A single adult southern right whale was sighted close to a mining camp within 100m from the shore on the southeastern side of Elizabeth Bay on 16 August 1996. Subsequently, this whale was sighted from the same camp virtually on a daily basis. As from the last week of August, it was observed accompanied by a young calf. The birth was

Table 1

Incidental sightings of southern right whales along the Namibian coast since 1971. All sightings were made within 3km from the coast. Categories of sightings (Cat.) follow the definitions given in the text for 'probable' (P) and 'confirmed' (C).

Date	No. whales	No. calves	Source	Cat.	Latitude S
5 Dec. 1971[1]	1	1	Aerial survey of seal colonies	C	28°03’
15 Oct. 1977[1]	1		Shipboard marine mammal survey	C	26°38’
18 Aug. 1978[1]	1		Sketched from shore	P	21°08’
15 Sep 1981[1]	1		Ichaboe Island headman	P	26°17’
12 Sep. 1986	1		From Shark Island lighthouse	C	26°37’
12 Oct. 1986	2		Photographed from shore	C	26°36’
8 Jul. 1987	2		Fishing boat *Hoddevik* - id. as humpback but description right whale	P	24°27’
8 Jul. 1989	1		Seen at close range from rubber dinghy	C	26°37’
18 Sep. 1990	2	1	Seen from aircraft by nature conservator	P	23°20’
9 Sep. 1991	1		Ichaboe Island headman	P	26°17’
17 Sep. 1992	1		Possession Island headman	P	27°01’
12 Oct. 1992	1		Seen breaching from fisheries survey vessel	P	17°16’
1 Sep. 1993	2		Observed for 4 hours from shore, apparent mating	C	26°37’
26 Jul. 1993	2	1	Reported by tugboat captain	P	22°53’
7 Nov. 1993	2		Seen at close range from diamond mining vessel	P	26°49’
8 Nov. 1993	1		Observed from shore by nature conservator	P	26°44’
25 Jul. 1994	1		Seen from fisheries survey vessel	P	26°38’
23 Sep. 1995	1		Photographed from shore	C	27°13’
10 Jul. 1996	1		Seen from diamond mining vessel	P	26°51’
11 Jul. 1996	1		Seen from diamond mining vessel	P	26°53’
16 Aug. 1996[2]	1		Observed from mining camp at close range, video taken	C	26°57.2’
25 Sep. 1996[2]	2	1	Observed from mining camp at close range, video taken	C	26°57.2’
17 Sep. 1996	1		Photographed at close range from skiboat	C	22°33’
30 Oct. 1996	2	1	Observed from shore by nature conservator	P	19°22’
24 Aug. 1997	2	1	Seen at close range by Mercury Island headman	C	25°43’
28 Sep. 1997	6	3	Seen from aircraft, video taken, Ministry of Environment	C	24°46.4’
15 Jul. 1998	2	1	Photographed from survey vessel	C	26°36.9’
16 Jul. 1998	1		Seen breaching from diamond mining vessel	P	26°42’
30 Jul. 1998	2		Observed by Mercury Island fisheries personnel	C	25°43’
12 Aug. 1998	1		Seen from diamond mining vessel	P	26°52.2’
14 Aug. 1998	1		Seen from diamond mining vessel	P	26°49’
6 Oct. 1998	2		Photographed from diamond mining vessel	C	26°44’
3 Nov. 1998	1		Seen from diamond mining vessel	P	26°46.4’
2 Jun. 1999	1		Observed by Ichaboe Island headman	C	26°17’
2 Aug. 1999	2		Observed by biologist from Mercury Island	C	25°43’
5 Sep. 1999	2		Video taken from aircraft	C	26°26.4’
14 Nov. 1999	2		Observed breaching from shore by nature conservator	P	19°50.5’

[1] From Best (1981). [2] Denotes first and last sightings of the same individual cow, which calved in Elizabeth Bay in August 1996.

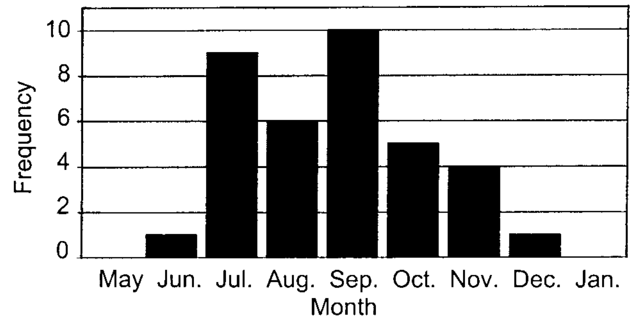

Fig. 2. Seasonality of incidental sightings of southern right whales along the Namibian coast (1971-1999).

not witnessed but is thought to have taken place within two days of 28 August. The mother and calf pair remained in the bay and were seen many times until 25 September. The calf was estimated to be less than one third of the adult's length when first observed and was seen only in close association with the adult. The last recorded sightings of the mother and calf pair were noted on 20, 23 and 25 September. Surveys of the bay by boat on 26 and 27 and along the shore on 28 September failed to locate the whales and they were not sighted again despite continued frequent observations from the shore until mid-November. As only one adult whale was sighted at any time, and because when seen at close range the observers could recognise the pattern of natural markings, it can be assumed that the same adult whale spent the whole period (41 days) inside or in the vicinity of the bay. This whale calved approximately 12 days after arriving and remained in the bay with the young calf for a period of 27 to 31 days after the birth, before departing.

DISCUSSION

Since 1971, southern right whales have been sighted between the Kunene River mouth on the Angolan border and the vicinity of the Orange River, on the South African border. Some of these whales were mature cows and at least one was a male. At least 10 small calves accompanied by adults were seen along the Namibian coast between 1996 and 1999.

The seasonal distribution of sightings in Namibian waters, from June to December with a peak in September, is supported by the seasonal occurrence of southern right whales in other calving areas in Australia (Bannister, 1986), Patagonia (Payne, 1986) and South Africa (Best and Scott, 1993). The average sighting date was 4 September; whales seem to be present inshore along the Namibian coast slightly earlier in the year on average than at higher latitudes in the

Table 2

Coverage and sightings of southern right whales during aerial surveys along the Namibian coast.

Date	Region	Coastline surveyed (km)	% Coastline	No. whales	No. calves	Position
28 Sep. 1978	Orange River - Walvis Bay	810	100	1	0	27°12'S, 15°15'E
				2	1	24°30'S, 14°35'E
29 Sep. 1978	Walvis Bay - Kunene River	660	100	0	0	
29 Sep. 1998	Lüderitz - Orange River	310	100	2	1	27°47.94'S
				1	0	28°16.82'S
	Orange River - Lüderitz	310	100	2	1	27°05.68'S
30 Sep. 1998	Lüderitz - Swakop River	67	13	0	0	
	Swakop River - Lüderitz	284	55	0	0	
7 Oct. 1999	Lüderitz - Swakop River	512	100	0	0	
	Swakop River - Lüderitz	390	76	0	0	
8 Oct. 1999	Lüderitz - Orange River	310	100	2	1	28°31.42'S
				2	0	28°35.24'S
				2	0	28°35.45'S
				3	0	28°35.59'S
	Orange River - Lüderitz	291	94	2*	0	28°35.73'S
				2*	0	28°35.45'S
				3*	0	28°35.31'S
				1	0	28°35.19 S
				2*	1*	28°33.07'S

* Assumed duplicate sightings.

South Atlantic where the peak of abundance inshore is late September (Payne, 1986; Best and Scott, 1993) or early October (Best, 1981).

With the exception of one sighting in early December 1971, cow-calf pairs were sighted between mid-July and the end of October; one calf was born at the end of August in 1996. Despite the small number of observations, this agrees well with the calving season and the residence time of cows and young calves in other calving areas (Whitehead and Payne, 1981; Best, 1994b). Best (1994b) estimated the calving season in South Africa to range from late June to late October with most calves (95.5%) born during a period of 118 days around the mean date of birth (24 August). Cow and calf pairs are usually resident in coastal waters of South Africa for about a month before starting their southerly migration (Best and Scott, 1993), but some pairs may stay in the same bay for more than two months (Best, 1981).

Historical records place the northernmost limit of the coastal distribution of the species prior to exploitation in southern Angola, and Baia dos Tigres was a well known whaling ground at the beginning of the exploitation of right whales in the southeastern Atlantic (although it is unclear if calving was taking place there). Best (1981) commented on the striking paucity of modern records for the species north of 32°S along the west coast of Southern Africa, and concluded that the species still had to recolonise much of its former range in the region. The analysis of survey data up to 1987 along the coast of South Africa confirmed that the South African population was increasing at a rate close to 7% per year. However, the bulk of the population is concentrated to the east of the Cape of Good Hope, and only one cow and calf pair and three unaccompanied adults were sighted along the west coast of South Africa north of 32°S in four aerial surveys between 1981 and 1986 (Best, 1990b). The sightings presented in this study show that the species has been present throughout its former range in the coastal waters of Namibia in recent years.

The sightings of a single adult off the Kunene River mouth and of a mother and calf pair swimming in a southerly direction on 30 October 1996 at Möwe Bay are particularly significant. They are the northernmost records of the species in Namibia since the end of the whaling era. In addition, considering the date and the swimming direction, the cow and calf pair had presumably started the southward migration. A pair of unidentified whales was sighted the following day from the shore at Terrace Bay, 80km south of Möwe Bay, and could have been the same animals (J. and B. Paterson, pers. comm.). Therefore, the calf was probably born earlier in the season and to the north.

Most mature cows calve every 3rd year (Best, 1990a), therefore, sightings of mother and calf pairs during four consecutive years seem to confirm the existence of a small established breeding stock off Namibia. This represents a northward extension of the hitherto known regular modern calving range of the species in the southeastern Atlantic by more than 1,000km.

No inference can be made on population size and trend from incidental sightings. A minimum of three complete successive aerial surveys of the area would be needed to assess the number of mature females calving in Namibian waters. Further survey data and photo-identification studies are required to estimate the size of the population frequenting the Namibian coast, its trend and its relationship with other sub-populations in the South Atlantic. On the other hand, from the results of the surveys (Table 2), the absence of recorded strandings during the 20th century and the paucity of incidental records, it is clear that the population frequenting the Namibian coast is still very small.

Available whaling records clearly document the extreme depletion of the local stock before the advent of modern whaling (Best and Ross, 1986) and it is possible that the breeding population of Namibia and southern Angola had been almost completely eradicated before any protection was granted to the species. In practice, the southern right whale was awarded partial protection only after 1935, and in the South Atlantic some right whales were taken illegally in the Antarctic, Brazil and around Tristan da Cunha until the 1970s (Best, 1981; 1988; Tormosov *et al.*, 1998). The taking of only a few individuals per decade since the beginning of the 20th century could have been sufficient to keep the local population at extremely low levels and to prevent any earlier noticeable recovery.

At least three of the historically important calving bays in Namibia (Walvis Bay, Lüderitz Bay and Elizabeth Bay), have been the sites of important habitat alterations during the 20th century. The first two have been developed into major harbours while a large part of Elizabeth Bay is being filled in by diamond mining operations. Inshore shipping and fishing have increased greatly since the middle of the 20th century and the past two decades have been marked by an accelerated development of coastal and marine mining as well as oil exploration. Anthropogenic factors, through habitat modification and increased mortality risk associated with ship collisions and entanglement in fishing gear (Kraus, 1990), might play a limiting role in the potential recovery of the Namibian right whale population.

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Overview of catch history, historic abundance and distribution of right whales in the western North Atlantic and in Cintra Bay, West Africa

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ABSTRACT

The catch history of the North Atlantic right whales (*Eubalaena glacialis*) in the western North Atlantic has been studied in a series of projects. Data from European archives on early Basque whaling, centred in the Strait of Belle Isle, showed that there were at least a few thousand right whales in the northern part of the range in the sixteenth century. Data from shore whaling in the eastern United States supplemented by British customs data indicated that there were still more than a thousand right whales in the southern part of the range (i.e. south from Nova Scotia) in the late seventeenth century. Right whales were depleted throughout the western North Atlantic by the middle of the eighteenth century, but small shore whaling enterprises persisted in some areas and pelagic whalers continued to kill right whales opportunistically. An increase in alongshore whaling occurred at Long Island (New York) beginning in the 1850s and in North and South Carolina, Georgia and northern Florida in the 1870s-1880s. By the start of the twentieth century only a few crews of shore whalers remained active in Long Island and North Carolina, and their whaling efforts were desultory. All evidence points to stock depletion as the primary reason for the demise of organised whaling for right whales in eastern North America. Recent sightings indicate that some right whales travel from the Bay of Fundy and Scotian Shelf far to the north and east, at least occasionally reaching the historic Cape Farewell Ground. Areas known to have been used regularly by right whales in the past (e.g. Gulf of St Lawrence, Delaware Bay) are now visited seasonally by only a few individuals. Recent surveys of Cintra Bay, a historic right whale wintering ground in the eastern North Atlantic, provided no evidence of continued use by right whales.

KEYWORDS: RIGHT WHALES; NORTH ATLANTIC; WHALING-HISTORICAL; ABUNDANCE ESTIMATE; DISTRIBUTION

INTRODUCTION

At the IWC workshop on right whales in June 1983, three papers (Aguilar, 1986; Reeves and Mitchell, 1986a; b) were presented concerning the catch history of North Atlantic right whales (*Eubalaena glacialis*) and several other papers contained relevant data (Brown, 1986; Cumbaa, 1986; Mead, 1986; Mitchell *et al.*, 1986). Additional reports on right whale catch history have been completed since then (Reeves and Barto, 1985; Reeves and Mitchell, 1988; 1990; Reeves, 1991; Reeves *et al.*, 1992; 1999). The present paper summarises the state of knowledge on the catch history of right whales in the western North Atlantic, and identifies work that remains to be completed. Studies of catch history have two primary objectives: estimation of historic abundance and identification of areas that might still be used by right whales.

ABUNDANCE ESTIMATION

Aguilar (1986) refrained from attempting to estimate the initial abundance of right whales in the western North Atlantic from Basque whaling returns, citing uncertainties about the proportion of bowheads (*Balaena mysticetus*) in the catch and the effects of density-dependence. Gaskin (1991) used Aguilar's (1986) data to estimate abundance in 1530, reasoning that if the Basque whalers secured about 200 right whales per year during the peak whaling decades at Red Bay (Labrador), 'with perhaps one third of struck-and-lost-animals dying (*sic*)', then the cumulative catch could have been as high as 21,000 over the period 1530-1600. He concluded that the initial population size was in the order of 12,000-15,000 right whales. The US 'recovery plan' for North Atlantic right whales (NMFS, 1991) assumed a pre-exploitation population size of at least 10,000 but provided no explanation of why this number was chosen.

Schevill *et al.* (1986) compared their recent observations in Cape Cod waters with Allen's (1916) compilation of newspaper and other accounts from the late 1600s-early 1700s, and made the somewhat provocative suggestion that 'the population of right whales passing near Cape Cod is at worst only slightly smaller now than it was in the 17th century'. After a crude preliminary analysis of oil and baleen imports from the North American colonies to London between 1696-1725, Reeves (1991) concluded that 'right whales are far less abundant in the western North Atlantic today than they were in the 17th century'. A less crude, but still preliminary, analysis of the same data suggested that well over 1,000 right whales were present in coastal waters of the eastern United States in the 1680s, at the beginning of an intense episode of shore whaling (Reeves *et al.*, 1992). The British customs data demonstrate that Schevill *et al.*'s (1986) comparison of sighting rates in the twentieth century with Allen's (1916) miscellaneous compilation of records from the late seventeenth and early eighteenth centuries was a questionable approach to assessing the whale population's current abundance relative to historic abundance (Reeves *et al.*, 1999). The numbers of right whales occurring off Cape Cod in the 1950s-1980s could not possibly have produced the quantities of oil and baleen exported from New England (*ca* 5,000,000 US gallons and 1,200,000 pounds, respectively) between 1696-1734.

Several attempts have been made to guess how small the western North Atlantic right whale population was when whaling stopped. S.D. Kraus ('pers. comm.' in Schaeff *et al.*, 1997, p.1075), for example, suggested that it 'may have been reduced to as few as 60 animals'. The context suggests that this estimate refers to some time in the first third of the twentieth century. Kenney *et al.* (1995) used a simple back-calculation equation and a range of possible annual rates of increase to explore possible numbers for the population in 1935. Using an annual rate of increase of 0.03

and a 1990 population size of 300, their estimate for 1935 was 58 whales. Preliminary trajectories using known removals and MSY rates of 0.01, 0.03 and 0.05 suggested that the right whale population off the eastern United States had been reduced to very low levels (< 100 individuals) several times but was recovering by 1935 (fig. 2 in Reeves *et al.*, 1992). In contrast to these estimates, the comment by Rosenbaum *et al.* (1997) that 'no recovery is apparent despite six decades of international protection from hunting' implies that there were about 300 whales in the population in the 1930s, as there are today.

Harmer (1928) noted that the right whale 'began to re-appear' in the North Atlantic about 1850 and that by 1880 'it had become the object of a moderate whaling industry off the Eastern United States'. A number of independent sources in the literature refer to a revitalisation of shore-based whaling for right whales in the 1850s at Long Island, New York (Reeves and Mitchell, 1986b) and in the early to mid-1870s in North Carolina (Clark, 1887; Earll, 1887; Reeves and Mitchell, 1988). In addition, a relatively intense episode of pelagic whaling on right whales in the southeastern US began in about 1875 (Reeves and Mitchell, 1986a). A striking feature of this episode was its short duration (1875/76 to 1881/82) and the low return on effort (e.g. only two right whales were taken in 343 vessel-days by the *Golden City* and *E.H. Hatfield* (Reeves and Mitchell, 1986a: their table 3) and the *Rising Sun* (Taylor, T., 1875-83, [MS])[1]. As the whaling was conducted in the only known calving ground in the western North Atlantic, it seems clear that the population of reproducing females must have been extremely small by the mid-1880s. In the 1880s a summer fishery that took mainly fin and humpback whales (*Balaenoptera physalus* and *Megaptera novaeangliae*, respectively) was prosecuted in the Gulf of Maine, including the lower Bay of Fundy (Reeves and Barto, 1985). Any right whales encountered in these waters certainly would have been pursued.

Tables 1 and 2 summarise the whaling effort and removals, respectively, for the crucial period 1850-1910. The evident decline in effort and catch in the 1890s and 1900s was not due to market factors because demand for right whale baleen had begun to increase in 1875 and remained strong until 1907 (Bockstoce, 1977). It is clear from numerous sources that by about 1900 right whales were extremely scarce in coastal waters of eastern North America. Dedicated efforts to find and catch them were no longer economically viable and right whales were chased only opportunistically after the early to mid-1890s. Thus, the western North Atlantic right whale population presumably experienced its most recent 'bottleneck' towards the end of the nineteenth century and into the early twentieth century.

Table 2

Removals of right whales along the Atlantic coast of North America, by decade, 1850-1910. Whales known to have been killed but lost are included as removed; all others struck-but-lost are not included. Numbers in square brackets are estimates; for details, see text of relevant source. Abbreviations as in Table 1. - = no known take.

	1850-59	1860-69	1870-79	1880-89	1890-99	1900-10
MA/RI shore[1]	5	3	1	5	3	1
MA/ME pelagic[1]	4	-	-	4	-	-
LI shore[1,2]	23	15	18	22	7	5
LI pelagic[2]	4	-	-	-	-	-
NJ shore[1]	-	2	2	1	-	-
NC shore[3]	1[20+]	1[20+]	10[40+]	3[20+]	6[10]	3
SE US pelagic[4]	-	-	5	14(+?)	-	-
Casual SC shore[3,4]	-	-	-	2(+?)	-	-
Unknown[5]	1	-	-	-	-	-
TOTALS	38[57+]	21[40+]	36[66+]	51(+?) [68+]	16[20]	9

References: [1]Reeves *et al.* (1999); [2]Reeves and Mitchell (1986b); [3]Reeves and Mitchell (1988); [4]Reeves and Mitchell (1986a); [5]Wood (no date, MS) indicates that the schooner *William Martin* of Orleans took a right whale sometime between 26 Dec. 1856 when it sailed from Orleans, and 27 Jan. 1857 when it was at Dominica.

STOCK STRUCTURE AND HISTORIC DISTRIBUTION

Three hypotheses for stock structure in the North Atlantic have been proposed: (1) a single stock throughout the North Atlantic; (2) two stocks – eastern and western; and (3) three stocks – eastern, central and western (Reeves and Mitchell, 1986a). Gaskin (1991) argued that the right whales summering in the Bay of Fundy and on the Scotian Shelf comprise a deme, or 'separate sub-stock.' This suggestion seems to accommodate some of the puzzling aspects of the catch history, as Gaskin points out, but it presupposes that right whales are much less mobile than they have been shown to be. Long-distance movements by photo-identified individuals have been documented between the Cape Farewell Ground (Fig. 1) and the east coast of North America (Knowlton *et al.*, 1992). Therefore, hypothesis (3) above is probably false but either of the first two could be true.

Patterns of resightings of photo-identified individuals, in combination with patterns of annual visitation to the Bay of Fundy by composite mitochondrial DNA morphs, have been

Table 1

Effort at taking right whales along the US Atlantic coast, by decade, 1850-1910. ME, Maine; MA, Massachusetts; RI, Rhode Island; LI, Long Island; NJ, New Jersey; NC, North Carolina; SE US, southeastern United States; SC, South Carolina. ? = may have been some effort; - = presumably no effort.

	1850-59	1860-69	1870-79	1880-89	1890-99	1900-10
Casual MA/RI shore [5]	Some	Some	Some	Some	Some	Some
MA/ME pelagic[5,6]	Some	Some	?	1 or more schooners; 2 or more steamers; at least 5 vessel-seasons	?	?
LI shore [4]	Many crews	Many crews	Many crews	Many crews	Several crews	Several crews
LI pelagic [4]	4(+?) vessel-seasons	-	-	-	-	-
Casual NJ shore [5]	-	Some	Some	Some	-	-
NC shore [1]	?	?	6-12 crews	6-18 crews	5-7 crews	1-2 crews
SE US pelagic[2,3]	-	-	6 vessel-seasons	14(+?) vessel-seasons	-	-
Casual SC shore [1]	?	?	?	Some	?	-

References: [1]Reeves and Mitchell (1988); [2]Reeves and Mitchell (1986a); [3]Taylor (1875-1883 MS), see footnote in text above; [4]Reeves and Mitchell (1986b); [5]Reeves *et al.* (1999); [6]Reeves and Barto (1985).

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[1] Taylor, T. 1875-1883 [MS]. Journal of T. Taylor kept aboard the schooner *Rising Sun* of Provincetown, T.S. Taylor, Master, 27 March 1875-12 September 1883. Phillips Library, Peabody Essex Museum, Salem, MA.

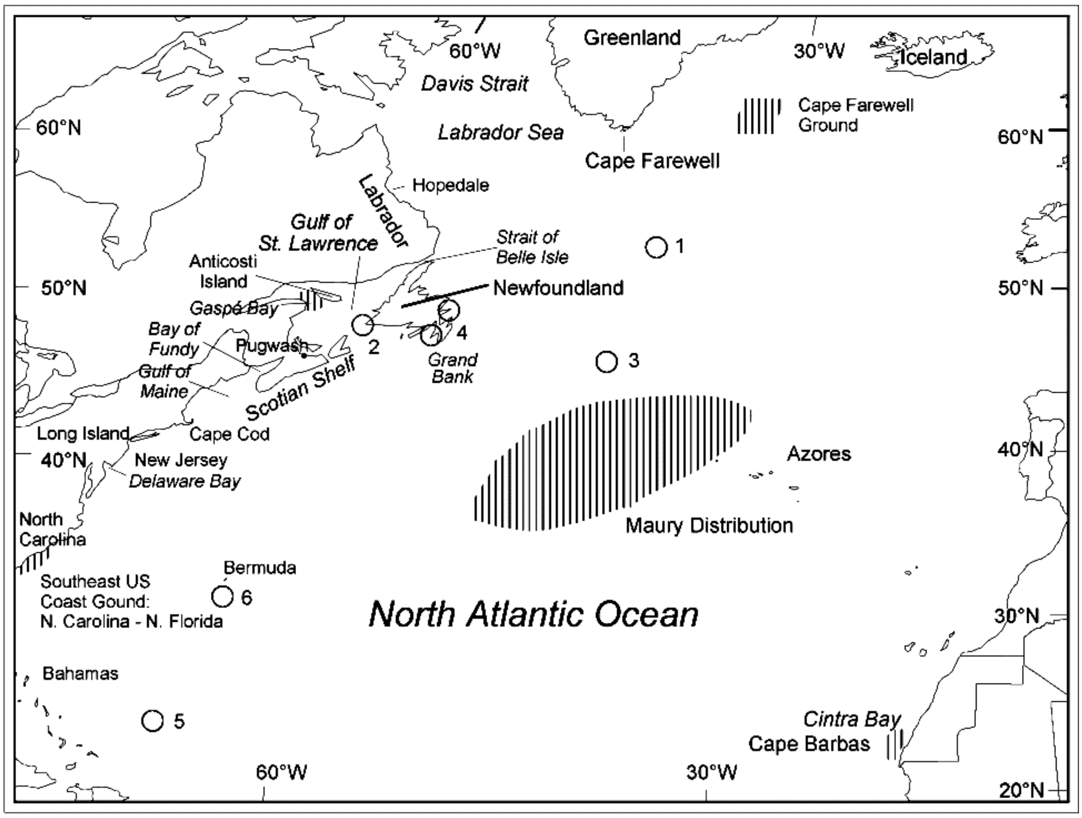

Fig. 1. North Atlantic Ocean, indicating whaling grounds and other areas mentioned in the text. The sightings mentioned in the text are shown as circles, with numbers keyed to text references.

interpreted to mean that the right whales found along the coast between the Scotian Shelf and the southeastern United States represent a single breeding population (Schaeff *et al.*, 1993). Some structuring within that population, on the basis of relative degrees of philopatry to particular summer 'nursery' areas, was also suggested by these initial analyses.

The following sections briefly consider the state of knowledge about past and current distribution in selected parts of the North Atlantic, including one area in the centre of the basin (Cape Farewell Ground) and one on its east side (Cintra Bay Ground).

Cape Farewell Ground

This former summer whaling ground for right whales was east of Cape Farewell, Greenland, centred at approximately 60-62°N, 33-35°W (Schevill and Moore, 1983; Reeves and Mitchell, 1986a). At least a few right whales still migrate to the area (Sigurjónsson *et al.*, 1989; Knowlton *et al.*, 1992). Also, some exchange occurs between this ground and the North American coast: one individual was photographed on the Cape Farewell Ground in early July 1987 and on the Scotian Shelf in mid-June 1989 (Knowlton *et al.*, 1992). The mother and calf seen in early August 1990 at 52°43'N, 38°36'W (Sigurjónsson *et al.*, 1991; No.1 in Fig. 1) may have been *en route* to or from the Cape Farewell Ground. Reeves and Mitchell (1986a) reported nineteenth-century sightings by whalers south to 56°10'N and west to 43°W (see below for further discussion).

Southeast US Coast Ground and alongshore north to Long Island

The reports of whaling activity alongshore from northern Florida to North Carolina in the winter and spring (Schevill and Moore, 1983; Reeves and Mitchell, 1986a; 1988) are consistent with recent observations that right whales regularly migrate to this area (Kraus *et al.*, 1986). Observations near the North Carolina (Outer Banks) coast are reported less frequently than would be expected judging by the historic shore-based whaling operations there (Reeves and Mitchell, 1988) but this could be due to relatively low sightings effort. The same might be said of the coastal waters of New Jersey (Reeves *et al.*, 1999) and Long Island, New York (Reeves and Mitchell, 1986b).

Mead and Mitchell (1984) suggested that some of the whales hunted in Delaware Bay in the mid-seventeenth century were gray whales (*Eschrichtius robustus*). While that may be true, right whales certainly occurred there in the late winter and early spring (Lipton, 1975; Reeves *et al.*, 1999). They also moved, at least occasionally, far inside the Bay and into the mouth of the Delaware River (Reeves *et al.*, 1978). The inner parts of Delaware Bay and the river mouth seem not to be used regularly by right whales today. The recent appearance of a right whale about 130km up the Delaware River was regarded as an anomaly (Hamilton, 1995). The lack of more observations in Delaware Bay can be interpreted as an indication that the carrying capacity has declined (i.e. this part of their range is no longer suitable habitat), that the population has yet to recover sufficiently to re-occupy all areas of past use (Winn *et al.*, 1986) or that search effort in the Bay during the appropriate season has not been intensive and regular enough to detect right whales other than occasionally.

Newfoundland, Labrador and Gulf of St Lawrence

Whaling records for these areas have been confounded by the fact that the historic range of bowheads overlapped that of right whales (Moore and Reeves, 1993; Ross, 1993). A substantial proportion of the balaenids killed by commercial whalers in the Strait of Belle Isle apparently were bowheads

(Cumbaa, 1986). Inuit hunted bowheads in the late autumn (mainly November) along the Labrador coast as far south as Hopedale (55-56°N) during early historic times (Taylor, 1988). Presumably, the overlap in range was out of phase, such that bowheads moved south along the Labrador coast and into the Strait of Belle Isle in the winter and left in the spring, prior to the arrival of right whales from the south. This would mean that most balaenids taken off Labrador, in the Strait of Belle Isle and in the northeastern Gulf of St Lawrence in summer and autumn months were right whales.

The records of New England whalemen sighting whales in the heavy ice of the Strait of Belle Isle in May and hunting 'right' whales in the northern Labrador Sea and southern Davis Strait in June and July could refer to bowheads (see table 1 in Reeves and Mitchell, 1986a). The balaenids hunted along the Labrador coast in August and in the Gulf of St Lawrence in summer and autumn months (e.g. Wakeham *et al.*, 1913; Mitchell and Reeves, 1983) were more likely right whales than bowheads. Recent observations of right whales in the northwestern Gulf off Gaspé Bay and the west end of Anticosti Island (Lien *et al.*, 1989; Richard Sears, pers. comm., 19 May 1999) are broadly consistent with what is known of the historic distribution. No balaenids have been sighted in recent surveys of the Strait of Belle Isle (Kingsley and Reeves, 1998; M.C.S. Kingsley, pers. comm., May 1999). However, the carcass of a 9m female bowhead was found adrift off the northeast coast of Newfoundland (49°40'N, 56°10'W) in mid-October 1998 (Daoust *et al.*, 1998). This is the first confirmed record of a bowhead in the western North Atlantic south of Hudson Strait in the twentieth century.

The sighting of a right whale off the southwestern coast of Newfoundland in February 1984 (Lien *et al.*, 1989; No. 2 in Fig. 1) seems like an exceptional event according to both historic and modern standards. The only other published record of a right whale in the southeastern Gulf of St Lawrence was a live-stranded animal at Pugwash, Nova Scotia, in October 1954 (Sergeant *et al.*, 1970). Gaskin (1991) suggested that some right whales may not migrate south but instead over-winter in offshore waters with high secondary production, and he recommended that winter surveys be conducted along the northern margins of the Gulf Stream to investigate this possibility. Mate *et al.* (1992) speculated that copepod concentrations in deep basin waters of the Scotian Shelf could represent an important resource for right whales in the autumn and winter.

Other areas

New England whalers hunted right whales east of the Grand Bank from July to September in the 1750s-1760s (Reeves and Mitchell, 1986a). The positions given in logbooks suggest that the whales were found off the eastern and northeastern edges of the Grand Bank. These eighteenth century observations probably account for the so-called 'Maury distribution', roughly bounded by 35-43°N and 30-49°W (Maury, 1853; see Reeves and Mitchell, 1986a). Observations of two right whales at 46°37'N, 43°19'W on 30 May 1897 (Reeves and Mitchell, 1986a; No. 3 in Fig. 1), the mother and calf at 52°43'N, 38°36'W on 5 August 1989 mentioned earlier (Knowlton *et al.*, 1992; No. 1 in Fig. 1) and single individuals off southeastern Newfoundland (*ca* 46°30'N-48°30'N) between mid-July and early September in recent years (Knowlton *et al.*, 1992; No. 4 in Fig. 1) are all consistent with the hypothesis that some right whales disperse far to the east and north of the Scotian Shelf in the late spring and summer. The photographic match of an individual seen off Cape Cod in May 1999 and again in a Norwegian fjord in September 1999 (Øien and Marx, pers. comm., as cited in IWC, 2001 [see p.66, this volume]) demonstrates that right whales sometimes move across the entire North Atlantic Ocean.

Rapid long-distance movements by satellite-monitored right whales provide support to the hypothesis that the northern 'summering' grounds are extensive both latitudinally and longitudinally. An adult male (NEA No.1421) travelled 3,056km in 42 days (12 September-24 October 1990), including an excursion offshore to waters 4,200m deep; a mother and calf (mother, NEA No. 1140) covered at least 3,764 km in 42 days (24 August-5 October 1990), remaining mainly in near-shore waters from the Bay of Fundy to New Jersey (Mate *et al.*, 1997). Another adult female (NEA No.1135), inferred to have been pregnant, was tracked for seven days (24-31 August 1990), moving between the Bay of Fundy and Emerald Basin on the Scotian Shelf and covering at least 779km for an average daily speed of 4.6km/hr (Mate *et al.*, 1997). Such mobility makes it easy to imagine that a right whale seen east of the Grand Bank in July or early August could be *en route* to or from the Cape Farewell Ground, with sufficient time to visit the summer and autumn feeding aggregation areas on the Scotian Shelf and in the Bay of Fundy. Whalers generally tried to arrive on the Cape Farewell Ground by mid-June and most left well before mid-August (Reeves and Mitchell, 1986a: their table 2).

A historical record of right whales in an area far offshore, east of the Bahamas and south of Bermuda, raises an interesting possibility in the ongoing search for one or more additional wintering areas. On 5 April 1870 the New Bedford bark *Ansel Gibbs* (1869-70, [MS])[2] was *en route* home from a sperm whaling voyage to the eastern North Atlantic. Two right whales were seen and chased, without success, at 23°58'N, 66°42'W (No. 5 in Fig. 1). To my knowledge, this is the only reliable record of right whales from this area although two animals were sighted 25 n.miles southwest of Bermuda on 13 April 1970 (Payne and McVay, 1971; No. 6 in Fig. 1) and another pair was seen in the Gulf of Mexico off Sarasota on 10 March 1963 (Moore, J.C. and Clark, 1963). These sightings, taken together, demonstrate that right whales, at least occasionally, disperse well away from their well-known near-shore wintering grounds between northern Florida and Cape Cod Bay. In my experience reading logbooks of voyages to the North Atlantic, most vessels that were west-bound from the Cape Verde Islands (as was the *Ansel Gibbs* in 1870) made a landfall at Barbados before heading north to the Bahamas, the Charleston Ground or the Southern Ground in pursuit of sperm whales (*Physeter macrocephalus*). The *Ansel Gibbs* did not take this route but angled northwestwards before reaching Barbados. Perhaps this helps to explain why more voyages circumnavigating the North Atlantic in the usual clockwise manner (New England east to the Azores, south to the Cape Verdes, west to the Antilles and north to home) failed to encounter right whales.

The Cintra Bay question

Schevill and Moore (1983) 'rediscovered' the Cintra Bay Ground where American whalers hunted right whales between 1855-1880 (for details see Reeves and Mitchell, 1986a; 1990). It is clear from the historical record that right

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[2] Ansel Gibbs. 1869-70 [MS]. Logbook of the bark *Ansel Gibbs* of New Bedford, Charles Stetson, Master, 20 October 1869-12 May 1870. New Bedford Whaling Museum, New Bedford, MA, Logbook 500B.

whales, including mothers and calves, visited coastal waters of northwest Africa between Cintra Bay and Cape Barbas during winter months (late November to mid-April). However, in two recent winter surveys (Lamarche and Vely, 1992; Notarbartolo-di-Sciara *et al.*, 1998) no evidence was found to suggest that right whales still use the area. Further investment of research effort in this region probably needs to be justified in some way other than as a search for right whales. The absence of evidence that right whales still visit the Cintra Bay region in the winter is consistent with the rarity of recent observations in European waters to the north (Brown, 1986; Martin and Walker, 1997; Notarbartolo-di-Sciara *et al.*, 1998), assuming that the whales from Cintra Bay traditionally migrated in the late spring and early summer to northern feeding areas off the British Isles, Norway and Iceland as proposed by Thompson (1928) and Brown (1986).

RECONSTRUCTION OF CATCH HISTORY: STATE OF COMPLETION

With completion of the catch history project for the northeastern United States (Reeves *et al.*, 1999), studies have now covered the entire US coast, including shore whaling at Long Island (Reeves and Mitchell, 1986b) and along the southeastern states (Reeves and Mitchell, 1988), American pelagic whaling (Reeves and Mitchell, 1986a) and the little whaling known to have taken place in the Bay of Fundy (Reeves and Barto, 1985). The only major geographic gap in coverage is the Newfoundland/Gulf of St Lawrence/Labrador region for which Aguilar (1986) provided valuable information from European archives and Mitchell and Reeves (1983) reviewed some of the literature from North American sources. Using conversion factors for oil production based on data from American shore whaling, and assuming that the catch was half right whales and half bowheads, Reeves *et al.* (1999) estimated from Barkham's (1984) production data that the sixteenth century Basque whalers may have secured 283-364 right whales in the western North Atlantic in some years. Aguilar (1986) estimated that 300-500 'mainly right whales' were secured annually by the Basques between 1530-1610. These catch levels by the Basques are much higher than the one-year estimates of the catch by shore whalers in the northeastern United States, which ranged only to as high as 158 based on baleen production (in 1724) and 250 on oil production (in 1734, by which time, however, oil from sperm whales and other species may have been mixed in the returns; Reeves *et al.*, 1999).

The next step, apart from trying to document catches in southeastern Canada in greater detail, is to compile annual removal estimates for all catching areas combined. This will need to include adjustments of catch to account for hunting loss but more importantly will require major interpolations and extrapolations to account for years with little or no documentation.

Estimating historic population levels for right whales in the western North Atlantic poses many challenges. Among them are that: (1) whaling began, and the largest catches were made, long before there was any systematic effort to document catch or production; (2) the period of exploitation was prolonged, lasting from at least the early 1500s to the early 1900s; (3) stock structure is uncertain; (4) climatic and other environmental variability has had unknown effects on the whales' distribution and seasonal migrations if not also on their abundance and vital rates; and (5) historical factors (e.g. changes in whaling technology, changes in the economic value of oil and baleen) probably influenced whaling effort and efficiency over the period of exploitation.

Given the many uncertainties, especially those related to changes in carrying capacity, there are severe limits on what historical research can provide. Even if one were to set aside concerns about climatic variability and changes in habitat quality, the great uncertainty about removals and stock structure would persist. With new techniques that make it possible to obtain DNA from baleen in museum collections (Rosenbaum *et al.*, 1997) and thus to supplement ongoing biopsy sampling of live and stranded whales, rapid progress towards understanding stock structure should be possible (e.g. see IWC, 2001). However, it is difficult to foresee a similar breakthrough to reduce the uncertainty about removals by whaling in early historic times.

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Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean

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ABSTRACT

Northern right whales in the western North Atlantic number about 300 animals and have shown little sign of recovery in recent decades. Mortality and serious injury due to human activities, particularly commercial fishing and shipping, are thought to be significant factors limiting their recovery. From 1970-1999, 45 right whale deaths were reliably documented. Sixteen of these fatalities (35.5%) were due to ship collisions, and three (6.7%) were due to entanglement in fishing gear. The remainder were neonates (13; 28.9%) and 'unknown cause' mortalities (13; 28.9%). Criteria for defining serious injuries and mortalities from entanglement or ship strikes were developed and include any animal carrying fishing gear, cuts from entanglement or ship strike deeper than 8cm, swelling or necrosis, evidence of poor health from such interactions, and, in carcasses, evidence of haematoma, haemorrhaging or broken bones. A total of 56 animals fitting the defined criteria were documented from 1970-1999: 31 (55.4%) from entanglement and 25 (44.6%) from ship strikes. Nineteen were fatal (16 ship strikes, 3 entanglements), 10 were possibly fatal (2 ship strikes, 8 entanglements) and 27 were non-fatal (7 ship strikes, 20 entanglements). The breakdown of potentially serious injuries by age and sex reveals no difference in levels between sexes but shows a 3.3:1 higher level of interaction in juveniles and calves *versus* adults. The data show that ship strikes are more immediately lethal, but entanglements can result in long term deterioration of an animal and may be responsible for higher levels of mortality than previously thought. Considering that some animals become entangled, drown and never return to the surface, even these levels may be underestimated. Between 1986 and 1999, 84 animals were presumed dead based on a lack of resightings for six years. There were 32 confirmed deaths during this time period suggesting that at least as many unreported deaths occurred as carcasses were reported. Definitive actions need to be taken to reduce the level and severity of anthropogenic injuries and deaths. Actions could include continued disentanglement efforts, gear modifications, seasonal closures for fisheries, mandatory ship reporting, ships' routing measures and speed restrictions for commercial shipping.

KEYWORDS: RIGHT WHALE; STRANDINGS; ENTANGLEMENT; MORTALITY; SHIP STRIKE; FISHERIES; NORTHERN HEMISPHERE; ATLANTIC OCEAN

INTRODUCTION

Northern and southern right whales (*Eubalaena* sp.) were heavily harvested during the whaling era in which they were considered the 'right' whales to kill because they swam slowly, yielded good quantities of oil and baleen and floated after they were killed. Harvesting of northern right whales (*Eubalaena glacialis*) in the North Atlantic began in the 1100s off the coasts of Spain and France, continued off the coasts of Labrador and Newfoundland in the 1500s and 1600s (Aguilar, 1986), and persisted along the east coast of the US into the early 20th century (Reeves and Mitchell, 1986b; Simpson and Simpson, 1988). Stocks were reduced to extremely low levels (Reeves and Mitchell, 1986a). Despite legal protection from hunting for both northern and southern right whales (*Eubalaena australis*) in 1935 by the 1931 Convention for the Regulation of Whaling and subsequent conventions (Donovan, 1992), the Northern Hemisphere populations have seen little to no recovery. This is in marked contrast to their Southern Hemisphere counterparts that have increased at a rate of 7-8% and have a current estimated abundance of about 7,000 animals (IWC, 2001b). Major factors thought to be contributing to this lack of recovery in the western North Atlantic include entanglement in commercial fishing gear and collisions with ships (IWC, 2001a). The purpose of this paper is to review available data on the extent and consequences of mortalities and serious injuries of right whales in this region.

Northern right whales have been studied extensively in the western North Atlantic by a collaboration of research organisations. Much of the work is based on photographically identifying individuals using callosity patterns on the head, as well as scars and markings on the body and tail (Kraus *et al.*, 1986). Monitoring individual whales over time allows for a determination of the population status, reproductive rates, mortality levels, movements and demographic parameters. The western North Atlantic population is considered extremely endangered with about 300 individuals surviving (Knowlton *et al.*, 1994; IWC, 2001a).

A previous review of right whale mortality and scarring rates (Kraus, 1990) indicated that 20% of the documented deaths were caused by ship collisions and 12% (later reduced to 6.7% - Kenney and Kraus, 1993; this manuscript) were caused by entanglement in fishing gear. Kraus (1990) also noted that 57% of all clearly-photographed living individuals bore evidence of entanglement interactions and 7% bore scars from ship collisions. The proportion of those injuries that would be considered serious was not assessed.

The impacts of serious injury from fishing gear on marine mammal populations were the focus of a workshop convened by the National Marine Fisheries Service (NMFS) in April 1997. One of the difficulties with assessing injuries in large cetaceans was identifying those likely to be 'serious', meaning reasonably likely to result in death or to impair reproduction (Angliss and DeMaster, 1998). Workshop participants felt an animal was not necessarily seriously injured if it was trailing gear and that a determination of effect would require a case-by-case assessment. It was generally agreed that any entanglement that impeded locomotion or feeding should be considered a serious injury. Although that particular workshop focused solely on entanglement injuries, the seriousness of injuries from other sources can also be difficult to assess. This paper attempts to outline criteria for assessing serious injury of right whales based on 20 years of observational data. It updates data on the number and causes of right whale deaths, provides information on the circumstances in which carcasses were first found (i.e. beached *versus* floating), the number of dead animals retrieved and the extent to which they were examined, and the location of carcasses relative to shipping lanes. Necropsy results and the indicators used to determine cause of death are reviewed. Information on the number of unconfirmed right whale mortalities is also provided.

Additional analyses are provided regarding the level and causes of serious injury observed in this population. Mortalities and serious injuries from human related activities are combined into categories based on the type of interaction, in order to assess the relative impact of each type of activity (e.g. fishing gear entanglement, ship strike) on the population beyond the figures calculated from known mortality data.

METHODS

Mortalities

The New England Aquarium maintains records of all right whale deaths documented by reliable means (e.g. photographs or positive identifications by persons trained in whale identification) from the western North Atlantic since 1970. These records typically include the location where the carcass was found, measurement data, a list of samples collected and a description of findings (including the cause of death, if determined). Not all records are complete. For example, in some cases, carcasses were observed at sea and never towed to shore for careful examination and in other cases carcasses were inaccessible or buried without a necropsy.

Determining cause of death is not a straightforward process. If there is external evidence of an interaction (propeller cuts, gashes, or entangled and drowned), assessing the cause of death can be relatively easy. However, other situations are much less obvious and require substantial effort and expertise to evaluate (broken bones, internal haemorrhaging, infection). Carcasses are usually several days old and have experienced severe decomposition, which masks histological and/or other features that might indicate trauma or stress. It has therefore recently been made a practice to flense each carcass to look for evidence of bone breakage. With apparent ship collisions, an assessment is made to determine if the incident was pre- or post-mortem. The indicators used to make an assessment include the four listed below:

(1) *The location of propeller cuts and gashes*

A dead right whale typically floats belly or side up, so post-mortem cuts or damage are likely to occur on the ventral side of the body. If an animal has evidence of cuts or gashes on the dorsal side of its body, it is assumed that the strike occurred pre-mortem (Kraus, 1990).

(2) *Length of time dead*

If an animal has been dead for less than a few days, as evidenced by the condition of internal organs, and there is evidence of ship collision, it is assumed that the ship strike led to the animal's death and did not occur post-mortem (Kraus, 1990).

(3) *Evidence of internal haemorrhaging or haematoma*

Histology of internal organs and fluid found in body cavities can be useful for even moderately decomposed animals to identify haemorrhaging and blood clotting, which would only occur pre-mortem. Haematomas, which require circulatory action to form, can be looked for in association with broken bones to determine if the break occurred pre-mortem. Large haematomas found along the blubber/muscle interface can also indicate that an impact occurred.

(4) *Evidence of infection*

This is the most difficult indicator to confirm without a freshly dead carcass for histological samples. In rare cases, this has been inferred as the cause of death when an animal had a severely necrotic cut or gash in which exposed muscle and bone indicated infection was likely to have occurred.

All confirmed right whale mortalities have been tabulated by date, latitude, longitude, age, sex, length, disposition when found, extent of examination (e.g. whether it was retrieved or necropsied) and distance from the nearest shipping channel or lane (as determined from nautical charts) when first sighted. For each carcass, the cause of death was listed as ship strike, entanglement or unknown. Mortalities attributed to ship strikes or entanglements were based upon necropsy data or external evidence (e.g. missing tails, propeller cuts, or entangled and drowned). Mortalities listed as unknown were further sub-divided into newborn calves which died on the calving ground with no obvious indication of a human-related interaction, and all other deaths due to unknown causes. Most, if not all, neonates probably died of natural causes. The remainder classified as unknown probably fall in one of the three categories (ship strike, entanglement or natural cause) but there are no data to support assignment to any of these categories.

Confirmed deaths have been tallied for each five-year period beginning with 1970-74 and sub-divided by cause of death to assess trends over time. The initial disposition of the carcass (i.e. floating *versus* beached) and the number of floating carcasses actually retrieved were examined for each of these time periods to evaluate whether reports of floating carcasses have increased with heightened awareness of the plight of right whales and whether increased effort to document mortalities has significantly increased the retrieval of floating carcasses.

Serious injuries and human-related mortalities

The New England Aquarium curates the photo-identification catalogue of individual animals which allows for an assessment of the apparent health of each animal. Each animal's photographs were reviewed to assess the extent of interaction with fishing and shipping activity. Criteria were developed to define a serious injury based on longitudinal observations of right whales and the types of injuries that have been photographically documented. For an injury type to be deemed serious, at least one animal must have been observed to have either died or suffered potentially fatal wounds from the given injury type. This is a more stringent criterion than that proposed by the NMFS workshop.

Criteria for serious injury and mortality caused by entanglements

Three main criteria are used to determine whether serious injury or mortality resulted from entanglements in fishing gear.

(1) *Animal seen carrying line*

Events in which an entanglement and subsequent assisted or unassisted disentanglement were witnessed and occurred on the same day were not included.

(2) *Open wound with a depth estimated to be greater than 8cm caused by an entanglement*

The 8cm depth was chosen as some animals with cuts appearing only slightly deeper than this (as estimated from photographs) have been seen in poor health. Wounds were determined to be caused by entanglement if the cut wrapped around the injured body part (Hamilton *et al.*, 1998).

(3) *Entangled animal, or animal with entanglement wounds appeared in poor health.*

Indicators of poor health could include any one or more of the following: slow swimming; evident skin lesions; graying of skin; not fluking; evidence of infection (i.e. necrosis or swelling); and high levels of orange cyamids present in animals older than one year. One year was used as the lower limit because calves are often seen with high levels of orange cyamids on the head and sometimes the tail. As animals grow older these orange cyamids disappear and are seen associated only with injuries or on animals that are in poor health and are swimming slowly (Rowntree, 1996; Osmond and Kaufman, 1998).

Criteria for serious injury and mortality caused by ship strikes

Four main criteria are used to determine whether serious injury or mortality resulted from ship strikes.

(1) *Propeller cut(s) or gashes which are more than approximately 8cm in depth (see category (2) above)*

(2) *Evidence of bone breakage which was determined to have occurred pre-mortem*

(3) *Evidence of haematoma or haemorrhaging*

(4) *Ship-struck animal appeared in poor health*

Indicators could include any one or more of the following: slow swimming; skin lesions evident; greying of skin; not fluking; and high levels of orange cyamids present in animals greater than one year old (see entanglement category (3) above), evidence of infection (i.e. necrosis or swelling).

Sub-categories of ship strikes and entanglements

The two human interaction categories, ship strike and entanglement, were each divided into four sub-categories based on the nature of the interaction. For entanglement these sub-categories were:

(1) line around tail;
(2) line through mouth;
(3) deep cuts but no line present;
(4) line around multiple body parts.

For ship strikes these sub-categories were:

(1) propeller cuts/gash;
(2) severed fluke(s);
(3) broken bones;
(4) haemorrhaging/haematoma.

The indications of poor health are potential secondary effects of each of these types of interactions and are described in individual animal accounts. Serious injuries from other causes are described only in the text. The mortality and photo catalogue databases were reviewed to determine the number of animals by sub-category. Each animal (living or carcass) in one or more of these sub-categories was then assigned an appropriate impact level: fatal; possibly fatal; or non-fatal. Fatal was only used for animals observed dead. Possibly fatal interactions included animals that were last seen in poor health or have not been seen since their initial injury sighting. This group was further subdivided into *presumed dead* if they have not been resighted for six or more years[1] (Knowlton *et al.*, 1994) or *fate uncertain* if they have not been resighted since being observed seriously injured within the past six years. Non-fatal interactions include animals that were seen with a serious injury but were subsequently observed alive and apparently healthy. Although some of the injuries in this non-fatal category could be deemed non-serious, there may be long-term impacts from such interactions that are impossible to measure. For the purposes of this paper, therefore, the non-fatal injuries are all considered serious injuries. Included in these summaries are animals that were not photo-identified but for which there exists either qualified observer information on a human activity/right whale interaction to suggest that the resulting injury was definitely serious, or carcasses with external evidence of a ship strike or entanglement interaction which could not be matched to the right whale photo-identification catalogue because of insufficient documentation.

To assess the combined effects of serious injuries and mortality over time, five categories (natural mortalities, unknown cause mortalities, fatal injuries, possibly fatal injuries and non-fatal injuries) have been plotted by year (Fig. 2). A linear regression was carried out for the years 1980-1999, the years in which data were collected systematically.

RESULTS

Mortality

Forty-five right whale mortalities were documented from 1970-1999 (Table 1). The number of carcasses observed per year ranged from 0-6 with a mean of 1.50 (SD = 1.36; Fig. 1). Out of the 30 years that mortality data have been collected, there were only six years during which a death was not documented, all prior to 1986.

Mortalities by cause of death for each five-year period beginning with 1970-1974 are shown in Fig. 2. The increase in total mortalities for each five-year period is significant at $p = 0.024$. *Ship strike* mortality shows a generally increasing but not quite significant trend over time ($p = 0.064$) and no trends are obvious for *newborn calves* ($p = 0.267$), *entanglement* ($p = 0.119$) and *unknown cause* ($p = 0.210$) mortalities.

Ship strikes account for the largest number of confirmed deaths (16/45, 35.5%). Nine out of the 16 ship strikes (56.3%) have occurred since 1990, representing 47.4% of the total mortalities for this period (9/19). Mortality of neonates with no evidence of human interactions represent 28.9% (13/45) of the total mortality[2]. Entanglement-related deaths represent 6.7% of total confirmed mortality (3/45) and deaths due to unknown causes represent 28.9% of total confirmed mortality (13/45).

The number of carcasses found floating *versus* beached, and the number of floating carcasses retrieved, were plotted for each five-year period (Fig. 3). The data indicate that in recent years, a greater number of floating carcasses was observed and reported which may account for the apparently increasing mortality trends. Of the 17 carcasses found floating, ten were retrieved. Seven of these ten carcasses were retrieved within the past five years, indicating the greater commitment to retrieving every right whale carcass. Three carcasses were first reported floating but subsequently washed ashore. These animals were included in the beached category.

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[1] The six year criterion was developed to account for animals in this population that may be dead. Between 1980 and 1999, 23 animals or less than 8% of the population exhibited sighting histories longer than six years. Although this *presumed dead* criterion may over-inflate the actual number of dead animals, it serves as a cautionary approach to monitoring this population (see discussion in IWC, 2001a).

[2] The foetus found on 10 September 1989 was probably the foetus of #1219 that died of unknown causes. The foetus was found three miles south of 1219's carcass and during a month when right whales are typically not sighted in that region. The foetus was counted as unknown cause mortality.

Table 1

Confirmed right whale deaths in the western North Atlantic: 1970–99. E = estimated.

Date	Sex, age, catalogue no.	Length (cm)	Location	Latitude/Longitude	Disposition of whale when first found	Notes	Necropsy	Distance from shipping channel (miles)
Ship strike								
30 Jan. 1972	Calf	600(E)	TX, Freeport	28°53’N, 95°19’W(E)	Beached	Tail severed	No	5
13 Apr. 1976	6 month old calf, male	760	MA, near Race Point	42°06’N, 70°12’W (E)	Floating, then beached	Large bruise anterior to skull - possible ship collision. Beached in Wellfleet 15 April	Yes	~4
5 Nov. 1976	Unknown	1,100(E)	ME, east of Portland Harbor	43°30’N, 69°50’W	Floating, not retrieved	Cuts and slashes in back	N/A	0
5 Mar. 1979	Juvenile	1,100(E)	NY, Wainscott	40°55.1’N, 72°14.5’W	Beached	Tail severed	Yes	24
21 Feb. 1983	2 year old male, No. 1128	1,100(E)	NJ, Island Beach State Park	39°54.0’N, 74°03.5’W	Beached	Tail severed	Yes	9
7 Aug. 1986	1 year old female, No. 1504	1,090	MA, Mass. Bay	42°12.7’N, 70°02.3’W	Floating, retrieved	2 deep longitudinal gashes	Yes	0
9 Jul. 1987	Juvenile male	800(E)	Nova Scotia, Seaforth	44°40’N, 63°16’W(E)	Beached	Several gashes in back	No	12
12 Mar. 1991	2 year old female, No. 1907	1,005	FL, Amelia Island	30°41’N, 81°26’W	Beached	Shattered skull	Yes	2
5 Sep. 1992	Adult female, No. 1223	1,360	Bay of Fundy, Grand Manan Island	44°32’N, 66°36’W	Floating, then beached	Death witnessed. With calf. Internal haemorrhaging. Probably ship strike	Yes	5
5 Jan. 1993	Calf, male	581	FL, St Augustine	30°02.4’N, 81°16.0’W	Floating, retrieved	Struck by CG cutter	Yes	22
6 Dec. 1993	Unknown age female	Unknown	VA, near Chesapeake Bay entrance	37°10.1’N, 75°31.5’W	Floating, not retrieved	Gash observed, right side. Probably ship strike	N/A	18
20 Oct. 1995	Unknown age male, No. 2250	1,270	Bay of Fundy, Long Island, Nova Scotia	44°18’N, 66°19’W	Beached	Gash in back	Partial	6.5
30 Jan. 1996	Adult male, No. 1623	1,415	GA, offshore	31°28.4’N, 80°59.6’W	Floating, retrieved	Shattered skull	Yes	26
10 Mar. 1996	Unknown age male, No. 2220	1,350	MA, Wellfleet	41°57.5’N, 69°59.5’W	Beached	3m gash in back	Yes	6.5
19 Aug. 1997	Unknown age female, No. 2450	1,259	Bay of Fundy	44°36.5’N, 66°13.8’W	Floating, retrieved	6m haematoma left flank, broken right mandible	Yes	1.6
20 Apr. 1999	Adult female, No. 1014	1,370	MA, Cape Cod Bay	14°54.3’N, 70°09.7’W	Floating, retrieved	Broken right mandible and 5 vertebral processes, oedema	Yes	16
Entanglement								
17 Nov. 1988	Unknown	Unknown	Bay of Fundy	Unknown	Entangled, dead, not retrieved	Caught in offshore lobster gear	N/A	N/A
17 Jul. 1995	2 year old male, No. 2366,	1,009	RI, Middletown	41°29.2’N, 71°16.0’W	Beached	Lobster line embedded – flipper	Yes	7.5
20 Oct. 1999	Adult female, No. 2030	1,350	NJ, Cape May	39°03.3’N, 74°38.4’W	Floating, retrieved	Gillnet gear around body and flippers. Cut into dorsal body cavity	Yes	14
Unknown cause								
Autumn 1971	Unknown	1,200(E)	NY, Atlantic Beach	40°35’N, 73°43’W(E)	Beached		No	7
13 May 1975	Juvenile, male	1,030	MA, Monomoy Island	41°40’N, 69°59’W(E)	Floating, retrieved		Partial	14
10 Dec. 1979	Adult, female	1,550	FL, Atlantic Beach	30°20.0’N, 81°23.3’W	Beached		No	4
19 Apr. 1982	Juvenile, female	900(E)	DE, offshore	38°58.5’N, 69°17.4’W	Floating, not retrieved		N/A	86
22 May 1987	Unknown	1,200(E)	MA, Cape Cod Bay	42°17.0’N, 70°27.4’W	Floating, not retrieved		N/A	0
15 Mar. 1988	Adult	1,500(E)	Newfoundland	Unknown	Beached	Decomposed	No	N/A
8 Sep. 1989	Adult female, No. 1219	1,200(E)	FL, St Augustine Beach	29°54’N, 81°17.5’W(E)	Beached	Carcass buried	No	30
8 Sep. 1989	Foetus	Not determined	FL, Crescent Beach	29°48’N, 81°15.5’W(E)	Beached	Buried as manatee. Retrieved. Probably foetus of No. 1219 (above)	No	N/A
17 Oct. 1990	Adult male	1,675 (E)	ME, Head Harbor Island	44°30’N, 67°31’W	Beached	Decomposed. Partially in trees	No	42
6 Dec. 1993	Male	1,400(E)	VA, near Chesapeake Bay shipping channel	36°45.0’N, 75°39.2’W	Floating, not retrieved		N/A	12
9 Jul. 1994	Male	1,155	Bay of Fundy, Kent Island, south end of Grand Manan	44°34.2’N, 66°44.6’W(E)	Beached	Decomposed	No	19
8 Feb. 1996	Female	1,100(E)	FL, offshore	30°18.7’N, 80°57.2’W	Floating, not retrieved		N/A	22
7 Oct. 1998	Adult male, No. 1333	1,460	NC, at VA state line	36° 33.0’N, 75° 52.0’W	Beached	Decomposed	Yes	18.5

cont.

Table 1 continued.

Date	Sex, age, catalogue no.	Length (cm)	Location	Latitude/Longitude	Disposition of whale when first found	Notes	Necropsy	Distance from shipping channel (miles)
Natural cause								
26 Jan. 1970	Calf, female	439	FL, Neptune Beach	30°18.7’N, 81°23.6’W(E)	Beached, alive		No	5
12 Jan. 1974	Calf, male	407	SC, Edisto Island	32°32’N, 80°15’ (E)	Beached		No	25
30 Dec. 1981	Calf, male	464	GA, Little St Simon’s Island	31°17.5’N, 81°17.0’W	Beached		Partial	10
20 Feb. 1982	Calf, female	457	GA	Unknown	Beached		No	N/A
17 Jan. 1988	Calf, male	438	FL, Cape Canaveral	28°05.5’N, 80°33.9’W	Beached		Yes	19
3 Jan. 1989	Calf, male	425	GA, Cumberland Island	30°50’N, 81°34’W(E)	Beached alive	Birth defects?	Yes	8
26 Jan. 1989	Calf	488	FL, Ormond Beach	29°16’N, 81°02’W(E)	Beached		Yes	70
15 Jan. 1993	Calf, female	473	FL, Cape Canaveral	28°43.8’N, 80°39.8’W	Floating, then beached	Decomposed	Yes	24
2 Jan. 1996	Calf, female	478	FL, Atlantic Beach	30°20.1’N, 81°23.7’W	Beached		Yes	4
19 Feb. 1996	Calf, female	513	FL, offshore	30°44’N, 80°59’W	Floating, retrieved		Yes	11
22 Feb. 1996	Calf, male	Not determined	GA, offshore	30°56.5’N, 80°47.7’W	Floating, retrieved		Yes	25
9 Jan. 1997	Calf, male	417	FL, Flagler Beach	29°25.8’N, 81°06.2’W	Beached		Yes	59
10 Jan. 1998	Calf, female	455	GA, 30 miles east of St Simon’s Island	31°07.9’N, 80°43.1’W	Floating, retrieved		Yes	29

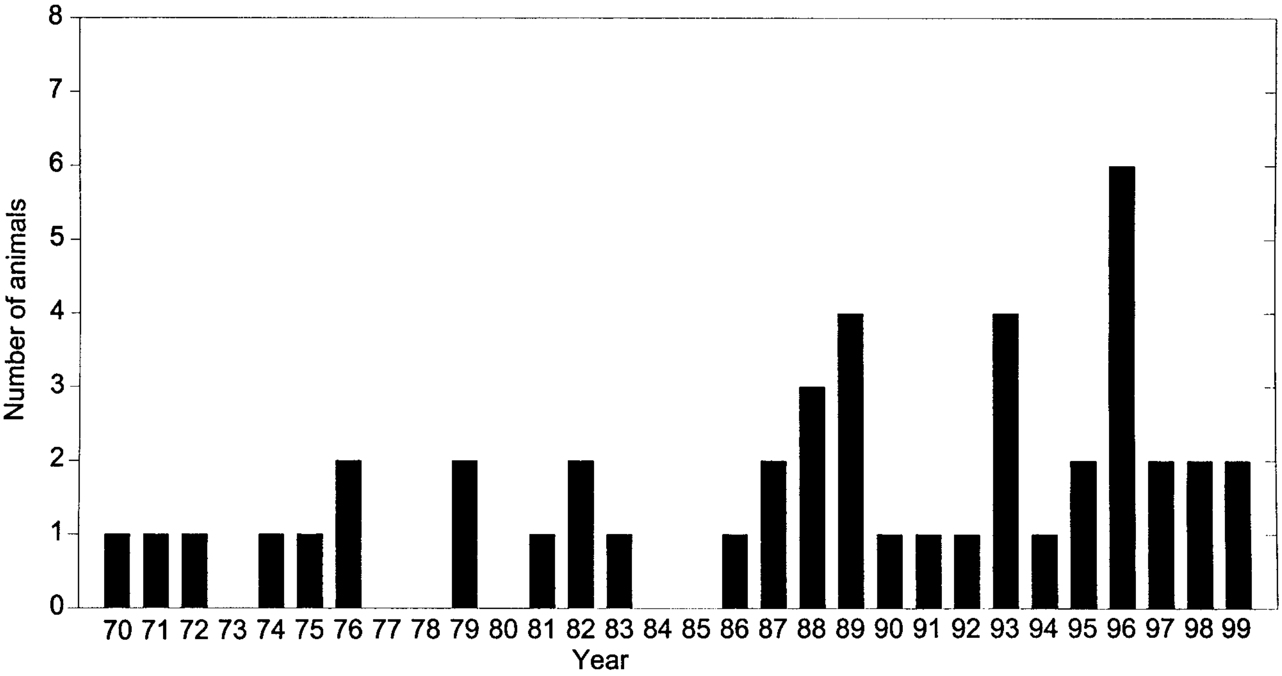

Fig. 1. Confirmed right whale fatalities by year.

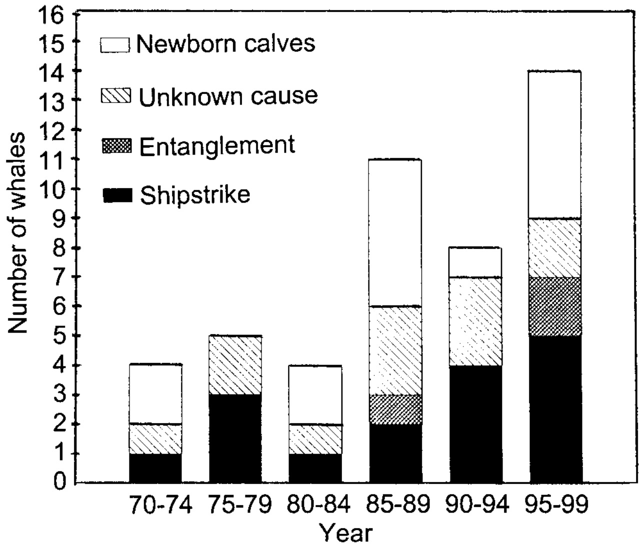

Fig. 2. Confirmed right whale fatalities by cause of death, 1970-99.

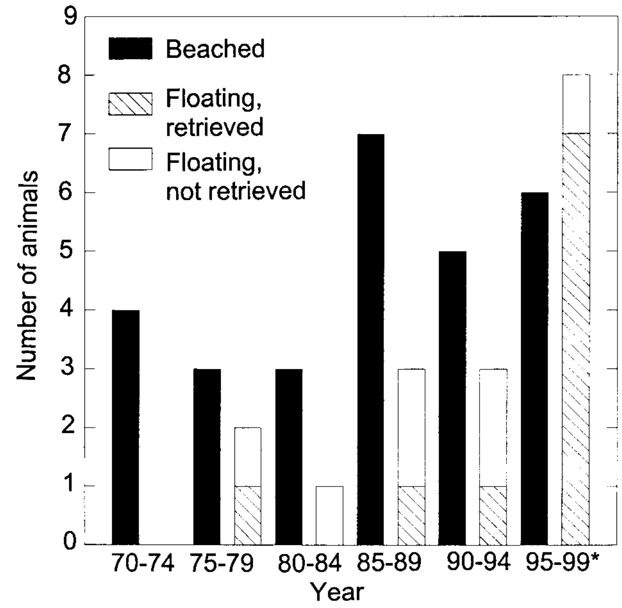

Fig. 3. Number of beached *versus* floating carcasses.

Of the 38 carcasses that were retrieved or beached, 26 were partially or fully necropsied (see Table 1). The thoroughness of each necropsy varied depending on the accessibility of the carcass, access to heavy equipment to move the carcass and aid in flensing, availability of qualified personnel, and availability of adequate funds to carry out the necropsy (note: the financial situation improved dramatically after 1996 when the US National Marine Fisheries Service (NMFS) committed resources to respond to all right whale mortalities).

For the 16 carcasses known to have been struck by ships, the distances to the nearest shipping channel ranged from 0-26 miles with an average distance of 9.9 miles (SD = 8.7 miles). For 25 of the 29 remaining carcasses (location data were not available for four animals), the distances to the nearest shipping channel ranged from 0-86 miles with an average distance of 23.1 miles (SD = 24.0 miles). This difference was not quite significant at a level of $p = 0.081$ (Mann-Whitney rank sum test). Three of the 13 non-neonatal, unknown cause mortalities were found within nine miles of shipping lanes and an additional five unknown cause mortalities were found between nine and 26 miles (maximum distance where ship struck carcasses were found) suggesting that some proportion of these unknown cause mortalities could be attributable to ship strikes. The locations of these 41 carcasses in relation to shipping lanes and the coastline are displayed in Figs 4-6.

There were three additional deaths that were initially reported as right whales but were not reliably confirmed as to species, and therefore were not included among the confirmed right whale deaths: (1) 15 February 1983 - a carcass pulled up by a fishing vessel was inconclusively identified as a right whale (Kenney and Kraus, 1993); (2) 6 July 1991 - a calf with two other larger whales was struck by the US Coast Guard cutter Chase approximately 73 miles east of the Delaware Bay shipping lanes. Although Coast Guard personnel identified the animal as a right whale, the

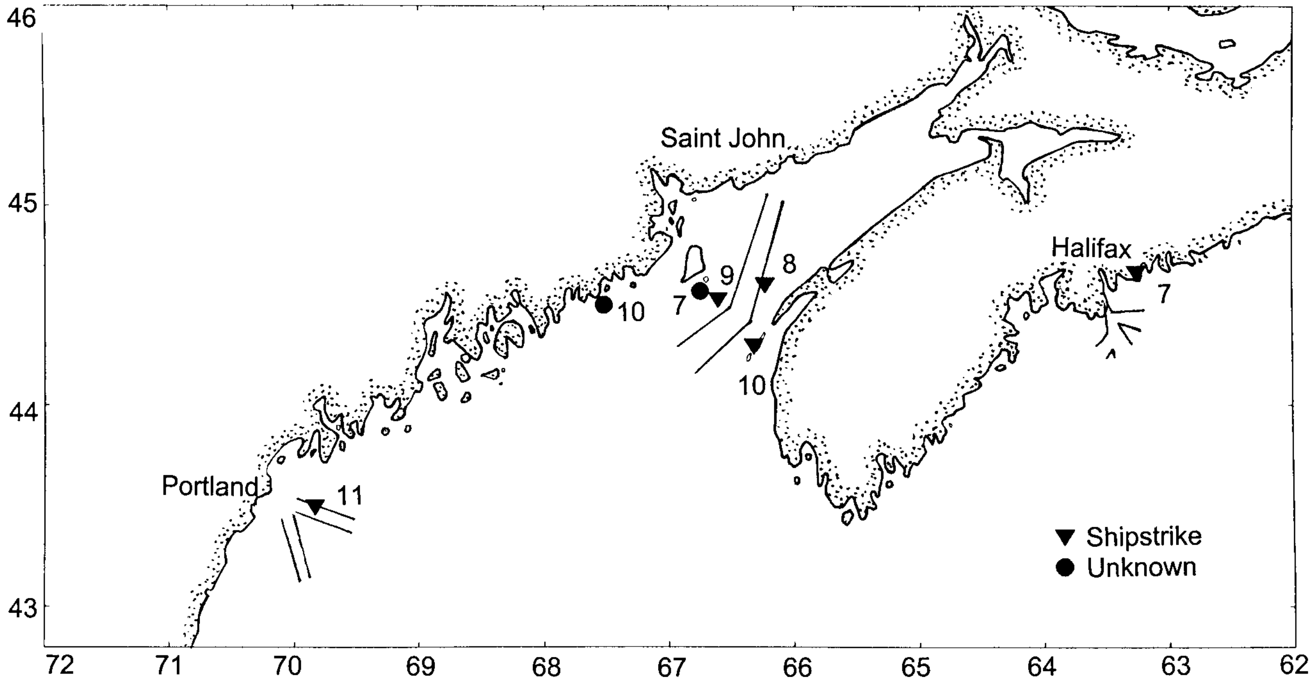

Fig. 4. Right whale fatalities and shipping lanes in the Gulf of Maine and Canada, 1970-99. Note: the number next to the symbol represents the month the carcass was detected.

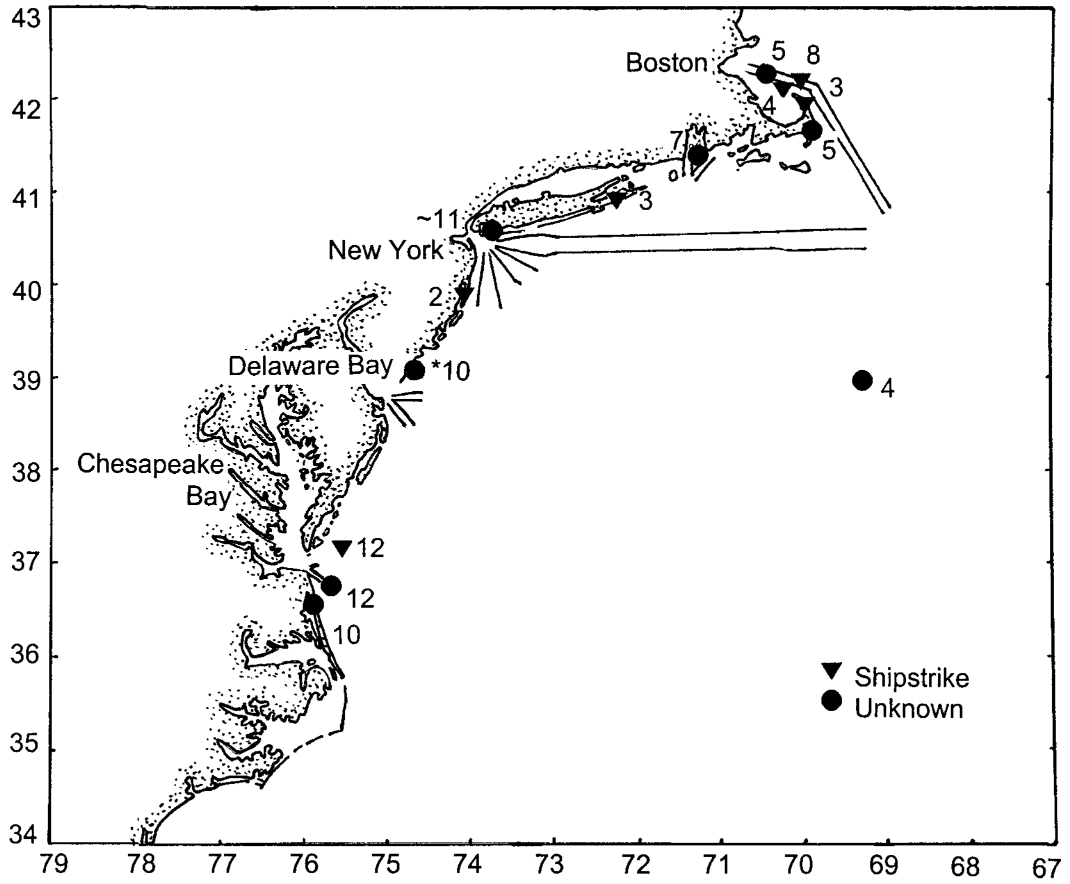

Fig. 5. Right whale fatalities and shipping lanes in southern New England and the mid-Atlantic coast, 1970-99. Note: the number next to the symbol represents the month the carcass was detected. An asterisk in front of the number indicates an entanglement mortality.

timing and location of the strike suggest it may have been a sperm whale. These two species are often confused by inexperienced observers; (3) 25 March 1996 - a possible right whale carcass was reported by a Navy submarine 80 miles east of the northeast Florida coast. The carcass was not relocated by aerial surveillance.

In addition, in the Kraus (1990) review of mortality, there was one event tallied as a definite right whale death that has been deleted from the above list of confirmed deaths because a carcass was not observed. This record involved a right whale observed in July 1984 entangled in a cod trap. The observer, a qualified whale biologist, was certain the whale

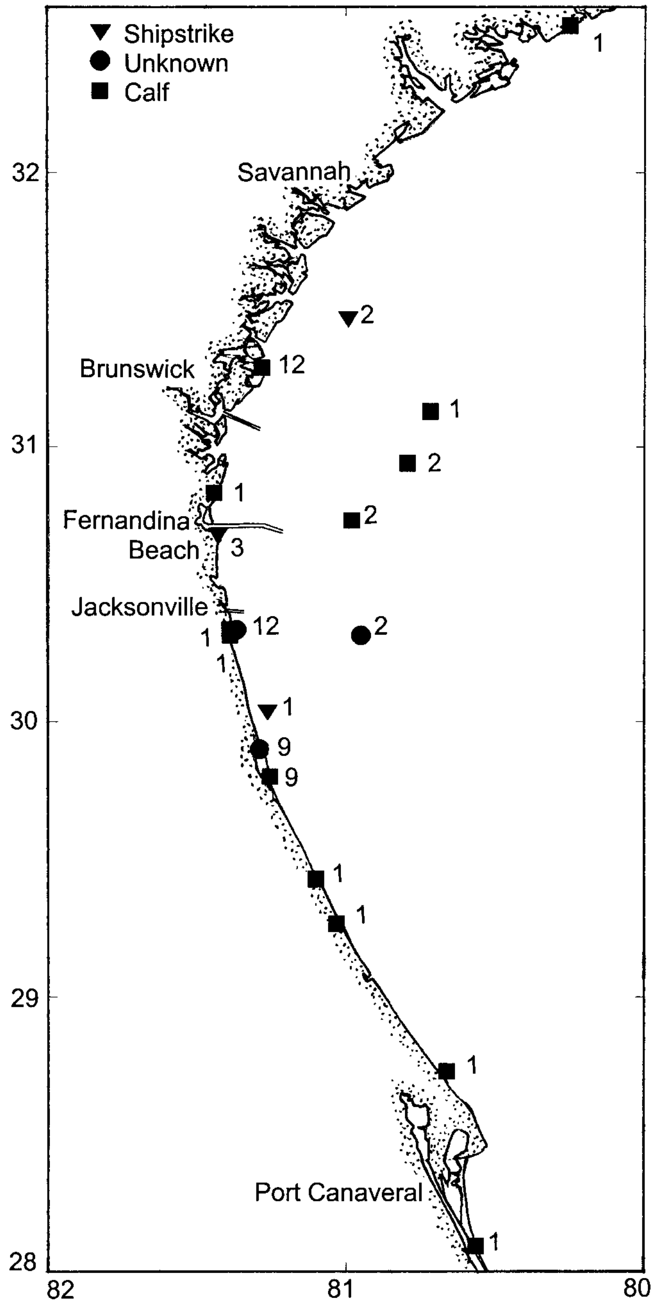

Fig. 6. Right whale fatalities and shipping lanes in the southeast US, 1970-99. Note: the number next to the symbol represents the month the carcass was detected.

would not survive the entanglement (Jon Lien, pers. comm.), but since a carcass was never detected, this event has been moved to the serious injury/presumed dead category as described below.

Table 2

The age and sex of right whales identified with serious injuries: 1970-99.

	Calf/juvenile	Adult	Unknown age	Total
Female	13	6	2	21
Male	9	3	7	19
Unknown sex	7	0	9	16
Total	30	9	18	56

Serious injuries and human-related mortalities

Fifty-six right whales fitting the serious injury criteria described above have been documented since 1970 (Table 2). Thirty-one (55.4%) were the result of entanglements in fishing gear and 25 (44.6%) were caused by ship strikes. Four animals bore serious injuries from both ship strike and entanglement but were counted in the category considered the more serious interaction; one animal suffered three separate serious entanglement events with two disentanglements. Nineteen of the 56 injuries (33.9%) have resulted in documented fatalities (16 ship strikes, 3 entanglements as described in the Mortalities section above). Ten other injuries (17.9%) were considered possibly fatal interactions, including seven animals presumed dead (i.e. not resighted for six or more years since being injured) and three others which were seen seriously injured since 1994 and, unless they are resighted, will become presumed dead in the years ahead. The remaining 27 animals (48.2%) suffered injuries that were determined to be non-fatal. Three additional animals not included in the above tally had serious injuries that were not attributable to human interactions. One animal (#1217) was missing about 1m of the left fluke due to attack by killer whales as evidenced by tooth marks around the injury. This was a non-fatal injury. A second animal (#1025, a reproductively active female) is presumed dead since she was last seen in 1983 with drooping flukes, the cause of which is unknown. A third animal (#1505, an adult male) was seen in April 1999 in very poor condition evidenced by emaciation, skin lesions and orange cyamids on the body. A longitudinal cut at least one metre long was observed near the tail stock but it was impossible to tell from the photos the depth of the cut or what caused it, thus the cause of this animal's condition is unkown.

The breakdown by age and sex of these 56 animals is provided in Table 2. There was no significant difference in injury levels by sex (19 male *versus* 21 female) when compared to the 1999 population sex ratio of 52% male to 48% female using a chi-square test ($0.9 > \chi^2_{0.061}$, > 0.5, d.f. = 1). However, the number of calves and juveniles recorded with serious injuries was more than three times higher than known adults (30 *versus* 9), which is significantly greater than the proportion of juveniles and calves in the population in 1999 (19%; $\chi^2_{58.560}$, $p < 0.001$, d.f. = 1). Eighteen animals of unknown age had injuries but some proportion of these animals likely acquired the injury as juveniles so the ratio of injured calves and juveniles to injured adults may well be greater than 3.3:1.

The level of impacts from each of the serious injury criteria is given in Fig. 7. A detailed description of each animal's serious injury is given in Table 3.

[Text continues on p. 205]

Table 3

Documented right whales with serious injuries due to interactions with human activities from 1970-99. Cells highlighted in **bold** are those where the date of the injury was known to have occurred within the same year (the animal was seen before and after the interaction in the same calendar year, or the incident was a mortality), the age of the animal when it acquired the injury is known and/or the area where it was injured is known. Under the column 'Date most recently observed': '-' indicates the animal not seen since injury observation; 'N/A' that the animal died and was not available to be seen or the identification of the animal was not known. 'Presumed dead' means the animal has not been sighted in six years or the interaction was considered definitely fatal. Photographs analysed up to October 2000 were used to assess status.

Date observed injured or dead (previous date seen uninjured)	Interaction type(s)	Serious injury category	Catalogue No.	Sex	Age at observation (age range when injury acquired)	Region observed with injury	Date most recently observed	Description
30 Jan. 1972	Ship strike	Fatal	Unid72	U	**Calf**	**Texas**	N/A	Body severed ~1m forward of tail stock. Only documentation is a photograph published in a local newspaper (Brazosport Facts) in Freeport, TX.
15 Apr. 1976	Ship strike	Fatal	Unid76	M	**Calf**	**Massachusetts**	N/A	Large area of bruising observed behind skull. Scientist noted as probable ship collision.
5 Nov. 1976	Ship strike	Fatal	Unid76	U	**Unknown**	**Maine**	N/A	Cuts and slashes observed on back.
5 Mar. 1979	Ship strike	Fatal	Unid79	M	**Juvenile**	**New York**	N/A	~2-3m of tail and body severed.
28 May 1980	Ship strike	Non-fatal	1401	M	Unknown	Great South Channel	5 Sep. 1989	~1.5m long, 15cm deep cut along back, crossing spine. Presumed dead in 1996 but before that, status: good.
13 Aug. 1980	Ship strike	Non-fatal	1019	M	Unknown	Bay of Fundy	29 Feb. 2000	Series of 8 propeller cuts running along left flank and over back. Maximum ~70cm long, 8cm deep, 11cm apart. Status: good.
27 Aug. 1981	Entanglement	Non-fatal	1152	M	Unknown	Bay of Fundy	6 Sep. 2000	Green netting tightly wrapped around tail. Unknown when acquired. Gone in 1990. No disentanglement action taken. Slightly disfigured tailstock resulted from embedded line. Status: good.
21 Feb. 1983 (18 Sep. 1981)	Ship strike	Fatal	1128	M	**2 years**	**New Jersey**	N/A	~2m of tail and body severed.
15 May 1983 (1 May 1983)	Entanglement	Non-fatal	1306	M	Unknown	Massachusetts Bay	27 Sep. 2000	Several wraps of lobster line and buoys around body. No disentanglement action taken. Line gone by next sighting on 15 September 1983. Status: good.
5 Aug. 1984	Ship strike	Non-fatal	1432	U	Unknown	Browns Bank	29 May 1988	Series of 5 propeller cuts, ~45cm long, 10cm deep, 20cm apart on left flank and near spine. Presumed dead in 1995 but before that, status: good.
26 Aug. 1984	Entanglement	Possibly fatal - presumed dead	Unid84	M?	**Unknown**	**Newfoundland**	N/A	Wrapped in a cod trap. Disentanglement efforts unsuccessful. After two days of attempts, the whale towed entire trap plus 12 grapnels out to sea leaving a 1m deep furrow in the sea bed. The observer felt certain the whale could not survive the entanglement. Status: uncertain.
6 Sep. 1984 (30 Sep. 1983)	Entanglement	Non-fatal	1308	F	1 year (0-1 year)	Bay of Fundy	17 May 1999	Strip of monofilament gillnetting through mouth, along body. No disentanglement action taken. Line gone by next sighting on 7 October 1984. Status: good.
2 May 1985 (9 Mar. 1985)	Entanglement	Non-fatal	1406	F	**1 year**	Coastal Maine	23 Aug. 2000	Lobster line around tail with buoys and traps attached. Disentangled. Status: good.
15 May 1986 (13 Oct. 1984)	Entanglement	Non-fatal	1411	M	2 years (0-2 years)	Great South Channel	7 Apr. 2000	Line of unknown origin tightly wrapped and embedded around tailstock. Line gone by 22 September 1990. Some disfigurement of tailstock. Skin lesions, greying of skin, orange cyamids around tail stock but condition improving with time. Status: fair to good.
7 Aug. 1986 (9 Sep. 1985)	Ship strike	Fatal	1504	F	**1 year**	**Massachusetts Bay**	N/A	2 propeller cuts, max ~4.5m long, 1m deep, 50cm apart running longitudinally along body. Severed spine.
14 Aug. 1986 (May 1984)	Ship strike	Possibly fatal - presumed dead	1006	F	7 years (5-7 years)	Bay of Fundy	3 Oct. 1986	1m diameter necrotic wound ~50cm behind blowholes. Last seen 3 October 1986 in Cape Cod Bay. Slow swimming, orange cyamids and evidence of infection at wound. Status: poor.
29 Aug. 1986 (19 Jun. 1986)	Entanglement	Non-fatal	1163	F	**5 years**	Massachusetts Bay	12 Feb. 1992	Line through mouth. Line gone by 12 February 1991. Skin lesions evident at most recent sighting in 1992 but may be unrelated to previous entanglement. Presumed dead in 1998. Status: poor..
14 Feb. 1987	Ship strike	Non-fatal	1704	F	**Calf**	**Southeast USA**	14 Mar. 1999	Series of 5 propeller cuts ~30cm long, 8cm deep, 5cm apart on left fluke tip. Fluke tip eventually came off because of cuts. Status: good.
9 Jul. 1987	Ship strike	Fatal	Unid87	M	**Juvenile**	**Nova Scotia**	N/A	2-3 observed propeller cuts on left flank, 20-25cm deep, 40cm apart. Shallow gash and swelling observed on right flank. Animal buried without a necropsy. Photographs taken. Unable to identify to catalogue.
10 Jul. 1987 (1980)	Entanglement (probable)	Non-fatal	1004	F	Adult	Massachusetts Bay	4 Jun. 2000	~1m of right fluke tip missing. Entanglement scars detected - line may have cut fluke tip off but not certain. Fully healed. Status: good.

cont.

Table 3 continued.

Date observed injured or dead (previous date seen uninjured)	Interaction type(s)	Serious injury category	Catalogue No.	Sex	Age at observation (age range when injury acquired)	Region observed with injury	Date most recently observed	Description
28 Aug. 1987	Ship strike	Non-fatal	1716	U	Unknown	Browns Bank	23 Sep. 2000	~1m of right fluke tip missing. Severed by propeller. Status: good.
25 Sep. 1987 (5 Sep. 1986)	Entanglement	Non-fatal	1113	M	Unknown	Browns Bank	27 May 2000	Yellow polypro line through mouth - loose. Gone in 1991. Unknown when acquired. No disentanglement action taken. Status: good.
9-14 Nov. 1988	Entanglement	Fatal	Unid88	U	**Unknown**	**Bay of Fundy**	N/A	Lobster fishermen hauled a full whale carcass to water's surface before detecting what it was. Released the whale and gear back into the water and reported to local whale naturalist on Grand Manan Island. Retrieved gear two weeks later (1 December 1988). All that remained of whale was skull, lungs, stomach and several 2m long baleen plates. Copepods in stomach.
11 Feb. 1991	Ship strike	Non-fatal	2143	F	**Calf**	**Southeast USA**	31 Aug. 2000	Series of 3 propeller cuts, max. 1.2m long, 15cm deep, 40cm apart on left flank. Cuts healed. Status: good.
12 Mar. 1991 (21 Feb. 1991)	Ship strike, entanglement	Fatal	1907	F	**2 years**	**Florida**	N/A	Seen in Bay of Fundy in August 1990 with line tightly wrapped around tailstock with buoys and gillnetting attached. Seen in Florida on 21 February 1991 with severe lesions on head and infection behind blowholes. Swimming slowly, greying of skin. Stranded on 12 March 1991 in Florida. Flensed carcass revealed a shattered skull from ship collision.
11 Jan. 1992	Entanglement	Possibly fatal - presumed dead	Unid92	U	Juvenile	Southeast USA	-	~1m long, 10cm deep gash on dorsal fluke, entanglement scars on tail, orange cyamids on tail, back and along lip edge, greying of skin, infection behind blowholes, emaciated. Status: poor..
5 Sep. 1992 (23 Aug. 1992)	Ship strike	Fatal	1223	F	**Adult**	**Bay of Fundy**	N/A	Death witnessed - rigorous thrashing of tail then rolled onto her right side dead. Her calf was in vicinity and eventually swam away. No external sign of injury. Necropsy revealed extensive internal haemorrhaging caused by impact from ship. Carcass flensed, no broken bones.
5 Jan. 1993	Ship strike	Fatal	Unid93	M	**Calf**	**Florida**	N/A	Two series of propeller cuts from a twin engine, 82ft Coast Guard cutter. 18 cuts running from the dorsal peduncle to behind the cranium. Propeller cuts range from 10-65cm long, 10-35cm deep, 14-26cm apart. 10 cuts starting along lower left flank and running down to the ventral throat and head. Propeller cuts range from 30-104cm long, 1.1-40.5cm deep, 14-50cm apart. Animal hit from behind. Not seen by vessel operators before impact. Vessel struck whale at a speed of 15 knots. Still alive at least one hour after impact when vessel lost sight of whale. Mother remained nearby. Relocated dead on 8 January, full necropsy 9 January.
9 Jul. 1993 (26 Sep. 1992)	Entanglement	Possibly fatal - presumed dead	2233	F	**1 year**	**Gulf of Maine**	22 Aug. 1993	Found entangled in swordfish drift gillnet gear near Munson Canyon, off the southern edge of Georges Bank on the morning of 9 July. Gear had probably been set the night before. Fishermen and NMFS observer disentangled whale from net after 4 hours. Some cuts and blood noted. The animal had some existing rope with buoys already wrapped around tailstock which was not removed. Photos also showed orange cyamids along lip edge. On 7 August whale seen on Stellwagen Bank. CCS responded and removed lobster gear from tailstock. There were 2 severe cuts from the gear into leading edge of tail extending ~30cm in towards tailstock. On 22 August this animal was seen off Montauk, Long Island in shallow water. Animal appeared in poor health with orange cyamids on body, emaciated appearance. Animal has not been resighted since. Status: poor..
6 Dec. 1993	Ship strike	Fatal	Unid93	F	**Unknown**	**Virginia**	N/A	Large straight gash running from right ventral side to right side lateral surface just anterior to flukes reported by NMFS observer. Found floating belly up, back side not observed. Not retrieved. Another dead floating right whale found on same day 28 miles to the south of this carcass with cause of death undetermined as carcass also not retrieved.
7 Jan. 1994 (3 Feb. 1993)	Entanglement	Non-fatal	1621	U	Unknown	Georgia	3 Sep. 2000	Cut ~2.4m long, max. 30cm deep running from lip edge on right side below rostrum across back. Entanglement scars around tail. Line gone. Fully healed in 1997. Status: good.
22 Feb. 1994 (27 Jan. 1994)	Entanglement, ship strike	Possibly fatal - presumed dead	2404	U	**Calf**	**Florida**	-	Several deep cuts on head and lower lip regions from line or cable. Probable propeller cuts on both sides of dorsal flukes. Injury may have occurred when a fishing vessel hauled whale in gear and it got cut by propeller before being released. Calf was supported by mother. Flukes not functional because of cuts. Status: poor.

cont.

Table 3 continued.

Date observed injured or dead (previous date seen uninjured)	Interaction type(s)	Serious injury category	Catalogue No.	Sex	Age at observation (age range when injury acquired)	Region observed with injury	Date most recently observed	Description
9 Sep. 1994 (uncertain)	Entanglement	Non-fatal	2320	F	Unknown	Bay of Fundy	5 Oct. 2000	Small piece of yellow line with gillnetting attached seen coming out of right side at corner of mouth. Very difficult to see unless animal rolls onto side so uncertain when entanglement occurred. Status: good.
21 Sep. 1994 (25 Sep. 1992)	Entanglement	Possibly fatal – presumed dead	1247	M	12 years (10-12 years)	Bay of Fundy	17 Aug. 1995	Tail stock tightly wrapped and embedded with several wraps of polypro line. Undetermined amount of line trailing behind. Orange cyamids on tail stock and lip edge, skin lesions. Status: poor.
17 Nov. 1994 (9 Aug. 1994)	Entanglement	Possibly fatal – presumed dead	2151	U	**3 years**	Jeffreys Ledge	-	Line tightly wrapped around forward end of rostrum with undetermined amount trailing behind. Embedded into gum. Orange cyamids on gum above baleen, skin lesions. Disentanglement attempted, unsuccessful. Status: poor.
17 Jul. 1995 (see description)	Entanglement	Fatal	2366	M	**2 years** (0 years)	Rhode Island	N/A	8 wraps of lines from lobster gear embedded 8cm into bone at base of right flipper. First seen entangled 21 December 1993. Previously seen not entangled 22 August 1993. Disentanglement not attempted as thought not to be life threatening at that time.
13 Aug. 1995 (22 Mar. 1992)	Ship strike	Possibly fatal - fate uncertain	1045	F	Adult (Adult)	Gulf of Maine	-	Cut ~60-90cm deep on right side of head below rostrum and cutting into the lower lip and extending down for undetermined length. Orange cyamids on tail and along lip edge, graying of skin. Status: poor.
16 Sep. 1995 (8 Sep. 1995)	Entanglement, ship strike	Non-fatal	2110	M	**4 years**	**Bay of Fundy**	8 Jul. 2000	Gillnet bottom to surface line through mouth and ~150m of line with buoys and hiflyer attached and trailing. Partial disentanglement, ~120m of line removed. Whale picked up gear only hours prior to observation. Remaining line gone in 1997. 8 propeller cuts along left tail stock and left fluke. Max. ~50m long, 8cm deep, 20cm apart. Acquired cuts between 0-1 years old. Status: good.
19 Oct. 1995 (8 Oct. 1995)	Ship strike	Fatal	2250	M	**Unknown**	**Bay of Fundy**	N/A	4.8m long gash in back, broken vertebral discs. Full necropsy impossible as whale found on inaccessible beach.
6 Jan. 1996 (3 Oct. 1995)	Entanglement	Non-fatal	1707	F	9 years (8-9 years)	Florida	22 Jun. 1998	Line of unknown origin wrapped around mid-body. Disentanglement effort. Satellite tag in buoy attached, no line could be removed. Line gone by sighting 6 August 1996. Status: good.
30 Jan. 1996	Ship strike	Fatal	1623	M	**Adult**	**Georgia**	N/A	No external sign of impact. Broken skull, vertebrae and ribs found when carcass flensed. Blunt impact from ship.
9 Mar. 1996 (3 Oct. 1995)	Ship strike, entanglement	Fatal	2220	M	**Unknown**	**Massachusetts**	N/A	3.3m long gash in back, broken skull. Lobster line including a trap caught through mouth and around tail. Entanglement occurred in December 1995, Bay of Fundy. Carcass severely decomposed.
12 Apr. 1997 (24 Feb. 1997)	Entanglement	Non-fatal	1505	M	**12 years**	**Massachusetts Bay**	21 Apr. 1999	Line of unknown origin through mouth with ~9m trailing along right side of body. Line gone by next sighting 18 August 1997. Severely emaciated at most recent sighting, but may not be related to entanglement. Status: poor..
Mid Jul. 1997 (27 Sep. 1996)	Entanglement	Non-fatal	1705	F	10 years (9-10 years)	Bay of Fundy	23 Sep. 2000	Small amount of line with several small, oval black buoys attached coming out of right side of mouth. Line gone in 1999. Status: good.
24 Jun. 1997 (20 Aug. 1996)	Entanglement	Non-fatal	1971	M	**8 years**	Great South Channel (see description)	23 Sep. 2000	Severely entangled through mouth and around body in lobster gear. Gear picked up between 18-24 June in an area (Stout Wright Swell) ~104 miles northeast of Chatham, MA. Disentangled. Status: good.
12 Sep. 1997 (26 Aug. 1997)	Entanglement	Non-fatal	2027	M	**7 years**	**Bay of Fundy**	25 Aug. 2000	~600 feet of line through mouth and trailing. Partial disentanglement, ~400 feet of line removed. Satellite and radio tags in buoys attached to remaining line. Tracked for ~1 week - animal left the Bay. All line gone by next sighting in February 1998. Status: good.
23 Aug. 1997 (16 Aug. 1996)	Entanglement, 3 times (see description)	Possibly fatal - fate uncertain	2212	M	5 years (4-5 years)	Bay of Fundy, Cape Cod Bay	14 Sep. 1998	Several wraps of line around tail with undetermined amount of line trailing. Disentangled on 24 July 1998. Re-entangled through mouth in lobster gear and disentangled on 12 September 1998. Re-entangled through mouth in lobster gear and disentangled 14 September 1998. Line remaining in gullet. Skin lesions on head, orange cyamids on tail and blowholes. Status: poor.
19 Aug. 1997	Ship strike	Fatal	2450	F	**Unknown**	**Bay of Fundy**	N/A	Carcass found floating left side down. No external sign of injury. Necropsy revealed 6m long haematoma along left side and broken right mandible.
29 Aug. 1997 (8 Feb. 1996)	Entanglement	Possibly fatal - fate uncertain	2557	F	2 years (1- 2 years)	Bay of Fundy	19 Sep. 1997	Line of unknown origin criss-crossed across body and around at least left flipper. Flipper may be necrotic. Implantable radio tag put in blubber but animal unable to be relocated for disentanglement. Orange cyamids, emaciated. Status: poor.

cont.

Table 3 continued.

Date observed injured or dead (previous date seen uninjured)	Interaction type(s)	Serious injury category	Catalogue No.	Sex	Age at observation (age range when injury acquired)	Region observed with injury	Date most recently observed	Description
3 Jan. 1998 (9 Sep. 1997)	Ship strike	Non-fatal	2705	U	1 year (0-1 year)	Georgia	31 Aug. 2000	Entire left fluke lobe extending beyond dorsal notch severed by propeller. Wound has healed. Status: good.
20 Apr. 1999 (15 Apr. 1999)	Ship strike	Fatal	1014	F	**Adult**	Cape Cod Bay	N/A	Carcass found floating right side down. No external sign of injury. Necropsy revealed broken mandible and 5 vertebral processes. Some callous formation observed in mandible indicating strike had occurred 7-10 days prior to death. Extensive oedema indicated the animal died of infection associated with bone breaks.
12 May 1999	Entanglement	Non-fatal	Unid.99	U	Unknown	Great South Channel	N/A	Animal trailing over 100 feet of line with hi-flyer attached. Line appeared to be coming out of mouth but animal not identified. Entanglement was not thought to be dangerous although impossible to be sure. Status: uncertain.
19 May 1999 (3 Mar. 1999)	Entanglement	Non-fatal	1158	F	**Adult**	Great South Channel	27 Sep. 1999	Line with hi-flyer attached wrapped around right flipper. Partially disentangled on 27 Sep. Hi-flyer removed. Some unknown amount of line remaining on flipper. Status: good.
5 Jun. 1999 (6 Aug. 1998)	Entanglement	Non-fatal	2753	F	2 years (1-2 years)	Bay of Fundy	14 Sep. 2000	Line through mouth and around body. Hi-flyer attached. Disentangled with small amount of line remaining in mouth. All line gone in 2000. Status: good.
21 Jul. 1999 (25 Apr. 1999)	Entanglement	Non-fatal	2710	F	**2 years**	Bay of Fundy	9 Aug. 2000	Line through mouth, around right flipper and across head and back. Partially disentangled and satellite telemetry buoy attached. Buoy came free with ~ 90 feet of line attached. All line gone in 2000. Status: good.
20 Oct. 1999 (see description)	Entanglement	Fatal	2030	F	**Adult**	New Jersey	N/A	Seen on 10 May 1999 by aerial survey team with 3 tight wraps from gillnet over back. Previously seen not entangled on 11 Sep. 1997. Resighted by vessel crew in Bay of Fundy on 3 Sep. 1999. Forward wrap had cut approximately 8cm into blubber. Disentanglement attempts unsuccessful. Animal travelled from Bay of Fundy to coast of New Jersey where it was found dead on 20 Oct. 1999. The line had cut into the dorsal body cavity and was wrapped around both flippers and underside.

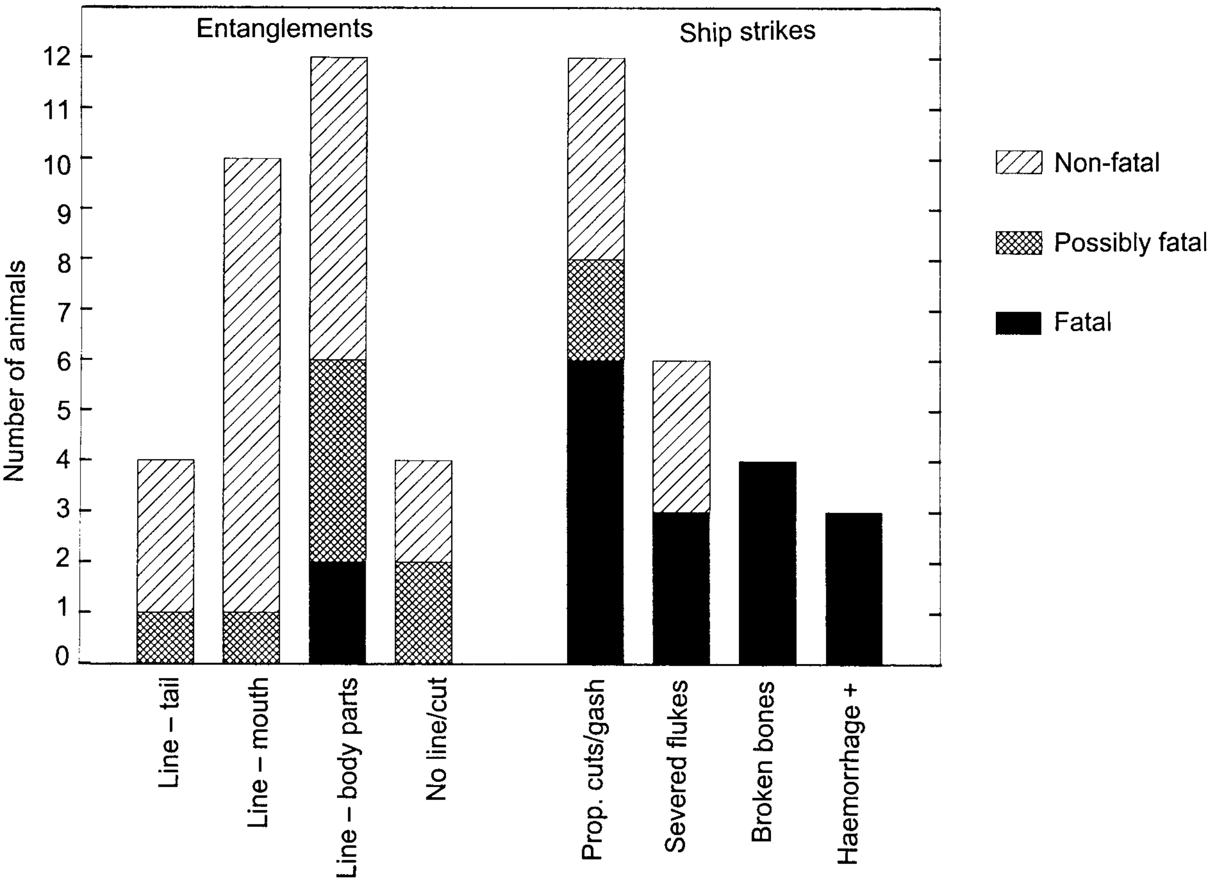

Fig. 7. Comparison of impacts of entanglements and ship strikes.

Ship strikes resulted in a high level of observed fatalities (28.6% of all serious injuries). *Propeller cuts* and *gashes* resulted in the most lethal injuries with six fatalities documented. Four fatalities occurred in the broken bones category, three fatalities in the severed flukes category and three fatalities were documented in the *haemorrhaging/haematoma* category. In the *severed fluke(s)* category, only those animals where the whole tail was severed were found dead. The animals that suffered non-fatal injuries from severed fluke(s) only had up to one side of the tail cut off. There were only two animals categorised as having possibly fatal injuries due to ship collision. With 18 documented or presumed mortalities among 25 recorded vessel-related serious injuries and only seven non-fatal ship strike injuries, it appears few whales successfully survive ship collisions.

Only three carcasses were found where the primary cause of death was attributed to entanglement (5.3% of all serious injuries). All had line around multiple body parts. One of these animals was found entangled and drowned in lobster gear (unid88). Another had line through the mouth and tightly wrapped around its flipper and embedded 8cm into the bone (#2366) – it is suspected that this animal died from infection. The third animal (#2030) had lines from a gillnet wrapped tightly around her body and both flippers. Despite extensive disentanglement efforts, the embedded line could not be cut and it eventually sawed into her body cavity resulting in death. In addition, eight of the 10 possibly fatal injuries were from entanglements. The *line around multiple body parts* sub-category accounted for four of the eight possibly fatal injuries. Although two of these animals were disentangled (#2233 and #2212), the injuries in #2233's case were so severe that this animal probably died. With respect to #2212, the animal looked in poor health during the latter disentanglement plus there was some line remaining in the gullet, so its fate remains uncertain. Considering that one of the right whales that died from entanglement drowned and never floated to the surface, entanglements may be responsible for an additional number of undocumented right whale deaths.

Nine of the 20 non-fatal entanglement injuries fell within the *line through the mouth* sub-category. Two of these 9 were partially or fully disentangled which may have reduced the severity of their situations. The high number of animals in this category suggests that catching line in the mouth is the most frequent type of serious injury, and if the animal can break away from the attached gear and not become further entangled, the impact may not be severe. Six of the 20 non-fatal entanglements were in the *multiple body parts* category. Full or partial disentanglement was carried out for four of the six which definitively reduced the severity of the impact.

If the possibly fatal injuries (10) are all assumed to be fatal and are added to the total of confirmed deaths (45+10 = 55), then entanglements (11) represent 20.0% of the right whale mortality between 1970 and 1999, ship strikes (18) account for 32.7%, and unknown causes (26) represent 47.3%. When neonate mortalities (13 or 23.6%) are excluded from the total, the resulting percentages are: entanglements 26.2%; ship strike 42.9%; and unknown cause 30.9%. Thus, once neonate mortalities are removed, anthropogenic interactions are responsible for a minimum of 69.0% of the confirmed and possible mortalities (29/42). This is substantially higher than that reported by Kraus in 1990 (53%).

A graph showing all potentially serious injuries and confirmed deaths by year (Fig. 8) indicates an increasing trend, especially evident in the mid 1990s. A regression analysis using natural log transformation of the dependent

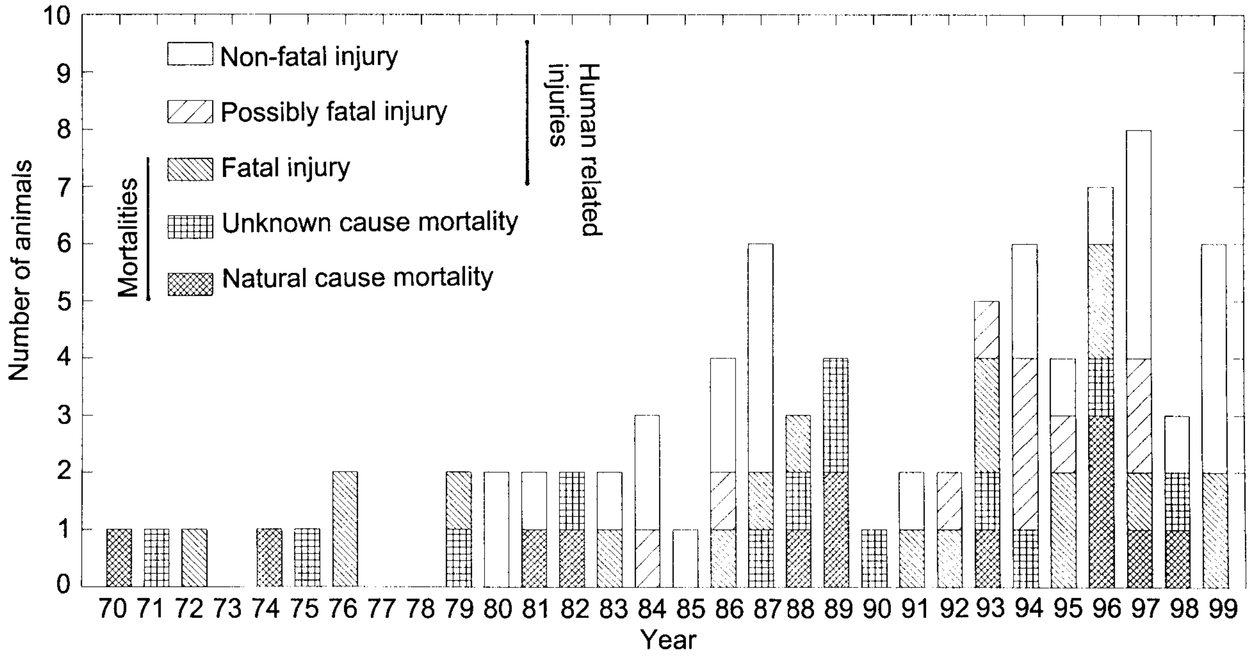

Fig. 8. All potentially serious injuries and mortalities.

variable for the data from 1980-1999 (data prior to 1980 were not collected systematically) reveals a significant increase over time ($p = 0.009$) with an annual rate of increase of 5.83% (95% CI = 1.85% to 9.81%).

DISCUSSION

Western North Atlantic right whales face significant impacts from interactions with ships and fishing gear that are impeding the populations' ability to recover from nearly a millennium of whaling pressure (Caswell *et al.*, 1999; IWC, 2001a). Previous analyses of the extent of these interactions have focused on confirmed deaths and the frequency of scars from interactions with human activities (Kraus, 1990). In the 1990s, a series of developments indicated that anthropogenic interactions resulting in serious injury to members of this population were a greater cause for concern than previously thought. Firstly, the observed number of severe entanglements which could potentially prove fatal to individual right whales increased. Of the 11 fatal or possibly fatal entanglements recorded, all but one were documented in the 1990s. Secondly, the number of documented ship strike deaths increased with nine out of the 16 occurring since 1990 (although some of this increase is probably due to increased attention to the reporting, retrieval and necropsy of right whale carcasses, which may simply mean that deaths attributable to ship collisions were underestimated in the past). Thirdly, an 'unusual mortality event' occurred during the winter of 1995/96 when eight right whales died over a nine month period: five along the southeast US coast, one near Rhode Island, one in Canadian waters and one near Cape Cod. Three of those animals died from ship collisions. Finally, the 1994 amendments to the US Marine Mammal Protection Act were passed which required that serious injury and mortality among endangered marine mammal species from entanglements in fishing gear would have to be reduced to levels approaching zero within five years of implementation of a Take Reduction Plan (TRP). An Interim Final Rule outlining the plan was put in place in July 1997, and a Final Rule was issued in February 1999.

There are a number of reasons to suggest mortality data alone provide an incomplete picture of anthropogenic interactions. The data show that ship strikes are often immediately fatal. If the animal in the collision is healthy with a thick blubber layer it will float and have a relatively high probability of being detected and reported. On the other hand, a whale that is entangled is less likely to die immediately unless it drowns, in which case it may be held underwater by attached gear and be less likely to be detected and reported. Moreover, if it survives for some time, an entangled whale that carries the gear could become emaciated because of impaired feeding or the extra energy expenditure imposed by carrying heavy fishing gear. If this animal dies, either the emaciation or the weight of the gear could cause the carcass to sink and not be detected. Therefore, mortalities resulting from entanglement may be considerably underestimated if only the documented mortality database is assessed.

The average annual rate of increase in serious injuries and mortalities (5.83%) exceeds the calculated population growth rates. Although the range falls within the average annual rate of increase for the population calculated as 2.5% by Knowlton *et al.* (1994) and 4.4% by Caswell *et al.*(1999) for the years 1986-1992, Caswell *et al.*'s (1999) results indicate that the population is presently decreasing at a rate of 2.4% per year. Thus, this increasing rate of serious injury and mortality does not appear to be correlated to population size. In addition, an analysis of the average mortality rate for the years 1993-1999 (as defined in Knowlton *et al.*, 1994) shows an average mortality rate of 3.37 %, up from the rate of 2.1% for 1986-1992. This rate is higher than the 1-2% mortality rates detected in healthy populations and is definitely cause for concern.

The long-term impacts of non-fatal injuries are difficult to assess. For example, animal #2143 suffered deep propeller cuts on the left flank but has been resighted numerous times since the injury and still appears healthy. This female was born in 1991 and should be approaching reproductive age, but it is not clear whether she will be able to reproduce as a result of her extensive injuries. Another female #1163, was entangled through her mouth in 1986 but had lost the gear by

1991. Although she seemed healthy while carrying and shortly after losing the line, she developed extensive skin lesions a year later and is now presumed dead; it is unclear whether these lesions were related to the entanglement.

The number of mortalities that go undetected could still be quite high even with increased awareness and reporting. Considering information on the number of right whale births, estimated population size and growth rates, and mortality, the Marine Mammal Commission (1995 Annual Report) suggested about two-thirds of all right whale mortality in the western North Atlantic goes unreported. Another means of estimating this proportion is through the analysis of presumed mortalities as indicated by the number of animals in the right whale photo catalogue that have not been seen for six years and which are presumed dead in the sixth year after the last sighting (Knowlton *et al.*, 1994). Between 1986 and 1999, 84 animals were presumed dead from the absence of resighting records in the photo catalogue as compared to 32 confirmed deaths for a ratio of 2.6:1. Although the number of presumed dead whales is likely to be inflated owing to the vagaries of survey effort and the fact that some confirmed deaths could not be examined to determine if they were among the presumed dead animals, it seems reasonable to believe that at least as many unreported deaths occurred as reported carcasses during this 14-year period.

Caswell *et al.* (1999) note a declining survival probability in this population in the 1990s which could lead to extinction within 200 years if not reversed. They also note that the population growth rate and extinction probability are more sensitive to changes in survival probability than to changes in fertility. Thus, to improve the situation for right whales, definitive action needs to be taken to reduce the level and severity of anthropogenic injuries and deaths. Right whale deaths and serious injuries have occurred all along the eastern seaboard and are not limited to the five high-use areas where right whales are seen most frequently. Although this is an important fact to consider as protective measures are proposed, focusing conservation strategies on the high-use areas would likely have the most immediate impact and should be pursued at least initially. Creating awareness of right whale conservation issues through education is certainly an important first step, yet considering the precarious status of right whales, further proactive measures are clearly needed. Disentanglement is one such effort that has met with positive results (only two out of the nine right whales that were disentangled suffered possibly fatal serious injuries), although these efforts may be considered more reactive than proactive. The effectiveness of these efforts strongly depends on the willingness of fishermen and others to report entanglements, the efficiency of response provisions and the severity of the entanglement. Disentanglement activity is extremely dangerous for the people involved and should not be considered a long-term solution. Other measures such as seasonal fishery closures and gear modifications may provide better long-term protection and are currently being implemented and evaluated for further improvements.

The impacts of ship traffic may be more complicated to remedy because the problem is international in scope. For example, measures focused only on US mariners would do little to alleviate the problem. However, a recent proposal developed by the US government to create two mandatory ship reporting systems for all ship traffic entering two defined high-use right whale areas along the eastern seaboard was adopted unanimously by the United Nations' International Maritime Organisation and was implemented in July, 1999 (NOAA Press Release 12/8/98). This system will increase awareness amongst mariners and hopefully reduce the level of interaction between right whales and ships. In other high-use areas, ships' routing measures to minimise travel distance through key habitats or speed restrictions may also be considered. In the long run, continued monitoring of the population throughout the extent of its range will be essential for evaluating the effectiveness of any measures undertaken to protect this severely endangered species.

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Anomalous 1992 spring and summer right whale (*Eubalaena glacialis)* distributions in the Gulf of Maine

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ABSTRACT

No right whales (*Eubalaena glacialis*) were sighted during aerial surveys in May-July 1992 in the Great South Channel region of the southwestern Gulf of Maine. This was the first year that spring surveys failed to detect right whales in this region. During the late spring/early summer season when right whales would normally be expected in the Great South Channel, a few were sighted in the central Gulf of Maine, none were found in their usual late summer/early autumn feeding areas near Nova Scotia and a few were seen in Massachusetts Bay. The absence of right whales in the Great South Channel in 1992 can be attributed to a shift in the regional zooplankton community. The usual spring zooplankton of the region is strongly dominated by the calanoid copepod *Calanus finmarchicus*, vertically and horizontally aggregated into dense patches which are the preferred foraging areas of right whales. The 1992 zooplankton was dominated by pteropods, distributed evenly throughout the water column. It is possible, although unlikely, that pteropods are unacceptable prey for right whales. A more likely explanation is that their local densities within small-scale patches were below the energetic threshold required for successful right whale feeding. The shift in zooplankton dominance in 1992 is likely related to significantly reduced water temperatures and a delay in the development of the usual hydrographic structure of the region. The 1992 temperature and hydrographic anomalies, in turn, can be attributed principally to an unusually large influx of colder and fresher Scotian Shelf Water, and may have been enhanced by widespread cooling of the Northern Hemisphere caused by sulphuric acid haze in the atmosphere from the June 1991 eruption of Pinatubo volcano in the Philippines.

KEYWORDS: NORTHERN RIGHT WHALE; ATLANTIC OCEAN; DISTRIBUTION; CLIMATE CHANGE; ECOSYSTEM; OCEANOGRAPHY; FEEDING GROUNDS; PREY; PATCHES

INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) is the most endangered large whale species in the world (Braham and Rice, 1984; IWC, 1986; NMFS, 1991), with a western North Atlantic population of around 300 animals (e.g. see IWC, 2001a). Right whales in the western North Atlantic have been studied intensively since the late 1970s, and a relatively clear picture of their patterns of distribution in space and time emerged by the early 1990s (Kraus, 1985; Winn *et al.*, 1986; Gaskin, 1987; 1991; Kraus *et al.*, 1988; Kraus and Kenney, 1991; IWC, 2001b). Four important right whale feeding habitats are found in the continental shelf waters off the northeastern United States and southeastern Canada (Fig. 1). Right whales first arrive in northeastern waters in late winter in the relative shallows of Cape Cod Bay, with peak occurrence there in April (Hamilton and Mayo, 1990). Cape Cod Bay is typically occupied each year by approximately 25-50 individuals (Hamilton and Mayo, 1990; Kraus and Kenney, 1991). Right whales are then found in late spring and early summer in the Great South Channel (GSC) region east of Cape Cod, which is the primary spring feeding habitat for the western North Atlantic population (CETAP, 1982; Winn *et al.*, 1986; Kraus and Kenney, 1991; Kenney *et al.*, 1995). Right whales are found during the rest of the summer and into the autumn in two habitats in Canadian waters (Gaskin, 1987; 1991; Kraus *et al.*, 1988; Murison and Gaskin, 1989). A smaller portion of the population, including nearly all of the mother/calf pairs, is found in the lower Bay of Fundy to the east of Grand Manan Island, an area known as the Grand Manan Basin. The majority of the adult population occurs in continental shelf waters off southern Nova Scotia, centred in the Roseway Basin just north of Browns Bank.

The University of Rhode Island (URI) collected a near-continuous time-series of springtime survey and sightings data for the GSC region from 1979 through 1991 (excluding 1990). These data suggest that at times the entire (or almost entire) population occupies the region (Kenney *et al.*, 1995). Right whales typically are found in the GSC area from April to June, with a peak in May (Winn *et al.*, 1986; Kraus and Kenney, 1991; Kenney *et al.*, 1995). Departure from the area (apparently differing between years) occurs between late May and early July (Kenney *et al.*, 1995). Right whale sightings in the GSC are primarily in the central portions of the region, mostly in waters deeper than 100m. They are found in aggregations which coincide with the dense patches of the zooplankton upon which they feed (CETAP, 1982; Scott *et al.*, 1985; Kenney *et al.*, 1986a; Wishner *et al.*, 1988; 1995; Macaulay *et al.*, 1995; Beardsley *et al.*, 1996). These aggregations occur north of a tidal-mixing front (roughly coincident with the 100m isobath) which divides deeper, stratified waters with warmer surface temperatures from shallow, totally-mixed waters with colder surface temperatures (CETAP, 1982; Scott *et al.*, 1985; Wishner *et al.*, 1988; 1995; Brown and Winn, 1989; Kenney *et al.*, 1995; Macaulay *et al.*, 1995). The stratified waters are north of the front and the tidally-mixed waters south of it (Wishner *et al.*, 1988; Brown and Winn, 1989; Chen *et al.*, 1995b).

The 1992 spring aerial surveys began in May. The results of the first surveys immediately suggested that the distribution of right whales in the GSC was atypical; none were sighted during two complete GSC surveys. The sampling design was then altered to expand the number and geographic range of the aerial surveys. The objectives of the expanded survey programme were to:

(1) conduct aerial surveys of the GSC area, and as much of the rest of the Gulf of Maine as possible – the goals were to survey the GSC to confirm/refute the apparent absence of right whales there, and to locate concentrations of right whales outside of the GSC, particularly in their normal late summer/autumn habitats in the Bay of Fundy and shelf waters south of Nova Scotia;

(2) explore the possible oceanographic mechanisms which might be responsible for atypical right whale distributions by using available information and, in particular, consultation with other researchers collecting physical and biological oceanographic data in the Gulf of Maine.

METHODS

Aerial surveys

The standard GSC aerial surveys conducted by URI followed a sampling design, protocol and survey block which remained constant since 1984 (Fig. 1), using methods standardised during the Cetacean and Turtle Assessment Program (CETAP, 1982; Scott and Gilbert, 1982). All surveys were flown in a twin-engine *Cessna* 337-G Skymaster, which was equipped with a Barnes PRT-5 infra-red radiometer to measure sea surface temperature (recorded by a computer data-logger with time and position at 15sec intervals). All right whale sightings were circled to obtain accurate counts, observe behaviour and take photographs for individual identification (see Kraus *et al.*, 1986 for details of photo-identification methods). Complete details of aerial survey methods can be found in Kenney *et al.* (1995).

Additional aerial surveys were conducted in 1992 in the Gulf of Maine and adjacent waters, with two different objectives:

(1) to search the normal late summer/autumn right whale habitats in Nova Scotian waters to see if right whales had arrived there much earlier than in previous years; and
(2) to search as much of the Gulf of Maine as feasible to locate right whale aggregations.

The survey lines were initially designed based on right whale sightings collected during the CETAP surveys, which covered the continental shelf waters from Cape Hatteras, North Carolina to Nova Scotia nearly completely. As the surveys progressed, 1992 right whale sightings made by our earlier surveys or contributed from other sources were factored into survey designs.

Other sightings data

Additional 1992 right whale sightings were obtained from the sources listed below:

(1) The National Marine Fisheries Service (NMFS) conducted several sampling programmes over the year, and right whales were sighted from three: (1) oceanographic and fisheries research cruises aboard NMFS ships; (2) a harbour porpoise (*Phocoena phocoena*) cruise aboard R/V *Abel J*; and (3) an aerial harbour porpoise survey.
(2) The Center for Coastal Studies (CCS) conducted research cruises aboard R/V *Halos* in Cape Cod Bay from February to April, and also collected data from observers aboard commercial whalewatching vessels from April to October.

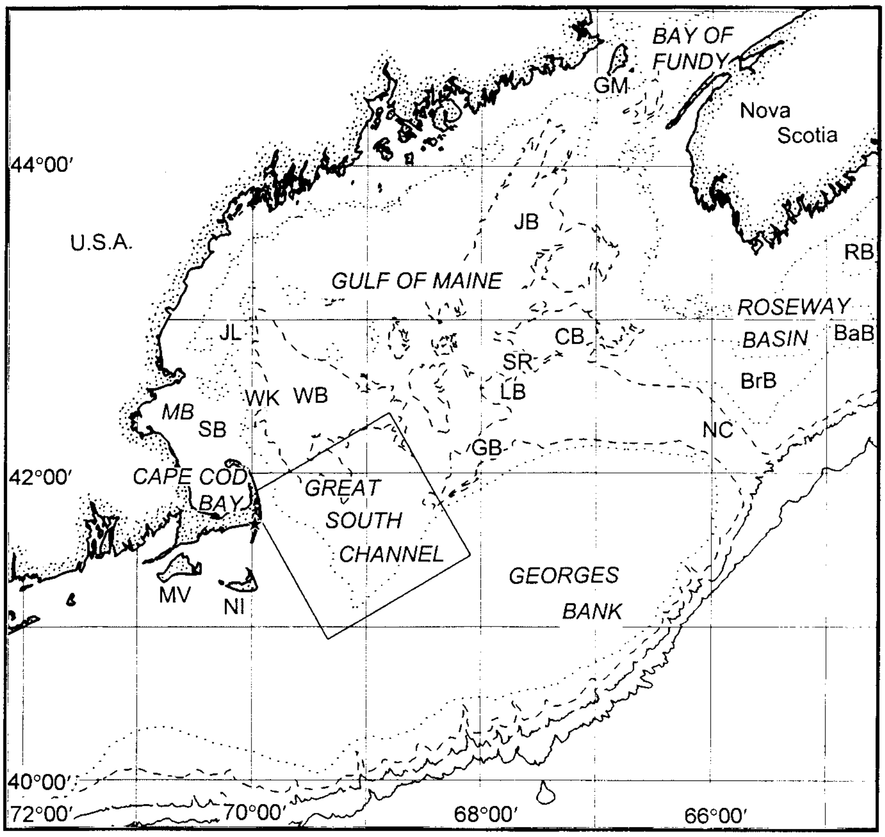

Fig. 1. The continental shelf region off the northeastern United States and southeastern Canada, showing the four important right whale feeding habitats and other areas referred to in the text. The block east of Cape Cod is the Great South Channel aerial survey block, and the star at the southeast corner of Cape Cod shows the location of the Chatham weather station. The isobaths shown are at 100, 200, 1,000 and 2,000m. Key to abbreviations: BaB = Baccaro Bank; BrB = Browns Bank; CB = Crowell Basin; GB = Georges Basin; GM = Grand Manan Island; JB = Jordan Basin; JL = Jeffreys Ledge; LB = Lindenkohl Basin; MB = Massachusetts Bay; MV = Martha's Vineyard; NC = Northeast Channel; NI = Nantucket Island; RB = Roseway Bank; SB = Stellwagen Bank; SR = Sewall Ridge; WB = Wilkinson Basin; WK = Wildcat Knoll. La Have Bank, Emerald Bank, and Sable Island Bank are located on the shelf south of Nova Scotia east of the area mapped here.

(3) The New England Aquarium (NEA) conducted vessel surveys aboard R/V *Nereid* in the lower Bay of Fundy from late July to early October.

(4) East Coast Ecosystems (ECE) conducted two days of vessel surveys in September in the Roseway Basin area in conjunction with NEA and Brier Island Ocean Studies (BIOS) aboard M/V *Cetacean Quest*, the BIOS whalewatching vessel.

(5) The Canadian Department of Fisheries and Oceans (DFO) collected sightings recorded by fisheries observers aboard commercial fishing vessels.

Data from all these sources were included into a common database which is maintained at URI as part of a cooperative research project involving all of the above organisations which has been underway since 1986. Another component of the cooperative effort is the maintenance of the photo-identification catalogue (Crone and Kraus, 1990) at NEA and the joint maintenance of the catalogue database by NEA and URI. The catalogue includes photographs submitted to NEA by a wide variety of sources, and any 1992 catalogue records from these other sources were also added to the sightings database.

Data analysis

All data were handled according to protocols designed for the cooperative research programme. All data processing and management have been accomplished on a series of IBM-compatible personal computer systems. Distributional analyses were performed by plotting the locations of sightings on a standard base map using CAMRIS (Computer Aided Mapping and Resource Inventory System: Ford, 1989) mapping software. All other data management, analysis, graphics and archival procedures have been accomplished using successive versions of Statistical Analysis System software (PC-SAS ver. 6.04; SAS for Windows ver. 6.11 & 6.12: SAS Institute, Inc., Cary, NC).

Zooplankton sampling

Zooplankton sampling was conducted in the GSC region during a submersible research cruise aboard R/V *Seward Johnson* on 4-8 June conducted by Howard Winn and Karen Wishner from URI. The study was planned as an investigation of zooplankton patches in the vicinity of right whale feeding aggregations. The 4 June aerial survey was scheduled to locate right whales at the beginning of the cruise, but found none in the GSC area, therefore the sites selected for sampling were based on previous years' whale sighting locations. Sampling was conducted by two methods: paired bongo and opening/closing nets (505 μm and 333 μm mesh) deployed from the support ship, and pump sampling (333 μm mesh filter) directly from the submersible. Samples were preserved and counted later using standard methods (see Wishner *et al.*, 1995). Summary data were provided by K. Wishner (pers. comm.).

RESULTS

1992 aerial surveys

The first survey was flown on 20 May, which was the first time in 13 years that a complete May survey in good weather conditions resulted in no right whale sightings. By the end of July, eight days of surveys had been completed, covering a wide area of the GSC, Gulf of Maine, Nova Scotian shelf and Bay of Fundy. In addition to the standard GSC survey area, the additional specific areas surveyed included, at least once, the perimeter of Georges Bank, the central and western Gulf of Maine, the western Nova Scotian shelf near Browns Bank and Roseway Basin, the Northeast Channel and the area east of Grand Manan Island in the lower Bay of Fundy (Table 1). Plots of the tracklines flown each day are included in Kenney (1994). Only 7-9 right whales were seen throughout all of the aerial surveys (Table 1), all in the central portion of the Gulf of Maine.

Table 1

Summary of 1992 aerial right whale surveys in the Gulf of Maine, showing the general area(s) surveyed and number of right whales sighted each day. (GSC = Great South Channel).

Date	Area surveyed	Right whales sighted
20 May	Standard GSC survey	0
29 May	Standard GSC survey, extended 37 km east; also Cape Cod Bay, Stellwagen Bank, Jeffreys Ledge and Wildcat Knoll in extreme western Gulf of Maine	0
4 Jun.	Central GSC; perimeter of Georges Bank (western 3/4)	1
17 Jun.	Central Gulf of Maine; with transits across GSC and along northwestern flank of Georges Bank	4-6
8 Jul.	Lower Bay of Fundy, western Roseway Basin	0
14 Jul.	Standard GSC survey	0
30 Jul.	Eastern Georges Bank, Northeast Channel, southern and western Browns Bank	0
31 Jul.	'Zig-zag' across Gulf of Maine from Nova Scotia to New England, between Georges Bank and about 44°N	2

Distribution of right whale sightings

Combining the data from the aerial surveys and all other sources, there were 678 right whale sightings totalling 904 animals in 1992 in the waters off New England and Nova Scotia which comprise the main feeding areas of this population (Fig. 2). Since the number of animals sighted exceeds the estimated size of the population, it is obvious that some individual whales were observed on multiple occasions, however since not all individuals at all sightings are identified, the exact percentage of resightings is not known. In addition, vessel surveys targeted at right whale photography identify a much higher proportion of the individuals encountered than aerial surveys or other vessel surveys. There were an additional 81 winter sightings in the calving grounds off the southeastern USA which will not be considered here, and one much further north. The late winter/early spring and late summer/autumn patterns were typical of most years, but the number and distribution of sightings during the late spring and early summer were unusual.

Late winter/early spring

Right whales were first observed in Cape Cod Bay on 4 February, and sightings were made until 13 April. There were 199 sightings of 268 whales, which were distributed entirely within the eastern half of Cape Cod Bay (Fig. 2). These sightings represented only 37 different identified right whales over the entire period, with 9 different individuals present in February, 21 in March and 24 in April.

Late spring/early summer

During the study period from late May to late July, very few right whales (only 7-9 on the aerial surveys) were seen anywhere in the Gulf of Maine, and those were almost all in two locations: the central Gulf of Maine and Massachusetts Bay (Fig. 2). The first sighting, of a single individual, was on 4 June on the northern edge of Georges Bank. On 17 June, a single adult was sighted northwest of the 4 June sighting location. Later in the 17 June flight, at least three (possibly five) more right whales were sighted about 50km further to the northwest. Three sightings were recorded: a single adult; a pair of adults with a possible third animal; and a sighting of a footprint and flukes only, which was identified as a 'possible' right whale. During the last survey on 31 July, a pair of right whales (#1056 and #1227) was seen and photographed in the deeper central basin north of Georges Bank and west of Browns Bank.

During the same period, three sightings, of a single right whale each, were reported by observers aboard NMFS research vessels. One was on 3 June, and the other two were on 11 July. All three sightings were in the same vicinity as our June and July sightings.

There were scattered right whale sightings in Massachusetts Bay in each month during late spring and early summer, totalling 11 sightings of 12 whales. Eight different whales were identified, with no individual seen on more than one day; two were sighted on 31 May, two were sighted on 22 June, a mother/calf pair was seen on 28 June and another mother/calf pair was sighted on 31 July. These sightings tended to be further north than the February-April sightings, outside Cape Cod Bay (Fig. 2).

DFO observers reported five sightings of six right whales between 20 April and 20 May on the outer Scotian Shelf in the vicinity of Emerald Bank and Sable Island Bank (beyond the eastern edge of the region mapped in Fig. 2). There was also one right whale sighted south of Iceland on 29 May.

Late summer/autumn

During the NEA surveys in the Bay of Fundy, right whales were first observed on 7 August, when 34 were sighted; the whales were still being seen in the Bay when the surveys ended in early October. There were 341 sightings of 475 animals, and 72 different individuals were identified (including four mother/calf pairs). The sightings were concentrated in the Grand Manan Basin between Grand Manan Island and Nova Scotia (Fig. 2).

The ECE surveys on the Scotian Shelf south of Nova Scotia on 9 and 10 September resulted in 23 sightings of 41 whales, with 17 individuals identified. The sightings were concentrated in the Roseway Basin north of Browns Bank (Fig. 2). There was also a sighting of 12 whales by a DFO observer on 21 October northeast of the September aggregation (Fig. 2). There was one additional DFO record of one right whale much further east near Emerald Bank on 3 August.

A total of 74 sightings was extracted from catalogue records in Massachusetts Bay and Cape Cod Bay during August-October, all to the north and west of the February-April concentration (Fig. 2). However, only eight identified individuals were seen. Two mother/calf pairs were sighted repeatedly, one from 10 August to 12 October and the other from 24 August to 10 October (the same pair seen

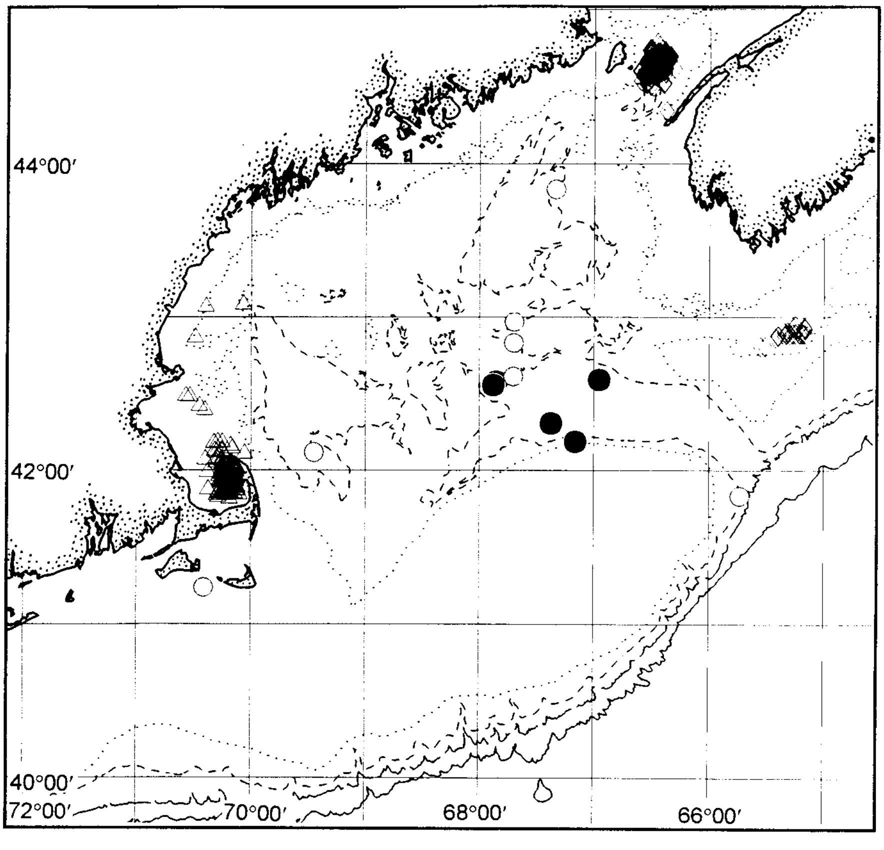

Fig. 2. All available sightings of right whales in 1992 ($n = 672$). The open triangles show the largely typical distribution of whales in the western Gulf of Maine from late winter through autumn ($n = 294$). The dense aggregation of sightings in Cape Cod Bay was in February-April, and the more scattered sightings on the periphery of the aggregation, to the north on Stellwagen Bank and further north on Jeffreys Ledge occurred from May to October. The open diamonds show the usual summer/autumn concentrations in the Bay of Fundy ($n = 341$; August-October) and just north of Browns Bank ($n = 24$; 9-10 September, with the sighting which is isolated from the others on 21 October). The circles show sightings outside the usual feeding habitats and seasons. The solid circles are sightings from the URI aerial surveys in June and July ($n = 6$). The open circles are sightings provided by other sources ($n = 7$): three near the URI sightings in June and July, one at the eastern end of Georges Bank in late July, one in the northern Gulf of Maine in late August, one east of Cape Cod in late October and one south of Cape Cod in early December. Five additional sightings in April-May and one in August occurred on the Nova Scotian shelf 150-200km east of the boundary of this map.

on 31 July). Two individuals were sighted from 13-18 August, and two others were seen only once on 20 or 23 October. The same two mother/calf pairs were also sighted on Jeffreys Ledge just north of Massachusetts Bay (Fig. 2), one on 8 August and 19 September, and the other on 21 August.

Three sightings were also reported by NMFS observers during the late summer and autumn (Fig. 2). One or more individuals was sighted in the north-central Gulf of Maine, on the edge of Jordan Basin, on 20 August. A single individual was sighted on 20 October on the edge of Wilkinson Basin just north of the GSC (the only sighting of the year within the GSC area). Finally, a single individual was seen on 10 December just south of the channel between Martha's Vineyard and Nantucket.

Biological and physical oceanographic parameters

Zooplankton

Zooplankton species patterns in the GSC in 1992 were also atypical (K.F. Wishner, pers. comm.). In previous spring seasons, the GSC zooplankton community has been strongly dominated by copepods, and the copepod assemblage in turn dominated by the calanoid species *Calanus finmarchicus*, frequently to the point that samples yielded nearly monospecific collections of *Calanus* (CETAP, 1982; Scott *et al.*, 1985; Kenney *et al.*, 1986a; Sherman *et al.*, 1987; Wishner *et al.*, 1988; 1995; Durbin *et al.*, 1995c). Large calanoid copepods, including *Calanus finmarchicus* and similar species, are the preferred prey of right whales (Matthews, 1938; Tomilin, 1957; Omura *et al.*, 1969; Watkins and Schevill, 1976; 1979; Scott *et al.*, 1985; Kenney *et al.*, 1986a; Gaskin, 1987; 1991; Wishner *et al.*, 1988; Murison and Gaskin, 1989; Mayo and Marx, 1990). In June 1992, copepods comprised only 53% of the total zooplankton abundance (on a numerical basis), and *Calanus* represented only 37% of the total copepod abundance (i.e. approximately 20% of the total zooplankton rather than the typical 90% or more). Other copepods, including *Metridia lucens*, *Pseudocalanus minutus* and cyclopoids, were nearly equal in abundance to *Calanus*. The dominant zooplankton species was the shelled pteropod *Limacina retroversa*. The average water column pteropod abundance in 1992 was 235,000/m^2, slightly lower than the average water column abundance of *Calanus* in 1989 - 255,000/m^2 (Wishner *et al.*, 1995).

Sea surface temperatures

The available sea surface temperature (SST) data (from the airborne radiometer) within the GSC survey block from all aerial surveys from 1985-1992 were extracted from the archived database. The data series is incomplete; no surveys were flown in 1990 and the aircraft used in 1986 was not equipped with a radiometer. There was a total of 33 surveys with SST data: four in 1985, six in 1987, nine in 1988, seven in 1989, three in 1991 and four in 1992 (Table 2). Mean SSTs for the four 1992 surveys were substantially colder than those for comparable dates in earlier years. SSTs in 1992 were also more variable than in earlier years; four of the six surveys with coefficients of variation in excess of 10% were in 1992 (Table 2).

To determine if SST patterns in 1992 were statistically different from those in earlier years, temperature data from surveys between 15 May and 15 June each year were compared. Mean values for all surveys pooled within years were calculated (Table 3). The mean SST in 1992 was 2.3°C lower than in 1985, the second coldest year, and over 6°C lower than the mean for 1989, the warmest year in the period analysed. All of the yearly mean SSTs differed significantly from all others (Duncan's multiple range test, $a = 0.05$). Non-parametric statistical comparisons of the 1992 SSTs with the data from each other year also showed that surface temperatures in 1992 were significantly lower than each of the others (Wilcoxon rank sum tests, $P < 0.001$ in all cases).

A second aspect of SST patterns in the GSC which has an apparent relationship to right whale distribution is the presence of a tidal mixing front (Chen *et al.*, 1995b). The front approximately coincides with the 100m isobath (see Fig. 1), although it oscillates to the north and south with the tidal cycle. This front is normally persistent through most of the spring and early summer. It is often visible as a distinct change in water colour, turbidity and surface characteristics. During aerial surveys, the radiometer readings frequently show shifts of several degrees when the aircraft crosses the line of a visible front. Surface temperatures north of the front are warmer than to the south, and right whales are most often found in those waters with warmer surface signatures, about 10-11km north of the front (CETAP, 1982; Scott *et al.*, 1985; Brown and Winn, 1989; Kenney *et al.*, 1995). The front marks a boundary between two different hydrographic structures or mixing regimes. To the north are thermally-stratified waters with a warm surface layer, thermocline and colder intermediate and deep layers. To the south the water column is completely mixed by strong tidal currents over the shoal areas, reducing the temperature in the upper layer by mixing up the colder bottom waters (Wishner *et al.*, 1988; Chen *et al.*, 1995b). It is likely that the tidal mixing front and thermal stratification are established for short intervals early in the season (April) and remixed during storm and wind events before being permanently established later (May) for the rest of the warm season (J.J. Bisagni, University of Massachusetts-Dartmouth, pers. comm.). Similar zones between tidally-mixed and stratified water masses occur in the lower Bay of Fundy and Browns/Bacarro Bank regions, where they are also associated with right whale feeding habitats (Murison and Gaskin, 1989).

In 1992, a small number of real-time images of SST patterns for the entire northeastern US shelf region were obtained as part of the survey planning process. These images were from the AVHRR (Advanced Very High Resolution Radiometer), an infrared remote-sensing system aboard an earth-orbiting satellite, and provided by the Northeast Area Remote Sensing Center at URI. Real-time images for 29 April, 30 April and 1 May showed no sign of development of any detectable front in the GSC region. On the image for 20 May, the date of the first aerial survey, there was some suggestion of temperature differences in the GSC area, but no clear front was visible on the image and no visual evidence of a front was seen by the observers during the survey. It was not until the 14 July survey that a clearly visible frontal zone, with a 3-5°C temperature gradient, was seen by the aerial observers. A retrospective search of processed and archived AVHRR images revealed that the seasonal tidal mixing front in the GSC was becoming established on 20 May 1992 and was well-established within the next few days (S. Wagner, University of Massachusetts-Dartmouth, pers. comm.). A detailed hydrographic transect across the region on 27-28 May 1992 at 41°17'N (Gallager *et al.*, 1996) showed weak stratification with a thermocline at 20m, as well as a frontal zone near the western end of the transect, although they suggested that the observed front was something more complex than a simple tidal mixing front.

DISCUSSION

Comparison of 1992 patterns with previous years

The patterns of right whale distribution and abundance in 1992 were consistent with distributions from previous years at the beginning and end of the year, but atypical in late spring and early summer. Right whale occupancy in Cape Cod Bay from February-April and in the Bay of Fundy from August-October was essentially the same as in previous years (Mayo, 1982; Winn *et al.*, 1986; Gaskin, 1987; 1991; Kraus *et al.*, 1988; Murison and Gaskin, 1989; Hamilton and Mayo, 1990). Although only two days of surveys were conducted in the Roseway Basin area in 1992, the right whales there were present in the expected location and numbers based on previous work (Winn *et al.*, 1986; Gaskin, 1987; 1991; Kraus *et al.*, 1988). Given the limited effort in 1992, it is probable that there were more whales present than the 17 animals identified, and that more would have been sighted and photo-identified if additional surveys had been possible. During 1986-1991, between 47 and 120 different animals per year (mean = 89) were identified from the Roseway Basin area (from data in the catalogue).

The major 1992 anomaly was that no right whales were sighted in the Great South Channel region between May and July, the season of usual occupancy, with only a handful of sightings in the central Gulf of Maine during that period. Except for 1990, spring survey data were available for the Great South Channel for every year between 1979 and 1992 (CETAP, 1982; Winn *et al.*, 1985; Kenney and Winn, 1986a; 1987; Kenney *et al.*, 1986b; 1995; Kraus and Kenney, 1991), and 1992 was the only year when few right whales were observed. Since there were no surveys in April, it is possible that right whales were present early in the season in 1992, but departed much earlier than usual. However, in 1985 right whales left the area earlier than observed in any other year, and were almost gone by the end of May (only five sighted on 30 May) and absent by mid-June. Anecdotal reports that year suggested that right whales also arrived earlier than normal in the Bay of Fundy, by the beginning of July (L.D. Murison, pers. comm.), which definitely did not occur in 1992. Unfortunately, 1992 was the last year when the aerial survey programme was funded and thus there are few data to address right whale occurrence in the GSC in 1993 and subsequent years.

The area in the central Gulf of Maine where right whales were found in 1992, in the area of Georges, Lindenkohl and Crowell Basins and Sewell Ridge, is not one where right whales have been frequently sighted in the past. Despite extensive, year-round survey coverage of the entire northeastern shelf during the CETAP study, only six right whale sightings were made in that vicinity (CETAP, 1982). In the area of the central Gulf of Maine where the 1992 sightings occurred (bounded by 42°00’ and 43°00’N, and 66°50’ and 68°00’W), there was a total of approximately 7,100km of aerial and shipboard surveys in good visibility and sea conditions in 1979 and 1980 (archived CETAP effort data used in Shoop and Kenney, 1992). Those surveys resulted in sightings on 25 April 1979, 19 October 1979, 2 November 1979, 31 May 1980 (two) and 13 June 1980. The aerial surveys in 1992 covered less than 900km within that same area, and the NMFS cruises may have covered another 200-300km (estimated assuming two or three transits across

Table 2

Comparison of Great South Channel sea surface temperatures (ºC) in 1992 (in ***bold italics***) with data collected in 1985, 1987, 1988, 1989 and 1991. The data are sorted in calendar order with all years mixed together for comparison of similar dates between years. All temperature data were obtained via airborne radiometry.

Date	*n*	Mean	SD	Minimum	Maximum	CV
26 Apr. 1988	390	10.83	0.304	10.0	13.2	2.81
26 Apr. 1989	1,117	12.62	0.753	11.1	15.9	5.97
26 Apr. 1991	1,272	7.71	1.233	1.3	12.4	16.00
04 May 1988	63	11.19	0.674	10.4	15.0	6.02
05 May 1988	343	11.19	0.447	10.0	12.5	4.00
07 May 1987	349	8.82	0.623	7.7	10.5	7.07
09 May 1985	936	9.19	0.621	7.4	10.9	6.75
09 May 1988	494	11.78	0.294	10.5	12.5	2.50
09 May 1989	1,138	13.53	0.636	11.3	15.2	4.71
09 May 1991	1,218	10.45	0.522	8.3	12.9	4.99
12 May 1988	476	12.74	0.484	11.7	17.8	3.80
15 May 1988	1,426	12.10	0.616	10.1	17.5	5.09
20 May 1992	***1,059***	***9.18***	***1.606***	***5.2***	***20.2***	***17.51***
21 May 1989	563	13.48	0.668	12.4	16.5	4.95
23 May 1985	954	11.21	0.561	9.5	12.5	5.00
26 May 1987	508	13.15	1.028	9.5	15.4	7.82
27 May 1988	554	14.99	0.614	13.2	22.3	4.10
28 May 1989	381	16.83	0.477	15.1	17.9	2.83
29 May 1989	1,120	15.63	0.746	12.9	18.5	4.77
29 May 1992	***1,424***	***9.24***	***1.026***	***5.2***	***12.1***	***11.11***
30 May 1985	410	12.13	0.854	9.3	13.5	7.04
01 Jun. 1987	404	12.70	0.775	9.0	15.4	6.10
03 Jun. 1988	645	16.38	0.916	13.5	19.0	5.59
04 Jun. 1992	***704***	***9.18***	***1.733***	***5.0***	***13.2***	***18.89***
07 Jun. 1987	471	14.39	0.937	10.5	15.9	6.51
07 Jun. 1991	1,117	11.79	1.686	7.4	17.7	14.30
11 Jun. 1988	1,150	16.50	1.273	12.8	19.2	7.71
19 Jun. 1987	52	15.90	0.614	14.8	17.4	3.86
19 Jun. 1989	1,400	17.56	1.050	12.2	19.4	5.98
21 Jun. 1985	1,132	14.95	1.016	10.3	18.5	6.79
30 Jun. 1989	1,444	19.44	1.120	14.8	26.3	5.76
07 Jul. 1987	173	17.47	1.629	12.2	20.1	9.32
14 Jul. 1992	***1,084***	***13.71***	***2.456***	***8.2***	***18.3***	***17.91***

Table 3

Yearly mean Great South Channel sea surface temperatures (°C, from airborne radiometry), in order from warmest to coldest years, limited to surveys between 15 May and 15 June.

Year	1989	1988	1987	1991	1985	1992
n	2,064	3,775	1,383	1,117	1,364	3,187
Mean SST	15.26	14.59	13.44	11.79	11.49	9.20

the area), yet together nine right whale sightings were made. If the CETAP observers had sighted right whales at the 1992 rate, they would have made 35 or more sightings in 1979-80.

An additional anomaly in 1992 was the occurrence of small numbers of right whales from May-October in the Cape Cod vicinity. Similar residencies, although of larger numbers of animals, were observed in 1986 and 1987 (Mayo *et al.*, 1988; Hamilton and Mayo, 1990; Payne *et al.*, 1990; Kraus and Kenney, 1991).

Had funding been available, it would have been interesting to have conducted aerial surveys further to the east on the Nova Scotian shelf, from La Have Bank eastward to Emerald Bank and the western end of Sable Island Bank (all east of the boundary on Figs 1 and 2) in May-July 1992. That was the location of a significant number of right whale sightings made by whalers operating out of Blandford, Nova Scotia from 1966-1972 (Mitchell *et al.*, 1986). The area between La Have and Emerald Banks was the location of most of their July sightings, as well as some in August and a few in June. Interestingly enough, the DFO fishery observer data for 1992 did include five sightings in that vicinity in April and May, although there are no data available for other years which might allow assessment of whether low numbers of right whales routinely occur in Nova Scotian shelf waters in most or all years.

Factors influencing cetacean distributions

What factors could be responsible for the anomalies in right whale distribution patterns observed in 1992 in the Gulf of Maine? It has been relatively well-established that the distributions of cetaceans are strongly affected by the distribution, abundance and patchiness of their prey populations (CETAP, 1982; Gaskin, 1982; Kenney and Winn, 1986b; Katona and Whitehead, 1988). The question then is, what was different about the prey resource exploited by Gulf of Maine right whales in 1992, and why? Spring zooplankton densities in the Great South Channel are among the highest published for any area of the western North Atlantic (CETAP, 1982; Scott *et al.*, 1985; Sherman *et al.*, 1987; Wishner *et al.*, 1988; 1995; Durbin *et al.*, 1995c; Macaulay *et al.*, 1995; Beardsley *et al.*, 1996; Meise and O'Reilly, 1996), although even higher densities have been measured in small patches near feeding right whales in Cape Cod Bay (Mayo and Goldman, 1992; C.A. Mayo, Center for Coastal Studies, pers. comm.). The question posed above can thus be refined to, what was different about zooplankton distribution and abundance in the western Gulf of Maine in 1992, and why?

The characteristics of the zooplankton community which make a specific area a desirable right whale feeding ground include the species composition, the abundance of the preferred species, the age (therefore size) structure of the preferred species and the patch structure (Kenney *et al.*, 1986a; Wishner *et al.*, 1988; 1995; Murison and Gaskin, 1989; Mayo and Marx, 1990; C.A. Mayo, Center for Coastal Studies, pers. comm.). All of these are affected by physical parameters and processes. Temperature can affect species composition directly, since each zooplankton species may have differing thermal preferences and physiological optima. Temperature and hydrography affect phytoplankton productivity and therefore zooplankton growth, productivity and abundance. Temperature affects growth and developmental rates, and therefore age and size. Temperature, hydrography and phytoplankton productivity can all affect the patch structure of the zooplankton. Temperature changes can affect or be caused by changes in circulation patterns, which influence advection of zooplankton.

Anomalous GSC zooplankton community in 1992

The available data for the GSC in 1992 show that the species composition of the zooplankton community, the abundance of zooplankton species, the water temperatures and the water column structure were all different from earlier years. Copepod abundances were greatly decreased, *Calanus finmarchicus* was in nearly equal abundance to other copepod taxa rather than strongly dominant, and the pteropod *Limacina retroversa* was the dominant zooplankter. Temperatures were significantly colder than normal, and the establishment of the expected hydrographic structure, i.e. the frontal zone between stratified and tidally-mixed water masses, was apparently delayed. Right whales either did not appear, or visited the region and quickly departed, so the most likely explanation is that something about the prey resource in the GSC in 1992 was sub-optimal.

Hypothesis 1 – pteropods are not acceptable prey

One possibility is that pteropods are not acceptable right whale prey for one or more of several different reasons:

(1) Right whales find pteropods distasteful. Pteropods can contain a black pigment with a sulphur-containing compound (dimethylsulphoniopropionate or DMSP) which they get from certain phytoplankton food, especially *Phaeocystis* and coccolithophores (Lalli and Gilmer, 1989; Keller, 1991; Liss *et al.*, 1994). Fish which have been feeding on pteropods are referred to by fishermen as 'black guts' or 'stinkers,' because the pigment leaches into and discolours the viscera and flesh, and the DMSP breaks down to dimethyl sulphide (DMS), causing an unpleasant odour (Wimpenny, 1966; Lalli and Gilmer, 1989). Perhaps either DMSP or DMS make pteropods taste objectionable to right whales. This does not seem likely, however. Descriptive publications on zooplankton or marine biology often mention that pteropods are fed upon by whales (e.g. Pratt, 1935; McConnaughey, 1978; Lalli and Gilmer, 1989), although the whale species is seldom clearly specified. Pratt (1935), for example, states that *Limacina* is 'an important food of whales' and that *Clione* 'forms an important source of food for right whales', though both statements are unsupported by literature citation and 'right whale' could refer to the bowhead ('Greenland right') whale. In addition, there are rare references in the cetacean literature to pteropods as right whale prey (Millais, 1906; Hentschel, 1937 – not seen, cited in both Tomilin, 1957 and Slijper, 1962; Gaskin, 1982), and somewhat more common mentions of pteropods as bowhead whale prey (Hjort and Ruud, 1929; MacGinitie, 1955; Tomilin, 1957; Marquette, 1978; Lowry and Frost, 1984; Lowry, 1993). Finally, right

whales have recently been observed in the Bering Sea in the midst of a coccolithophore bloom, suggesting that the whales were not especially sensitive to the DMS produced by the bloom (C. Tynan, NMFS, pers. comm.).

(2) The size and/or shape of pteropods makes filtration through right whale baleen difficult or inefficient. It is unlikely that this is the case based on size alone. Mayo (pers. comm.) tested the filtration efficiency of a section of right whale baleen collected from a stranded animal. He found a direct correlation between zooplankter size and baleen filtration efficiency, with 89% efficiency for the largest zooplankton size class tested, 505-700 μm (defined by the mesh sizes of filters used to sort the zooplankton samples into size categories). The shell diameter of adult *Limacina retroversa* ranges from 2,000-7,000μm, with the total size of the animal larger, varying depending on the degree of extension of the foot (Hardy, 1956; Wimpenny, 1966; Lalli and Gilmer, 1989). The individuals in the GSC in 1992 represented a range of ages and were on the smaller end of that size range at 0.5-2mm, which was slightly smaller than the 1.2-2mm *Calanus* sampled at the same time (Gallager *et al.*, 1996). Lowry and Frost (1984) found prey items of 3-30mm in bowhead whale stomach contents. Mayo (pers. comm.) tested only crustacean zooplankton, so it is not possible to address at this time whether pteropod shape or surface characteristics may affect filtration efficiency.

(3) Pteropods swim too fast to be effectively captured by right whales. This possibility may be considered as unlikely based on indirect evidence. Zooplankton nets are generally towed at about 1 knot (1.9 km/hr), about the same as or slightly slower than the swimming speed of a feeding right whale (Watkins and Schevill, 1976; 1979; Mayo and Marx, 1990). Therefore, zooplankton species which readily avoid capture by nets might also avoid capture by right whales. Because of their faster swimming speeds, krill (*Meganyctiphanes* and *Thysannoesa* in the Gulf of Maine), are under-sampled due to net avoidance (Brodie *et al.*, 1978; Wishner *et al.*, 1988; 1995; Macaulay *et al.*, 1995). However, pteropods can be collected readily by plankton nets (Hardy, 1956; Sherman *et al.*, 1987; Lalli and Gilmer, 1989; K. F. Wishner, pers. comm.) and probably also by right whales.

Hypothesis 2 – pteropod patch density was energetically inadequate

A second and more likely possibility is that pteropods are acceptable right whale prey, but in 1992 they were not aggregated into patches dense enough to provide a net energetic gain to feeding right whales, even though their average abundance was only slightly lower than the average abundance of *Calanus* in 1989, a year when right whales were feeding in the GSC. Kenney *et al.* (1986a) and Mayo and Marx (1990) have shown that right whales need prey concentrated above some threshold density (on the order of 10^4-10^5/m^3) to obtain a net energetic benefit from feeding. Pteropod populations in the GSC in 1992 were distributed throughout the water column, with an average water column abundance of 235,000/m^2 and a maximum measured patch density (at a depth of 12m) of 3,700/m^3 (K.F. Wishner, pers. comm.). *Calanus* in 1989, with only slightly higher average water column abundance (255,000/m^2), was horizontally and vertically aggregated, with a relatively thin near-surface layer in one location containing a maximum measured patch density of 331,000/m^3 (Wishner *et al.*, 1995). Mayo (pers. comm.) has found that the threshold zooplankton density which triggers right whale feeding behaviour in Cape Cod Bay is about 4,000/m^3, slightly higher than the peak pteropod density measured in the GSC in 1992.

Gallager *et al.* (1996) reported the results of a Video Plankton Recorder (VPR) towyo transect across the GSC at about 41°17’N on 27-28 May 1992. Because the VPR photographically samples very small volumes at 60 samples per second, it can measure micro-scale (< 1m) zooplankton patch densities. The peak density they detected for a single sample within a patch of *Limacina* was 7,000/m^3. Interestingly, they observed some adult *Limacina* near the surface to be releasing streamers of embryos, with the peak density of embryos over 6,000,000/m^3, however at only 200μm the embryos are too small to be effectively filtered by right whale baleen (C.A. Mayo, pers. comm.).

Differences in caloric content between *Calanus* and *Limacina* may further decrease the relative food value of the latter to right whales. *Calanus* is relatively high in energy content, approximately 4,000-8,000 cal/gm dry weight, varying with season and life-stage (Comita *et al.*, 1966; Lawrence, 1976). *Clione limacina*, an Arctic pteropod eaten by bowhead whales (Lowry and Frost, 1984), has a caloric density of 3,310-4,000 cal/gm dry weight (Percy and Fife, 1981). *Clione* is a shell-less species (Hardy, 1956; Lalli and Gilmer, 1989). *Limacina* should have an even lower caloric density, since the shell would add to the weight but not the energy content.

Pteropods in the GSC before 1992

The presence of pteropods in 1992 in the GSC region is neither unprecedented nor necessarily anomalous. Sherman *et al.* (1987) summarised the NMFS zooplankton data for Georges Bank and adjacent waters, with their ‘northern deep water’ zone approximately equivalent to the GSC region. They showed that pteropods were a normal component of the zooplankton of the area, comprising over 80% of the non-copepod zooplankton in late spring and early summer with a peak occurrence in June. Their peak average pteropod density was approximately one-fifth the magnitude of and somewhat later than the peak average *Calanus* density. The observed dominance of pteropods in 1992 may simply have resulted from the very reduced populations of *Calanus* in the GSC, without substantial differences in pteropod abundance from previous years.

Temperature and hydrographic effects on GSC zooplankton

It is unlikely that temperature or hydrography affect right whale distribution in the GSC directly. Right whales are well-insulated by a thick blubber layer, and have been sighted in water as cold as 2.2°C off the northeast US coast (Winn *et al.*, 1986). They also have been observed in recent years as far north as Greenland and Iceland (Knowlton *et al.*, 1992). It is similarly unlikely that the cooler temperatures in 1992 affected GSC zooplankton by a direct thermal effect, i.e. by being below the range of temperatures at which *Calanus* can persist. *Calanus* and *Pseudocalanus* are boreal species which are the dominant copepod taxa in the Gulf of Maine/Georges Bank region in winter and spring, and are largely replaced in summer by a warmer-water assemblage dominated by *Metridia lucens* and *Centropages typicus* (Sherman *et al.*, 1987). During the warmer part of the year in the Gulf of Maine/Georges Bank region, *Calanus* abundance is consistently higher in colder water masses (Meise and O'Reilly, 1996). However, it is probable that the hydrography of the GSC has a significant effect on the development of the extremely dense zooplankton patches on which right whales feed. Gaskin (1987; 1991) and Murison and Gaskin (1989) showed that the boundary zones between stratified and mixed water masses off Nova Scotia were important in the formation of dense *Calanus* patches. Similar processes, probably augmented by the behaviour of the copepods themselves, are believed to be responsible for zooplankton patch structure in the GSC (Scott *et al.*, 1985; Wishner *et al.*, 1988; SCOPEX results – see below; Miller *et al.*, 1998). The low temperatures and anomalous hydrographic structure in the GSC in 1992 probably did not cause the observed absence of right whales in the region directly, but rather indirectly through effects on the zooplankton.

The results of the SCOPEX study of the oceanography of the GSC relative to right whale ecology enable further refinement of the hypothesis that low temperatures and delayed development of stratification in 1992 affected the regional zooplankton community and, therefore, right whales. To briefly summarise the conclusions of the study:

(1) patterns of right whale occurrence in the GSC are directly related to the occurrence of dense patches of *Calanus finmarchicus* (Kenney *et al.*, 1995; Macaulay *et al.*, 1995; Wishner *et al.*, 1995; Beardsley *et al.*, 1996);
(2) right whale distribution and feeding is also strongly correlated with the proportion of larger, more energy-dense *Calanus* life stages (fourth- and fifth-stage copepodites and adults – Wishner *et al.*, 1995);
(3) observed interannual differences in the location of the main right whale aggregation are correlated with sea surface temperatures north of the tidal mixing front in early May, with the aggregation usually on the west side of the region, but on the east side in colder years (Kenney *et al.*, 1995);
(4) the development of exceptionally dense *Calanus* patches is principally a result of hydrographic processes, with the copepods being advected into the GSC region and concentrated rather than growing *in situ* as a result of trophic processes (Wishner *et al.*, 1988; 1995; Chen *et al.*, 1995a; b; Durbin *et al.*, 1995b) – concentration is probably enhanced by the behaviour and swimming of the copepods, i.e. swarming and diel vertical migration (Beardsley *et al.*, 1996); the *Calanus* which aggregate in the GSC likely originate from source regions throughout the Gulf of Maine and Nova Scotian shelf (Bucklin and Kocher, 1996; Miller *et al.*, 1998);
(5) the general circulation in the region is cyclonic with the main currents entering from the northwest, flowing southeastwards to the centre of the region and then turning to the northeast along the flank of Georges Bank (Chen *et al.*, 1995a; Fig. 3);
(6) *Calanus* growth and development is temperature dependent, with faster rates in warmer temperatures (Durbin *et al.*, 1995a);
(7) when water temperatures early in the season are lower, *Calanus* development from one stage to the next is slower, and consequently the location where the proportion of C-4 and larger stages preferred by right whales is reached is on the east side of the area, rather than the west (Durbin *et al.*, 1995a; Kenney *et al.*, 1995; Wishner *et al.*, 1995).

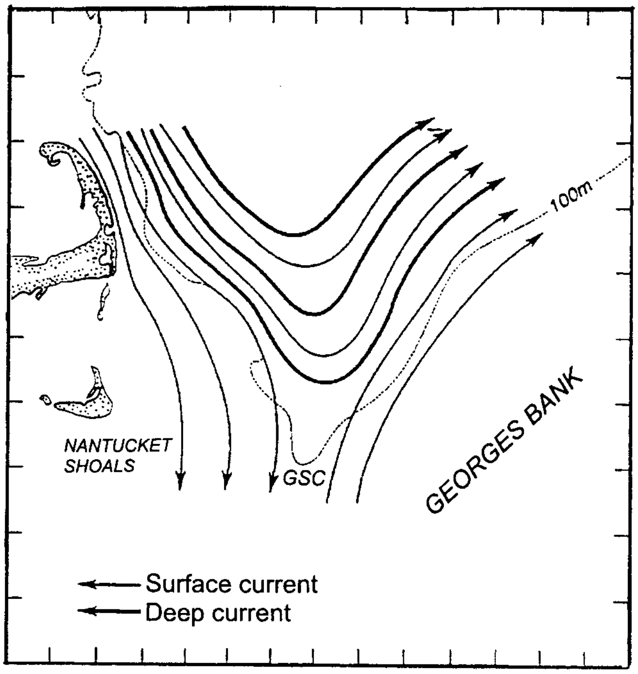

Fig. 3. Simplified conceptual model of the surface and deeper circulation in the Great South Channel region during late spring, based on SCOPEX Acoustic Doppler Current Profiler and satellite-tracked drifter data (from Chen *et al.*, 1995b). The tidal mixing front which is usually established during spring and summer approximately follows the 100m isobath, with north-south oscillations on a tidal cycle.

Extension of this scenario then illuminates what may have occurred in 1992. With water temperatures averaging 2-6°C colder than in previous years, the *Calanus* cohort did not mature to C-4 until after the currents had moved them through and beyond the GSC region. The high proportions of large copepods preferred by right whales were never attained within the area. (Substantial increases in current velocity could have the same effect as reduced temperature by advecting the growing cohort through the region more quickly. This was probably unlikely in 1992 – see discussion under *Labrador Current* below.) Additionally, the degree of *Calanus* diel vertical migration is often tied to ontogeny, with younger-stage individuals typically remaining more in surface waters and older-stage copepodites and adults more likely to strongly migrate (Marshall and Orr, 1972; Williams and Lindley, 1980; Durbin *et al.*, 1995c). Since vertical migration may be involved in their concentration by hydrographic processes, delayed initiation of migration may have enhanced the advection of *Calanus* through and out of the area without the development of dense patches. Two observations from 1992 provide additional support for this hypothesis: (1) the area of the late spring/early summer right whale sightings, in the central Gulf of Maine, is northeast and 'downstream' of the GSC, and where one might expect to find *Calanus* populations which have been advected through the GSC by currents; (2) a Sea Education Association (SEA) cruise which went to the GSC area in June with the objective of sighting right whales and sampling zooplankton in their vicinity, but failed to locate any right whales, did collect some zooplankton samples with high *Calanus* densities in the northeast portion of the area, near the northern edge of Georges Bank (M. Lesser, SEA, pers. comm.).

Even though the GSC was apparently not an acceptable right whale feeding ground in May and June 1992, some very dense copepod patches were present nevertheless. The VPR transect on 27-28 May (Gallager *et al.*, 1996) showed a horizontal patch of *Calanus finmarchicus*, about 2km in width and at a depth of about 15-20m within and just above the thermocline, with densities exceeding 2,500/m^3 throughout and a peak density of 285,000/m^3. They also observed a peak patch density of 3,000,000/m^3 for *Pseudocalanus* sp. The simultaneous hydrographic data they collected during their transect showed that the GSC is extremely complex. Within one east-west transect, they observed twelve different identifiable water masses or types. *Limacina* and *Calanus* were found primarily within the same water masses, but were very different in their fine-scale distributions. *Limacina* was densest in the centre of the water mass, where the temperature gradient was smallest, leading to low stability and high mixing. *Calanus* was densest at the lower edge of the water mass in/near the thermocline, where stability and resistance to mixing is highest. This seems to support the SCOPEX hypothesis that species-specific behaviour enhances the physical aggregation of *Calanus* in the GSC (Kenney and Wishner, 1995; Beardsley *et al.*, 1996), although Miller *et al.* (1998) have suggested that strictly physical mechanisms may be sufficient.

Underlying physical factors in 1992

There are several large-scale oceanographic or atmospheric phenomena which may have influenced the temperature and hydrography within the GSC region in 1992, thereby leading to a different pattern of zooplankton occurrence and the subsequent absence of right whales. These include the North Atlantic Oscillation, the Gulf Stream, the Labrador Current and associated inputs, North Atlantic thermohaline circulation and the cooling effect of the 1991 Pinatubo eruption. Many of these vary on decadal or longer time scales, so information on short-term variability or anomalies is rare. In addition, the atmosphere, surface currents and deep circulation of the North Atlantic are probably inter-connected in some complex manner which as yet is not fully understood (Reid *et al.*, 1998). Finally, the lack of directed right whale surveys in the GSC in 1993 and subsequent years has made it very difficult to establish whether the absence of right whales there in 1992 was a one-time anomaly or the beginning of a longer-term change in their distribution. However, even though there are no GSC survey or sightings data for 1993-1997, there were between one and ten right whale photo-identifications in the GSC during the March-June period each year which have been included in the catalogue from a variety of sources. Therefore, right whales have not been entirely absent in spring from the GSC in later years like they were in 1992, which suggests that their absence in 1992 was, in fact, a single-year anomaly.

North Atlantic Oscillation

The North Atlantic Oscillation (NAO) is a pattern of alternating phases in atmospheric pressure between Iceland and the Azores, leading to different patterns of jet stream trajectory, winds and weather at both extremes of the cycle (van Loon and Rogers, 1978; Hurrell, 1995). The dimensionless NAO index is the standardised difference between the Iceland and Azores pressures, and is calculated on a monthly basis. Because the impact of NAO fluctuations is most apparent during the winter, standard practice is to average the monthly values across four or five months, December through March or April (Hurrell, 1995; Fromentin and Planque, 1996). Positive values of the winter NAO correspond to cold winters in Greenland and Iceland and mild winters in Europe, while negative values correspond to relatively warmer Greenland and colder European winters, and the index tends to remain in one phase or the other for some number of successive years, then switch to the opposite phase (Hurrell, 1995).

Fromentin and Planque (1996) showed that the NAO can influence *Calanus finmarchicus* and *C. helgolandicus* abundance in the eastern North Atlantic around the British Isles. Changes in NAO cause changes in the relative strength of west wind stress, which lead to changes in water temperature patterns, frequency and intensity of upwelling and phytoplankton productivity, all of which influence zooplankton populations. To test whether a short-term change in the NAO, or a recent switch from one state to the other, may have affected the GSC in 1992, monthly NAO index data for 1980-1998 were obtained from the Climate and Global Dynamics Division, National Center for Atmospheric Research (*http://www.cgd.ucar.edu/cas/climind/nao_monthly.html*). The winter mean index for a given year was calculated from the four monthly values from December of the previous year through March, following Hurrell (1995). The 1992 value was 0.975, which is not significantly different from the 1980-1991 average of 0.670 (SE = 0.316; range = –0.775 to 3.959). The NAO has been in a largely positive phase in the 1980s and 1990s (Hurrell, 1995), with a period of very high values from 1989-1995 (the three highest values recorded were in 1989, 1994 and 1995). There is no obvious short-term fluctuation in or shortly preceding 1992 in the time-series, and the index had been in a positive phase for about a decade before 1992. The most obvious change in the time series is the large increase in 1989, and one would have to both presume a three-year time lag for an effect on right whales in 1992, and expect the effect to have persisted until 1998, which does not appear to be the case. For comparative purposes, during the late 1960s and early 1970s, when there were substantial numbers of right whale sightings on the Nova Scotian shelf (Mitchell *et al.*, 1986), there was a strongly negative phase of the NAO, quite different than the more recent period (Hurrell, 1995).

Gulf Stream

The Gulf Stream is a north and eastward-flowing, warm, western boundary current in the western North Atlantic. Taylor *et al.* (1992) and Taylor (1995) have shown that interannual variability in the latitudinal position of the north wall of the Gulf Stream in the western North Atlantic can be correlated with variability in zooplankton abundance in the eastern North Atlantic. Taylor (1995; 1996) developed the Gulf Stream Index (GSI), a single dimensionless number based on mean monthly Gulf Stream position (calculated from the first principal component of latitude where the current crosses six different meridians of longitude). The monthly and annual mean GSI data were obtained from the Plymouth Marine Laboratory (*http://www.pml.ac.uk/pml/srpl/gulfstream/inetdat.htm*). Examining the annual means, there was no short-term anomaly in 1992. The value in 1992 was 1.208, which was a slight decrease from a value of 1.359 in 1991. The index was continuously positive from 1988 to the maximum value of 2.264 in 1995. Interestingly, approximately 60% of the interannual variability in Gulf Stream position can be attributed to variability in the NAO (Taylor *et al.*, 1998), and this period of continuously positive GSI corresponds very closely to the series of high NAO years. One might therefore have expected either both indices to show some short-term fluctuation which could be related to the 1992 changes in the GSC, or that neither would, which appears to be the case.

Hays *et al.* (1993) showed a strong linear relationship between GSI and annual mean total copepod abundance for an area in the vicinity of the shelf break between Scotland and the Faroe Islands. The relationship held from 1966-1988, but beginning in 1989 copepod abundance was significantly lower than predicted from their model. Again, that period coincides with the time of very high NAO values, although no connection was established in their results.

Labrador Current

A dominant influence on the properties and circulation of water in the Gulf of Maine is the influx of cooler, somewhat fresher water flowing southwestward across the Nova Scotian shelf and inward at depth through the Northeast Channel (Chapman and Beardsley, 1989; Townsend, 1992; Petrie and Drinkwater, 1993; Khatiwala and Fairbanks, 1999). Buoyancy forcing from this inflow is the major driver of Gulf of Maine circulation, and the freshwater inputs are derived about one-third from the St. Lawrence River and two-thirds from high latitude inputs (glacial melt and river run-off) into polar waters feeding into the Labrador Sea and Labrador Current, with only a small contribution from local river inputs (Khatiwala and Fairbanks, 1999). Petrie and Drinkwater (1993) described a widespread cooling and freshening trend across the Scotian shelf and Gulf of Maine from 1952-1967, during which time there was a quadrupling in transport of the Labrador Current, followed by a reversal. The period 1952-1967 was a time of steady decrease in long-term average NAO (Hurrell, 1995), however Petrie and Drinkwater (1993) were unable to correlate variability in Labrador Current transport with NAO. Labrador Current transport is a much more difficult parameter to measure than simple atmospheric pressure at two locations (Han and Tang, 1999), so there is no readily accessible data time-series available for correlation.

Bisagni *et al.* (1996) described a substantial influx of cold Scotian Shelf Water (SSW, identified by salinity less than 32.0 psu) onto Georges Bank in April 1992. They reviewed the occurrence of SSW on Georges Bank from available hydrographic data going back to 1912. Typically, the peak near-surface flow of SSW westward just south of Nova Scotia into the Gulf of Maine occurs in February. There is also a so-called ‘cold band’ of SSW extending westward along the southern edge of Georges Bank. In 30% of the years where there were appropriate data, SSW could be detected on the southern flank of Georges Bank in May (from where clockwise circulation around the bank advects the water into the GSC). In 1992, temperatures within the SSW cold band were below 2°C in February. SSW was observed on the bank in April, which was not seen in any previous year. Colder than normal conditions persisted throughout the spring of 1992 all along the southern flank of Georges Bank (Bisagni *et al.*, 1996), with seasonal warming increasing the temperature within the SSW plume to 6-7°C by early June. Monthly average water temperatures at a meteorological buoy on southern Georges Bank were up to 3°C colder than the long-term means. Conditions on southern Georges Bank returned to ‘normal’ in 1993, so the patterns observed in 1992 were a short-term phenomenon (Bisagni *et al.*, 1996).

The strong influx of colder SSW onto Georges Bank and then into the GSC in 1992 is probably the immediate cause of the reduced temperatures observed in the GSC, however its underlying cause is not clear. Bisagni *et al.* (1996) hypothesised that the large influx of SSW in 1992 was consistent with higher than average discharge from the St Lawrence River the preceding year, since the peak SSW inflow lags the peak river discharge by about nine months. However, they were unable to correlate longer-term variability in SSW with lagged variability in St Lawrence discharge and suggested that other factors were likely involved. SSW is the end of the Labrador Current branch which flows south of Nova Scotia (Chapman and Beardsley, 1989). Although no Labrador Current transport data are available for 1992, a hypothesis of higher transport in and preceding 1992, when NAO was high, would not be consistent with the observations of Petrie and Drinkwater (1993) of high transport during a period of low NAO.

Presuming that near-surface SSW influx south of Nova Scotia was also greater in 1992, one might expect that enhanced buoyancy forcing might have intensified the Gulf of Maine circulation, increasing current velocities through the GSC. This would have the same effect as lower temperature on shifting the location of *Calanus* maturation to the ‘whale-food’ size class further eastward. Lacking current data, this possibility is difficult to address. However, the hydrographic data from the 27-28 May transect by Gallager *et al.* (1996) showed the leading edge of the surface plume of warmer, fresher water derived from coastal rivers in New England had just reached the extreme western end of their transect. This is similar to the conditions observed in 1988, when current velocities were lower than in 1989 (Chen *et al.*, 1995a; b).

Thermohaline circulation

Saline Gulf Stream water transported to high latitudes mixes with colder Arctic waters, then cools during the winter forming very cold, salty water which sinks because of its increased density. In the Labrador Sea between Labrador and Greenland, the process causes the development of a water mass at mid-depths known as Labrador Sea Water (LSW), while North Atlantic Deep Water (NADW) is formed in the Greenland and Irminger Seas north and west of Iceland (Sverdrup *et al.*, 1942). These water masses flow slowly southward at depth, eventually remixing to the surface in a gradual convective cycle at a time scale on the order of a thousand years (Sverdrup *et al.*, 1942). Recent work has shown than NAO variability has a strong effect on the formation of these water masses. Under high NAO conditions, formation of NADW is inhibited and that of LSW is enhanced, and the opposite occurs under low NAO (Reid *et al.*, 1998). The period of very high NAO between 1989 and 1995 was a time of greatly enhanced LSW formation (Curry and McCartney, 1996; Reid *et al.*, 1998). However, the transport rates of deep water masses are very slow; Read and Gould (1992) estimated that it took 18 or 19 years for LSW to reach the area west of Ireland. Because of the slow flows and long time scales, it seems unlikely that fluctuations in rates of deep water formation could cause short-term fluctuations in hydrography in the Gulf of Maine.

Reid *et al.* (1998) suggested that deep convective circulation, surface circulation and atmospheric cycles in the North Atlantic are inter-related in some complex, not well-understood manner. The data summarised in Curry and McCartney (1996) show a strong freshening of LSW during the 1990s period of high NAO and enhanced LSW formation. This suggests that Labrador Current transport of lower salinity water at the surface might be reduced at the same time. Conversely, Labrador Current transport increased in 1952-1967 (Petrie and Drinkwater, 1993) while NAO, deep convection in the Labrador Sea and LSW formation were low (Read and Gould, 1992; Curry and McCartney, 1996). If there is some degree of inverse relationship between Labrador Current transport and NAO, perhaps transport has been reduced during the 1990s, weakening the Gulf of Maine circulation. This might have an effect on GSC hydrography, however it seems that the effect would be over a longer term and not in a single year, as observed.

Global cooling from the Pinatubo eruption

One other potentially important factor in the significantly lower ocean temperatures in the GSC in the spring and summer of 1992 is the 15 June 1991 eruption of Pinatubo volcano on Luzon Island in the Philippines (Bernard *et al.*, 1991; Luhr, 1991; Brasseur and Granier, 1992). The eruption plume included an estimated 20 million metric tons of sulphur dioxide (two-thirds of the total aerosols produced during the eruption) ejected to altitudes of 20-30km (Bluth *et al.*, 1992; Brasseur and Granier, 1992). The SO_2 gas became a long-lasting aerosol haze of sulphuric acid, which significantly reduced the amount of solar radiation reaching the surface (Luhr, 1991; Brasseur and Granier, 1992; Kerr, 1993; Blumthaler and Ambach, 1994; McCormack *et al.*, 1995). The aerosol clouds completely circled the globe within 22 days after the main eruptions, and eventually extended into most of the Northern and Southern Hemispheres (Bluth *et al.*, 1992).

Hansen *et al.* (1992) predicted in advance, based on a simplified computer model of the atmosphere, that the cooling effect from the Pinatubo eruption would be widespread, lowering the mean global temperature by 0.5°C for 1992, 1993 and possibly 1994. Atmospheric temperature measurements from satellites showed a decrease in global mean temperature for the 12 months following the eruption of 0.6°C from the year preceding the eruption (Dutton and Christy, 1992; Kerr, 1993; McCormack *et al.*, 1995). The average temperature in 1992 was 0.5°C below the long-term mean and 1993 was 0.2°C below, while 1994 saw a return to the pre-eruption warming trend (McCormack *et al.*, 1995). Additionally, the cooling effect was not evenly distributed in space and time. The most intense cooling, greater than 1.0°C below the long-term mean, was in the middle latitudes of the Northern Hemisphere between March and August of 1992 (Dutton and Christy, 1992; Kerr, 1993). It should be noted that all of these temperature data were based on satellite measurement of atmospheric temperatures in the lower troposphere, and that no studies of effects of Pinatubo cooling on ocean temperatures have been published, although a reduction in the intensity of solar radiation could be expected to retard warming of surface waters. On the other hand, regional and local effects, some dramatic, of the cooling were seen on land. Jones and Kelly (1996) showed decreases in 1992 surface temperatures measured at land-based weather stations attributed to the Pinatubo cooling effect, with the most intense cooling in eastern North America. Abdalati and Steffen (1997) showed that ice-sheet melting in Greenland decreased by 68% in 1992 over 1991, while Shuman *et al.* (1996) showed a 2°C negative temperature anomaly in 1992 at a station in the centre of the Greenland ice-sheet.

Air temperatures in 1992 in southeastern New England were significantly lower than normal. Monthly summary data from the National Weather Service station at Chatham, Massachusetts (Fig. 1; located at the 'elbow' of Cape Cod and therefore the station closest to the GSC area) showed that average daily minimum, mean and maximum temperatures at Chatham in March, April and May 1992 were all 2.2-3.3°F (1.2-1.8°C) below the 1979-1991 averages (Table 4; NCDC, 1979-1992). In fact, for the two-month period of March and April 1992 for the entire New England region, 'the combined March/April average for the region was 2.8° below normal, which was the coolest such combination since 1978' (NCDC, 1992, no. 4).

Table 4

Average daily minimum, mean and maximum air temperatures (°F) at the Chatham, Massachusetts National Weather Service station in March, April, May and June of 1992 compared to 1979-1991 averages (NCDC, 1979-1992).

Month(s)	Minimum	Mean	Maximum
March 1992	29.5	34.8	40.1
March 1979-91	31.7	37.6	43.4
April 1992	36.3	42.1	47.9
April 1979-91	39.4	45.1	50.8
May 1992	45.0	51.3	57.6
May 1979-91	47.5	53.7	59.8
June 1992	55.7	62.1	68.4
June 1979-91	55.4	61.8	68.3

Conclusions

The absence of right whales in the GSC in 1992 was probably a direct result of the lack of sufficiently dense patches of *Calanus finmarchicus*, their preferred prey. The pteropod populations which were present may have been unacceptable prey for right whales regardless of density, but more likely were not aggregated into sufficiently dense patches for efficient right whale feeding. These changes in the GSC zooplankton community probably resulted from a significant decrease in water temperature, and consequent changes in circulation and mixing patterns and water structure.

The direct cause of the observed 1992 GSC temperature and hydrographic anomalies appears to be an anomalous influx of cold Scotian Shelf Water which began in late winter and resulted in below-average temperatures over much of Georges Bank through the spring (Bisagni *et al.*, 1996). The underlying cause of this phenomenon is not clear, although it appears that high discharge from the St. Lawrence River in 1991 is involved. It is also possible that reduced air temperatures related to global cooling caused by atmospheric sulphate aerosols from the eruption of Mount Pinatubo in June 1991 may have exacerbated the effect by retarding the seasonal warming of surface waters. Fluctuations in other phenomena, including the Labrador Current, Gulf Stream, North Atlantic Oscillation, and Labrador Sea Water formation may all affect hydrography within the Gulf of Maine and Great South Channel, however the time-scales of variability are longer, and no short-term anomalies have been observed which can be related to the 1992 anomalies in GSC hydrography, zooplankton, and right whale occurrence.

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Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis*

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ABSTRACT

In order to define the trophic requirements of the North Atlantic right whale, a series of experiments were designed to examine the food capture characteristics of the species. The food filtering efficiency of the baleen of an immature right whale was tested in a flume using graded samples of zooplankton, primarily calanoid copepods, collected in the path of surface-feeding whales. The filtering capacity decreased with decreasing prey organism size, so that greater than 95% of the available caloric content of the zooplankton samples was captured in size fractions collected on 333µ mesh nets. The experiments demonstrate that the filtering efficiency of the baleen narrowly focuses the right whale's feeding on an energy-rich, yet spatially and temporally variable, portion of the mid-water food resource.

KEYWORDS: FEEDING; EUPHAUSIIDS/COPEPODS; NUTRITION; RIGHT WHALE; NORTH ATLANTIC

INTRODUCTION

With a population of about 350 individuals (Fairfield, 1990; NMFS, 1991; Knowlton *et al.*, 1994; IWC, 2001), the North Atlantic right whale (*Eubalaena glacialis*) is among the rarest of the world's baleen whales. Although intensive whaling which began in the 17th century initially depleted the right whale stock (Reeves *et al.*, 1978; Reeves and Mitchell, 1986), lack of recovery today is thought to be the result of a number of factors including mortality caused by collision with ships and entanglement in fishing gear (Kraus, 1990; IWC, 2001). The recovery plan for the northern right whale (NMFS, 1991) also identifies disruption of critical habitats as a potential contributing factor to the lack of recovery. Although the impact of such disruption on the health of the population is not easily assessed, both the recent decline in calving rate (Kraus *et al.*, 2001) and the decreased use of historically exploited feeding areas (A. Knowlton, pers. comm.) could reflect profound changes in food resources. Hence, the relationship between the whales and the marine ecosystem is an important consideration in the effort to conserve the species.

The most obvious connection between the whale and its habitat is embodied in the whale's feeding activities. To capture food, the right whale filters its zooplanktonic prey from seawater. The efficiency of the right whale's filtering structure fundamentally defines the relationship between the whale and its mid-water resources and thus characterises the whale's reliance on marine planktonic productivity.

The filtering structure of the right whale is formed by two rows of keratinous baleen plates whose function and morphology are reviewed by Pivorounas (1976). Rows of between 250 and 390 plates per side (Leatherwood *et al.*, 1976) form tightly packed filtering walls, or racks, beneath the lateral margins of the upper jaw. With the mouth open, seawater enters the buccal cavity through a gap at the front of the mouth between the racks. In the mouth, filaments arising from the frayed inner edges of adjacent plates overlap across the narrow openings between the plates, forming a filter mat through which water trapped in the mouth is expelled. Because such filter feeding is relatively indiscriminate with respect to food types, food consumption is determined by two characteristics of available mid-water prey items, filterability and avoidance behaviour.

Planktonic food resources in most of the North Atlantic habitats where right whales are thought to feed are dominated by the calanoid copepods *Calanus finmarchicus* (Winn *et al.*, 1986; Wishner *et al.*, 1988; Murison and Gaskin, 1989; Woodley and Gaskin, 1996), *Pseudocalanus* sp. and *Centropages* spp. (Mayo and Marx, 1990). Although a variety of other food organisms including euphausids (Hamner *et al.*, 1988), swarming galaethiads (N. Patenaude, pers. comm.) and colonial siphonophores (C. Mayo, unpublished data) have occasionally been reported or inferred as the food of right whales worldwide, the dependency of North Atlantic right whales on calanoid copepods is widely accepted. Copepods and other forms found in the zooplankton community range from approximately 0.05-10.0mm in length, thus requiring for their capture the fine mesh filter mat found in right whales. Movement and orientation of the whale at many scales as it chooses to find patches of zooplankton may permit some degree of prey selection. However, during feeding it is likely that selection is passive and determined solely by the filtering capacity of the baleen once the water has entered the mouth.

Although important in assessing the relationship between the whale and the ecosystem, the filtering efficiency of right whale baleen has not been quantified. This paper estimates the capture efficiency of baleen from the results of filtration experiments using zooplankton collected on the edge of the feeding paths of right whales in Cape Cod Bay, Massachusetts, USA and baleen extracted from the mid-rack of a dead, immature whale.

METHODS

To test zooplankton capture efficiency, a series of experiments were designed to flush water containing plankton through a section of a rack of right whale baleen. In these experiments, we did not compensate for the escape behaviour and orientation of living copepods, for tissue changes in preserved zooplankton, or for the possible

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influences on filtration resulting from the Bernoulli effect at the outer plate margins hypothesised by Orton and Brodie (1987) and Lambertsen *et al.* (1989). The effects on filtration of active or passive conditioning of the filament mat by the whale as suggested by P. Brodie (pers. comm.) were also not controlled for in this study. Instead, the experiments were designed to use food organisms encountered by right whales to test baleen capture efficiency in a simple experimental environment controlled for the density of zooplankton, the velocity of flow and the total filtration time.

The baleen used in the tests was extracted from a 10.1m, 18 month old female (North Atlantic catalogue #1504, P. Hamilton, pers. comm.) killed in a collision with a ship off Cape Cod in August 1986. Our estimates of zooplankton capture efficiency thus refer to the characteristics of #1504's baleen. The section of the left rack used in the experiments included plates 125-150, counting from the front and the test area was approximately 35cm below the upper margin of the plates. During the year between the collection of the baleen and its use in the filtration tests, the baleen was washed and conditioned with a commercial hair conditioner every four months. While the baleen became brittle after collection and drying, the periodic washing and conditioning appeared to restore the supple quality of the filaments found in fresh material.

The zooplankton samples used in the filtration tests were collected in Cape Cod Bay. During the winter of 1987, thirty-nine samples were collected by towing a 471μ mesh conical plankton net within 3m of the path of right whales feeding at the surface. Samples of zooplankton in the $170\text{-}471\mu$ size range were collected separately using fine mesh nets. All collections were combined to make a standard zooplankton test sample with a density distribution approximating the mean density of the 1987 feeding path collections (Fig. 1). Zooplankton samples were preserved in 10% formalin and graded into seven size fractions by washing through screens. To determine the filtration efficiency of the baleen for different zooplankton sizes, five to nine individual tests were run using each graded fraction. To control for density effects, a sample of a size fraction was counted and injected into the flume to produce a density that approximated that found in the feeding path of the whales. The preserved zooplankton samples were used in the tests within 14 months of collection and preservation.

To flush water through the baleen section, a flume (Fig. 2) was constructed of plywood. It was built around a reservoir containing approximately 125 litres of water and a submersible pump rated at 167 litres/min^{-1}. Connected to the reservoir were input and return channels, each 1m long and 15 × 15cm in cross section. Water was pumped by hose from the reservoir into the input channel with the volume of flow controlled by a restrictor. Water flowed in a loop from the reservoir through the restrictor and input channel and back to the reservoir via the parallel return channel. The baleen section with its plate surfaces parallel to the flow was sealed to the end of the return channel by support frames clamped on each side of the rack section. Thus, the matted filtering surface of the baleen blocked the flow of water returning to the reservoir.

During each experiment, a counted sample was injected into the flow of the return channel 30cm before the water reached the baleen. A window in the face of the return channel permitted the operator to observe the progress of the plankton injection and capture. Observation of the plankton and baleen surface assured that no holes developed in the baleen mat and that the zooplankton was distributed evenly through the water column at the point of impact with the filaments. Such experiments were conducted for 2.5mins to approximate the mean interval between behaviour that Mayo *et al.* (1987) proposed may indicate harvesting of plankton from the baleen surfaces.

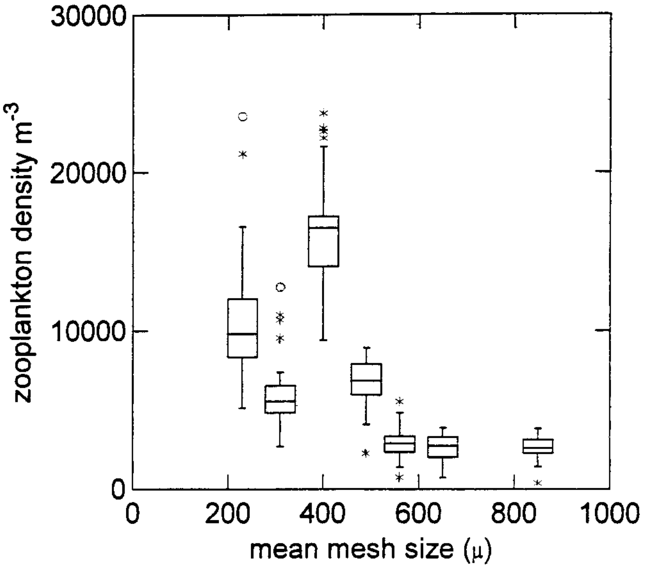

Fig. 1. The distribution of zooplankton collected in the path of feeding right whales in 1987. The size fractions are expressed as the mean of the mesh sizes used to grade the standard 1987 zooplankton sample.

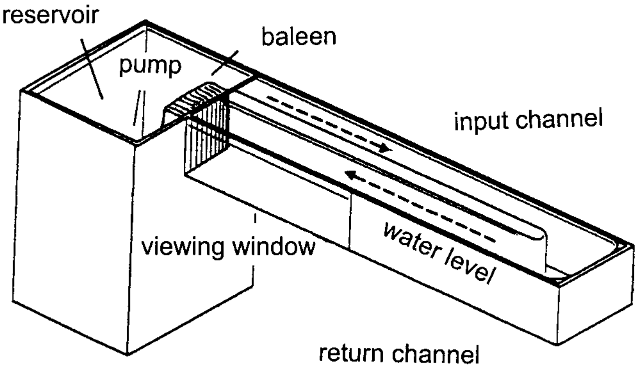

Fig. 2. The experimental flume.

In order to set the water transport volume of the flume to the approximate velocity with which water passes through the baleen of a feeding whale, we used the relationship:

$$Vb = (Ag/Ab) \times Vs$$

where:

Vb is the estimated velocity through the baleen filtering surface;

Ag is the area of the free gape of the mouth of whale #1504;

Ab is the surface filter area of the baleen of whale #1504;

Vs is the mean swimming velocity of feeding whales observed during our studies.

To determine the size of the gape, the mouth of #1504 was measured, a 1/20 scale model of the head constructed, and the approximated free gape projected on a grid. The left baleen rack was removed from the mouth intact, measured and similarly projected on a grid to estimate the filtering area.

Swimming speed was determined from plotted tracks of the research vessel following surface feeding whales. Onto these tracks were superimposed the paths of the whales using the methods described by Mayo and Marx (1990). Twenty-three segments of right whales' feeding paths from approximately eight hours of observations were analysed to determine swimming velocity during feeding.

With the pump running at the end of a test, the captured zooplankton was removed from the surface of the baleen by siphoning the sample off the mat and into fine mesh screens. The baleen segment was then lifted from the reservoir and any organisms adhering to the filaments were collected. An estimate of the filtration efficiency for the zooplankton size fraction being tested was obtained by comparing the number of zooplankton captured on the baleen filaments with the number injected. To determine both the injection density and the capture numbers, organisms were counted using a dissecting microscope.

In order to examine the energetic implications of the zooplankton capture characteristics of the baleen, the caloric content of the size fractions used in the filtration tests was estimated. Laurence (1976) determined the mean dry-weight caloric content of the adult forms of several taxa of copepods collected from the shelf waters of the northeastern USA, including three taxa that dominated the 1987 Cape Cod Bay feeding path samples: *Calanus finmarchicus* (6,425 kcal kg^{-3}); *Centropages* spp. (4,999-5,245 kcal kg^{-3}); and *Pseudocalanus minutus* (5,071 kcal kg^{-3}). To permit a comparison with Laurence's estimates of caloric content, five weighed sub-samples of the mixed test sample were frozen and the caloric content of each was determined by bomb calorimeter. Three additional sub-samples of each size fraction were counted and weighed to produce an estimated wet weight per organism and, using the calorimeter data, a caloric content per organism was determined. The wet weight to dry weight values were converted using the 1/5 fractional relationship between wet and dry weight caloric content in order to compare our caloric content estimate with those reported by Laurence (1976).

RESULTS

By projecting the opening of the mouth on a scaled grid, the area of the gape at the front of the racks was determined to be 1.21m^2. The left side rack area was estimated by projection to be 4.35m^2, yielding a total baleen surface area of 8.70m^2 for whale #1504. The mean velocity of feeding whales determined from our field observations was 1.34±0.41m sec^{-1} (SE = 0.08) with a range of 0.41-2.20m sec^{-1} for the 23 segments of feeding paths analysed. This swimming velocity differs from that reported by Mayo and Marx (1990, 0.63m sec^{-1}, SE = 0.03) because of the incorporation of information not previously available. For comparison, the velocity of feeding right whales was roughly estimated by Watkins and Schevill (1979) at 3kts or 1.54m sec^{-1}.

From the above values, the calculated mean through-baleen velocity for feeding whales was estimated at 0.188m sec^{-1}. To approximate this velocity, water was pumped from the reservoir of the flume into the channels and through the baleen at 0.11-0.19m sec^{-1} (mean = 0.13m sec^{-1}).

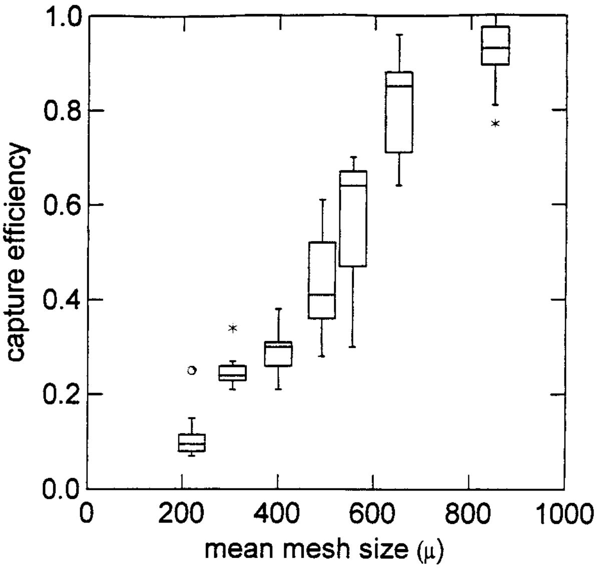

Fig. 3. Baleen capture efficiency determined from flume experiments. The size fractions are expressed as the mean of the mesh sizes used to grade the standard 1987 zooplankton sample.

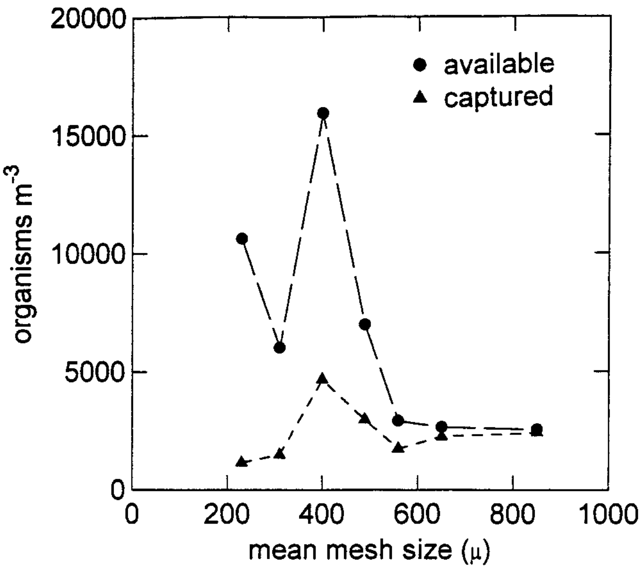

Fig. 4. The estimated mean number of zooplankton organisms available in and captured from the 1987 feeding path samples.

The mean caloric content of the zooplankton sub-samples was 914 kcal kg^{-1} wet weight. Although this value was approximately 10% lower than the caloric content reported by Comita (1966) and Laurence (1976), it was used here as a conservative estimate of the quality of the zooplanktonic food of right whales in Cape Cod Bay.

Sixty-six flume tests were run using the zooplankton size fractions. The zooplankton capture efficiency summarised in Fig. 3 is reported as the number of organisms captured divided by number injected. The effect of the mesh size on the capture of zooplankton is shown by comparing the number of organisms available and captured (Fig. 4). The calculated wet weight and caloric content of individual zooplankters in each size grade are reported in Table 1. Combining the filtering efficiency with the estimated caloric content by test fraction, permits a comparison between the cumulative caloric content of zooplankton available to right whales and the predicted cumulative caloric capture and loss during filtration (Fig. 5). In our tests, greater than 95% of the available energy was obtained from zooplankton sizes greater than those captured on a 333μ mesh net, despite the significant number of organisms available in the lower size fractions of the test sample.

Table 1

Characteristics of 1987 zooplankton size fractions used in the filtration experiments.

Experimental fraction (m)	Capture efficiency	Mean no. organisms m^{-3}	Weight/ organism in g x 10^{-5}	Available kcal m^{-3}	Captured kcal m^{-3}
170-280	0.11	10,621	1.46	0.15	0.02
280-333	0.25	6,012	1.63	0.09	0.02
333-471	0.29	15,922	2.00	0.30	0.09
471-510	0.42	6,997	4.05	0.27	0.11
510-600	0.60	2,915	5.76	0.16	0.09
600-700	0.85	2,661	15.30	0.38	0.33
700-1,000	0.95	2,555	46.50	1.12	1.06
Total		47,683		2.47	1.72

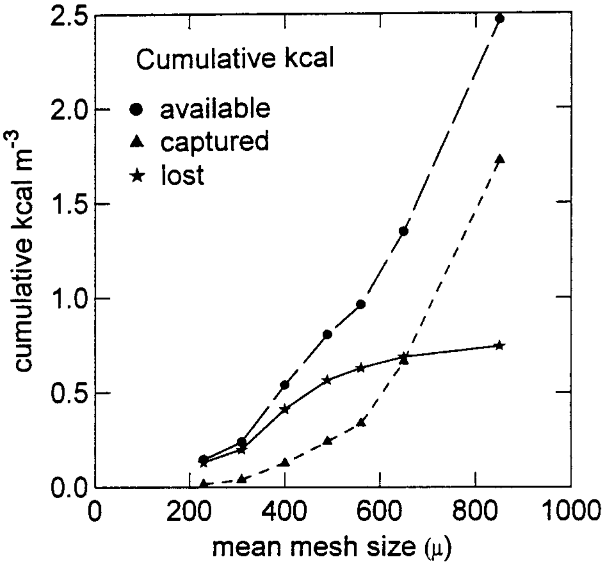

Fig. 5. The cumulative caloric availability, capture and loss during the filtration of $1m^3$ of seawater in the path of feeding right whales in 1987.

DISCUSSION

There are a number of factors that it was not possible to control for in the experimental design which should be considered when applying our findings to a full consideration of right whale foraging efficiency. The stiffening of the baleen filaments in the dried test rack and the softening and shrinkage of copepod tissues resulting from preservation may have decreased the filtering efficiency in the experimental apparatus as compared to that in a foraging whale. Furthermore, in living whales the filtration rate might be greater than in our experiments as a result of increased flow through the mat because of pressure differences hypothesised by Orton and Brodie (1987) and Lambertsen *et al.* (1989). The considerable escape behaviour of living copepods should also be considered as a factor influencing an application of our results to the living whale. However, our interpretation of the experimental results compensates for the effects of escape behaviour because the estimation of available zooplankton in the path of the whales was calculated from net tows also influenced by copepod avoidance behaviour. The activity of a captured copepod on the surface of the baleen may also increase the escape rate, thus reducing the efficiency of filtration in foraging whales (P. Wiebe, pers. comm.). In our study, it was not possible to assess the impact of the hypothesised differences between the filtration rates in the living whale and in our experiments. Nevertheless, it seems likely that the identified influences balance one another to some degree, making the results of the experiments useful in assessing the limitations of the right whale's capacity to capture food organisms.

The relationship between capture efficiency and zooplankton size (Fig. 3) is expected if the filter surface is of non-uniform pore size, as are the matted filaments of the baleen rack. In such a filter system, the capture of zooplankton would be expected to increase in efficiency as the size of the available organism increases. In a feeding right whale, this direct relationship between filtration efficiency and organism size would probably continue until the motility of the prey becomes significant. In collections from the feeding paths of whales from Cape Cod Bay, large, mobile organisms such as euphausids are not encountered and our observations do not, therefore, establish the upper limit of successful foraging. Organisms available as food within the feeding path samples in Cape Cod Bay have a relatively low motility and, once trapped within the mouth, are selected on the basis of the filterability demonstrated in our experiments. Thus, the right whale is well adapted to the harvest of larger, energy-rich zooplankton organisms such as the later life-stages of *C. finmarchicus*, but is less effective at capturing smaller prey items. These smaller prey are both inefficiently filtered and produce less caloric content per organism and are, therefore, less valuable to foraging whales. Nevertheless, right whales feeding in midwater environments dominated by exceptional densities of small zooplanktonic forms could be successful if the density of organisms is so great as to overcome the coincident factors of low efficiency and low organism mass. Fig. 5 demonstrates the importance of the larger size zooplankton fractions in caloric capture by feeding right whales in Cape Cod Bay, where the potential prey is dominated by late larval and adult stages of calanoid copepods. In the bay and perhaps in the other remaining feeding habitats of the western North Atlantic, the right whale's feeding options are therefore limited. Restricted to the capture of large zooplankton by the baleen's filtering characteristics, yet limited in their ability to harvest larger and more mobile nektonic prey by their ponderous filtering apparatus, the right whale's trophic position is narrowly focused on the most productive but labile part of the marine food web. The success of the right whale, as for all filter feeders, is thus determined by the availability of a limited variety of prey organisms whose occurrence may vary widely and unpredictably in the natural system.

Our observations have implications for the methods of zooplankton sampling used to measure the quality of right whale habitats. Using the results of the zooplankton capture tests, it is possible to estimate the size of the net mesh which best approximates the filtering characteristics of the baleen. This estimation is also useful because it presents an approach to evaluate the quality of habitats for which the zooplankton resource has been described from studies using various sampling techniques. We propose that the net mesh that best approximates the capture characteristics of right whale baleen is 333μ, based on the assessment here that more than 95% of the energy captured during the tests came from size fractions captured on mesh greater than 333μ. However, the use of the 333μ mesh as a general functional model of right whale baleen is dependent on the assumptions that the distribution of planktonic prey is similar to the distribution found in our study and that baleen filtration characteristics do not vary significantly with the demographic class of the whales.

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Reproductive parameters of the North Atlantic right whale

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ABSTRACT

North Atlantic right whale reproduction was assessed for the period 1980 through 1998. At the end of this period, we estimated there were between 299 and 437 right whales alive, including 70 mature females. Using maximum and minimum population estimates for the entire period, mean values for gross annual reproductive rate were 0.36 and 0.49 respectively, and the mean value for calves per mature female per year was 0.25. There is a significant decreasing trend in calves per mature female per year over the entire study period. The mean age at first calving is 9.53 years. The mean number of cows recruited annually since 1985 is 3.8. Mean annual calving intervals have increased significantly during the study period from 3.67 years (1980-1992) to over 5 years (1993-1998). Although the North Atlantic population is affected by significant anthropogenic mortality, diminishing reproductive rates are probably also responsible for the plight of this species.

KEYWORDS: REPRODUCTION; TRENDS; RIGHT WHALE; NORTH ATLANTIC

INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) is the rarest species of large whale in the world (Brownell *et al.*, 1986). Despite protection for over 60 years, estimates of current abundance for this species indicate that only about 300 animals survive today (Knowlton *et al.*, 1994; IWC, 2001). Contemporary studies show low levels of recovery, and many years of data are being examined to assess the potential problems in this population. The photographic identification of individual whales has proved to be invaluable in evaluating a variety of life-history parameters for the North Atlantic population, including: sex ratios; birth and death rates; inter-birth intervals; and population abundance and trends (e.g. Kraus *et al.*, 1986a; b; Fairfield, 1990; Hamilton and Mayo, 1990; Kraus, 1990; Kenney and Kraus, 1993; Schaeff *et al.*, 1993; Brown *et al.*, 1994; Knowlton *et al.*, 1994; Hamilton *et al.*, 1995; 1998; Caswell *et al.*, 1999).

Knowlton *et al.* (1994) summarised the then available information on reproductive biology of the western North Atlantic right whale population based on data obtained by repeated sightings of photographically identified individuals. From 1980-1992, 145 calves were born to 65 different females. Mean age at first birth was 7.57 years, which was expected to increase with the duration of the study. The number of reproductively active females was stable at around 51 animals from 1987-1992, with newly mature recruits balancing mortalities. The mean interval between calves was estimated at 3.67 years. Although the data suggested that this interval was increasing with time, the trend was not statistically significant. The total number of individuals in the population was estimated at 295. Gross annual reproductive rate (GARR), mortality rate and population growth rate were estimated at 4.5%, 2.0% and 2.5%, respectively. The population growth rate was substantially lower than southern right whale populations off Argentina and South Africa (Best, 1990; Payne *et al.*, 1990). Anthropogenic mortality caused by collisions with ships and entanglement in fishing gear were identified as among the primary causes of poor population recovery. However, other potential problems were suggested as factors that may lead to reduced reproductive rates, including inbreeding depression, competition for food from other species, climatic changes resulting in reduced food availability and sub-lethal effects of toxic contaminants. Since Knowlton *et al.* (1994), additional information has become available and some parameters have changed. An updated analysis is presented of North Atlantic right whale life history parameters, including data collected through 1998 which suggest that reproduction has recently been compromised.

METHODS

Right whales in the North Atlantic have been individually identified and catalogued since the 1950s using the callosity patterns and scars found on their heads and bodies (Payne *et al.*, 1983; Kraus *et al.*, 1986a). Right whale identification photographs have been obtained through both aerial and shipboard surveys over the last twenty years. Although there has been significant variation in effort from year to year, photographic surveys for right whales have been undertaken annually in the southeastern US wintering ground since 1984, in Cape Cod Bay since 1982 and in the Bay of Fundy since 1980. Right whale surveys started in the Great South Channel in 1979, but there have been several years in the early 1990s with no effort in that area. Surveys on the Nova Scotian Shelf started in 1983, and have continued sporadically to the present. Since photographic identifications provided repeated records of individual whales, information on population size, mortality and reproductive parameters (including annual calf production, calving intervals, age at first parturition and the number of new cows recruited annually) was available from the North Atlantic right whale catalogue (Hamilton and Martin, 1999). A supplementary genetics study has provided gender information for 270 individuals (Brown *et al.*, 1994). Subsets of the data were used to examine different questions.

In the present paper, population estimates were obtained in two ways. The total catalogued population minus the cumulative numbers of presumed dead[1] for that year was chosen as a lower estimate (Table 1, $n_{min} = i\text{-}m_p$). This

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[1] i.e. Not seen for five years following Knowlton *et al* (1994), and see below.

estimate is likely to be low, since not all calves are photographically identified in a given year, and some animals presumed dead may be re-sighted after a five year gap in the sighting record. The second estimate (Table 1, n_{max}) was obtained using the back-calculating method of Knowlton *et al.* (1994) for the entire period, but assuming zero presumed mortalities. The starting year was 1998 as all catalogued whales minus those known to be dead plus all calves known to be born but not photographically identified ($n = 53$). Previous years were then estimated by subtracting the calves of year x for year$_{(x\text{-}1)}$ and adding any mortalities known to have occurred in the catalogued whales in that year (known mortalities are given in brackets in Table 1 under catalogued whales). Since additional unreported mortality probably occurred, and some calves not identified in their first year may have been added to the catalogued whales at a later date, these estimates are considered to be too high.

Right whale mortality was documented through strandings, although not all dead animals are reported or come ashore. Mortality was therefore estimated for the population by presuming death in the sixth year for any individual with a hiatus of five years or more in the sighting records (Table 1, m_p). Where dead stranded right whales were identified ($n = 10$), those individuals (identified in brackets) were removed from the cumulative count of catalogued whales (Table 1, i) in the year in which they died. Prior to 1986, the study period was not long enough to meet the presumed dead criterion, so the early (m_p) estimates are unreliable. After 1992, offshore survey effort in the Great South Channel and the Nova Scotian Shelf was reduced. It is believed that not all whales presumed dead in this period were really dead – they may just be missing from the limited photographic samples.

For estimating reproductive parameters, adult females were classified as mature beginning in the year in which they were first seen with a calf, and were eliminated from all subsequent counts if they died or were presumed dead after a six-year hiatus in sightings. GARR was estimated from the number of calves expressed as a proportion of the total estimated population for both the lower and upper abundance estimates. Calves per mature female per year (CMFY) was estimated from the number of calves expressed as a proportion of the total number of mature adult females in that year.

All data on calving were used to estimate age at first parturition. New cows were counted as recruited to the population using data starting in 1985, to try and eliminate recruits who were in fact older cows that had not been observed with calves during the early part of the study period.

Annual calf production is presented for the years 1980-1998. We believe most calves have been reported in this population since 1991 because of intensive survey effort (*ca* 90 aerial survey days per year) in the only known calving ground off the southeastern US in the winter. However, reliable photo-identification requires that young right whales have fully developed callosity patterns which in fact do not stabilise until they are six months old. Since all cows do not use the same summering habitats, not all calves are photographed between 6 and 12 months, and these therefore remain unidentified. Whales added to the catalogue as animals of unknown age probably represent unidentified calves that grew up without being sighted or clearly photographed in their first year rather than animals from an un-photographed population of adults. For this paper, annual calf count (Table 1, c) includes all calves, even those that

Table 1

Estimated measures of reproduction by year for North Atlantic right whales.

Year	Catalogued whales (i) [1]	Presumed dead (m_p) [2]	Abundance [3]		Mature females [4]	Calves (c) [5]	GARR [6]		CMFY [7]
			(n_{min})	(n_{max})			($c/(n_{min})$)	(c/n_{max})	
1980	96	2	94	240	17	6	0.064	0.025	0.35
1981	149	4	145	246	21	8	0.055	0.033	0.38
1982	173	5	168	254	28	12(1)	0.071	0.047	0.43
1983	189(1)	5	184	265	34	9	0.049	0.034	0.26
1984	203	5	198	273	39	12	0.061	0.044	0.31
1985	220	5	215	285	41	11	0.051	0.039	0.27
1986	242(1)	5	237	296	47	13	0.055	0.044	0.28
1987	258	9	249	308	51	11	0.044	0.036	0.22
1988	277	13	264	319	53	8(1)	0.030	0.025	0.15
1989	297(1)	19	276	326	52	18(2)	0.065	0.055	0.35
1990	308	20	288	341	54	13(1)	0.045	0.038	0.24
1991	321(1)	28	293	353	54	17	0.058	0.048	0.31
1992	333(1)	32	301	369	55	12	0.040	0.033	0.22
1993	343	34	309	380	57	8(2)	0.026	0.021	0.14
1994	357	48	309	386	60	9	0.029	0.023	0.15
1995	364(2)	62	302	395	60	7	0.023	0.018	0.12
1996	377(2)	72	305	400	70	22(1)	0.072	0.055	0.31
1997	390(1)	77	313	419	75	20(1)	0.064	0.048	0.27
1998	389	90	299	437	70	6(1)	0.020	0.014	0.09
				1980-1998 means and SDs			0.049 (0.017)	0.036 (0.012)	0.25 (0.094)

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[1] Includes all whales cumulatively identified in the North Atlantic up to and including that year, minus ten whales known to have died during the period (i). Known mortalities are given in brackets. [2] Includes all animals cumulatively presumed dead in that year (m_p). [3] Minimum population size (n_{min}) equals the total number of catalogued whales minus presumed dead for that year (i-m_p). Maximum population size (n_{max}) is back-calculated following the method of Knowlton *et al.* (1994), but in this case assuming zero presumed mortality. [4] Includes those observed at least once with a calf, minus those presumed dead. [5] Includes unidentified individuals (known deaths are in brackets). [6] GARR (gross annual reproductive rate or crude birth rate) is the number of calves expressed as a proportion of the total estimated population for both estimates. [7] CMFY (calves per mature female per year) is the number of calves expressed as a proportion of the number of adult females recorded as mothers in that or in any previous year.

remained unidentified (but whose mothers were recorded) and those that were known to have died in their first year (known calf mortalities are given in brackets in Table 1).

Calving intervals were examined for every cow in the population who calved more than once. Mean calving intervals were calculated from the annual totals, with intervals longer than seven years excluded because of gaps in the sighting records. Because of the possibility that females are calving in one or more unknown locations, and to examine whether the probability of sighting mature females had declined, the rate at which mature females were sighted annually throughout the study period was analysed. The intervals between sightings of both juvenile and mature females for the 1980s and the 1990s were also compared to see if there were differences in sighting probability. Finally, the sightings histories of mature females with six- or seven-year calving intervals were evaluated to determine whether the longer calving intervals could have included a missed calving record due to a reduced number of sightings prior to calving. To achieve this, it was assumed that no cow had a calf within the first two years of calving or within two years prior to calving. This assumption is based upon the low probability of a two-year calving interval. Of 127 calving intervals recorded since 1980, only one (less than 1%) was two years. Therefore, in this analysis of sighting histories, it was assumed that calves could have been missed in our database if cows were not observed in years three and four of a seven-year interval, or year three of a six year interval.

RESULTS

Estimates of population size and mortality

The population size in 1998 was estimated to be at least 299 and no more than 437 (Table 1). The current catalogue includes all known photographs of members of this population since 1935, and currently includes documentation of 389 individual right whales, ten of which are known to have died (Table 1, *i*) (Hamilton and Martin, 1999). The number of whales included in the catalogue at any one time does not represent an absolute count of North Atlantic right whales. The actual number may be lower (since unreported mortality is certain to occur) or higher (because not all calves born in any year are photographically identified). Between two and 14 animals were presumed to have died annually using the presumed mortality criterion, and the cumulative ‘presumed dead’ estimates are given in Table 1 by year. An additional negative bias is that there may be individual animals which are not approachable or which rarely or never use habitats where photographic sampling occurs, and therefore have never been photographed. Prior to the present paper and the consideration of abundance estimates given in IWC (2001), the only other published estimate is that of Knowlton *et al.* (1994). As noted in IWC (2001) recapture heterogeneity and changes in survey effort make capture-recapture estimates of abundance problematic.

Reproductive females

The number of reproductively active females has increased slowly throughout the study period, although it remained stable in the low fifties, from 1987-1992. Of 21 photographed mothers in 1996, 10 were new mothers, 10 had calved previously and 1 remains to be identified. An additional 8 new females calved in 1997, bringing the total number of cows to 75, although presumed mortalities reduced this number to 70 in 1998 (Table 1).

Calving rate

The number of calves born per year from 1980-1998 ranged from 6-22, with a high level of inter-annual variability. The mean annual calving rate for 1980-1998 was 11.32 calves per year (SE = 1.09). The calving rate was well below the mean for three successive years with 8, 9 and 7 calves in 1993, 1994 and 1995, respectively. In 1996 and 1997, however, the number of calves increased to record highs of 22 and 20 respectively. In 1998, calf production fell to a record low of 6 calves.

Calving intervals

Apparent calving intervals (the number of years between observed calves) have increased across the population of repeatedly calving females since 1992 (Table 2). Knowlton *et al.* (1994) reported a mean calving interval of 3.67 years (SE = 0.11; $n = 86$; range = 2-7). The most frequently observed interval was three years, with 53 observations (61.6%). They also reported an apparent trend toward increasing intervals with time, though it was not statistically significant ($p = 0.083$). Since 1992, there have been 40 new observations of calving intervals added, including only three observations of a three-year interval, representing 7.5% of the total.

Table 2

Distribution of calving intervals by year for North Atlantic right whales. Mean intervals are calculated from annual totals, with intervals longer than 7 years excluded because of inconsistency in the sighting records.

	Calving intervals in years							
	2	3	4	5	6	7	8+	Mean interval
1980	-	1	-	-	-	-	-	3.0
1981	-	-	1	1	-	-	-	4.5
1982	-	1	-	1	-	-	-	4.0
1983	-	2	1	-	-	-	-	3.3
1984	-	7	-	-	-	-	-	3.0
1985	1	6	-	2	-	-	-	3.1
1986	-	5	2	-	-	-	-	3.3
1987	-	4	-	1	-	1	-	4.0
1988	-	2	1	1	1	-	-	4.2
1989	-	7	2	4	-	-	-	3.8
1990	-	7	1	1	1	-	-	3.6
1991	-	4	3	3	2	1	-	4.5
1992	-	7	1	-	1	-	-	3.4
1993	-	-	3	1	-	-	-	4.3
1994	-	-	3	1	-	-	-	4.3
1995	-	1	1	1	1	-	1(13yr)	4.5
1996	-	-	1	6	2	1	-	5.3
1997	-	2	1	2	3	3	1(13yr)	5.4
1998	-	-	1	-	3	1	-	5.8
Totals	1	56	22	25	14	7	2	

The mean calving interval for multiparous cows for 1996 and 1997 ($n = 22$) was 5.3 years. In the 1993-1998 period, two females gave birth after apparent gaps of 13 years, although these animals were not observed in many of the intervening years. Calving intervals in the two periods 1980-1992 and 1993-1998 are significantly different (Wilcoxon Rank Sum Test; $P < 0.001$) whether the two 13-year intervals are included or not (Fig. 1). The 13-year intervals were dropped from all subsequent analyses.

A non-parametric one-way ANOVA (Kruskal-Wallis Test) showed statistically significant variability in calving intervals between years ($p < 0.001$); but no significant inter-individual variability ($p = 0.749$). A bi-variate ANOVA (parametric), looking at effects of year and

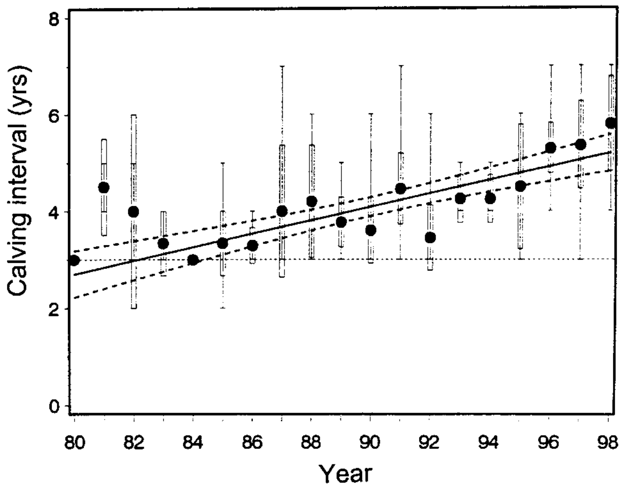

Fig. 1. Trends in calving intervals in the western North Atlantic right whale population, 1980-98. For each year, the mean is shown as a solid circle, one standard error to each side of the mean with a vertical box, and the range by a vertical line with a small horizontal tick at each end. The solid sloping line is the increasing trend shown by least-squares regression on all individual data points ($n = 127$), with the 95% confidence interval shown by dashed lines. The fine dashed line shows the 'typical' three-year interval expected in right whales for reference.

individual on calving intervals, showed that changes were statistically significant by year but not by individual cow ($n = 120$; YEAR: $F = 3.11$; $p < 0.001$; $n = 120$; INDIVIDUAL: $F = 0.67$; $P = 0.930$).

Linear regression analyses of trends in calving interval over time demonstrate that calving intervals have been increasing significantly between 1985 and 1998 (slope = 0.209; $n = 112$; SE = 0.037; $p < 0.001$). To determine whether changes in sighting rates of adult females could be affecting apparent calving intervals, sighting rates for mature females (those seen in a given year as a proportion of those available to be seen) were calculated. They have not changed significantly in 19 years, although there has been a slight increase over the period (Table 3).

A comparison of sighting intervals between the 1980s and 1990s for both juvenile and adult females shows no significant difference between the decades (Table 4).

Table 3

Sighting rate for adult females by year. Number of cows sighted in a year as a proportion of available cows for that year.

Year	No. of cows available	No. of cows sighted	Sighting rate
1980	17	9	0.53
1981	20	10	0.50
1982	28	15	0.54
1983	34	13	0.38
1984	39	22	0.56
1985	41	21	0.51
1986	47	21	0.45
1987	51	18	0.35
1988	53	23	0.43
1989	52	28	0.54
1990	54	27	0.50
1991	54	26	0.48
1992	55	23	0.42
1993	57	18	0.32
1994	60	31	0.52
1995	60	32	0.53
1996	70	44	0.63
1997	75	50	0.71
1998	70	40	0.57

Table 4

Intervals between sightings for females in the 1980s and 1990s.

Category	Period	*n*	Mean (yrs)	SD
Juvenile females	1980-1989	161	1.37	0.56
	1990-1998	129	1.40	0.65
Adult females	1980-1989	118	1.93	0.84
	1990-1998	253	1.93	0.97

An analysis of individuals shows that the longer calving intervals in 1997 and 1998 can be attributed to animals with long gaps in the sighting records (Table 5), making it possible that calvings by those individuals were missed. For 21 females with calving intervals of six or seven years, 12 could have had calves that were missed in this study. Of the nine females with long calving intervals that had adequate sighting records to exclude missed calvings, eight occurred in the 1990s. However, of the 21 females with long intervals, 19 appear to use the southeastern US as their only calving ground. The remaining two cows (No.1242 and No.1248) have only been seen in the summer with calves in the Gulf of Maine and their calving location is unknown. We believe that the consistent survey effort in the southeastern calving ground since 1990 renders it unlikely that cows would be missed in that area. Given that calving areas do not appear to be feeding areas, they are probably less subject than northern habitats to re-distribution of whales in poor food years. We therefore suspect that these longer calving intervals are real, and not artefacts of missed sightings in calving years.

Table 5

Prior sighting histories for cows with six and seven year calving intervals. Calves could have been missed if cows were not observed in years 3 and 4 of a seven-year interval, or year 3 of a six year interval.

Whale ID	Year	Interval (years)	Missed years prior to calving (by year)						Missed calves possible	Southeast calving?
1004	1987	7	0						No	Y
1242	1988	6	1	2	3		5		Yes	N
1142	1990	6		2	3		5		Yes	Y
1145	1991	7	1	2		4		6	Yes	Y
1204	1991	6	1						No	Y
1240	1991	6	1	2					No	Y
1612	1992	6	1	2	3		5		Yes	Y
1241	1995	6	0						No	Y
1114	1996	6	0						No	Y
1142	1996	6	1	2			5		No	Y
1281	1996	7	1						No	Y
1014	1997	6	1	2	3				Yes	Y
1118	1997	7	1	2	3				Yes	Y
1240	1997	6	1						No	Y
1243	1997	6	1	2					No	Y
1248	1997	7	1	2	3	4	5	6	Yes	N
1310	1997	7	1		3	4	5		Yes	Y
1233	1998	6	1	2	3	4	5		Yes	Y
1315	1998	6	1	2	3	4			Yes	Y
1321	1998	7	1	2	3	4	5		Yes	Y
1515	1998	6	1	2	3	4	5		Yes	Y

Age at first parturition

Knowlton *et al.* (1994) reported a mean age at first calving of 7.57 years (SE = 0.63). Since 1992, an additional 12 known-age females have given birth for the first time, more than doubling the sample size. The mean age at first calving is now 9.53 years (SD = 2.32), consistent with those reported for the southern right whale (Best *et al.*, 2001; Cooke *et al.*, 2001).

Cow recruitment

Since 1985, there have been between 0 and 10 new cows recruited into the population annually (mean 3.8 per year). Although younger females recruited into the breeding pool in the 1990s might be expected to have longer calving intervals (as less-experienced foragers and mothers), the analyses of interval by year and individual suggest this is not the case.

Estimates of GARR

The mean estimates of GARR for the entire period are 0.036 for the lower estimate and 0.049 for the upper estimate. Annual GARR estimates range from 0.020-0.072 for the lower population estimates, and from 0.014-0.055 for the upper population estimates (Table 1). Linear regressions on both GARR estimates show no statistically significant trends.

CMFY

The mean number of calves per mature female per year (CMFY) for the period is 0.25 ($SD = 0.094$). The mean CMFY for the 1980s is 0.30 ($SD = 0.077$) and for the 1990s is 0.20 ($SD = 0.078$). The annual variation in CFMY values is high, ranging from 0.09-0.42. A linear regression shows that the CMFY has decreased over the study period ($slope = -0.0109$, $p = 0.0004$).

DISCUSSION

The application of capture-recapture models to estimate biological parameters for this population are made problematic by the cumulative effects of capture heterogeneity (especially calving females), changes in survey effort since the 1990s, and large shifts in spring and summer whale distribution during the study period (Kenney, 1994). The application of models used by Best and Underhill (1990), Payne *et al.* (1990), and Barlow (1990) are rendered impractical because many of the assumptions of these models are violated. In addition, if subsets of the population are used that meet the assumption requirements, sample sizes become extremely small, the confidence intervals around those estimates are consequently large and the estimates are unhelpful in a management context. A cumulative identification approach was therefore used to put upper and lower bounds on the estimates of population used in this paper. Estimates of the population prior to 1986 are likely to be underestimates, as survey effort was inconsistent in all areas, and animals were still being ‘discovered’ photographically at a fairly high rate. Insufficient survey effort and photographic discovery may also increase presumed mortalities by making capture probabilities lower for offshore survey areas. Further discussion of the question of estimating abundance and the ‘presumed mortality’ concept is given in IWC (2001).

Annual calf production shows large variability, ranging from 6-22 calves during the study period, around a mean of 11.3. The three years (1993-1995) in which calving dropped well below the mean, followed years in which the distribution of the population on its feeding grounds was anomalous. In 1992, right whales apparently did not use the Great South Channel feeding habitat, and did not appear in the Nova Scotian Shelf feeding habitat during the ‘expected’ seasons, based upon all survey data from the 1980s (Sutcliffe and Brodie, 1977; Kenney, 1994). From 1993-1998, right whales were rarely observed on the Nova Scotian Shelf feeding ground but somewhat larger numbers than expected were observed in the Bay of Fundy. However, the lack of survey effort in the Great South Channel from 1993-1997 means that nothing is known of right whale occurrence during that period there. Clearly, a female right whale must obtain sufficient energy from feeding to have a surplus over her own energetic needs stored for pregnancy and lactation. If right whales were forced to spend more time than usual in searching for appropriate foraging locations, then mature females may have had more difficulty in assimilating sufficient food.

One dramatic feature of North Atlantic right whale reproduction is the significant increase in calving intervals over the 19 year period of study. No definitive causes for the increase exist, and hypotheses currently being examined to account for it include inbreeding, pollutant effects and food limitations (IWC, 2001). Other possibilities include large numbers of senescent mothers and/or an unstable age structure, although the analysis conducted by Hamilton *et al.* (1998) of age structure in this population does not provide much support to either hypothesis.

Mean GARR estimates for the study period are 0.049 and 0.036, which bracket the estimate of 4.5% made by Knowlton *et al.* (1994). Data collection in the North Atlantic includes large portions of the year-round range of the population and thus GARR values may not be comparable to Southern Hemisphere estimates, where study areas are limited to wintering calving grounds where segregation is known to occur. GARR data from Argentina shows ratios of calves to the total population vary between 10% and nearly 60% (Payne *et al.*, 1990). Patenaude and Baker (2001) report that the calf/total whale ratio in the Auckland Islands wintering grounds ranged from 9-14% during the 1995-1997 period. Since the GARR data do not reflect mortality information, it is not possible to estimate population growth rate from these estimates. Nevertheless, the data presented here suggest that reproductive rates in the North Atlantic population are currently less than one half the rates of comparable right whale populations in the Southern Hemisphere. The North Atlantic population is clearly suffering from significant anthropogenic mortality, but a diminishing reproductive output may be equally responsible for the plight of this species (IWC, 2001). Comparative studies using the Southern Hemisphere right whales as ‘controls’ provide one option for identifying the reproductive issues in the North Atlantic population (and see NMFS, 2000).

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Sighting heterogeneity of right whales in the western North Atlantic: 1980-1992

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ABSTRACT

The population of western North Atlantic right whales (*Eubalaena glacialis*) is distributed primarily between Florida, USA and Nova Scotia, Canada, aggregating seasonally in five geographically distinct, high-use areas. To test the effectiveness of monitoring all demographic classes (juvenile and adult males and females) of the population in these five habitat areas, an evaluation was carried out of the identification records of catalogued right whales collected between 1980 and 1992, for which the age, sex and reproductive status (for adult females) were known. The mean annual identification frequency of adult females was significantly lower than that of adult males, juvenile females and juvenile males. Among adult females, reproductively active females were seen significantly more often than expected when lactating (with a calf) than during their pregnancy or resting years. These data suggest that, while research efforts in the five high-use habitat areas have had relatively equal success at monitoring juvenile males and females and adult males, many adult females are segregated at times from the rest of the population. Lower variability in annual identification frequencies of adult females indicates that they may be more site specific in their distribution than males, particularly during the years when they are pregnant or resting from a previous pregnancy. Re-running these analyses using sighting records updated through 2000 will help determine if the trends continue to be documented regardless of changes in survey effort and patterns of habitat use of some animals.

KEYWORDS: POPULATION ASSESSMENT; MONITORING; NORTHERN HEMISPHERE; NORTH ATLANTIC; RIGHT WHALE

INTRODUCTION

Western North Atlantic right whales (*Eubalaena glacialis*) are known to occur seasonally in at least five geographically distinct habitat areas between Florida, USA and Nova Scotia, Canada (Fig. 1): the southeast USA between Savannah, Georgia and Cape Canaveral, Florida; the Great South Channel (between Cape Cod and Georges Bank); Cape Cod Bay; the lower Bay of Fundy; and Roseway Basin between Browns and Baccaro Banks on the southern Scotian Shelf (NMFS, 1991). Between 1980 and 1992, research efforts were conducted annually in these areas to monitor the population.

A large database of identification records of individually catalogued right whales now exists, the result of intensive photo-identification efforts since 1980 (Kraus *et al.*, 1986a; Crone and Kraus, 1990; Hamilton and Martin, 1999). Annual sightings records of individuals of the best known portion of the population were evaluated (i.e. individuals for which both age and sex have been documented and for adult females, reproductive status). This paper investigates whether research efforts in the five high-use areas have been equally successful at monitoring the demographic classes of the population. It was assumed that the majority of right whales in the western North Atlantic have been photo-identified because the number of new identifications, other than of calves, has been low since 1989 (approximately three per year, New England Aquarium, NEAq, unpublished data). The annual sightings records of individuals from 1980 to 1992 only have been used for this study because in the following years there was a decrease or loss of survey effort in two of the high-use areas, Roseway Basin and the Great South Channel respectively. The null hypothesis is that there is no difference in the rate of identification between groups of best known animals due to age and sex.

METHODS

The dataset was analysed for right whales for which both age and sex were known from standardised systematic surveys in the five high-use areas, from 1980 to 1992. Each identification record included the date and location, age and sex of the animal, details on associations and observed behaviours, and the name of the observer.

Demographic classifications

The sex of recognisable individuals was identified by photographic observation of the genital area, by molecular sex identification (Brown *et al.*, 1994), or, for reproductively active adult females, by consistent association with a new-born calf (Knowlton *et al.*, 1994). Age classification was based on year of birth, length of sighting history or, sometimes, behaviour (see below). Not all right whales could be classified at the initial identification. Observations collected in subsequent years were used to 'back-classify' some animals based on status changes observed later, i.e. reproductive states (resting and pregnant) of adult females were assigned based on the years in which they were seen with a calf.

Animals were classified into one of two age categories: juvenile or adult.

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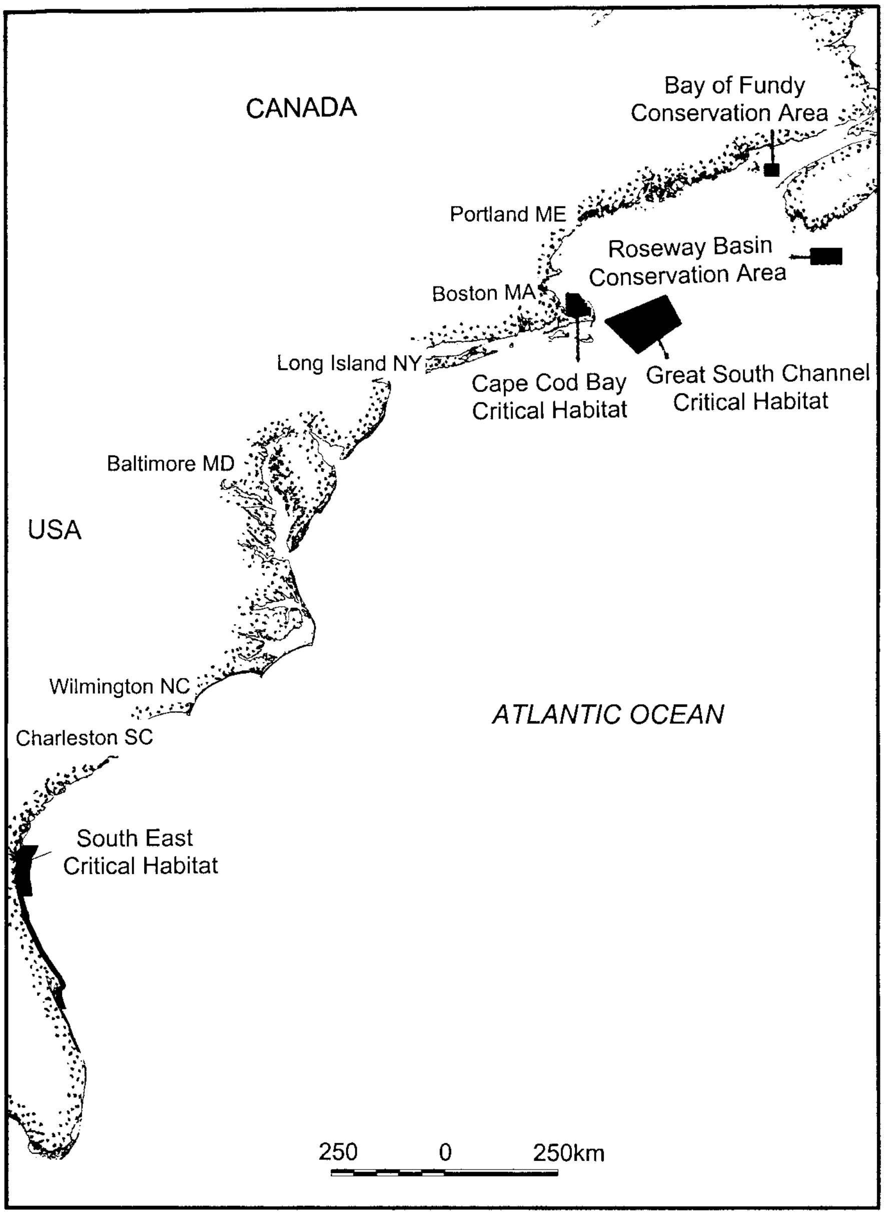

Fig. 1. Critical habitats of the Atlantic coast.

Juvenile

All pre-reproductive right whales, first seen as calves, were classified as juveniles. The mean age at sexual maturity for right whales is unknown, but Payne *et al.* (1990) reported that most first calves were born to female South Atlantic right whales (*Eubalaena australis*) of at least nine years of age. For western North Atlantic right whales, Hamilton *et al.* (1998) estimated the mean age of first parturition at 9.6 years (SD = 2.33). Animals first seen as calves were therefore classified as juveniles until they reached age nine (Hamilton *et al.*, 1998). The age classification of some animals changed from juvenile to adult during the study period.

Adult

Animals were classified as adults based on a known age of nine or more years, a sightings history of at least nine years or for males, body size and positioning as alpha males in surface-active groups (presumptive mating groups) (Kraus, 1991). For females, adults were classified by the presence of a closely associated calf (Knowlton *et al.*, 1994). Juvenile females were back-classified as adults the year before their first known parturition if they gave birth before age nine.

Adult females were further sub-divided into reproductively active females (resting, pregnant or lactating) and non-reproductive females (nulliparous) based on their reproductive history.

REPRODUCTIVELY ACTIVE ADULT FEMALES

Adult females were considered reproductively active once they had been seen with a calf (Knowlton *et al.*, 1994) and as lactating for the entire birthing year based on the estimated weaning time of 10-12 months for northern right whales (Hamilton *et al.*, 1995). The length of gestation for northern right whales is not definitely known. Best (1994) estimated a gestation length of 321-397 days for right whales in the eastern South Atlantic based on the relationship between length and growth rates of foetuses. Payne (1986) assumed a year-long gestation period for right whales in the western South Atlantic, similar to that of other mysticetes (Lockyer, 1984). On this basis, it was assumed that northern right whales have a three-year interval between birthing events divided into a resting year, a year of gestation, and a year of lactation (Knowlton *et al.*, 1994). The mean calving interval for adult female right whales from 1980-1992 was 3.67 years (Knowlton *et al.*, 1994). Reproductively active females producing calves on longer than three-year intervals were classified as resting for two years (four-year interval), three years (five-year interval), or four years (six-year interval). Non-lactating adult females were back-classified as pregnant or resting in particular years on the basis of an observed subsequent birth. There are no means for determining pregnancy other than the presence of a calf the following year. Thus, the number of pregnant females is biased downward and the number of resting females is biased upwards because miscarriages or stillborn calves are unaccounted for.

NON-REPRODUCTIVE (NULLIPAROUS) ADULT FEMALES

Adult females not observed with a calf since 1980 were considered nulliparous. Included was one female, catalogue #1045, sighted with a calf in 1935, but not seen with a calf since (Hamilton *et al.*, 1998). Juvenile females were classified as nulliparous from age nine until the year of the first known pregnancy (back-classified by the presence of a calf the following year). The number of nulliparous females is biased downward in the first eight years of the study because there is no reliable method of estimating age for animals not first seen as calves. Adult females not seen with a calf were not classified as nulliparous until their sightings history spanned nine years.

Identification frequencies

Annual identification frequencies were calculated for each age (juvenile and adult) and sex (male and female) category by dividing the number of individuals identified each year (i.e. photographed and subsequently identified in the catalogue), by the total number in that class 'available to be seen' (i.e. known to be in the population in that year). To avoid any bias from unequal numbers of identifications of individuals in different habitat areas, which could result from unequal survey effort or variations in patterns of habitat use, each animal was scored simply as present or absent from the records within a given year, regardless of the number of times or the location where that individual was seen. Annual identification frequencies were summed to give a measurement of the probability that individuals within each category would be seen in any particular year. The identification records of adult females were further sub-divided based on their reproductive status (nulliparous, resting, pregnant and lactating).

Statistical analysis

Tests were made of the effects of age and sex on sighting probabilities, and the presence of a time trend in these probabilities, through binary logistic regression using the software package SPSS. Both age and sex were transformed into categorical variables with values of 0 or 1 (age 0 = juvenile; age 1 = adult; sex 0 = male, sex 1 = female). Through stepwise removal of parameters, their significance was tested from the ensuing changes in deviance and degrees of freedom of the regression model. Regression parameter values for the logit models were estimated by maximum-likelihood. Given the large number of individuals ($n = 337$), each whale's presence or absence in a given year was treated as one case, regardless of whether the same whale was observed in previous or later years, i.e. each observation was treated as independent from others of the same individual. Effects due to individual histories were therefore not tested here.

Differences in the rate of identification between adult females in different reproductive states were examined using a chi-square analysis. Using the mean calving interval of 3.67 years (Knowlton *et al.*, 1994) expected values were generated for sightings based on the null hypothesis that there was no difference in the rate of identification of adult females due to reproductive state. It was assumed that adult females were pregnant for one year, lactating for one year and resting for 1.67 years. These values were tested against the actual number of adult females seen in each of the three reproductive categories.

RESULTS

In total, there were 6,209 sightings of 1,700 right whales representing 337 catalogued individuals identified between 1980 and 1992; 92% of those sightings were from survey efforts in the five high-use habitat areas. Of those 337, both age and sex were known for 231 animals (69% of the known population). Following each of these known individuals over their respective periods of availability for sighting, yielded 1,430 records (Table 1). Table 2a presents the results from the logistic regression; total sighting frequency estimates by age and sex from the regression are given in Table 2b. No significant time trend in presence or absence of known individuals was found, and age alone did not explain a

Table 1

Number of right whales of known age and sex identified (n=858) as a proportion of the number available to be identified (n=1,430) within each demographic category by year. Multiple indications within a year have been eliminated.

	Adult females			Juvenile females			Adult males			Juvenile males		
	Seen	Available	Frequency	Seen	Available	Frequency	Seen	Available	Frequency	Seen	Available	Frequency
1980	9	17	0.53	0	2	0.00	0	1	0.00	0	0	0.00
1981	9	21	0.43	3	4	0.75	0	2	0.00	0	1	0.00
1982	16	29	0.55	3	6	0.50	2	4	0.50	4	7	0.57
1983	13	35	0.37	5	10	0.50	2	3	0.67	6	11	0.55
1984	22	36	0.61	9	12	0.75	1	3	0.33	9	12	0.75
1985	22	38	0.58	7	16	0.44	3	5	0.60	8	18	0.44
1986	22	41	0.54	14	17	0.82	8	8	1.00	19	21	0.90
1987	20	46	0.43	13	19	0.68	10	12	0.83	18	27	0.67
1988	26	50	0.52	23	26	0.88	32	34	0.94	27	31	0.87
1989	37	59	0.63	21	24	0.88	50	61	0.82	30	33	0.91
1990	35	61	0.57	25	33	0.76	30	71	0.42	21	32	0.66
1991	31	65	0.48	20	33	0.61	48	78	0.62	22	34	0.65
1992	26	68	0.38	23	35	0.66	35	81	0.43	19	37	0.51
Total identified	288			166			221			183		
Total available		566			237			363			264	
Mean id frequency			0.51			0.63			0.55			0.62
Standard deviation			0.08			0.24			0.32			0.25

Table 2a

Results of the stepwise binary logistic regression of the dependent variable, presence of a whale in the sighting records, against year, age, sex and age x sex interaction term. Value of coefficients B are for the log-odd ratio transforms (log (y/1-y)). Wald values test for significance of parameters, given the change in degrees of freedom (df) when parameters are added or removed from the model. Parameters contributing significantly to the model are in **bold**.

Variables	B	SE of B	Wald	df	Significance
Constant	**0.831**	**0.097**	**73.153**	**1**	**<0.001**
Year	-	-	1.240	1	0.266
Sex	-	-	0.031	1	0.860
Age	**-0.389**	**0.145**	**7.197**	**1**	**0.007**
Age by Sex Interaction	**-0.407**	**0.137**	**8.888**	**1**	**0.003**

significant amount of variation in the data. The final model includes an intercept (the constant), age, and the interaction of age by sex, all of which are highly significant ($p < 0.01$). The intercept alone describes the probability of juvenile males (i.e. age = 0 and sex = 0) being present. Juvenile females have the same predicted probability as juvenile males, because sex has no effect on presence or absence from the records, unless individuals are adults (i.e. through the interaction term). Adults have a lower probability of being present than juveniles, and adult females have a lower probability of presence than adult males.

The relative numbers of the three categories (pregnancy, lactation and resting) of reproductively active adult females were examined to determine what proportion of adult females seen could be attributed to a phase of the reproductive cycle (Table 3a). It was tested whether their proportions were as expected given a calving interval of 3.67 years and an even chance of observations among categories.

Table 2b

Observed frequencies (from Table 1) and probabilities of presence predicted from the regression model in Table 2a of each age and sex category.

	Observed frequencies		Predicted probability of presence	
Sex	Juvenile	Adult	Juvenile	Adult
Male	0.693	0.609	0.697	0.509
Female	0.700	0.509	0.697	0.609

The proportions were highest among lactating animals and lowest among pregnant ones. Among the three classes of reproductively active adult females, lactating females were seen significantly more often than expected ($\chi^2 = 76.917$, $p < 0.001$) and pregnant and resting females significantly less often than expected ($\chi^2 = 9.508$, $p = 0.002$), ($\chi^2 = 19.508$, $p = 0.001$) respectively (Table 3b). It was not possible to calculate identification frequencies for adult females by reproductive status because it was unclear how many were available to be seen in each category. Only the total numbers of reproductively active adult females or nulliparous females were known.

The individual sightings records of reproductively active adult females were further examined to assess their use of the southeastern USA calving ground. Of 65 known reproductively active adult females that have produced 145 calves between 1980 and 1992, 16 (25%) have never been seen on the calving ground with a calf and only 19 (13%) have been seen in the southeast with all of their calves. There were 56 (86%) which were available to be monitored (identified) both the year before parturition (during pregnancy) and the year after weaning (resting) for 124 calvings. In a significant portion of these calvings (51%),

Table 3a

Number of individual adult females identified annually. The annual sightings of reproductively active females were further subdivided into resting, pregnant or lactating status. The number of non-reproductive adult females (nulliparous) was subtracted from the total adult females seen to obtain a proportion of reproductive females seen by reproductive status (n=256). The percentages of resting, pregnant and lactating females are given in brackets. Identification frequencies were not calculated for reproductively adult females because it was not known how many were available to be seen in each category.

	Adult females	Non-reproductive	Reproductively active		
Year	No. seen/available	Nulliparous seen/available	Resting (%)	Pregnant (%)	Lactating (%)
1980	9/17	2/4	1 (14.3)	1 (14.3)	5 (71.4)
1981	9/21	0/4	0 (0.0)	2 (22.2)	7 (77.7)
1982	16/29	1/4	3 (20.0)	2 (13.3)	10 (66.6)
1983	13/35	0/4	3 (23.0)	1 (7.7)	9 (69.2)
1984	22/36	0/4	6 (27.3)	4 (18.2)	12 (54.5)
1985	22/38	3/4	6 (31.6)	2 (10.5)	11 (57.9)
1986	22/41	0/4	7 (31.8)	2 (9.1)	13 (59.1)
1987	20/46	2/3	6 (33.3)	1 (5.5)	11 (61.1)
1988	26/50	2/3	9 (37.5)	8 (33.3)	7 (29.2)
1989	37/59	8/9	9 (28.6)	3 (10.7)	17 (60.7)
1990	35/61	6/10	7 (24.1)	10 (34.5)	12 (41.4)
1991	31/65	4/9	4 (14.8)	7 (25.9)	16 (59.3)
1992	26/68	4/10	8 (36.4)	1 (4.5)	13 (59.1)
No. seen/available	288/566	32/72	69	44	143
Mean percentage			24.8	16.1	59.0
Standard deviation			10.6	10.0	12.6

Table 3b

Results of the chi-square analysis on the three categories of reproductively active adult females using observed frequencies from Table 3a, a calving interval of 3.67 years to generated expected values and an even chance of observations.

Frequencies	Resting	Pregnant	Lactating
Observed	69	44	143
Expected	116.49	69.75	69.75
χ^2	19.508	9.508	76.917
Significance	<0.001	0.002	<0.001

adult females were only seen in the year in which they gave birth (63/124, $\chi^2 = 19.898$, $p < 0.001$). Reproductively active adult females were identified during the year before parturition for 25% (30/124) of calvings, and the year after weaning for 11% (14/124). There were only 17 calvings (13%) where adult females were identified both the year before and the year after. Of the 61 calvings for which adult females were identified before and/or after parturition, most of these identifications (61%) were recorded in the spring in Cape Cod Bay or the Great South Channel, but not during the summer and autumn in the Bay of Fundy or Roseway Basin (Brown, 1994). On average, 72% of the cow-calf pairs seen in other areas between 1989 and 1992 (years of increased survey effort in the calving ground) were also seen the same year in the southeast USA (Kraus *et al.*, 1993).

DISCUSSION

The similarity in the frequency of identifications of male and female juveniles and adult males (Table 1) demonstrates that survey efforts in the five high-use seasonal habitat areas have had relatively equal success in monitoring these segments of the catalogued right whale population over the 13-year study period. The same monitoring efforts however, have yielded significantly lower identifications for adult females suggesting that many are segregated from the rest of the population, particularly during the inter-birth years. Overall, these analyses indicate that the identification rate among the best known animals is not homogeneous by age and sex. There is now strong evidence for segregation by age, by sex (in adults) and by reproductive state (for adult females), in the western North Atlantic right whale population.

There are several ecological and behavioural reasons why adult female right whales might be seen less often in the high-use areas than other age/sex classes. One is that there could be a dietary difference compared to males or juveniles due to the higher energy demand while producing and rearing offspring (Lockyer, 1984). Female right whales invest heavily in their offspring, giving birth in the winter months to a calf that averages 4.5m in length and about 800kg in weight. By the time the calf is weaned it may be 8.5m long with an estimated weight of 5,000kg (NEAq, unpublished data). Lactation is estimated to last 10-12 months (Hamilton *et al.*, 1995) followed by a year or more of rest, presumably to replenish energy reserves depleted during lactation (Lockyer, 1984). Adult females may also be feeding on different prey types at different times of their reproductive cycle. Dietary differences between pregnant and lactating animals have been found for spotted dolphins, *Stenella attenuata* (Bernard and Hohn, 1989) and harbour porpoises, *Phocoena phocoena* (Recchia and Read, 1989).

Another possible reason could be avoidance of areas where other right whales aggregate, especially those areas where there is a high percentage of males. Given the high costs of reproduction (both in terms of time and energy) and the prevalence of surface-active groups in the northern habitat areas (Kraus, 1991), it may be beneficial for non-calving adult females to avoid areas where males predominate, until they are ready to reproduce. This might explain the low numbers of adult females seen on Roseway Basin, the only area where juvenile and adult males predominate and the area with the highest occurrence of surface-active groups (Kraus and Brown, 1992; Brown, 1994).

The only known calving ground for right whales in the southeastern USA was identified in the early 1980s (Kraus *et al.*, 1986b) but speculation on additional calving grounds exists in the North Atlantic. In the western South Atlantic population, two adult females were observed with newborns in a second calving ground in the waters off the coast of Brazil (Best *et al.*, 1993). These females, observed in previous years with calves in Argentine waters, were using an alternative calving area in some years. In the western North Atlantic, the evidence suggests that the southeastern USA is certainly the primary, and possibly the only, calving area for this species. There have been no confirmed reports of calvings in other areas. Between 1980 and 1992, 74% of the reproductively active adult females were seen in the southeast. The remaining cow-calf pairs may have also used this area but experienced early (before January) or late season (after the end of March) births.

However, annual counts of cow-calf pairs seen in the southeastern USA have increased with increasing survey effort in the latter years since 1989. The size of the survey area in the early years (pre-1989) was large, ranging from North Carolina to southern Florida. In the latter years, a similar amount of effort over a longer season was concentrated in a smaller area between Savannah, Georgia and Cape Canaveral, Florida, suggesting the increase in the annual counts reflects a concentrated distribution of animals over a protracted season in this region.

There have been no identifications of non-calving adult females in the southeastern USA in the year preceding or following their parturition. However, there were sightings of reproductively active adult females in a year in which they were expected to give birth, but in which no calf was recorded. These individuals may have experienced a near-term abortion or a still birth. Several deaths of young right whales (less than 5m in length) have been documented in the coastal waters of Florida and Georgia (Kraus, 1990). In 1989, five adult females were seen in Florida and later that year in other areas without calves, and three neonatal mortalities were recorded in southeastern USA. Analysis of DNA from tissue samples collected from stranded neonates and those adult females could reveal the maternal parentage resulting in a better assessment of reproductive success of females and providing an explanation for the longer calving intervals observed in some adult females.

Research efforts between 1980 and 1992 were concentrated in the five high-use areas because of the remarkable consistency with which right whales were seen there. Right whales migrate to areas with high spring, summer and autumn concentrations of *Calanus finmarchicus* copepods (Winn *et al.*, 1986; Wishner *et al.*, 1988; Murison and Gaskin, 1989; Mayo and Marx, 1990; Woodley, 1992; Kenney, 1994; Kenney *et al.*, 1995). Since 1992, there have been several interesting variations in the general pattern of seasonal movements. For example, no right whales were seen in the Great South Channel in the spring of 1992 (Kenney *et al.*, 1995). Analysis of plankton samples suggested the whales' absence might have been related to a shift in zooplankton dominance, caused by significantly reduced water temperatures and a delay in the development of the usual hydrographic structure of the region (Kenney, 1994). No right whales were seen in surveys of Roseway Basin in August of 1993, 1994, 1996-1999, nor were there any sightings of sei whales (*Balaenoptera borealis*), a species commonly seen in association with right whales in this area and also considered (Mitchell, 1975) to be a primarily calanoid copepod feeder in the North Atlantic. Water surface temperatures in 1993 were 4-6°C lower than in previous years (NEAq, unpublished data).

In another respect, reliance upon specific areas makes whales vulnerable to fluctuations in the availability of prey.

Assuming that the whale's selection of these feeding areas is based on the density of food items, then it is not necessarily the distinct area that is important but the set of oceanographic conditions that result in the concentration of food to sufficient densities required by right whales, as suggested by Winn *et al.* (1986). Documented shifts in seasonal distribution in the 1986 summer in Massachusetts Bay (Hamilton and Mayo, 1990), in 1992 in the Great South Channel (Kenney, 1994), and in the Bay of Fundy and Roseway Basin from 1993 to 1999 (NEAq, unpublished data), may indicate flexibility in their use of available spring, summer and autumn feeding areas. Under large shifts in oceanographic patterns, movements among and changes in foraging areas by individual whales are likely, as are differences in habitat use among age and sex categories. Re-running these analyses using sightings records updated through 2000 will help determine if the trends continue to be documented regardless of changes in survey effort and patterns of habitat use of some animals.

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Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses

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ABSTRACT

Western North Atlantic right whales (*Eubalaena glacialis*) utilise several important foraging habitats off the northeastern United States and eastern Canada, where they feed on dense patches of zooplankton. At a fundamental level, a right whale's optimal strategy should be to locate and exploit the prey patches with the highest net energetic return from foraging. There remain many questions, however, concerning their migration and foraging strategies and the environmental cues and sensory modalities involved in migration and foraging, all of which are likely to vary at different spatial scales. For example, a right whale most likely uses different mechanisms and strategies for location of primary feeding grounds than those used for detection of optimum prey patches within a feeding area. This paper proposes a multi-scaled, hierarchical, conceptual model of right whale migratory and foraging strategies and presents a variety of hypotheses concerning the mechanisms involved. Right whales may return to the general area of their feeding grounds based on prior experience. The locations of successful foraging in the immediately preceding years are likely to be re-visited, as are habitats to which an animal was exposed while accompanying its mother during its first year of life. It is also possible that the whales utilise large- or medium-scale environmental cues, such as currents, temperature discontinuities, or salinity signals indicating coastal plumes, to locate likely areas of high zooplankton patch density. Whilst on their feeding grounds, right whales tend to be aggregated, but there are usually outliers which may represent occasional excursions in search of other prey patches, though there is currently no evidence to address whether they communicate information about prey to other individuals. Their behaviour whilst actively feeding indicates that they can detect differences in patch density and adjust their behaviour accordingly. A likely sensory mechanism for quantification of patch density and triggering of feeding behaviour would be the vibrissae around the anterior opening of the mouth.

KEYWORDS: NORTH ATLANTIC RIGHT WHALE; BEHAVIOUR; HABITAT; FEEDING GROUNDS; PATCHES; ATLANTIC OCEAN; MIGRATION; MOVEMENTS; DISTRIBUTION; SITE FIDELITY

INTRODUCTION

Howard Winn developed a preliminary conceptual model of the annual migratory cycle of western North Atlantic right whales (*Eubalaena glacialis*) based on sightings data collected to that time (Winn and Price, 1982; 1983). The model was descriptive, partitioning the annual cycle into six phases: winter calving and breeding; late winter/early spring northward migration; spring feeding; early summer shift of feeding grounds; summer/autumn feeding; and autumn/early winter southward migration. The model did not specifically address either foraging strategies or the environmental cues and sensory mechanisms which right whales might use in their migrations and movements and in locating prey. The model was later incorporated into a broader description of western North Atlantic right whale distribution patterns (Winn *et al.*, 1986), which similarly did not address migratory or foraging strategies.

The range of right whales in the western North Atlantic extends from the Gulf of Mexico to Iceland and Norway (Winn *et al.*, 1986; Kraus *et al.*, 1988; Gaskin, 1991; Knowlton *et al.*, 1992; IWC, 2001), although the vast majority of sightings occur in continental shelf waters off the eastern United States and Canada, from Florida to Nova Scotia (Fig. 1). There are five important habitats in this range which have been consistently utilised by right whales on a seasonal basis, although they occur more-or-less regularly in other habitats and sometimes have exhibited marked departures from the general pattern described below.

(1) During the winter, right whales occur in nearshore waters off southeastern USA, along the coasts of Georgia and northeastern Florida (Winn *et al.*, 1986; Kraus and Kenney, 1991; Kraus *et al.*, 1993). This habitat is apparently the principal or only calving ground for the population, and most of the animals sighted are adult females and mother/calf pairs. A small number of other animals, mostly juveniles, also occurs in this area. The winter habitat of the majority of the population remains undiscovered at this time.

(2) Right whales arrive in northeastern US waters in late winter in the relative shallows of Cape Cod Bay and Massachusetts Bay, with peak occurrence in these areas in March and April (Hamilton and Mayo, 1990; Kraus and Kenney, 1991). During 1986, and to a lesser degree in 1987, numbers of right whales remained in these waters through the summer and autumn (Mayo *et al.*, 1988; Hamilton and Mayo, 1990; Payne, P. *et al.*, 1990; Kraus and Kenney, 1991). In recent years there have been increased numbers of sightings in December and January (M.W. Brown, pers. comm.), but it is not clear whether these have resulted from a change in occurrence or increases in survey effort.

(3) Right whales are found in late spring and early summer, typically from April through June with a peak in May, in the Great South Channel region east of Cape Cod. This area is the primary spring feeding habitat for the majority of the western North Atlantic population (CETAP, 1982; Winn *et al.*, 1986; Kraus *et al.*, 1993; Kenney *et al.*, 1995). The whales apparently abandoned this feeding ground in 1992; available data for 1993 and subsequent years have been sparse (Kenney, 2001).

(4) Right whales are found through the rest of the summer and into the autumn season in two feeding grounds in Canadian waters (Gaskin, 1987; 1991; Kraus *et al.*,

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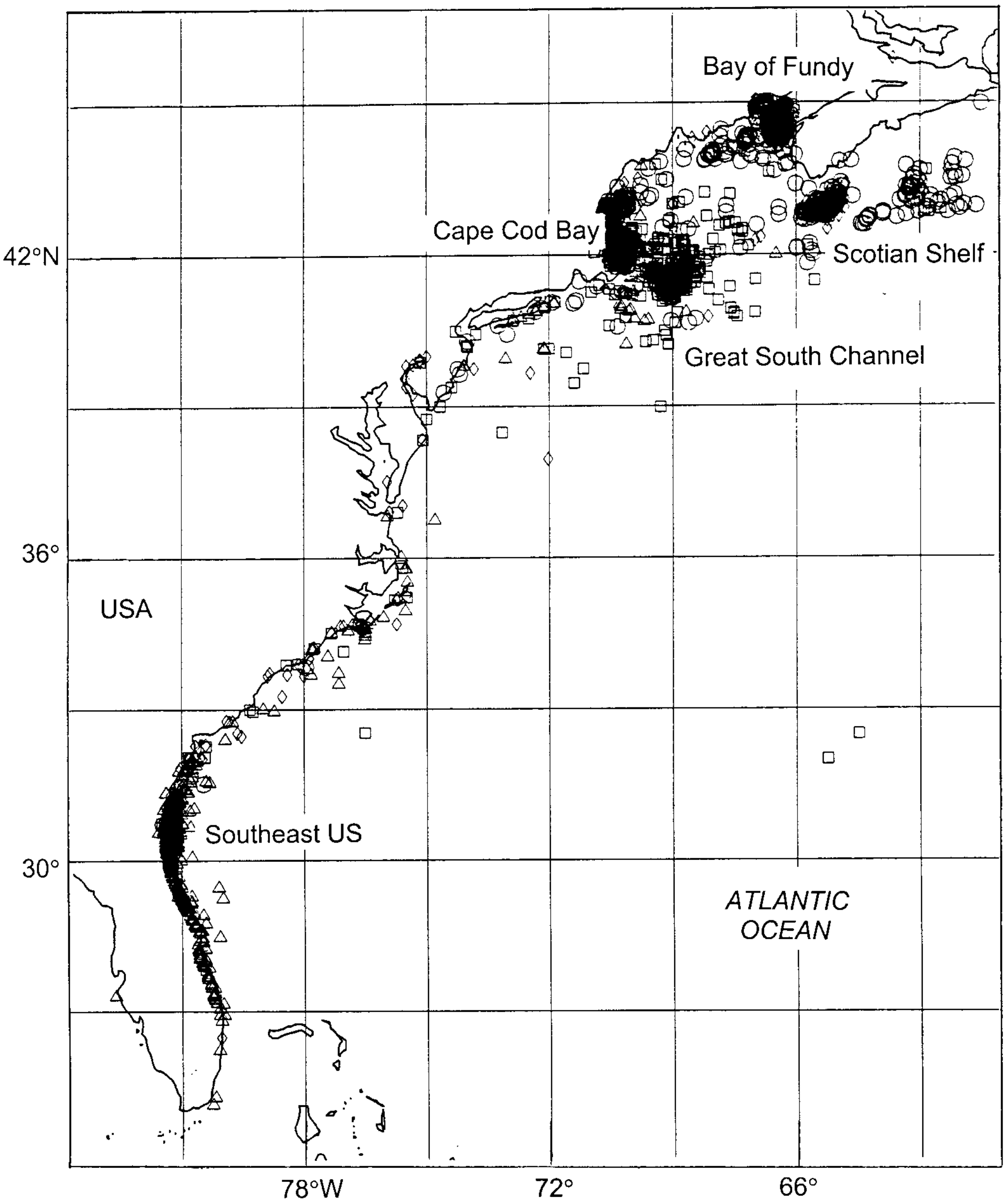

Fig. 1. Distribution of all western North Atlantic right whale sightings in the main range from Florida to Nova Scotia, through the end of 1997 (*n* = 14,910, with an additional 30 sightings beyond the boundaries of the map). Approximate seasons are differentiated by different symbols: Δ = January-March (*n* = 2,231); □ = April-June (*n* = 2,137); O = July-September (*n* = 9,346); ◊ = October-December (*n* = 1,188).

1988; Murison and Gaskin, 1989). One portion of the population is found in the lower Bay of Fundy to the east of Grand Manan Island. The majority of summer/autumn sightings of mother/calf pairs occur here, although some females consistently take their calves to other unknown summer nursery habitat(s) (Schaeff *et al.*, 1993; Malik *et al.*, 1999).

(5) The second well-known summer/autumn habitat is the continental shelf waters off southern Nova Scotia, especially the Roseway Basin just north of Browns Bank, where mother/calf sightings are very rare (Kraus *et al.*, 1988; Brown *et al.*, 2001). Beginning in 1993, right whales apparently abandoned the Scotian Shelf and occupied the Bay of Fundy habitat in much higher numbers (Brown *et al.*, 2001; IWC, 2001). The whales depart these Canadian habitats for their winter grounds in late autumn.

Other habitats which sometimes have significant numbers of right whales include Jeffreys Ledge in the western Gulf of Maine, especially in autumn (Weinrich *et al.*, 2000), and the edges of Georges Bank and some of the ledges and banks in the central Gulf of Maine (P.J. Clapham, pers. comm.).

All of the known right whale high-use habitats except for the winter habitat off southeastern USA are feeding grounds. Right whales feed on zooplankton, primarily copepods and especially large calanoid copepods such as *Calanus* (Matthews, 1938; Tomilin, 1957; Omura *et al.*, 1969; Nemoto, 1970). A right whale's mass is ten or eleven orders of magnitude larger than that of its prey (an adult *Calanus finmarchicus* is approximately the size of a small grain of rice). Right whales are therefore very specialised and restricted in their habitat requirements – they must locate feeding areas where copepods are concentrated into high-density patches. Kenney *et al.* (1986) estimated that such zooplankton patches must reach concentrations on the order of tens to hundreds of thousands per cubic metre in order to obtain a long-term net energetic benefit from feeding. Copepod densities of that magnitude have rarely been measured in the North Atlantic, primarily because of limitations of sampling methodology (Brodie *et al.*, 1978; Kenney *et al.*, 1986; Wishner *et al.*, 1988). Although the actual extent of such high-density zooplankton patches in the western North Atlantic is very poorly known, some of the highest densities have been measured near feeding right whales (Kenney *et al.*, 1986; Murison and Gaskin, 1989; Mayo and Marx, 1990; Mayo and Goldman, 1992; Macaulay *et al.*, 1995; Wishner *et al.*, 1995; Beardsley *et al.*, 1996).

It is clearly of interest to determine how right whales find their feeding grounds and, once there, how they locate dense zooplankton patches. This is true from both a general scientific and a management perspective. For example, it may provide insight into how and why right whales become entangled in fishing gear and how they may cope with potential changes in prey distribution caused by anthropogenic climate change. However, there are obvious methodological difficulties in studying the behavioural ecology of large whales. Under such circumstances, the formulation of plausible (but perhaps ultimately untestable) hypotheses has a role to play. Given the relatively extensive information on right whale distribution patterns and migratory timing along with some data on oceanographic conditions and zooplankton distribution on the feeding grounds, this paper reviews this information, along with foraging mechanisms and strategies for other species, and uses this to develop hypotheses for right whales.

The underlying assumption in this paper is that a right whale's optimal foraging strategy is to: (1) locate areas where high zooplankton patch density provides the maximal net return of energy relative to energy expended in foraging; and (2) remain there as long as the prey concentrations persist. An optimal strategy will also be to maximise time spent feeding and minimise time spent searching for or travelling between prey patches. Whilst it is probable that the strongest environmental cue for a foraging right whale will be the density of prey within small, exploitable patches in its immediate vicinity, it is unclear that the patches themselves will provide cues at any distance.

The objective of this paper is to expand on Winn's original model of the right whale annual cycle, incorporating hypotheses relative to the environmental cues, sensory modalities, and/or navigation mechanisms potentially utilised by migrating and foraging right whales. Given that there are few data on the sensory capabilities or mechanisms of large whales, it is inevitable that many of the hypotheses presented here are speculative. Despite this we will attempt to refine the speculations on whale migration presented by Norris (1967), with the benefit of three decades of additional research on large whales and especially other vertebrate species from which extrapolations may be informative. The intent is not to present an exhaustive review of the literature on sensory biology, but to provide enough references to give an interested reader an entry to the broader literature. One of the objectives here is to collate a range of hypotheses into a coherent conceptual framework which might then serve as a beginning for future research, a tool for beginning to address questions of critical management importance and a target for constructive criticism.

MODEL AND HYPOTHESES

The suite of strategies utilised by right whales in locating feeding grounds and prey concentrations undoubtedly varies with the spatio-temporal scale involved – from long-distance seasonal migrations over weeks or months down to minute-by-minute selection of the optimal prey patches within a particular feeding area. The strategy of this paper is to similarly begin from the largest scale and work down to the smallest.

Basin scale – 1000's of kilometres

Question: How do right whales navigate during their long-distance migrations between their wintering grounds and their feeding grounds in the Gulf of Maine region, and between feeding grounds?

The distribution of all right whale sightings to date largely confirms the general pattern described by Winn (Winn and Price, 1982; Winn *et al.*, 1986; Fig. 1) of a north-south feeding/calving migration typical of mysticetes (Norris, 1967). As the intensity of sampling effort increases, the number of sightings in areas and seasons outside of the core habitats/seasons has been increasing. Additionally, there have been observed anomalies in the distribution patterns, such as the abandonment of the Great South Channel in 1992 and of the Roseway Basin beginning in 1993.

The location of winter grounds for most of the population is still not known. It is possible that there is no specific winter ground, and that the animals are broadly dispersed. It is also possible that some individuals, perhaps even significant numbers, winter within the range of habitats described as spring-summer-autumn feeding grounds and that they have been missed due to a combination of dispersed and inconsistent distribution, inadequate survey coverage and generally poorer weather and sightability.

The navigation mechanisms used at this scale are probably more related to geography than to prey distributions. There are a number of potential mechanisms which might be used as discussed below.

(*1*) *Topography*

Right whales might simply follow the topography, such as the coastline, continental shelf break, particular isobaths, or undersea landmarks such as seamounts. Knowlton (1997) concluded that the majority of recent right whale sightings off the USA mid-Atlantic were relatively nearshore. Historically, there were shore-based right whale fisheries on the Outer Banks of North Carolina and at eastern Long Island, New York (Reeves and Mitchell, 1986; 1988). Homing pigeons (*Columba livia*) appear to use visual landmarks within the vicinity of their home loft (Berthold, 1996). The use of landmarks, learning and memory is believed to be common in terrestrial mammals, particularly in movements within a home range (Bovet, 1992). Pike (1962) concluded that gray whale (*Eschrichtius robustus*) movements from headland to headland along the west coast of North America were evidence for migration via landmarks. Norris (1967) speculated that migrating mysticetes could follow a given depth contour, or use consistent sound sources as acoustic 'landmarks'. He also hypothesised that low-frequency sounds produced by mysticetes could be used for coarse-scale echolocation during migration, perhaps by measuring water depth or imaging large topographic features. Ellison *et al.* (1987) similarly suggested that bowhead whales used reverberation from their vocalisations to detect leads in the pack ice.

(*2*) *Sun*

Right whales might use the sun as a compass cue. Sun-compass orientation is well-known in birds (Berthold, 1996) and has also been shown in fishes (Quinn and Dittman, 1992; Dittman and Quinn, 1996) and small mammals

(Bovet, 1992). Pilleri and Knuckey (1969) concluded that common dolphins (*Delphinus delphis*) in the Mediterranean used solar cues.

(*3*) *Magnetism*

Right whales might utilise the Earth's magnetic field for migratory cues, either as a compass mechanism or as a geomagnetic map system. In some areas, at least, studies have correlated cetacean stranding patterns with geomagnetic anomalies (Klinowska, 1985; 1990; Kirschvink *et al.*, 1986; Kirschvink, 1990), suggesting that cetaceans possess some type of magnetic sense. Walker *et al.* (1992) suggested that fin whales in the western North Atlantic utilised geomagnetic anomaly patterns as cues during their migrations; these magnetic 'stripes' on the seafloor trend north-south in the Atlantic basin (Gross, 1996) and thus may serve as ideal cues for north-south migrating mysticetes. There is good evidence that hatchling loggerhead sea turtles (*Caretta caretta*) are capable of detecting the geomagnetic field and using it as a compass, as well as evidence that geomagnetic cues might also be used as a bi-coordinate map (Lohmann and Lohmann, 1996). Use of a geomagnetic compass is also documented or hypothesised in migrating and homing birds (Wiltschko and Wiltschko, 1996), sharks (Kalmijn, 1982), salmon (Dittman and Quinn, 1996), tuna (Walker, 1984), amphibians (Sinsch, 1992) and rodents (Bovet, 1992). One potential mechanism for magnetoreception is possession of magnetite particles in the brain, which have been detected in common dolphins (Zoeger *et al.*, 1981) and humpback whales (*Megaptera novaeangliae*) (Fuller *et al.*, 1985). However, Gerrits and Kastelein (1990) have proposed a neural mechanism for magnetoreception in cetaceans which does not involve magnetite.

(*4*) *Sounds*

Right whales and other mysticetes are probably capable of hearing and localising the direction of very low-frequency sounds (Ketten, 1991; Richardson, 1995) and transmission distance of sound in water is inverse to frequency (Malme, 1995). Consistent sources of these infra-sounds (e.g. surf zones along the coast, zones of seismicity along the mid-ocean ridge) might be useful as an acoustic 'map' of a region, as suggested by Norris (1967) for more typical acoustic sources. Infra-sound has been hypothesised to be used for geographic location cues by homing pigeons, which are capable of hearing sounds below 20Hz, and other birds (Berthold, 1996).

(*5*) *Ocean currents*

Right whales might use ocean current patterns, either for directional cues or for a locomotory assist in one or both directions. Hatchling sea turtles from the eastern USA are believed to follow the Gulf Stream/North Atlantic gyre system to developmental habitats in the eastern North Atlantic (Carr, 1980; 1982; 1987; Hamner, 1988). Norris (1967) suggested that 'currents or water masses might serve as guideposts' for migrating whales. Although Winn *et al.* (1986) suggested that northward-migrating right whales in the spring could save energy by following the Gulf Stream for some part of the way, there have been no sightings of right whales in Gulf Stream waters and most northbound migrants which have been observed have been relatively close to shore (Knowlton, 1997).

Regional scale – 10's to 100's of kilometres

Question: Once a right whale arrives in the vicinity of the Gulf of Maine from its wintering habitat, how does it find the location of feeding grounds?

The primary hypothesis considered is that right whales return to particular feeding grounds based largely on prior experience i.e. that learning is important. If so, it seems probable that there may be a hierarchy of preferred areas. For example, one could envisage a situation where the location of successful foraging in the previous year is ranked highest, with previous years' locations ranked lower.

Under such an hypothesis, matrilineal learning is probably important, as has been shown for feeding site fidelity in humpbacks (Baker *et al.*, 1986; 1990; Clapham and Mayo, 1990; Clapham *et al.*, 1993). Both resighting and genetic data support the hypothesis of maternally directed habitat fidelity in western North Atlantic right whales (Malik *et al.*, 1999; Brown *et al.*, 2001). A female right whale accompanied by a calf was tracked via a satellite-monitored radio tag in August-October 1990 (Mate *et al.*, 1997). The pair moved from the Bay of Fundy to Massachusetts Bay, then southward to near New Jersey, and finally back to Massachusetts Bay, a minimum distance of at least 3,833km in 41 days. This suggests that at least some mothers with calves range widely and visit several potential feeding grounds.

Satellite tag studies (Mate *et al.*, 1997) have also shown that individuals can make occasional excursions over long distances, possibly in search of alternate feeding areas. This suggests the possibility for communication of foraging information between individuals, though direct evidence for this is lacking. Although Watkins and Schevill (1976) found that feeding right whales rarely vocalised, the possibility of communication between individuals with respect to foraging areas cannot be ruled out.

Norris (1967) hypothesised that another environmental cue which whales could utilise to locate feeding areas within a general region might be water mass characteristics, which could include temperature, currents, salinity, stratification, and chemistry. One cue which migrating right whales might use to locate the Gulf of Maine from offshore south of New England might be the spring run-off plume (with reduced salinity and containing organic compounds which originate in freshwater systems) that exits the Gulf via the Great South Channel (Chen *et al.*, 1995a). Mysticetes are believed to possess a limited olfactory sense (Anderson, 1969; Pilleri and Gihr, 1970; Berta and Sumich, 1999; Wartzok and Ketten, 1999) but it would probably not be useful at this spatial scale. However, cetaceans do possess gustatory (taste) and other intra-oral chemoreceptors which might be useful in this regard (Nachtigall, 1986; Kuznetzov, 1990; Pryor, 1990; Wartzok and Ketten, 1999). Sorensen (1986) showed that migrating elvers of the American eel, *Anguilla rostrata* (entering freshwater systems for the first time after hatching in mid-ocean), are attracted to organic compounds produced via microbial breakdown of plant detritus; such compounds are a generic signature of freshwater run-off from terrestrial sources. Raymond M. Gilmore (pers. comm., cited by Norris, 1967) believed that gray whales located the entrances to their breeding lagoons in Mexico by 'tasting' the water. Interestingly, in the spring of 1998 the largest numbers of right whales in recent memory were seen off Rhode Island, with 23 individuals sighted 25-30km south of the entrance to Narragansett Bay on 19 April (P. Gerrior, pers. comm.). Although it may have been entirely coincidental, this occurrence of right whales followed a period of heavy rains. If migrating right whales moving north and east over or beyond the continental shelf use the spring run-off plume exiting the Great South Channel as their cue to 'turn left' into the Gulf of Maine, the heavy rainfall in Rhode Island may have simply supplied the cue early.

Mesoscale – 1 to 10 kilometres

Question: Once in the general area of their Gulf of Maine feeding grounds, how do right whales locate zooplankton concentration areas?

A number of studies have shown that dense *Calanus* concentrations in the Great South Channel occur in areas of convergence near a persistent tidal mixing front which separates water masses of differing temperature, salinity and biological properties (CETAP, 1982; Wishner *et al.*, 1988; 1995; Brown, C.W. and Winn, 1989; Macaulay *et al.*, 1995; Beardsley *et al.*, 1996). A similar phenomenon appears to occur in right whale feeding grounds in Nova Scotian waters (Murison and Gaskin, 1989). Other similar oceanic discontinuities may also be locations of zooplankton concentration – in September 1990, a satellite-tagged adult male right whale made an extensive excursion beyond the continental shelf along the eastern edge of an anti-cyclonic warm-core ring, where an entrained plume of cooler shelf water was located (Mate *et al.*, 1997).

At this scale, several of the mechanisms proposed at greater distances will no longer be of value; it is difficult to see how compass orientation mechanisms could prove useful, for example. It is also unlikely that copepod patches produce significant far-field detection cues, although predators aggregating to exploit zooplankton concentrations (e.g. fish schools and flocks of seabirds) might produce enough sound to be detected at some distance. Chemosensory cues by contrast might be useful indicators. Salinity or other water mass properties might indicate the location of appropriate conditions for the development of dense copepod patches, whilst organic compounds produced by zooplankton may even be direct indicators of dense patches. An alternative hypothesis to that given above for the spring 1998 occurrence of right whales in Rhode Island Sound is that the whales detected the presence of zooplankton concentrations directly. They then remained in the area for about two weeks feeding on concentrations of zooplankton that the local fishermen characterised as unusual (another alternative is that they accidentally came across a suitable prey patch while moving through the region, and stayed until the patch was depleted or dispersed). Any chemical cues from zooplankton would probably be detected by the gustatory sense. Humans are sometimes able to smell patches of zooplankton-rich productive water, therefore right whales might also detect such airborne chemical cues. However, localisation of the source of such odours also requires the ability to detect wind direction. Procellariiform seabirds (petrels, albatrosses, shearwaters and storm petrels) have been shown to use olfaction to return to their nests at night and to locate prey; after detecting an odour they fly upwind to locate the source (Wenzel, 1980).

Temperature cues might also be useful indicators. In the Great South Channel the *Calanus* patches that right whales feed upon are typically located north of the tidal mixing front, in a water mass which is stratified with a warmer surface layer (Wishner *et al.*, 1988; 1995; Brown, C.W. and Winn, 1989; Chen *et al.*, 1995b). South of the front, in shallower water, the water column is completely mixed by strong tidal currents and is colder at the surface. A right whale might detect water temperature using sensors which could be either cutaneous or intra-oral.

At this scale, right whales are highly aggregated, often with several tens of animals within a radius of a few kilometres (Kraus *et al.*, 1988; Murison and Gaskin, 1989; Kenney *et al.*, 1995). However, there are frequently scattered individuals located well beyond the main aggregations. As has been suggested earlier, one possibility is that these may be 'scouts,' searching for other prey patches. Alternatively, they might be poorer competitors who are forced into suboptimal habitats (perhaps younger individuals). Hain *et al.* (1995) noted that the Gulf of Maine humpback whales which they observed with pronounced wounds on the sides of one or both jaws, attributed to abrasions incurred from contact with the sea bottom during feeding, were largely juveniles, possibly forced by intra-specific competition into a suboptimal foraging strategy.

Microscale – centimetres to 10's of metres

Question: Within a feeding ground, how do right whales detect the optimal (i.e. densest) zooplankton patches?

A foraging right whale should feed in the patch or layer of zooplankton which provides the maximum net energy benefit, i.e. the highest return relative to energy expended in foraging. For example, feeding right whales in the western North Atlantic typically swim at 1-3 knots (2-6 km/hr) (Watkins and Schevill, 1976; 1979; Mayo and Marx, 1990), while Hamner *et al.* (1988) observed a southern right whale (*E. australis*) feeding on Antarctic krill (*Euphausia superba*) while swimming at 8-9 knots (15-17 km/hr). A whale with a choice of feeding on a copepod patch of lower caloric concentration or a richer krill patch would get a better return from the copepods if it had to swim much faster (with the resulting increased cost of locomotion) in order to overcome the avoidance response of the stronger-swimming krill. An optimally foraging whale ought to be able to quantify at least the abundance of zooplankters within small-scale patches, and ideally their individual masses and size distribution, and consequently biomass or energy density. The behaviour of feeding right whales suggests that they are capable of detecting fine-scale variations in zooplankton density in both the horizontal and vertical dimensions and adjusting their behaviour accordingly. In the horizontal dimension, the path of a feeding whale is typically sinuous, with many turns, as it apparently attempts to remain within the area of maximum copepod density (Mayo and Marx, 1990). Turns in apparent response to changes in the fine-scale horizontal distribution of zooplankton are most easily observed at the margins of surface patches (Mayo and Marx, 1990). In the vertical dimension, Mayo and Goldman (1992) reported that whales feeding on zooplankton layers in the upper 2m of the water column regularly adjusted their swimming depth, apparently in response to changes in the depth of the most dense parts of the layer. Simultaneously-collected zooplankton data demonstrated that vertical adjustments of as little as 20cm could increase the whale's energy intake by as much as 20% above that predicted if the animal simply swam at a constant depth.

Visual cues may be used by whales skim-feeding during daylight hours at the surface or in the near-surface layer – a whale might simply see the thickest zooplankton layer or some manifestation of it (e.g. shadowing). However, visual cues are probably less useful when feeding at depth as occurs most often in the Great South Channel (Kenney *et al.*, 1995; Winn *et al.*, 1995) and Bay of Fundy (Murison and Gaskin, 1989; Goodyear, 1993) or when feeding at night. One interesting possibility is that right whales might be able to detect dense zooplankton layers at depth or in total darkness if there are significant numbers of bioluminescent individuals, e.g. the copepod *Metridia lucens*.

Waterborne chemical signals given off by zooplankton aggregations may be useful cues, although their utility will be a complex function of chemical persistence, turbulence and rate of diffusion or dispersal. A substance with a long persistence might be less useful as an immediate indicator of zooplankton concentration; however, very short persistence times or rapid dispersal would also reduce the value of a chemical cue. If the sensory receptors for chemical cues are in the mouth, detecting such cues might entail a significant energetic cost if it required frequent mouth opening and subsequent increases in drag, unless the whale is capable of 'sampling' by drawing in small volumes of water without opening the mouth significantly. Airborne chemical cues may also be detectable, but are probably less useful to whales, as discussed above.

Tactile cues are probably the most reliable indicator of zooplankton density at this scale. A right whale could utilise the sinus hairs ('vibrissae') on its head for detection of individual zooplankton organisms. The vibrissae are concentrated near the front of the mouth opening; Payne (1976) includes an excellent photograph which clearly shows the vibrissae on the tip of the rostrum and chin of a southern right whale. Cetacean vibrissae are richly enervated and appear to be sensitive tactile organs (Ling, 1977). An individual zooplankter contacting one of the vibrissae as the whale is swimming forward will deflect the hair to some degree. The frequency of deflections will be a measure of zooplankton density, while the magnitude of each hair deflection is a measure of the mass of an individual zooplankter. Summation of the two would be an indication of biomass density, possibly triggering open-mouth feeding when a threshold is reached. Differential signals from vibrissae in separate locations would cue the whale to adjust its mouth opening up/down or left/right. However, the system may be even simpler, based only on organism density, not biomass density. Comparison of small-volume zooplankton samples taken in Cape Cod Bay as near as possible to the mouth of feeding right whales with those collected near non-feeding whales and where no whales are present suggests that concentrations of approximately 4,000m^{-3} represent the threshold for releasing open-mouth feeding behaviour, but that the size of the zooplankters which are present has little effect on the threshold (Mayo and Goldman, 1992; unpublished data). Gustatory and/or intra-oral tactile cues may be the final indication of prey patch suitability. Right whales in Cape Cod Bay are occasionally observed to feed on dense patches of cyprids (the free-swimming larvae of barnacles), but those feeding bouts end very quickly, perhaps because the small size of the cyprids means they are not filtered very effectively and therefore do not provide the whale with the feedback cue(s) indicating successful feeding.

DISCUSSION

This paper represents a first attempt to construct a conceptual model of the mechanisms and strategies that may be involved in the annual cycle of distribution, migration, movements and foraging of western North Atlantic right whales. A nested framework of hypotheses is given, some testable and some probably not, spanning a range of spatial and temporal scales. Four different spatial scales were considered and it is very likely that multiple redundant mechanisms operate at each of them. At two of the scales, basin scale and mesoscale, the available information is not sufficient to conclude that any particular mechanism is more likely than any other. At the regional scale, the concordance of resighting, genetic and habitat use data lead to the conclusion that prior experience, learning and habitat philopatry comprise the principal mechanism. At the microscale, the use of the tactile sense, mediated via the vibrissae, is most consistent with observed foraging behaviour. With the possible exception of long distance seasonal migrations, it is presumed that feeding is the principal underlying drive. It is certain that there are other factors which drive a right whale's decision making (e.g. reproduction and social considerations) however, for the most part these are not considered here. There may also be additional unknown factors.

It is proposed that the movements of right whales in western North Atlantic continental shelf waters reflect adaptive responses to the distribution of prey at many scales. It is advantageous for whales to locate and forage in those areas which return the greatest energy value to them. Because zooplankton productivity and exploitability can vary at many temporal and spatial scales, some flexibility in the responsiveness of right whales to environmental variability should be expected. If it is to be adaptive, the life history of a species which moves and forages over large, variable, and at times, unpredictable marine habitats should incorporate a wide range of sensory capabilities, as well as a capacity for appropriate decision-making. The responses of right whales to variability in prey result in distribution patterns that will vary from minutes to decades and from metres to hundreds of kilometres. It is likely that the unexpected changes in right whale distribution which have been observed in the last decade (which may be 'anomalous' only within the limited time scale of our observations) are examples of right whales responding to variation in the distribution and quality of zooplankton resources, about which little is understood. However, there is certainly a limit to the effectiveness of adaptive responses to environmental change for any species, and there are very likely levels or rates of changes to which right whales will have difficulty responding. Broad regional changes in zooplankton productivity, or wide-scale alterations in hydrography which shift the locations of optimum zooplankton-aggregating conditions, might be expected to profoundly impact a population which would otherwise be capable of successfully responding to more local and/or short-term changes in their prey.

There is much that remains unknown about the migratory and foraging strategies of right whales and other mysticetes. This paper has attempted to set forth a series of hypotheses concerning these strategies. However it is accomplished and however unlikely it may be that we will completely understand the mechanisms involved, it is clear that right whales are capable of detecting the dense patches of zooplankton which constitute their preferred prey resource. The highest measured copepod densities in the western North Atlantic have been in right whale feeding grounds, dating back at least to Henry Bigelow's (1926) report of extremely high summer densities of *Calanus finmarchicus* on the Nova Scotian shelf near Browns Bank. However, questions relative to the possibility that right whales may at times have difficulty in locating sufficient food, and hence be energy-limited, may be critically important in managing the recovery of the western North Atlantic population.

The annual rate of increase in the abundance of western North Atlantic right whales until 1992 was estimated at 2.5% (Knowlton *et al.*, 1994), substantially lower than the rates observed in Southern Hemisphere populations (Best and Underhill, 1990; Payne, R. *et al.*, 1990). Since 1992, the trend has reversed to a decline (Caswell *et al.*, 1999; IWC, 2001; Kraus *et al.*, 2001) and inter-birth intervals have lengthened significantly (Kraus *et al.*, 2001); the continued survival of the population is now in question (Caswell *et al.*, 1999; IWC, 2001). The shift from population growth to decline coincided with significant changes in distribution such as the abandonment of the Great South Channel in 1992 (Kenney, 2001) and the Scotian Shelf beginning in 1993 (Brown *et al.*, 2001; IWC, 2001). At the same time, there is evidence of thinner blubber layers in North Atlantic animals (Moore *et al.*, 2001). All of this is strongly suggestive that the availability or distribution of prey changed, and that the whales have been unable to locate alternative feeding grounds which are sufficient to completely supply their energetic needs.

The present abundance of the western North Atlantic population is estimated at about 300 animals (IWC, 2001; Kraus *et al.*, 2001). The historical abundance is poorly known; the early North Atlantic whaling which depleted the population (Aguilar, 1986) left behind only a sparsely written catch record (Reeves *et al.*, 1992). It is sometimes assumed, however (e.g. in the USA right whale recovery plan – NMFS, 1991), that the original population was around 10,000 or more. The present population is therefore far below carrying capacity (assuming there has not been a drastic alteration in the availability of zooplankton and/or abundance of competitors in the last several hundred years), and the whales should be relatively immune to any effects of intra-specific competition for resources. However, observed statistical correlations between reproduction and global atmospheric cycles (Kenney, 1998 and unpublished) and the increase in calving intervals corresponding in time to marked distributional shifts (Kraus *et al.*, 2001) suggests that they are sensitive to oceanographic changes acting through prey availability. If a better understanding of how right whales locate their feeding grounds is achieved, it might be easier to understand these phenomena and to predict future changes.

One important question which arises is how right whales were able to cope with interannual and decadal-scale environmental variability before commercial whaling began, when the population was much higher and presumably closer to carrying capacity. Zooplankton concentrations sufficiently dense to support right whale feeding must have existed in many portions of the range from New England to Labrador. Assuming that the overall abundance of appropriate zooplankton prey is not drastically lower today, why then have right whales not re-colonised the northernmost portions of their historic range? An understanding of their strategy for locating feeding grounds might help to answer this question and to address the related issue of the long-term absence of any substantial recovery of the population. The hypothesis presented here is that:

(1) The surviving western North Atlantic population is a remnant of the historic stock which represents only the southern periphery of the original range. One should expect that the quality of the habitat on the periphery of any species' range would be lower than at the core of the range.

(2) Prey availability in the current range has probably always fluctuated with natural environmental variability. This would lead to alternating periods of prey abundance and energy limitation.

(3) Genetic studies indicate that the population has been small for hundreds of years (IWC, 2001). The combination of intervals of prey limitation, leading to increased mortality and/or reduced fecundity, with continued anthropogenic mortality has maintained the population at a very small size since the original reduction by Basque whaling. Mortality at first was directed and opportunistic killing by whalers, but presently whales are killed by ship strikes and entanglement in fishing gear (Kraus, 1990; Kenney and Kraus, 1993; Waring *et al.*, 1999; Knowlton and Kraus, 2001).

(4) The population has simply never re-occupied the original core of its range. Given the evidence for maternally-directed habitat fidelity in North Atlantic right whales, one might predict that it could take a very long time to re-colonise habitats from which they had been extirpated.

It would be very interesting to do some fine-scale zooplankton sampling in the waters off Newfoundland and Labrador where the Basque fishery was prosecuted to learn whether high-density copepod patches capable of supporting right whales can be found there, as well as to compare zooplankton densities to those measured in current right whale feeding grounds. If the prey resource exists, and if management efforts can be successful at reducing or eliminating anthropogenic sources of mortality, it might be expected that some individuals would eventually re-occupy the northern portion of the range. Right whales have been occasionally observed as far north as Iceland and Norway in the last two decades (e.g. Knowlton *et al.*, 1992; IWC, 2001). Interestingly, while the 1999 sighting in Norway was an adult male (IWC, 2001), of nine individuals photo-identified as of 1997 from northern areas (Gulf of St. Lawrence, Newfoundland, Labrador and Iceland), seven have been adult females, one was of unknown age and sex, and one was a male calf accompanying its mother (unpublished North Atlantic Right Whale Consortium photo-identification catalogue data). The best hope for the long-term recovery of western North Atlantic right whales may be those females taking their calves on 'the tour' of the foraging grounds, some day leading to re-occupation of the historic right whale habitat off eastern Canada.

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Preliminary estimates of whaling-induced mortality in the 19^{th} century North Pacific right whale (*Eubalaena japonicus*) fishery, adjusting for struck-but-lost whales and non-American whaling

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ABSTRACT

This study develops preliminary estimates of total whaling-induced mortality of northern right whales in the 19th century North Pacific pelagic whale fishery. Best's (1987) study of American whaling returns resulted in estimates of the total American catch of 14,480 and 15,374 northern right whales during the period 1839-1909. The present study offers adjustment factors to estimate total mortality from these catch data. Quantitative data from 14 pelagic expeditions for northern right whales in the North Pacific from 1838-1860 and additional anecdotal information about struck-but-lost animals is reviewed. On 12 voyages, 327 northern right whales were struck with harpoons, but only 133 landed. Adjusted for the subsequent recovery of struck whales, this implies a ratio of 2.43 whales struck for each whale eventually secured and flensed by whaleships. Data from four voyages show that of 148 northern right whales struck with harpoons, 14 sank before they could be processed. From a sample of five voyages, 80 northern right whales were landed and 31 carcasses sank without being secured. During the height of pelagic whaling in the North Pacific, approximately 10% of the fleet was non-American, primarily French. Adjusting recorded catch estimates for struck-but-lost mortality and non-American whaling yields preliminary estimates of total mortality in this fishery in the range of 26,500-37,000 animals during the period 1839-1909. In the single decade of 1840-49, between 21,000-30,000 northern right whales may have been killed in the North Pacific, Sea of Okhotsk and Bering Sea, representing about 80% of the northern right whales killed in this region during the period 1839-1909.

KEYWORDS: WHALING-HISTORICAL; PACIFIC OCEAN; NORTHERN HEMISPHERE; ABUNDANCE ESTIMATE; NORTH PACIFIC RIGHT WHALE

INTRODUCTION

In 1840, the North Pacific right whale (*Eubalaena japonicus*)* was common or abundant during summer in the Gulf of Alaska, North Pacific, southeast Bering Sea, among the Kuril Islands and in the southern Sea of Okhotsk (Scarff, 1991). Ten years later, it was rare; 20 years later it was nearly extinct. The cause for this rapid decline was pelagic whaling. Measurement of the magnitude of the mortality associated with this early pelagic whaling will be an important factor in the estimation of the initial population size of northern right whales in these seas.

Pelagic whaling for northern right whales began in the North Pacific in 1835 when the French whaleship *Gange* killed seven whales (Webb, 1988, p.40). It took about five years for the many whalers operating in the South Pacific to leave those depleted waters and head north to the new whaling grounds in the Gulf of Alaska, in the Sea of Okhotsk and off Kamchatka. Beginning in 1840, and continuing for the next nine years, a tremendous concentration of whaleships, mostly American, searched the North Pacific, Bering Sea and Sea of Okhotsk, hunting northern right whales (Scarff, 1986; Webb, 1988). In 1846 alone, over 290 American whaleships hunted these waters (Starbuck, 1878, p.104). From 1840-1849, American whalers took at least 11,000 northern right whales in the North Pacific, Bering Sea and Sea of Okhotsk, probably more than 75% of the northern right whales that would ever be caught in this region (Scarff, 1986; Best, 1987). In the following decade, 1850-59, American whalers took an additional 2,400 northern right whales, bringing the total catch to 92% of the northern right whales caught prior to 1910. By 1850, the fishery in the Gulf of Alaska was largely over and the whalers moved north to hunt the larger and still abundant bowheads (*Balaena mysticetus*). The fishery persisted for another decade in the more remote Sea of Okhotsk (Henderson, 1983).

Prior to the use of steam-powered whale catchers and explosive harpoons, probably no large population of whales was so severely depleted so quickly. Today, northern right whales remain extremely rare in the Bering Sea and central and eastern North Pacific, with population estimates in the low hundreds. Only in the Sea of Okhotsk does it appear that a remnant population persists, optimistically estimated at less than 1,000 (IWC, 2001).

Initial population size

Published estimates of pre-1840 northern right whale populations in the North Pacific and adjacent seas have been speculative rather than analytical. Berzin and Vladimirov (1981) estimated that the 'pre-exploitation' number of northern right whales in the North Pacific and adjacent seas was about 10,000. They gave no basis for this estimate. Braham and Rice (1984) estimated that the *combined* initial Northern Hemisphere right whale populations were between 30,000-100,000 (one-third of an estimated worldwide population of 100,000-300,000) based 'on recorded catch data' with no further detail provided. Based upon an estimate of American catches in the North Pacific in the 1840s of over

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* *Editors' note*: The IWC agreed that the North Pacific right whale (*E. japonicus*) comprised a separate species after this paper was ready for press. In order to avoid extensive changes at a late stage it was decided not to change the common name 'northern right whale' which is used throughout the rest of the paper. That was the common name used for right whales in both the North Pacific and North Atlantic which had been considered a single species, *E. glacialis*.

11,000, the Right Whale Recovery Team (NMFS, 1991) stated that the initial North Pacific population level was ‘higher than 11,000’. Neither of the two International Whaling Commission workshops on right whales (IWC, 1986a; 2001) have included estimates of the initial size of any northern right whale stock.

Scarff (1991) argued that the size of the pre-1835 North Pacific population of northern right whales may have been substantially higher than previous minimum estimates of 10,000. He cited the indices of abundance of northern right whales he derived from Maury’s (1852) Series F Whale Charts that showed whalers in the 1840s finding northern right whales on 50+% of the days they searched over large areas of the Gulf of Alaska, along the Aleutian Islands, off the coasts of Kamchatka and in the Kuril Islands. He believed that these high sighting frequencies strongly suggested larger initial population(s) of northern right whales in the North Pacific.

Total mortality and struck-but-lost whales

It might be possible to model at least the historic population(s) of northern right whales if the number of whales killed by 19th century whalers can be estimated with sufficient accuracy. Such an analysis was recently presented in IWC (2001) for Southern Hemisphere populations of right whales. Previous studies on North Pacific right whales have analysed only that portion of total mortality reflected in the recorded catch figures where the best data were available. Based on total US import figures for whale oil and baleen and the proportion of species and yield/whale in Townsend’s (1935) data, Best (1987) separately estimated the American catch of northern right whales in the North Pacific between 1805-1909 at 15,374 based on oil production up to 1879 and whalebone production thereafter, or 14,480 based on the estimated catch per voyage.[1]

In addition to the northern right whales whose oil or baleen were reflected in the catch data in the 19th century pelagic fishery, many whales were struck with harpoons but lost before they could be secured and processed. Some of these were dead at the time they were lost, while others were suffering from injuries ranging from minor to fatal. The mortality associated with these struck-but-lost whales greatly increased the impact of pelagic whaling on the northern right whale populations but has received relatively little attention in past studies.

Previous studies of 19th century pelagic whaling in the North Pacific have focused on the whaling culture and history (Webb, 1988), the historic distribution of northern right whales (Scarff, 1986; 1991) or the recorded catch by American whalers (Best, 1987). None of these studies discussed total mortality of northern right whales caused by whaling. Scarff (1991, p.479) suggested that the northern right whale’s current scarcity in the North Pacific might be the result of a larger kill by 19th century whalers than previously thought, from an initial population size that was also larger. He suggested that the mortality of struck-but-lost whales in the fishery might have been significantly greater than the adjustment factor used in IWC (1986a).

With no new data to review, the IWC Scientific Committee (IWC, 2001) stated that:

> about 14,500 were taken as a total by American pelagic whalers in the North Pacific in 1835-1904, with 90% in 1840-59, but they cannot be allocated to grounds. No allowance can be made in North Pacific catches for hunting loss, nor for catches by other nationalities.

The present study describes a small amount of data that allow preliminary estimates of both struck-but-lost mortality and non-American whaling in the North Pacific.

Prior adjustments for struck-but-lost whales

Best (1987, p.417) explicitly qualified his catch estimates by stating:

> It should also be stressed that the figures produced here are estimates of the landed catch; further work is needed to determine the number of animals that were struck and lost, and the proportion of these that might have died.

The various published catch-to-mortality adjustment factors and struck-but-lost ratios for northern right whales are summarised in Table 1.

IWC (1986a, p.5) noted that to estimate total whaling-induced mortality, the recorded catch figures would have to be adjusted to account for struck-but-lost whales that died. It suggested that:

> an average mortality factor, pertaining to [northern right whale] fisheries in which hand harpoons and lances (non-explosive) were used, would be between 1.2 and 1.5.

The higher estimate assumes that all struck-but-lost whales died from their injuries. In other words, the higher estimate reflects a judgement that on the voyages recorded, of 150 northern right whales struck only 100 whales were secured and the oil or baleen captured. The higher estimate assumes that all of the 50 struck-but-lost whales died. The lower estimate assumes that less than half the struck-but-lost whales died. Both estimates assume implicitly that none of the struck-but-lost whales are ever recovered and used later by another or the same whaleship.

IWC (1986a) also noted significant differences in loss rates by whaling area, time period and technology in use and such differences should be recognised in any reconstruction of the catch history. It noted that losses ‘seem to have been higher on the open seas than they were in bay whaling’.

As an indication of how the struck-but-lost ratios may vary between regions and periods, IWC (1986a) described separate high and low bounds for struck-but-lost mortality for seven separate areas/periods. In calculating resulting ratios, it assumed for the high bound that all struck-but-lost whales died; whereas for the lower bound that of those whales lost, 50% of those still alive when lost died later. The first six include: South Atlantic 1783-1794 (1.42-1.61), Bay whaling, South Africa 1804-1837 (1.32-1.50), South Atlantic 1817-1837 (1.21-1.41), New Holland ground

[1] Best (1986) provisionally estimated the total catch of northern right whales in the North Pacific between 1840 and 1909 by the American whaling fleet alone as 15,244. As noted in Scarff (1991, p.479, footnote 4), both Townsend’s (1935) and Best’s (1986) estimates are cited in Scarff (1986, table 3). Several changes should be made to Scarff’s table 3 to make it consistent with Best (1986) and Townsend (1935). First, the citation to Du Pasquier (1986) was to an earlier version of the study finally appearing as appendix 7 in IWC (1986a), but should more precisely be to Best (1986). Second, two typographical errors need to be corrected. The heading of the second column in Scarff (1986) table 3 which reads ‘L’ should read ‘L_t’; this is the summary of Townsend’s (1935) data. In addition, the record of whale catches in column 3 for the period 1840-44 which reads ‘985’ should read ‘2,985’, the number reported in Best (1986).

In addition, two related typographical errors should be mentioned. In appendix 7 of the 1983 IWC Right Whale Workshop Report, in the table on North Pacific Whale Catches, 1840-1969 (IWC, 1986a), the reference for the second column, labelled ‘Okhotsk Sea’, which currently is ‘(SC/35/RW26)’ (Scarff, 1986), should be to Henderson (1983). Also the brackets surrounding these same data indicate that these catches are included in the subtotal data contained in the seventh column labelled ‘US Whalers’.

Table 1

Ratio of whales struck to catch, or Catch-to-mortality adjustment factors for pelagic right whaling in the literature.

Ratio of whales struck to processed whales	Comments	Source
1.2-1.5:1	'[A]verage mortality factor, pertaining to [northern right whale] fisheries in which hand harpoons and lances (non-explosive) were used, would be between 1.2 and 1.5'	1983 IWC Workshop on Status of Right Whales (IWC, 1986, p.5)
1:53-1.83:1	Recorded struck-but-lost ratios for the North Pacific, South Atlantic and Indian Ocean (see text)	(IWC, 1986, appendix 8)
1.2:1	Factor for all oceans, may be based on Scammon (1874, p.251)	Starbuck (1878 p.661 table J, footnote)
1.35 and 1.5	Adjustments used by 1998 IWC Right Whale Workshop participants to estimate whaling-induced mortality on right whales in the Southern Hemisphere by pre-modern pelagic whalers	(IWC, 2001)
1.33:1	Estimate for northern right whales in the Sea of Okhotsk	Henderson (pers. comm., 1991)
1.41:1	Data from 48 voyages of French whalers in the South Atlantic 1821-37 (942 right whales processed out of 1,330 struck)	Du Pasquier (1986)
1.5:1	Of 20 whales struck on the Cape Farewell Grounds off the south coast of Greenland 1868-1897, 6 were killed but lost, 1 escaped, 13 were captured but 1 calf secured was discarded	Reeves and Mitchell (1986b, pp.254, 260)
1.93:1	Weighted average 'loss rate factor' (LRF) for three voyages to the Northwest Ground	Reeves and Mitchell (1986b, p.254)
2.46:1	Crude struck-but-lost ratio without adjustment for survivors or subsequent captures based on sample of 327 North Pacific northern right whales	This study, Table 3
1.39:1	Adjustment to reflect only the proportion of northern right whales which sank before escaping or being processed	This study, Table 3

1838-1839 (1.18-1.35), Cintra Bay, northwest Africa 1855-1858 (1.25-1.25) and 60/35 (Cape Farewell, North Atlantic) ground 1868-1898 (1.50-1.54).[2]

For the North Pacific, South Atlantic and Indian Ocean (1834-1864) appendix 8 of the 1983 Workshop Report (IWC, 1986b) shows ratios of total mortality to landed catches of 1.53-1.83:1, based on reports of 170 right whales struck between 1834-64. Although SC/35/RW22 is cited as the source of this information, this is clearly an error.[3] It appears that the reference for the North Pacific, South Atlantic and Indian Ocean data was also intended to be to Reeves and Mitchell (1986a, table 5) which discusses struck-but-lost data for these areas for this period.

However, the data in the IWC (1986) appendix do not quite match the data in Reeves and Mitchell (1986a). The differences are described in Table 2.

The most data on struck-but-lost right whales were reported by Du Pasquier (1986) regarding French pelagic whaling primarily in the South Atlantic. During ten voyages between 1787-1792, 294 right whales were struck. Of these, 181 were processed, 41 sank before being processed and 1 sank while it was being flensed; 70 whales 'escaped'. Du Pasquier (1986) suggested using an adjustment factor of 1.14 to adjust for the whales which sank prior to being flensed. He made no estimate of the number of whales that escaped and later died.

The recorded ratios for struck-but-lost northern right whales in IWC (1986a) were higher than previously published adjustment factors. In estimating the total number of northern right whales killed, Starbuck (1878, p.661, table J, footnote) assumed that for every 80 right whales caught, secured and processed, another 20 were struck-but-lost and died: Loss Rate Factor (LRF) = 1.25. Best (1987) and Reeves and Mitchell (1986b) described Starbuck as relying on Scammon (1874, p.251), who wrote that 'one-fifth' more whales were killed than estimates of the processed catch (LRF = 1.2). However, Scammon stated this in a chapter on California shore whaling which refers mainly to whaling for gray whales (*Eschrictius robustus*) and humpback whales (*Megaptera novaeangliae*). Northern right whales were exceedingly rare in the catch of California shore stations (Scarff, 1986) and Scammon does not appear to have ever engaged in hunting northern right whales, so his estimate may not be relevant to the pelagic northern right whale fishery.

Reeves and Mitchell (1986b, pp.209-10) reviewed data on struck-but-lost whales in the northern right whale shore fishery off Long Island, New York. They concluded that the LRF in that fishery was probably closer to 1.2-1.6 than to 1.85.

Attempts at categorising the logbook data

IWC (1986a, p.5) listed four different categories of struck whales described in the logbooks:

(1) struck, killed and processed;
(2) struck but escaped (and presumably survived);
(3) struck but escaped, moribund
    (a) lanced and/or spouting blood, or
    (b) with whaling gear attached; and

---

[2] The data regarding the Cape Farewell Ground appears to be derived from Reeves and Mitchell (1986a, p.250). In which case, the total number of whales struck should be 20, not 19 as reported in the table, and the ratios would be 1.50-1.54.

[3] SC/35/RW22 does not discuss struck-but-lost whales. The immediate prior citation in the table to whaling in Cintra Bay is also to SC/35/RW22 and is also an error. The data on Cintra Bay appear to be derived from SC/35/RW23, Reeves and Mitchell (1986a, table 4, pp.252-54).

Table 2

Comparison of struck-but-lost data in IWC (1986b, p.31) and the source data from Reeves and Mitchell (1986a, p.254).

Source	Period	Struck (a)	Struck, killed and not processed (b)	Struck and escaped (c)	Struck, killed and processed (d)	Mortality factor**	
						'one'	'two'
Appendix 8 (IWC, 1986)	1834-64	170	22	55	93	1.83	1.53
Table 5, Reeves and Mitchell (1986a)	1834-80	228	33	71	124*	1.84	1.56

*Includes 'dryskins'. **Mortality factor 'one'=a/d, mortality factor 'two'=(d+0.5c+b)/d.

(4) struck, killed, but not processed; and
   (a) recovered later as a drift whale or stinker, or
   (b) not recovered (due to sinking, rough seas, etc.).

The high estimate assumed that all the 'struck-but-escaped' animals died later and were not recovered, whereas the low estimate assumed that less than half of these died later and were not recovered.

Reeves and Mitchell (1986a, p.254) used a slightly different set of categories in their discussion of struck-but-lost mortality in the North Atlantic northern right whale fishery. They split the data into six groupings:

s	whales killed but lost, including those lost spouting blood;
u	struck and lost but 'unspecified';
d	struck and lost because the iron drew;
p	struck and lost carrying whaling gear;
c	calves orphaned; and
T	whales secured (including carcasses found) and taken alongside, as well as those secured but not tried out because of low oil yield ('dry skins').

From these groupings they derived an LRF to adjust catch records to total mortality according to the following equation:

$$\text{LRF} = [T + s + 0.5(u) + 0.5(d) + p + c] / T$$

This assumes that *all* of the whales spouting blood or carrying whaling gear when lost died, and that 50% of the whales that escaped when the harpoon pulled out or for unspecified reasons also died. With these assumptions, their LRF is intermediate between the high and low boundary assumptions given in IWC (1986a).

The LRF for the 15 voyages Reeves and Mitchell (1986b) described ranges from 1.0 (the minimum possible, one whale struck for each one landed) to 3.13 (4 whales landed out of 15 struck). In their data set, no calves were recorded as being orphaned. The three North Pacific voyages they report for the *Mary* (1 June to 8 August 1846) and *Braganza* (30 May to 17 August 1841, and 1 May to 17 July 1842) yield LRFs of 1.79, 2.09 and 1.83 respectively. The weighted average of these three voyages is 1.94.

Whales sinking before processing

It is popularly thought that right whales were the first large whales hunted because, among other factors, they tended to float when killed (e.g. Gilmore, 1978). Although right whales are more likely to float when dead than balaenopterids, they can sink, frequently enough for this loss factor to need explicit consideration when developing an adjustment for struck-but-lost mortality.

Du Pasquier (1986) reported that of 224 southern right whales (*Eubalaena australis*) killed by French whalers primarily in the South Atlantic between 1787-92, 41 (14%) sank before they could be flensed, whilst one sank during flensing. More examples of northern right whales sinking when killed, and the efforts of the shore whalers on Long Island, New York, to keep the carcasses afloat are described in Reeves and Mitchell (1986b, p.209).

Whales found dead

Some whales struck with a harpoon but subsequently lost were later found by the same or another whaleship, retrieved and processed. Best (1987, p.415) found that 103 of the right whales recorded in Townsend's (1935) abstracts (2.9% of the landed catch) were already dead when found by the whaleship. He wrote:

> these figures might be underestimates if (as seems likely) not all whales found dead were recorded as such in the logbooks or logbook extracts. If so, this fact should be borne in mind when corrections are applied to the landed catch to account for whales struck and lost that subsequently died.

Non-American whaling for northern right whales in the North Pacific

Although most of the whaling for northern right whales in the North Pacific was carried out by American whaleships, there were significant numbers of non-American whalers also taking them in these waters. The first northern right whale taken in the North Pacific was probably landed by a French ship, the *Gange* (Webb, 1988).

Immediately prior to the advent of right whaling in the North Pacific, non-American whalers were very active in hunting southern right whales in the South Pacific. French whalers caught *ca*. 4,000 southern right whales in the South Pacific from 1835-39, nearly 30% of a total catch of just under 14,000 southern right whales (IWC, 1986a, p.30). Du Pasquier (1986) noted that in 1839, 20 French whaling ships were whaling near southern Australia, Tasmania and New Zealand; in 1841, 27 French whalers were in these southern waters. The number dropped to eight in 1842 and nine in 1843. Du Pasquier stated that at least these latter whalers went to the North Pacific or the Sea of Okhotsk in subsequent years, presumably following the other French whalers who had departed for these grounds previously.

Webb (1988) reported that of the 161 whaling ships that called at Honolulu in 1845, 21% were of non-American registry: 19 from France, 6 from Bremen, 3 from New Brunswick, 2 from Denmark, and 1 each from Prussia, Hanover, Norway, and Hamburg.

Non-American whaling also occurred near and in the Sea of Okhotsk. Kugler (1984) mentions that in 1845, 11 whaleships, consisting of 8 American, 2 French and 1 Danish whaleship (*Neptun*) called at Petropavlosk, Kamchatka. The French whalers reported catching eight northern right whales in the Sea of Okhotsk that year (Kugler, 1984). In 1847, of the 30 whaleships reported in the Sea of Okhotsk, four were French (Kugler, 1984). Altogether, these 30 whalers took 341 northern right whales that year. Du Pasquier (1986) states that after 1848, French participation in North Pacific whaling declined, and ended in 1868.

Despite its potential significance, the effect of non-American whalers on total northern right whale mortality in the North Pacific has not been quantified in most previous estimates of the catch of northern right whales in the North Pacific (IWC, 1986a; Best, 1987).

Adjustment for 'incomplete' voyages

Not all the vessels that cruised for northern right whales in the 1840s and 1850s returned to port. In 1846 alone, the *Konohasset* of Sag Harbour sank off Kamchatka and the *Baltic* of Fairhaven was lost on Bering's Island (Webb, 1988). Right whales killed during such voyages would not be accounted for in the lists of returns. Nearly 10% of the voyages listed by Starbuck (1878) and Hegarty (1959) were recorded as 'incomplete'. Best (1987) explicitly adjusted his estimates of whale catches arbitrarily assuming that on average incomplete voyages caught half the number of baleen whales as completed voyages. No additional review was made in this study to test the reasonableness of this assumption.

SOURCES

This study incorporates quantitative data from 10 voyages between 1838-52 described in Webb (1988) and additional anecdotal information and impressions from Webb (1988) not previously considered. In addition, data from North Pacific voyages reported in Reeves and Mitchell (1986b; 1986a) are reviewed in the specific context of North Pacific 19th century whaling. Due to logistical constraints, no attempt was made to examine the actual logbooks themselves for these data, and it is thus possible that substantial additional data are available therein.

RESULTS

North Pacific data on struck-but-lost mortality

Table 3 describes quantified data on the number of northern right whales struck, the number which sank and the number which were landed and processed for 14 voyages of American pelagic whalers in the North Pacific between 1838 and the '1850s'. Webb (1988, p.70) states that his portion of the data 'were an average of the lot'.

In the North Pacific, what little data have been published since IWC (1986a) suggest that the report's estimates of struck-but-lost animals may be too low. Based upon his review of North Pacific logbooks, Webb (1988, p.69) stated:

> The success rate among whaleboat crews on the Northwest Coast during the 1840s was dismal. Even the most experienced men brought back fewer than 50 per cent of the [right] whales they struck with their harpoons; in some ships barely 20 per cent of the whales struck were killed; those crews losing four of five whales…
>
> …The common ways to lose a whale were these: by the harpoon breaking, or by a line being accidentally cut with a second harpoon; by a harpoon 'drawing' from soft blubber, by a deep dive, necessitating a quick cut to prevent the swamping of the whaleboat; by a fluke or flipper knocking a boat to pieces or capsizing it.

Whalers sometimes had to cut loose from a whale if it was pulling the whaleboat upwind, particularly if the whaleboat was getting out of sight of the whaleship due to fog or other reasons.

Webb suggested that the high percentage of struck-but-lost animals was due in large part to reliance on the double-barbed harpoon in the North Pacific during the 1840s. The much more effective single-barbed toggle harpoon did not reach the North Pacific until the 1850s (Webb, 1988, p.71). Between 75-85% of the total 19th century catch of northern right whales in the North Pacific pelagic fishery occurred in the period 1835-49, prior to the advent of the single-barbed toggle harpoon in the North Pacific (Best, 1987).

In the Sea of Okhotsk, Henderson (pers. comm., 1991) estimated that one northern right whale was killed but lost for every three northern right whales processed (1.33:1 ratio of total mortality:catch). This is lower than the 1.5:1 ratio attributed to Henderson previously in Kugler (1984). Henderson believed loss rates for northern right whales were greater than for bowheads in the Sea of Okhotsk as a result of right whaling occurring offshore whereas bowhead whaling occurred in the bays where many of the struck-but-lost whales could be later recovered.

Gross ratio of struck whales/catch data

As shown in Table 3, on 12 voyages in the North Pacific, 327 northern right whales were struck with harpoons, but only 133 landed. This reflects a crude ratio of total whales struck:whales landed of 2.46:1. This ratio contains no adjustment for struck whales which either survived their injuries, or died from their injuries but were later recovered by whalers as drifting carcasses.

Table 3

Struck-but-lost records for northern right whales in the North Pacific pelagic fishery 1838-1860. n/a = data not available. Sources: A = Webb (1988, pp.65-72), B = Reeves and Mitchell (1986b, table 5), C = Cheever (1850, p.99) cited in Webb (1988, p.72), D = Reeves and Mitchell (1986a, p.209).

Year	Ship	Lowerings	Right whales Struck	Sank	Landed	Source
1838	*Timoleon*	n/a	12	n/a	2	A
1841	*Superior*	n/a	58	5	26	A
1841	*Orozimbo*	n/a	5	n/a	3	A
1841	*Braganza*	44	38	5[1]	17	B,D
1842	*Braganza*	39	25		12	B,D
1842	*Elisa*	n/a	44	n/a	15	A
1842	*Angelina* (French)	n/a	20	n/a	14	A
1844	*Magnet*	n/a	26	n/a	13	A
1845	*Hibernia*	n/a	46	n/a	13	A
1846	*Mary*	37	14[2]	n/a	7	B
1848	*Julian*	n/a	12	n/a	3	A
1840s	unknown	n/a	n/a	6	0	C
1852	*Golconda*	70	27[3]	4	8	A
1850s	*Julian*?	n/a	n/a	11	17	D[4]

[1] Of the 63 whales struck by the *Braganza* in 1841 and 1842, 8 whales in 1841 and 1 whale in 1842 were lost. Of these 9 whales, 5 sank and 4 swam away spouting blood. Reeves (pers. comm.) assumes these latter whales also died.

[2] Of the 7 whales struck-but-lost by the *Mary*, 1 was lost either dead or spouting blood, 1 was lost without explanation, for 2 whales the harpoon drew out and for 3 whales the animals escaped carrying whaling gear on them.

[3] Webb (1988 p.70) summarises from the log of the *Golconda*: 'In the summer of 1852, the crew of the ship *Golconda* remained on the Northwest Coast until 2 September, lowering seventy times for whales and realizing a return of only eight animals. Forty-nine attempts ended in total failure, the oarsmen not able to bring the boatsteerer close enough to the gallied [=frightened] animals. During twenty-one other attempts only twelve whales were killed, and four of these sank irretrievably. The men lost fifteen more to causes beyond their control: three by irons drawing, four by irons breaking, another four escaping when the twisted strands of the whaling line parted. They intentionally cut from two whales, and accidentally separated themselves from a third when a second harpoon severed the fast line. In another case a loose whale stove a boat and forced a cancellation of the hunt.' These numbers suggest that more than one whale was struck on some lowerings otherwise it is difficult to reconcile the 12 whales killed with the 15 whales escaped and the 21 lowerings with some success.

[4] Reeves and Mitchell (1986a, p.209) cite Winegar, S.P. (1860). Cruise of the whaleship *Julian*. *Whalemen's Shipping List, and Merchants' Transcript*, 18(33), 23 October, for this information. They do not specify whether Winegar was referring to the *Julian* or some other ship.

Whales lost because the carcasses sank

The North Pacific data reviewed is consistent with the findings discussed above. The sinking of northern right whale carcasses before 19th century pelagic whalers could flense them occurred frequently. Bowles (1845) stated, apparently in reference to northern right whales:

> Within the deep bight formed by the peninsula of Aliaska [sic.] and near the Island of Kodiak, I have also seen large numbers of whales, but they were of a much smaller size than those we had found more to the Southward, and more than half we captured, sunk when dead. I have known the boats of one ship to kill six whales here in a day, and all of them sunk. Nor can this sinking of whales be at all accounted for. I have known a whale of the largest size, which in cutting him in, was found to be a dry skin (another singular fact in their physiology not to be accounted for, the blubber contained a milky fluid instead of oil) and yet this whale floated as light as a cork. Again, I have killed a whale with a single lance and he sunk like a stone, when another was lanced a hundred times, with the same result. As I said before, the cause of their sinking is unknown, and will be until we are better acquainted with their natural history than at present.

Cheever (1850, p.99, cited in Webb, 1988, p.72) reported:

> The havoc they make of whales is intense…I have heard of one ship that sunk twenty-six whales after she had killed them; of another that killed nine before she saved one; of another that killed six in one day, and all of them sunk.

As shown in Table 3, on the six voyages which data on the number of whales landed and the number which sank was recorded, 31 carcasses sank and 80 northern right whales were landed.[4] This is substantially higher than Du Pasquier's (1986) finding of 41.5 whales sinking out of 182.5 processed in the South Atlantic from 1787-92. Using the sunk/processed ratio from the North Pacific sample suggests that a multiplier of 1.39 should be applied for this factor alone, compared to a multiplier of 1.23 from Du Pasquier's study. The four North Pacific voyages in Table 3, which contain data on both the numbers of whales struck and whales which sank, show that of 148 northern right whales struck with harpoons, 14 sank before they could be recovered.

The analysis is complicated by the fact that whalers were probably able to recover some of the 'sinkers' if they remained attached to the whale. The whaleboat provided some offsetting buoyancy, more if two or more whaleboats were attached to the whale. Mitchell and Reeves (1986b) described the efforts of shore whalers in Long Island to use the buoyancy of the whaleboats to prevent a whale from sinking out of reach. Presumably similar techniques were used by the pelagic whalers in the North Pacific.

Whales found dead

As mentioned earlier, Best (1987) reported that in Townsend's abstracts a minimum of 2.9% of the catch of right whales from all oceans were already dead when found and processed by the whalers. Best (1987) suggested that the actual percentage of the landed catch which represented carcasses found floating might be significantly higher. The small amount of new information from this study supports the idea that the catch of already-dead carcasses may have been greater than 2.9%. Webb (1988, p.71) commented that:

> almost every logbook from the Northwest Coast reports the discovery of a [northern right whale] carcass or two, some bearing in their flesh the identifiable harpoons from the fatal struggle.

He suggested that most of the carcasses found were too decomposed to be rendered into oil and would not be reflected in the lists of returns (oil and baleen) used to estimate catches. As Best (1987) noted, such 'stinkers' may also not have been regularly reported in the logs.

Because 2.9% of the northern right whales reflected in the catch data relied on by Best (1987) were dead when found, it is necessary to adjust the crude struck-but-lost ratio of 2.46:1 described above to avoid double-counting these whales found dead. Accordingly the ratio was adjusted by 2.9% to result in a *net* struck-but-lost ratio of 2.43:1. This is the ratio that is used to calculate total mortality in Tables 4 and 5. If further study shows that more of the right whales eventually flensed were found dead, this would tend to *reduce* the struck-but-lost ratio further.

Adjusting for non-American whaling

These fragmentary data suggest that the non-American registered ships may have constituted as much as 15-20% of the whaleships on the northern right whale grounds. This indicates that more research to quantify their catch is warranted.

Estimates of total mortality

Estimates of total mortality were extrapolated from catch data and are reported in Tables 4 and 5. The catch data used were an average of Best's (1987) two estimates of catches in the American whale fishery developed using production and catch-per-voyage methods. For the period 1840-1909, Best's two methods yield estimates for the catch of northern right whales in the North Pacific (15,374 and 14,480 respectively) that differ by only 6%. Over five-year time periods, the methods differ more due to delays in reporting inherent in the oil production method.

Estimates of mortality from the American fishery were calculated by multiplying the catch data by either the IWC (1986a) struck-but-lost adjustment factors or the adjustment factors recommended in this study. In the first instance, the catch data were adjusted by the adjustments of 1.2 and 1.5 (IWC, 1986a, p.5) for the entire period 1835-1909 to get upper and lower estimates of total mortality.

In the second instance, the catch data were adjusted by struck-but-lost factors derived in this study. A gross struck-but-lost mortality factor of 2.46 was chosen based on Table 3. This was adjusted to reflect the opportunistic recovery of already killed whales, assuming that 2.9% of the total catch fit into this category based on Townsend's (1935) records described in Best (1987), resulting in a net struck-but-lost adjustment factor of 2.43. This factor was applied for 1835-54. Given the change to the much more efficient single toggle harpoon around 1855, a struck-but-lost adjustment factor of 1.4 was chosen for 1855-1909. During both periods, the lower estimates were calculated assuming that 50% of the struck-but-lost whales died; upper estimates were calculated assuming that all the struck-but-lost whales died.

Finally, the impact of non-American whalers was incorporated by assuming that they comprised 10% of the whaling fleet and made 10% of the catch during the period 1835-1859, 0% after 1859, and had struck-but-lost rates similar to the American fleet's. The latter seems reasonable since many officers of these foreign ships were American.

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[4] *Superior* 1841, *Braganza* 1841-42, unknown 1840s, *Golconda* 1852 and *Julian* 1850s.

Table 4

Estimates of total mortality of right whales in the 19th century North Pacific pelagic fishery. All the estimates of total mortality reflect adjustments to the average of Best's (1987) two estimates of the catch of the American pelagic fishery.

				Adjusted estimates of total mortality					
	Estimated catches by American whalers[1]			Mortality with only an adjustment for struck-but-lost whales				Including foreign whalers	
Years	Oil production[1]	Catch/ voyage[1]	Average	low bound*[2] (1.2:1)	high bound*[2] (1.5:1)	low bound**[3] (1.69:1)	high bound**[3] (2.43:1)	low bound**[4]	high bound**[4]
1835-39		149	75	89	112	126	181	140	201
1840-44	2,957	5,728	4,343	5,211	6,514	7,339	10,552	8,154	11,725
1845-49	8,001	5,578	6,790	8,147	10,184	11,474	16,498	12,749	18,332
1850-54	1,364	951	1,158	1,389	1,736	1,956	2,813	2,174	3,125
1855-59	1,381	1,221	1,301	1,561	1,952	1,561	1,821	1,735	2,024
1860-64	585	152	369	442	553	442	516	442	516
1865-69	441	434	438	525	656	525	613	525	613
1870-74	58	52	55	66	83	66	77	66	77
1875-79	85	16	51	61	76	61	71	61	71
1880-84	8	48	28	34	42	34	39	34	39
1885-89	356	90	223	268	335	268	312	268	312
1890-94	39	26	33	39	49	39	46	39	46
1895-99	56	16	36	43	54	43	50	43	50
1900-04	38	19	29	34	43	34	40	34	40
1905-09	5		3	3	4	3	4	3	4
Total	15,374	14,480	14,927	17,912	22,391	23,971	33,633	26,466	37,173

* Both high and low bounds apply struck-but-lost factors of 1.5:1 for each whale reported captured 1835-1909. The low bound assumes that 40% of the whales struck-but-lost (SBL) die (1.2:1); the high bound assumes that all the SBL whales die. ** Both high and low bounds apply SBL factors of 2.46 for each whale reported captured 1835-54. The high bound assumes that all of the struck whales die; the low bound assumes that 50% of the struck whales die. Both factors are adjusted to reflect an assumed 3% of the catch being of whales already killed by whalers, yielding net SBL adjustment factors of 1.69 and 2.43 respectively. For the period 1855-1909, it is assumed that the single-toggle harpoon dramatically reduced the number of whales lost, so a SBL estimate of 1.4:1 was used.

[1] Best (1987). [2] Using the SBL factor from the 1983 IWC Workshop Report (IWC, 1986). [3] Using the SBL factors from this study. [4] Assumes 10% foreign participation 1840-59 on SBL factors from this study.

Table 5

Cumulative American catch and estimated total mortality of right whales in the pelagic North Pacific fishery 1835-1909.

			Cumulative mortality				
	Cumulative American catch		Using SBL factors from IWC (1986)		From this study		
Period	No.	%	low	high	low	high	% (high)
1835-39	75	<1%	89	112	140	201	1%
1840-44	4,417	30%	5,300	6,626	8,294	11,926	32%
1845-49	11,207	75%	13,448	16,810	21,043	30,258	81%
1850-54	12,364	83%	14,837	18,546	23,217	33,383	90%
1855-59	13,665	92%	16,398	20,498	24,952	35,407	95%
1860-64	14,034	94%	16,840	21,050	25,394	35,922	97%
1865-69	14,471	97%	17,365	21,707	25,919	36,535	98%
1835-1909	14,927	100%	17,912	22,390	26,466	37,173	100%

Sources: Cumulative American catch is the average of Best's (1987) two estimates. The cumulative mortality is from this study (Table 4, adjusted for foreign whaling). The cumulative percentage is based on the high bound estimate from this study including the adjustment for foreign whaling.

Table 5 presents the same data on a cumulative basis. The total mortality estimates are those (a) from American whaling alone using the IWC (1986a) adjustment factors (1.2, 1.5) giving a range of 17,912-22,391 and (b) those using the adjustment factors recommended in this study giving a range of 26,466-37,173. These estimates illustrate that struck-but-lost mortality combined with non-American whaling may have been as great a factor in overall northern right whale mortality as the recorded catch by American whalers.

Given the rarity of northern right whales in these areas today, the estimated total whaling-induced mortality of 20,000-30,000 northern right whales in a single decade, the 1840s, is particularly striking.

DISCUSSION

How different was pelagic right whaling in the North Pacific from right whaling in other oceans?

IWC (1986a, p.5) stated that there:

> are significant differences in loss rates by whaling area, time period, and technology in use. These should be recognised in any reconstruction of catch history…. Losses seem to have been higher on the open seas than they were in bay whaling.

The North Pacific is not specifically identified as warranting a special adjustment factor; however, combined data for the South Atlantic, North Pacific and Indian Ocean whaling suggest that use of a higher adjustment factor is appropriate (IWC, 1986b, appendix 8). Among those three areas, the particularly bad conditions in the North Pacific and Sea of Okhotsk were well noted by contemporary whalers.

Given the sea conditions frequently found in the Gulf of Alaska, along the Aleutian Islands and along the Kamchatka coast, it is quite plausible that the ratio of the number of animals struck-but-lost to the number of whales reflected in the catch data in the North Pacific was greater than in other regions. Webb (1988, p.65) summarised conditions described in the logbooks he reviewed:

> Accounts of the Northwest Coast voyages are saturated with weather, often 'rugged' with rain, sleet, fog, and snow, punctuated by living gales from the Arctic North and every other point on the compass. 'Thick', they wrote. 'Thick and rain'. 'Thick, wet and disagreeable'.
>
> Coming with the fog, and sometimes apart from it, were the 'strong breezes', gales, and 'near hurricanes' which drove the seas to frothy crests and necessarily inhibited the whaling. The phrase 'Too rugged to lower' pervades the journals; too rugged to chase whales, too rugged to start the tryworks, too rugged to make sail. And if a whale was somehow taken in such dismal conditions…[i]n the deep Pacific swell, the rolling of the whales against the fluke chain and the hull often caused its body to part company with the ship.

The data described in this study represent a very small sample from a very large, albeit brief, fishery. The purpose of the study was to suggest again that the 19th century pelagic whaling on northern right whales in the North Pacific may have depleted an initial population that was substantially larger than may have been previously thought. It seems likely that more data exist in the logbooks that could increase the sample size examined and provide more reliable estimates of struck-but-lost ratios. This study suggests that further examination of those logbooks would be a worthwhile effort.

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Conservation status of North Pacific right whales

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ABSTRACT

The North Pacific right whale (*Eubalaena japonica*) is among the most endangered of all great whales, having been subject to intensive commercial whaling in the 19th century. All available 20th century records of this species in the North Pacific were reviewed. There has been a total of 1,965 recorded sightings since 1900; of these, 988 came from the western North Pacific, 693 from the eastern North Pacific and 284 had no location specified. Thirteen strandings (all but one from the western North Pacific) were recorded. Known catches for commercial or scientific purposes totalled 742 (331 in the western North Pacific, 411 in the eastern North Pacific). Most of the reported Soviet 'sightings' in the eastern North Pacific were actually catches, as may be the case for Soviet sightings in the Okhotsk Sea. In addition, the impact of known Soviet illegal catches in the Okhotsk Sea may be reflected in an apparent decline in sightings after the 1960s (although this may be partly explained by low observer effort). Overall, the data support the hypothesis that at least two stocks of right whales exist in the North Pacific. Any recovery in the western North Pacific population was compromised by the Soviet catches in the Okhotsk region, although recent sightings suggest that this population is still large enough to sustain reproduction. By contrast, Soviet catches in the now-smaller eastern North Pacific population have severely reduced its prospects for recovery. Although the prognosis for this population is poor, a long-term monitoring programme is required to better understand its conservation status and to determine whether it may be affected by human-related problems that would require mitigation.

KEYWORDS: RIGHT WHALE; PACIFIC OCEAN; NORTHERN HEMISPHERE; WHALING-MODERN; WHALING-HISTORICAL; CONSERVATION; DISTRIBUTION

INTRODUCTION

The North Pacific right whale, *Eubalaena japonica*, was once abundant in much of the North Pacific. The crew of the American whaler *Ganges*, one of the first vessels to work in the so-called 'Northwest Ground' (the Gulf of Alaska region), reported seeing 'millions' of right whales in 1835-36 (Webb, 1988). Contemporary records, compiled from the logs of 19th century whaling ships by the American naval officer Matthew Fontaine Maury, reveal an abundance of right whales across a broad range that stretched from Alaska to Japan (Scarff, 1986a; 1991). However, intensive commercial whaling proved devastating, and today the North Pacific right whale populations are among the most endangered of all the great whales (IWC, 2001b).

Aboriginal whaling for this species was conducted by various peoples from Washington state and British Columbia to eastern Asia (Tomilin, 1957; Mitchell, 1979; Omura, 1986; Scarff, 1991; Mitchell and Reeves, 2001). However, it does not appear that right whales were usually the primary target of these hunts, nor were they taken in significant numbers. Right whales were taken with some regularity in coastal Japan, where net whaling began in the 17th century (Omura, 1986). Net whaling also occurred for a short time off southern Sakhalin Island prior to 1904 (Tomilin, 1957). Catch records from these fisheries are incomplete so it is not known whether this method of exploitation had any significant effects on the population.

By contrast, the impact of commercial whaling was rapid and devastating. Pelagic whaling for right whales started first in the Sea of Japan during the 1820s. From 1835, from what came to be known as the Kodiak or Northwest Ground, whaling effort quickly spread across the Pacific. By 1845, American vessels were operating in the southern Okhotsk Sea (Webb, 1988; Scarff, 1991). By 1847-48, catches of right whales had already declined, and the discovery of bowhead whales (*Balaena mysticetus*) in high latitudes north of the Bering Strait resulted in a change of focus for the majority of vessels in the American fishery. Best (1987) estimated that American pelagic whalers in the North Pacific (including the Okhotsk Sea but not the Sea of Japan) killed an estimated 14,500 right whales. These catches do not make any allowance for hunting loss and do not include catches by British, French and other European whalers. The total North Pacific catch of right whales has been variously estimated at 20,000 (Du Pasquier, 1986), or between 26,500 and 37,000 (Scarff, 2001). Right whales continued to be taken after 1849, although the paucity of catch records after 1900 is testament to the damage inflicted upon these populations during the period of extensive exploitation. The species was never again the principal focus of commercial whaling. Although a Japanese coastal fishery, using modern methods, took 192 right whales in the western North Pacific between 1900 and 1948 (Omura, 1986), documented legal catches elsewhere for either commercial or scientific purposes were infrequent.

The Convention for the Regulation of Whaling was concluded in Geneva on 24 September 1931. Article 4 of the Convention states that 'The taking or killing of right whales, which shall be deemed to include North-Cape whales, Greenland whales, southern right whales, Pacific right whales, and southern pigmy right whales, is prohibited'. After the close of the meeting numerous whaling nations ratified the Convention but Japan and the USSR were not parties to the Convention. After World War II, Japan was allowed to conduct whaling operations again under the regulations established by the Supreme Commander for the Allied Powers in 1945. One of these regulations stated that the killing of gray and right whales in the North Pacific was prohibited. Japan joined the IWC in April 1951. The USSR joined the IWC in 1948. Furthermore, it is now known that the Soviet Union conducted illegal whaling on a large scale, beginning in the Southern Hemisphere in the 1949/50 season (Zemsky *et al.*, 1995) and that this included large numbers of

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right whales (Tormosov *et al.*, 1998); related operations subsequently took hundreds of right whales in the Okhotsk Sea, around the Kuril Islands, in the southeastern Bering Sea and the Gulf of Alaska and maybe beyond (Yablokov, 1994; Doroshenko, 2000). The species has been so rare in the eastern North Pacific that, over the past forty years, even single sightings have merited publication (Gilmore, 1956; Woodhouse and Strickley, 1982; Carretta *et al.*, 1994; Rowlett *et al.*, 1994; Gendron *et al.*, 1999). In the western portion of their former range, right whales have been observed with greater frequency in the Okhotsk Sea (Miyashita and Kato, 1998) but sightings elsewhere are still comparatively rare.

Much is unknown or uncertain regarding even some basic aspects of the biology and behaviour of the North Pacific right whale. There is no agreement on the number of populations that exist, the current population size is unknown for either the eastern or western population, and the location of the calving grounds remains a mystery. Indeed, with the exception of a series of Soviet and Japanese papers, based primarily on 23 animals killed for research purposes (Omura, 1958; Klumov, 1962; Omura *et al.*, 1969), virtually nothing has been published on the biology of the species.

The purpose of this paper is to review knowledge concerning the right whale in the North Pacific, and to attempt to assess the status of those animals that remain. For the purpose of conservation, it is important to take a basin-wide approach to understanding population structure and abundance. A complete listing of all known sightings, strandings and catches in the 20th century is provided.

METHODS AND MATERIALS

All available records of North Pacific right whales from the 20th century were reviewed. Scarff (1986a; 1991) provided a thorough analysis of the right whale's historic distribution as determined from 19th century whaling manuscripts collected by Maury (1852; 1853) and additionally summarised sighting records for the eastern North Pacific since 1855. The current paper is based on a complete listing of all known sightings, strandings or catches of right whales, including numerous published and unpublished sources that were either not covered by, or were unavailable to, Scarff. The review begins in 1900 because it represents a convenient division and the beginning of modern-type whaling in the North Pacific (Tonnessen and Johnsen, 1982).

There is sometimes confusion in records between the right whale and the closely related bowhead. For example, we believe that the right whales referred to by Tomilin (1957) were bowheads, since their reported distribution and timing of occurrence in the western Okhotsk Sea closely fits known patterns for this species. Similarly, it is clear that all of the right whales reported by Klumov (1962) in the vicinity of the Shantar Islands were in fact bowheads (Brownell, unpublished). The Russian language contains words specific to each species (Японский кíт = *E. glacialis/E. japonica;* and Гренландский кíт = *B. mysticetus*), as well as a more generic term ('smooth whales') which can imply either. In cases where the species identity was in question, the original texts were examined to verify the reliability of the English translation. The Russian originals were also examined when two or more papers gave conflicting accounts of the same sighting event(s). Where possible, authors (both Japanese and Russian) were queried for clarification of confusing or contradictory data.

In certain cases, numbers have been extrapolated from plots in the original papers, notably Berzin and Rovnin (1966) and Omura *et al.* (1969). It should be noted that it is not possible to obtain a precise count from these sources. In the case of Omura *et al.* (1969), one of us (TK) obtained the original data (those for the period 1959-62) on which some of this paper was based. Since these data give more detail in terms of sighting dates, locations and numbers of whales they have been incorporated into this review. For the remainder of the plotted sightings in Omura *et al.* (1969), each plot has been counted as a single whale, although it is known from the detailed data that this is not always the case[1]. Similarly, the two types of symbol used in the plots of Berzin and Rovnin (1966, fig. 6) represent sightings of either '1-3' or '15-20' animals; consequently, calculations from counts of these plots yield a range for each area rather than a single total. In all cases where a sighting has been reported as a range, the midpoint of that range has been used when calculating the total number of sightings for each area.

Sources and effort

The majority of records of North Pacific right whales come from vessels associated with the whaling industry. These include incidental sightings by catcherboats, factory ships and marking cruises, as well as much more extensive records provided by scouting boats or by research vessels engaged in directed sighting surveys for the specific purpose of establishing the abundance and distribution of whales. Of particular value is the series of extensive annual surveys conducted since 1964 by Japan. These surveys have covered virtually the entire North Pacific north of 20°N, although largely confined to the summer months. Their effort and results are summarised by Wada (1975) and by the annual Japanese national progress reports on whale research to the International Whaling Commission from 1976 onwards.

Almost all other sources of sightings are incidental in nature. They range from scientific research vessels (notably those of the Soviet Union) and recent aerial surveys off the west coast of the USA, to opportunistic sightings from a variety of vessels and individuals.

With the exception of the Japanese sighting surveys, it is generally not possible to meaningfully quantify the effort invested by these various sources. However, some general remarks concerning coverage are possible, and these are incorporated into the Discussion.

Study area and regional divisions

The study area includes the entire North Pacific Ocean from the equator northwards, including bodies of water outside the Pacific proper (e.g. Bering Sea, Okhotsk Sea). Since there is disagreement regarding the number and boundaries of right whale stocks in the North Pacific, the study area was arbitrarily divided into eastern and western halves at the 180° line of longitude.

In addition to listing all records chronologically within event type (sighting, catch, stranding), a record was also assigned to a general region. Regional divisions are necessarily somewhat arbitrary, and are used solely for the purpose of more clearly summarising the data. The principal divisions of the North Pacific used here can be broadly defined as follows.

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[1] There is an error in table 14 of Omura *et al.* (1969). The 'pelagic' sighting totals reported for the years 1954-57, which are based upon table 2 from Omura (1958), are incorrect. They represent the *total* of pelagic plus coastal sightings from Omura (1958). Pelagic data in table 14 should read: 1954 (24), 1955 (8), 1956 (75) and 1957 (25).

Japan
The waters within approximately 200 miles of the Japanese coast, including outlying islands such as the Amamis (Amami Oshima) and the Bonins (Ogasawara Guntō). However, the region around the southwestern Kuril Islands is excluded.

Kurils
Any area in the immediate vicinity of the Kuril Islands, whether on the Okhotsk Sea or Pacific side.

Okhotsk Sea
Any region within the Okhotsk Sea, including Sakhalin Island, but excluding the Kurils.

Aleutians
Any area within a hundred nautical miles of the Aleutian Islands, either the Bering Sea or Pacific side. The Aleutians are divided into eastern and western halves, separated by the 180° line of longitude.

NW Pacific
Any offshore waters (further than approximately 200 miles from land) west of 180°, including the Commander Islands.

NE Pacific
Any offshore waters (further than 100 miles from land) east of 180°, within the exception of the Northwest Ground as defined below.

West Coast
Waters off the western coast of North America, from British Columbia to Baja California, within 100 miles of shore.

Northwest Ground
This name is borrowed from the whaling literature, since it nicely describes an important area for which there is otherwise no convenient name. It has been arbitrarily defined as extending from the Gulf of Alaska south to 50°N. Waters to the south of this area are considered NE Pacific.

Bering Sea
Any portion of the Bering Sea except for those waters within 100 miles of the Aleutian Islands or the Alaska Peninsula. (Nineteenth century whalemen developed their own terminology for the North Pacific whaling grounds. They divided the Bering Sea into four major sections: Bristol Bay, Kamchatka Sea, Anadyr Sea and the Bering Straits. However, these are not used here).

Hawaii
Any area within the vicinity of the Hawaiian Island chain.

RESULTS

The total number of sightings, commercial takes, strandings and incidental catches since 1900 are summarised for both the eastern and western North Pacific in Table 1. It should be noted that, while we have been careful to exclude cases where two reports have either clearly or probably used the same data, no allowance for possible resightings of individual animals at different times can be made in the sighting records. Totals reported here are necessarily approximate. On the one hand, cases of duplication will inflate the number of individual whales observed; conversely, some sightings counted here as single animals probably represent two or more whales, thus negatively biasing our totals.

Table 1

Total numbers of sightings, catches and strandings/entanglements of right whales recorded in the North Pacific between 1900 and 1999. For the purpose of this paper, the boundary between the western and eastern regions is set at the 180° line of longitude.

Region	Sightings	Catches	Strandings or entanglements	Total
Western North Pacific	988	331	12	1,331
Eastern North Pacific	693	411	1	1,105
Area not specified	284	-	-	284
Total	1,965	742	13	2,720

Sightings

Excluding animals that were either stranded or taken by whalers, there have been 1,965 sightings[2] of living right whales in the North Pacific since 1900. Of these, 988 were reported from the western portions of this ocean basin and 693 from the eastern (Tables 2.1 and 2.2). There were an additional 284 sightings of right whales by Japanese and Soviet vessels with the location described only as 'North Pacific', without reference to area (Table 2.3). Although all but twenty of these are plotted in several figures by Omura *et al.* (1969), it is largely impossible to count the number of sightings in each half of the region since the plots represent an amalgamation of data from several sources and time periods; the exceptions are sightings from the period 1959-62, for which original data were available, as noted above. In addition, a few sightings have no or confusing numbers associated with them (e.g. the sightings from 1948 reported by Sleptsov, 1952), and these are not included in the totals.

Sightings are summarised by area in Table 2.4. In the western North Pacific, three areas accounted for more than 90% of the 988 sightings: Japanese waters (370 sightings, or 37.4%); the Kuril Islands (331 sightings, 33.5%); and the Okhotsk Sea (195 sightings, 19.7%). Of the 693 sightings in the eastern North Pacific, the greatest number (269, or 38.8%) were from the area of eastern Aleutians. More than a quarter (177, or 25.5%) were from the Northwest Ground; however, 139 of these sightings were derived from ranges given in the plots of Berzin and Rovnin (1966), and should therefore be interpreted with caution.

If one calculates the number of sightings on the Northwest Ground from the plots of Berzin and Rovnin (1966), one obtains a range of from 88 to 189 right whales observed by Soviet research vessels in the period 1958-1964 (the midpoint of this range, which we use for the totals given in Tables 1 and 2.4, is 139). These plots show right whales observed over a wide area within this region; the text of this paper notes that 200 right whales were encountered in 1963 in all of the northeastern Pacific. By contrast, Berzin and Doroshenko (1982) give a much more specific location on the Northwest Ground (51°N 145°W) for a single sighting of 200 right whales in 1963000, made by the same Soviet research vessels.

Text continues on p. 278

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[2] This total ignores certain and probable duplicates, and counts the sighting of '40-45' whales by Kuzmin and Berzin (1975) as 43. It uses the midpoints of the various ranges calculated from fig. 6 of Berzin and Rovnin (1966); these total 20 and 324 for the western and eastern North Pacific, respectively.

Table 2.1

Sightings of right whales since 1900 in the western North Pacific. Where possible, exact positions are given. Location information, given as a range of latitudes and longitudes, reflects either a series of sightings within this range, or sightings for which the source reported position only to within a particular survey block (e.g. Wada, 1975). NRIFS=National Research Institute of Far Seas Fisheries; ICR=Institute of Cetacean Research.

Date	Latitude	Longitude	Location	No.	Source	Remarks
May 1931			Off Akkeshi, eastern Hokkaido	9	Shino, 1932	12 whales sighted, but 3 were killed (see Table 3.1)
Apr. 1941-1957			East and southeast of Hokkaido, Japan	37	Omura, 1958	Japanese catcherboat sightings
May 1941-1957			East and southeast of Hokkaido, Japan	46	Omura, 1958	Japanese catcherboat sightings
			Lat 46/47 east of Kurils	3		
Jun. 1941-1957			SE of Hokkaido, Japan	4	Omura, 1958	Japanese catcherboat sightings
			SE of Paramushir I., Kurils	2		
			S of Commander Islands	10		
Jul. 1941-1957			SE of Hokkaido, Japan	2	Omura, 1958	Japanese catcherboat sightings
			SE of Paramushir I., Kurils	3		
			SE of Kamchatka	2		
Aug. 1941-1957	52°N	163°E	SE of Kamchatka	2	Omura, 1958	Japanese catcherboat sightings
1948			Northeast Okhotsk Sea	?	Sleptsov, 1952	Cited in Tomilin (1957) as ‘small groups of from 2-3 to 15 animals’
Apr.-Nov. 1951	39-52°N	140-158°E	Kuril Is (both Okhotsk Sea and Pacific sides)	57	Klumov, 1962	Russian catcherboat sightings
Apr.-Nov. 1953	39-52°N	140-158°E	Kuril Is (both Okhotsk Sea and Pacific sides)	16	Klumov, 1962	Russian catcherboat sightings
Apr.-Nov. 1954	39-52°N	140-158°E	Kuril Is (both Okhotsk Sea and Pacific sides)	6	Klumov, 1962	Russian catcherboat sightings
Pre-1955			NE Okhotsk Sea and western Kamchatka	?	Sleptsov, 1955	
1955			Amami Is, Japan	1	Miyazaki and Nakayama, 1989	Autumn
Apr.-Nov. 1955	39-52°N	140-158°E	Kuril Is (both Okhotsk Sea and Pacific sides)	85	Klumov, 1962	Russian catcherboat sightings
Apr.-Nov. 1956	39-52°N	140-158°E	Kuril Is (both Okhotsk Sea and Pacific sides)	50	Klumov, 1962	Russian catcherboat sightings
Apr.-Nov. 1957	39-52°N	140-158°E	Kuril Is (both Okhotsk Sea and Pacific sides)	109	Klumov, 1962	Russian catcherboat sightings
1958-1964			Western Aleutians	10-30	Berzin and Rovnin, 1966	Soviet sighting cruises. Shown (Fig. 6) as ten plots of ‘1-3’ whales
1 Jun. 1959	53°42’N	167°23’E	Western Aleutians	1	ICR data	Japanese catcherboat sighting
28 Jun. 1959	53°05’N	179°33’E	Western Aleutians	1	ICR data	Japanese catcherboat sighting
1965			‘Coastal’ Japan	102	Omura *et al.,* 1969	Japanese catcherboat sightings
Between 1965 and 1970			Near Muroto, Shikoku, Japan	1	T. Kasuya, unpub.	Caught in trap net, but broke free and escaped.
1966			‘Coastal’ Japan	34	Omura *et al.,* 1969	Japanese catcherboat sightings
1966	45-50°N	160-170°E	NW Pacific, southeast of Kamchatka	1	Wada, 1975	Japanese scoutboat sighting
1967			‘Coastal’ Japan	83	Omura *et al.,* 1969	Japanese catcherboat sightings
1967			Cape Terpeniya, eastern Sakhalin I.	70	Berzin and Vladimirov, 1989	Seen by RV *Vityaz*
1967			Okhotsk Sea	14	Berzin and Doroshenko, 1981	Unclear; may be part of 70 reported by Berzin and Vladimirov (1989)
1967			Okhotsk Sea side of Urup I. (Kurils)	?	Berzin and Vladimirov, 1989	‘Single individuals’
Jul. 1968	48°N	145-146°E	SE Sakhalin I., Okhotsk Sea	Few	Omura, 1968	Japanese catcher vessel sighting. Whales associated with those taken in research catch; 5 or fewer whales.
1968	45-50°N	160-170°E	NW Pacific, southeast of Kamchatka	5	Wada, 1975	Japanese scoutboat sighting
1968	45-50°N	170-180°E	NW Pacific, south of Aleutians	1	Wada, 1975	Japanese scoutboat sighting
1968	50-55°N	170-180°E	Aleutians, Pacific side	1	Wada, 1975	Japanese scoutboat sighting
1969	40-45°N	160-170°E	NW Pacific	2	Wada, 1975	Japanese scoutboat sighting
1969	45-50°N	160-170°E	NW Pacific, southeast of Kamchatka	2	Wada, 1975	Japanese scoutboat sighting
1969	45-50°N	170-180°E	South of Aleutians	1	Wada, 1975	Japanese scoutboat sighting
1970	40-45°N	150-160°E	NW Pacific, southeast of Kurils	1	Wada, 1975	Japanese scoutboat sighting
1970	45-50°N	160-170°E	NW Pacific, southeast of Kamchatka	1	Wada, 1975	Japanese scoutboat sighting
1970	45-50°N	170-180°E	South of Aleutians	1	Wada, 1975	Japanese scoutboat sighting
1971			Muroto, Shikoku, Kochi Prefecture, Japan	1	Kasamatsu and Miyashita, 1991	Escaped from fishing gear
1971	45-50°N	150-160°E	Near Kurils, Pacific side	1	Wada, 1975	Japanese scoutboat sighting

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Table 2.1 continued

Date	Latitude	Longitude	Location	No.	Source	Remarks
1971	40-45°N	160-170°E	NW Pacific	1	Wada, 1975	Japanese scoutboat sighting
1971	45-50°N	170-180°E	South of Aleutians	4	Wada, 1975	Japanese scoutboat sighting
1972	40-45°N	160-170°E	NW Pacific	3	Wada, 1975	Japanese scoutboat sighting
1972	45-50°N	160-170°E	NW Pacific, southeast of Kamchatka	3	Wada, 1975	Japanese scoutboat sighting
1972	35-40°N	170-180°E	NW Pacific	1	Wada, 1975	Japanese scoutboat sighting
1972	45-50°N	170-180°E	South of Aleutians	3	Wada, 1975	Japanese scoutboat sighting
Sep. 1973			Eastern Okhotsk Sea	16	Berzin and Vladimirov, 1989	Seen by factory ship *Vladivostok*
Aug.-Oct. 1974			Central and northeastern Okhotsk Sea, NE of Kashevarov Bank	40-45	Kuz’min and Berzin, 1975	Seen by RV *Tamango*
1974	30-50°N	160-180°E	West central North Pacific	4	Anon., 1976	Japanese scoutboat sighting
1974			Coast of Japan	32	Anon., 1976	No further details
1975	30-50°N	160-180°E	West central North Pacific	4	Anon., 1977	Japanese catcherboat sightings
1976	40-45°N	170-175°E	South of central Aleutians	1	Wada, 1978	Japanese sighting cruise
Summer 1981	30-40°N	140-150°E	Coastal Japan	3	Anon., 1983	Japanese catcherboat sightings
1983	30-40°N	140-160°E	Northwestern Pacific east of Japan	2	Anon., 1985	Japanese sighting cruise
1983	30-40°N	120-140°E	Coast of Japan	2	Anon., 1985	Japanese sighting cruise
13 Jan. 1984	35°44’N	141°35’E	Coast of Japan, off eastern Honshu	2	Miyashita and Kato, 1998	Japanese sighting cruise
21 Jan. 1984	33°40’N	138°28’E	Coast of Japan, off eastern Honshu	2	Miyashita and Kato, 1998	Japanese sighting cruise
1985	30-40°N	140-150°E	Coast of Japan	1	Anon., 1987	Japanese catcherboat sighting
Jun. 1986	50°N	156°E	10-11m east of Paramushir I.	2	Blokhin, 1988	One 13-14m, one 10-11m
18 Aug. 1989	53°41’N	146°12’E	Okhotsk Sea, E of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise; individual resighted 17 Sep. 1992
8 Apr. 1990	27°09’N	142°10’E	Chichi-jima I. (Bonin Is), Japan	1	Mori *et al*., 1998	
11 Aug. 1990	50°10’N	154°27’E	Okhotsk Sea, W of Paramushir I.	1	Miyashita and Kato, 1998	Japanese sighting cruise
6 Sep. 1990	54°28’N	151°08’E	Okhotsk Sea	4	Miyashita and Kato, 1998	Japanese sighting cruise
6 Sep. 1990	54°29’N	152°07’E	Okhotsk Sea	1	Miyashita and Kato, 1998	Japanese sighting cruise
7 Aug. 1992	51°17’N	148°38’E	Central Okhotsk Sea	1	Miyashita and Kato, 1998	Japanese sighting cruise
26 Aug. 1992	51°52’N	155°10’E	Okhotsk Sea, off western Kamchatka	1	Miyashita and Kato, 1998	Japanese sighting cruise
26 Aug. 1992	51°50’N	155°20’E	Okhotsk Sea, off western Kamchatka	5	Miyashita and Kato, 1998	Japanese sighting cruise
26 Aug. 1992	51°46’N	155°19’E	Okhotsk Sea, off western Kamchatka	1	Miyashita and Kato, 1998	Japanese sighting cruise
26 Aug. 1992	51°47’N	155°23’E	Okhotsk Sea, off western Kamchatka	4	Miyashita and Kato, 1998	Japanese sighting cruise
26 Aug. 1992	51°47’N	155°22’E	Okhotsk Sea, off western Kamchatka	1	Miyashita and Kato, 1998	Japanese sighting cruise; animal’s tail stock entangled in heavyrope
27 Aug. 1992	51°26’N	155°59’E	Okhotsk Sea, off western Kamchatka	2	Miyashita and Kato, 1998	Japanese sighting cruise
27 Aug. 1992	51°20’N	156°02’E	Okhotsk Sea, off western Kamchatka	1	Miyashita and Kato, 1998	Japanese sighting cruise
27 Aug. 1992	51°21’N	156°04’E	Okhotsk Sea, off western Kamchatka	2	Miyashita and Kato, 1998	Japanese sighting cruise
27 Aug. 1992	51°22’N	156°07’E	Okhotsk Sea, off western Kamchatka	1	Miyashita and Kato, 1998	Japanese sighting cruise
27 Aug. 1992	51°16’N	155°52’E	Okhotsk Sea, off western Kamchatka	1	Miyashita and Kato, 1998	Japanese sighting cruise
6 Sep. 1992	55°48’N	147°33’E	Okhotsk Sea, northeast of Sakhalin I.	2	Miyashita and Kato, 1998	Japanese sighting cruise
9 Sep. 1992	54°07’N	152°14’E	Central Okhotsk Sea	2	Miyashita and Kato, 1998	Japanese sighting cruise
15 Sep. 1992	53°45’N	145°07’E	Okhotsk Sea, northeast of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise
15 Sep. 1992	53°42’N	145°12’E	Okhotsk Sea, northeast of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise
16 Sep. 1992	53°12’N	146°31’E	Okhotsk Sea, east of Sakhalin I.	2	Miyashita and Kato, 1998	Japanese sighting cruise
17 Sep. 1992	51°32’N	144°47’E	Okhotsk Sea, east of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise; individual previously observed 18 Aug. 1989
18 Sep. 1992	50°21’N	145°00’E	Okhotsk Sea, east of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise
18 Sep. 1992	50°18’N	145°01’E	Okhotsk Sea, east of Sakhalin I.	2	Miyashita and Kato, 1998	Japanese sighting cruise
18 Sep. 1992	50°19’N	145°11’E	Okhotsk Sea, east of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise
18 Sep. 1992	50°17’N	145°12’E	Okhotsk Sea, east of Sakhalin I.	1	Miyashita and Kato, 1998	Japanese sighting cruise

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Table 2.1 continued

Date	Latitude	Longitude	Location	No.	Source	Remarks
12 Apr. 1993	27°06'N	142°10'E	Chichi-jima I. (Bonin I.), Japan	2	Mori *et al*., 1998	With humpback whales
15 Apr. 1993	27°02'N	142°10'E	Chichi-jima I. (Bonin I.), Japan	1	Mori *et al*., 1998	One animal from pair on 12 Apr.
12 Aug. 1994	42°10'N	142°08'E	Northwestern Pacific	2	Fujise *et al*., 1995	Cow (51') and calf (27')
21 Jun. 1995	47°28'N	163°19'E	Northwestern Pacific	1	Fujise *et al*., 1996	
9 Aug. 1995	45°00'N	165°34'E	Northwestern Pacific	1	Fujise *et al*., 1996	
13 Mar. 1996	27°04'N	142°08'E	Chichi-jima I. (Bonin Is), Japan	1	Mori *et al*., 1998	Estimated length 10m; with humpback whales
1 May 1996	34°45'N	138°44'E	Off coast of Izu, Japan	1	T. Kasuya, unpub.	Estimated length 10m
8 Aug. 1996	45°52'N	159°38'E	Northwestern North Pacific	1	NRIFS data	Japanese sighting cruise
12 Apr. 1997			Yakiuchi-wan, Amami-Oshima	1	S. Uchida, unpub.	Japanese sighting cruise
15 May 1997	51°06'N	166°08'E	East of Japan (sub-area 9)	1	JARPN 1997 cruise report	Japanese sighting cruise
26 May 1997	46°10'N	162°30'E	Northwestern Pacific	2	Ishikawa *et al*., 1997	Japanese sighting cruise
Apr.-Jun. 1998	39-41°N	145-150°E	East of Japan (sub-area 7)	3	Zenitani *et al*., 1999	Japanese sighting cruise
9 Jun. 1999			10-15 miles off Taiji, Wakayama, Japan	1	K. Mori, pers. comm.	Observed by M. Hohana, Taiji, Japan
10 Sep. 1999	50°08'N	145°31'E	Okhotsk Sea, east of Sakhalin Island	2	Miyashita *et al*., 2000; NRIFS data	Japanese sighting cruise
15 Sep. 1999	53°01'N	153°59'E	Okhotsk Sea, off western Kamchatka	2	Miyashita *et al*., 2000; NRIFS data	Japanese sighting cruise
16 Sep. 1999	52°13'N	154°27'E	Okhotsk Sea, off western Kamchatka	3	Miyashita *et al*., 2000; NRIFS data	Japanese sighting cruise
16 Sep. 1999	52°04'N	154°06'E	Okhotsk Sea, off western Kamchatka	1	Miyashita *et al*., 2000; NRIFS data	Japanese sighting cruise
16 Sep. 1999	51°46'N	153°30'E	Okhotsk Sea, off western Kamchatka	2	Miyashita *et al*., 2000; NRIFS data	Japanese sighting cruise
17 Sep. 1999	51°24'N	152°46'E	Okhotsk Sea, off western Kamchatka	1	Miyashita *et al*., 2000; NRIFS data	Japanese sighting cruise

Table 2.2

Sightings of right whales since 1900 in the eastern North Pacific. Where possible, exact positions are given. Location information given as a range of latitudes and longitudes reflects either a series of sightings within this range, or sightings for which the source reported position only to within a particular survey block (e.g. Wada, 1975). NRIFS=National Research Institute of Far Seas Fisheries; ICR = Institute of Cetacean Research.

Date	Latitude	Longitude	Location	No.	Source	Remarks
27 Jun. 1928			20m SE of Rootok I. Alaska	2	Reeves *et al*., 1985 (table 8)	Chased for 1hr by catcherboat *Paterson*
4 Aug. 1928			Off Akutan, Alaska	1	Reeves *et al*., 1985 (p.455)	Struck and lost during whaling by catcherboat *Unimak*
3 Sep. 1929			40m off Rootok I. Alaska	1	Reeves *et al*., 1985 (table 8)	Chased for 6hr 20min by catcherboat *Unimak*
11 May 1937			*Ca* 20m SE of Twohead I. (Kodiak)	2	Reeves *et al*., 1985 (table 8)	Chased by catcherboat *Moran*
14 May 1937			*Ca* 1m SE of Twohead I. (Kodiak)	1	Reeves *et al.,* 1985 (table 8)	Chased for 1hr by catcherboat *Tanginak*
20 Jun. 1937			SE of Unalaska I. Alaska	1	Reeves *et al*., 1985 (table 8)	Chased by catcherboat *Paterson*
24 Aug. 1937			28m SE of Rootok I. Alaska	1	Reeves *et al*., 1985 (table 8)	Seen by catcherboat *Kodiak*
17 Aug. 1939			Area of Akutan Pass	1	Reeves *et al*., 1985 (table 8)	Seen by catcherboat *Kodiak*
Jun. 1941-1957			Central and eastern Aleutians (Pacific side)	19	Omura, 1958	Japanese catcherboat sightings
			Eastern Aleutians, in SE Bering Sea	2		
Jul. 1941-1957			E Aleutians (both sides), and SE Bering Sea	92	Omura, 1958	Japanese catcherboat sightings
Sep. 1941-1957	53°N	168°W	E Aleutians (Pacific side)	3	Omura, 1958	Japanese catcherboat sightings
31 Mar. 1955	32°50'N	117°30'W	La Jolla, California	1	Gilmore, 1956	
1955-1958	40-50°N	170-180°W	South of Aleutians	4	Slijper *et al*., 1964	Opportunistic sightings, Dutch vessels
1958			'East of longitude 180 degrees'	12	ICR data	Japanese catcherboat sightings
Post-1958?	50°N	145°W	Northwest Ground	2	Pike and McAskie, 1969	Weather ship sightings

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Table 2.2 continued

Date	Latitude	Longitude	Location	No.	Source	Remarks
1958-1964			Eastern Aleutians (both sides) SE Bering Sea NE Pacific Northwest Ground	65-120 63-114 2-6 88-189	Berzin and Rovnin, 1966	Soviet sighting surveys. Shown (fig. 6) as plots of either '1-3' or '15-20' whales. Includes 200 reported in 1963 by Berzin and Doroshenko (1982), but locations in two papers conflict
8 Apr. 1959	45°55'N	125°25'W	80m W of Tillamook Hd, Washington	3	Fiscus and Niggol, 1965	Seen during fur seal research cruise; probably same group resighted near this position two days later
13-15 May 1959	37°25'N	122°48'W	16m SW of Pt Montara, California	1	Rice and Fiscus, 1968	40 feet
6 Jul. 1959	57°23'N	174°01'W	Central Bering Sea	1	Japan Whaling Association Data	Japanese catcherboat sighting
7 Jul. 1959	56°02'N	171°28'W	SE Bering Sea	5	Japan Whaling Association Data	Japanese catcherboat sightings
8 Jul. 1959	54°25'N	167°53'W	Eastern Aleutians	2	Japan Whaling Association Data	Japanese catcherboat sightings
14 Jul. 1959	54°57'N	167°11'W	Eastern Aleutians	4	Japan Whaling Association Data	Japanese catcherboat sightings
15 Jul. 1959	54°27'N	168°10'W	Eastern Aleutians	5	Japan Whaling Association Data	Japanese catcherboat sightings
11 Jun. 1960	52°34'N	175°16'W	Central Aleutians	1	Japan Whaling Association Data	Japanese catcherboat sighting
13 Jun. 1960	54°25'N	169°55'W	Eastern Aleutians	5	Japan Whaling Association Data	Japanese catcherboat sightings
15 Jun. 1960	55°45'N	168°48'W	Eastern Aleutians	10	Japan Whaling Association Data	Japanese catcherboat sightings
19 Jun. 1960	54°30'N	168°22'W	Eastern Aleutians	3	Japan Whaling Association Data	Japanese catcherboat sightings
21 Jun. 1960	55°31'N	169°41'W	SE Bering Sea	1	Japan Whaling Association Data	Japanese catcherboat sighting
22 Jun. 1960	55°45'N	170°40'W	SE Bering Sea	5	Japan Whaling Association Data	Japanese catcherboat sightings
23 Jun. 1960	56°12'N	170°03'W	SE Bering Sea	3	Japan Whaling Association Data	Japanese catcherboat sightings
24 Jun. 1960	56°10'N	170°39'W	SE Bering Sea	6	Japan Whaling Association Data	Japanese catcherboat sightings
25 Jun. 1960	54°48'N	167°51'W	Eastern Aleutians	4	Japan Whaling Association Data	Japanese catcherboat sightings
26 Jun. 1960	54°38'N	167°59'W	Eastern Aleutians	1	Japan Whaling Association Data	Japanese catcherboat sighting
28 Jun. 1960	53°49'N	170°17'W	Eastern Aleutians	1	Japan Whaling Association Data	Japanese catcherboat sighting
30 Jun. 1960	55°51'N	171°18'W	SE Bering Sea	3	Japan Whaling Association Data	Japanese catcherboat sightings
1 Jul. 1960	56°19'N	171°21'W	SE Bering Sea	1	Japan Whaling Association Data	Japanese catcherboat sighting
2 Jul. 1960	55°48'N	171°19'W	SE Bering Sea	5	Japan Whaling Association Data	Japanese catcherboat sightings
6 Jul. 1960	50°44'N	167°27'W	S of eastern Aleutians	2	Japan Whaling Association Data	Japanese catcherboat sightings
9 Jul. 1960	54°05'N	160°20'W	S of Alaska Peninsula	2	Japan Whaling Association Data	Japanese catcherboat sightings
10 Jul. 1960	54°49'N	158°06'W	S of Alaska Peninsula	2	Japan Whaling Association Data	Japanese catcherboat sightings
12 Jul. 1960	54°34'N	155°11'W	Northwest Ground	1	Japan Whaling Association Data	Japanese catcherboat sighting
15 Jul. 1960	53°39'N	164°04'W	S of Alaska Peninsula	2	Japan Whaling Association Data	Japanese catcherboat sightings
16 Jul. 1960	52°51'N	165°53'W	S of eastern Aleutians	1	Japan Whaling Association Data	Japanese catcherboat sighting
20 Jul. 1960	50°05'N	174°21'W	Central Aleutians	1	Japan Whaling Association Data	Japanese catcherboat sighting
21 Jul. 1960	52°47'N	171°40'W	Eastern Aleutians	4	Japan Whaling Association Data	Japanese catcherboat sightings
22 Jul. 1960	54°33'N	169°39'W	SE Bering Sea	13	Japan Whaling Association Data	Japanese catcherboat sightings
9 Aug. 1960	58°36'N	174°47'W	Central Bering Sea	2	Japan Whaling Association Data	Japanese catcherboat sightings
10 Aug. 1960	58°16'N	174°42'W	Central Bering Sea	2	Japan Whaling Association Data	Japanese catcherboat sightings
12 Aug. 1960	56°41'N	173°25'W	SE Bering Sea	1	Japan Whaling Association Data	Japanese catcherboat sighting
14 Aug. 1960	53°42'N	170°35'W	SE Bering Sea	4	Japan Whaling Association Data	Japanese catcherboat sightings
21 Jun. 1961	56°11'N	172°13'W	SE Bering Sea	2	Japan Whaling Association Data	Japanese catcherboat sightings
6 Jul. 1961	55°01'N	167°48'W	Eastern Aleutians	2	Japan Whaling Association Data	Japanese catcherboat sightings
8 Aug. 1961	58°04'N	149°24'W	Gulf of Alaska	1	Japan Whaling Association Data	Japanese catcherboat sighting
21 Aug. 1961	56°32'N	152°14'W	Kodiak Island	4	Japan Whaling Association Data	Japanese catcherboat sightings
22 Aug. 1961	56°03'N	153°00'W	Kodiak Island	3	Japan Whaling Association Data	Japanese catcherboat sightings
29 Aug. 1961	52°44'N	173°58'W	Central Aleutians	2	Japan Whaling Association Data	Japanese catcherboat sightings

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Table 2.2 continued

Date	Latitude	Longitude	Location	No.	Source	Remarks
1961			Gulf of Alaska	1	Omura and Ohsumi, 1964	Marked; may be duplicate of 8 Aug. sighting above
13 Jul. 1962	50°22'N	165°32'W	Northeastern North Pacific	3	NRIFS data	Japanese catcherboat sightings
16 Jul. 1962	52°07'N	169°44'W	Eastern Aleutians, Pacific side	1	NRIFS data	Japanese catcherboat sighting
1962			Eastern Bering Sea	1	Omura and Ohsumi, 1964	Marked
1962			'East of longitude 180 degrees'	4	Japan Whaling Association Data	One may be duplicate of sighting on previous line
11 Apr. 1963	37°08'N	123°05'W	33m W of Pigeon Pt., California	1	Rice and Fiscus, 1968	<30 feet
10 May 1963	37°20'N	123°10'W	24m SSW Farallon Is., California	1	Rice and Fiscus, 1968	45 feet
1963	51°N	145°W	Northwest Ground (but see Remarks)	200	Berzin and Doroshenko, 1982	Sighting by Soviet research vessels. Berzin and Rovnin (1966) say 200 in all eastern North Pacific in 1963, and their plot (fig. 6) shows no large sightings near this location
Jan. 1964	40°N	157°W	NE Pacific	?	Berzin and Doroshenko, 1982	'Right whales' seen by Soviet RV
11 Mar. 1965	26°39'N	113°40'W	6-7m SW of Pta Abreojos, Baja California	2	Rice and Fiscus, 1968	Both approx. 50 feet
1965	50-55°N	160-170°W	Aleutians, Pacific side	1	Wada, 1975	Japanese scoutboat sighting
1965	55-60°N	140-150°W	Gulf of Alaska	1	Wada, 1975	Japanese scoutboat sighting
1965	45-50°N	170-180°W	S of Aleutians	1	Wada, 1975	Japanese scoutboat sighting
1966	50-55°N	170-180°W	Aleutians, Pacific side	1	Wada, 1975	Japanese scoutboat sightings
1966	50-55°N	150-160°W	S of Alaska Peninsula	3	Wada, 1975	Japanese scoutboat sighting
1966	55-60°N	140-150°W	Gulf of Alaska	1	Wada, 1975	Japanese scoutboat sightings
17 Jan. 1967	48°20'N	125°06'W	15m WSW Cape Flattery, Washington	3	Rice and Fiscus, 1968	
1967	55-60°N	160-170°W	Eastern Bering Sea	1	Wada, 1975	Japanese scoutboat sighting
1967	50-55°N	150-160°W	S of Alaska Peninsula	1	Wada, 1975	Japanese scoutboat sighting
1969	50-55°N	160-170°W	Aleutians, Pacific side	1	Wada, 1975	Japanese scoutboat sighting
1969	45-50°N	170-180°W	S of Aleutians	1	Wada, 1975	Japanese scoutboat sighting
1970	50-55°N	130-140°W	W of Queen Charlotte Is, British Columbia	2	Wada, 1975	Japanese scoutboat sightings
1973	50-55°N	160-170°W	Aleutians, Pacific side	1	Wada, 1975	Japanese scoutboat sighting
1973	45-50°N	140-150°W	NE Pacific, S of Gulf of Alaska	1	Wada, 1975	Japanese scoutboat sighting
13 Sep. 1974	39°35'N	124,45°W	33m W of Fort Bragg, California	1	NMFS Platform of Opportunity data; Scarff, 1986a	Weather ship sighting
1974	40-50°N	140-160°W	NE Pacific	1	Anon., 1976	Japanese catcherboat sighting
1975	40-45°N	140-150°W	NE Pacific, S of Gulf of Alaska	2	Wada, 1977	Japanese sighting cruise
1976	50-55°N	155-160°W	Kodiak I.	1	Wada, 1978	Japanese sighting cruise
1976	45-50°N	150-155°W	NE Pacific, S of Alaska Peninsula	1	Wada, 1978	Japanese sighting cruise
Summer 1977	20-30°N	160-180°W	Hawaiian Is region	2	Anon., 1979	Japanese catcherboat sighting
1977	45-50°N	150-155°W	NE Pacific, S of Alaska Peninsula	1	Wada, 1979	Japanese sighting cruise
1977	45-50°N	140-145°W	NE Pacific, S of Gulf of Alaska	1	Wada, 1979	Japanese sighting cruise
1977	45-50 N	135-140°W	NE Pacific, S of Gulf of Alaska	2	Wada, 1979	Japanese sighting cruise
Summer 1978	50-60°N	140-160°W	Northwest Ground/Alaska Peninsula region	2	Anon., 1980	Japanese scout boat sightings
25 Mar. 1979	20°40'N	156°53'W	Off Maui, Hawaii	1	Rowntree *et al.,* 1980 Herman *et al.,* 1980	15-16m; associated with humpback whales. Resighted 10 Apr.
Summer 1979	40-45°N	145-150°W	NE Pacific	1	Wada, 1981	Japanese sighting cruise
1979	40-50°N	140-160°W	NE Pacific	1	Anon., 1981	Marked by Japanese
17 Apr. 1981	34°07'N	119°18'W	Santa Barbara Channel, California	1	Woodhouse and Strickley, 1982	14m
20 Mar. 1982	37°30'N	122°30'W	Half Moon Bay, near San Francisco	1	Johnson, 1982; Scarff, 1986b	15m
26 Jul. 1982	60°48'N	175°18'W	NW of St Matthew I., Bering Sea	2	Brueggeman *et al.,* 1984	Sighting details provided by G. Joyce
28 Aug. 1983	48°33'N	124°39'W	Juan de Fuca Strait, British Columbia	2	Reeves and Leatherwood, 1985	
8 Sep. 1985	56°54'N	163°56'W	SE Bering Sea	1	Goddard and Rugh, 1998	Photographed

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Table 2.2 continued

Date	Latitude	Longitude	Location	No.	Source	Remarks
5 Feb. 1988	32°50’N	117°30’W	La Jolla, California	1	Scarff, 1991	
9 May 1990	33°28’N	118°25’W	8m N of Santa Catalina I., California	1	Rae-Dupree and Krikorian, 1990	Photographed
4 Aug. 1991	43°03’N	179°09’W	Northeastern North Pacific	1	NRIFS data; NMFS Platform of Opportunity data	Photographed
24 Mar. 1992	32°14’N	118°42’W	70km SW of San Clemente I., California	1	Carretta *et al.*, 1994	Length 12.6m
24 May 1992	47°17’N	125°11’W	65km W of Cape Elizabeth, Washington	1	Rowlett *et al.,* 1994	Seen from aerial survey and reidentified 6hrs later 48km W of Destruction I.
12 Apr. 1993	54°43’N	165°03’W	Southeastern Bering Sea	1	Goddard and Rugh, 1998	Sighting K. Vicknair, NMFS Platform of Opportunity data
7 Aug. 1993	57°46’N	166°27’W	Southeastern Bering Sea	2	Goddard and Rugh, 1998	Sighting D. Morse, NMFS Platform of Opportunity data
3 May 1995	35°40’N	121°17’W	Off Piedras Blancas, California	1	Rowlett, unpub.	Seen from shore
20 Feb. 1996	23°02’N	109°30’W	15 miles off Cabo San Lucas, Mexico	1	Gendron *et al.,* 1999	Photographed from aeroplane
2 Apr. 1996	20°56’N	156°46’W	Off Maui, Hawaii	1	Salden and Mickelson, 1999	
30 Jul. 1996	57°36’N	163°21’W	Southeastern Bering Sea	4	Goddard and Rugh, 1998	Possibly included calf?
25 Sep. 1996	56°48’N	164°24’W	Southeastern Bering Sea	2-4	Goddard and Rugh, 1998	Sighting T. Lewandowski
20 Jul. 1997	57°08’N	162°50’W	Southeastern Bering Sea	4-5	Tynan, 1998	Biopsied and photographed
22-23 Oct. 1997	56°50’N	164°30’W	Southeastern Bering Sea	1+	M. Bomlander, unpub.	Sighting M. Bomlander, NMFS Platform of Opportunity data, photographed
27 Feb. 1998	35°44’N	121°30’W	Big Sur Coast, California	1	Evans, 1998	Photographed
14-19 Jul. 1998	56°46’-57°05’N	164°15’-164°51’W	Southeastern Bering Sea	6	Perryman *et al.,* 1999	Photographed from aeroplane
14 Jul. 1998	57°08’N	151°51’W	S of Kodiak I.	1	K. Wynne and J. Waite, unpub.	Photographed
8-17 Jul. 1998	56°39’-57°07’N	163°11’-164°18’W	Southeastern Bering Sea	5	LeDuc *et al.,* 2000	Photographed from aeroplane
15 Jun. 1999			Southeastern Bering Sea	1	Tynan, 2001	
31 Jul. 1999	56°53’N	163°33’W	Southeastern Bering Sea	2	Moore *et al.*, 2001	Photographed from RV *Miller Freeman*
29 Oct. 1999	56°26’N	164°32’W	Southeastern Bering Sea	1	K. Williams, unpub.	Sighting K. Williams, NMFS Platform of Opportunity data, photographed

Table 2.3

Sightings of right whales in the North Pacific, with location not specified.

Date	Latitude	Longitude	Location	No.	Source	Remarks
1954 to ?	-	-	North Pacific, north of 40ºN	20	Ivashin and Rovnin, 1967	All marked; no details given
1958-1962	-	-	‘Pelagic’ region	193	Omura *et al.,* 1969, table 14	Japanese catcherboat sightings; table 14 shows 310 sightings, but 117 for which details are available from unpublished ICR data sources are given separately above
1963	-	-	‘Northern North Pacific’	49	Omura *et al.,* 1969, table 15	May include 3 whales killed as scientific research take. Table 15 includes whales in other years, presumably duplicating those listed in table 14 and noted above
1966-1967	-	-	‘Pelagic’ region	22	Omura *et al.,* 1969	Japanese catcherboat sightings

Notes: Two reports of 8 right whales observed off Washington state in 1959 by Fiscus and Niggol (1965) have been excluded because of the unreliable nature of the sightings; see the critique of Scarff (1986a, p.52).
Nasu (1960) reports 2 right whales in the Chukchi and northern Bering seas in Aug 1958, but these were probably bowheads.
Berzin and Doroshenko (1982) note a ‘recent’ sighting at 58º30’N (longitude given in Berzin and Rovnin 1966 as 167º32’W), with no further details.
Possible but unconfirmed sightings of right whales are reported in Zenkovich (1934), Klumov (1962), DeBus (1975), Morris *et al.* (1983, p.141), Reeves and Leatherwood (1985), Scarff (1986a), and Blokhin (1988).
Several other tentative sightings were recorded between 1959 and 1989 by NMFS Platform of Opportunity data.

Table 2.4

Summary of sightings since 1900 by area. Excluded are 284 sightings with no location specified. The 41 NE Pacific sightings include 16 reported only as 'East of 180°'.

Western North Pacific		Eastern North Pacific	
Japan	370	Northwest Ground	177[1]
Kuril Islands	331	West Coast	24
Okhotsk Sea	195	Bering Sea	178
NW Pacific	69	NE Pacific	41
Western Aleutians	23	Eastern Aleutians	269
		Hawaii	4
Total	988	Total	693

[1] This total includes sightings in 1958-64 reported by Berzin and Rovnin (1966) but not the 200 animals reported for 1963 by Berzin and Doroshenko (1982). See text for discussion of the conflict between these two papers.

The latter report represents a striking anomaly in an area where subsequent sightings of this species have been rare, and have generally been of single animals. Data given in Wada (1975) for Japanese sighting cruises made between 1965 and 1973 revealed no right whale sightings in the area of the Soviet sighting, and a total of only ten whales in the survey blocks that surround it for several hundred miles in all directions. More significantly, Berzin and Rovnin's (1966) plots of sightings from the same source show a scatter of animals across the northeastern Pacific, with no concentrations near the position given by Berzin and Doroshenko (1982). Finally, although the English translation of Berzin and Rovnin (1966) could be verified, Berzin and Doroshenko (1982) was submitted only in English and we could not locate the original Russian manuscript to check various details. In light of all this, and the seeming improbability of the existence of such a large concentration of right whales, it has been assumed that the scattered distribution shown by Berzin and Rovnin (1966) is accurate. There appears no way of determining the extent to which these data include duplicate sightings or other errors, and they are reported with this caveat.

Catches

In all, 741 right whales are recorded as being caught for either scientific or commercial purposes since 1900. Of these, 330 were killed in the western North Pacific (Table 3.1), 160 of which were taken in the waters of Japan and the Okhotsk Sea by the Japanese (Omura, 1986). A total of 411 were killed in the eastern North Pacific (Table 3.2). Twenty-eight were taken in the Gulf of Alaska or eastern Bering Sea between 1911 and 1938. Eleven were taken by Japanese and Soviet whalers as scientific catches, but the remaining 372 were killed during Soviet illegal pelagic whaling from the Bering Sea and Gulf of Alaska. There is only a single catch record from the west coast of the continental United States: a whale killed on 9 April 1924 near the Farallon Islands off central California (Gilmore, 1956). Another whale was accidentally killed off the northwest coast of Vancouver Island, Canada in May 1951 (Pike and MacAskie, 1969). The single right whale killed on 1 June 1964 (Table 3.1) by the USSR and reported as an infraction is included in the 1964 illegal USSR catches from the Gulf of Alaska.

A number of sources list animals taken off the northwestern coast of North America and give different numbers. Kellogg (1931) reports 17 right whales taken; one of which was reported killed off British Columbia in 1924 but is not included in the total of 27 given for the period 1914-1935 by Reeves *et al.* (1985). We have not found this whale in original record summaries for British Columbia and believe Kellogg to be in error. Tomilin (1957) reported that 28 right whales were killed in this region between 1911 and 1938; however, he provided neither details nor sources. Our records for this same period agree with Tomilin.

Other right whales may have been illegally caught but not recorded by the Soviet Union in the western North Pacific. For example, Yablokov (1994) noted that right whales had been taken in the late 1950s by a whaling station on Paramushir Island in the northern Kurils.

Among the recorded catches, 23 were animals taken for the purpose of scientific research (9 and 14 in the eastern and western North Pacific, respectively). All of these have been previously reported, including ten taken by the USSR (Klumov, 1962), and 13 by Japan (Omura, 1958; Omura *et al.*, 1969).

Best (1987) estimated that seven right whales were taken by American whalers throughout the North Pacific between 1900 and 1909. However, this figure does not come from specific catch records; rather, it was calculated based upon imports of oil and baleen during this period. Consequently, they have not been incorporated into the present review.

Strandings and entanglements

The 13 records of strandings and entanglements are listed in Table 4; all but one are from the western North Pacific. Five of the 12 western records are from the Commander Islands, three from Kamchatka, two from Japan, and one each from the Kuril Islands and Sakhalin Island. The sole eastern North Pacific record, from California, dates from 1916.

DISCUSSION

Population structure and migration

Distribution

Nineteenth-century whaling records show that right whales were once abundant across much of the North Pacific (Maury, 1852; 1853; Townsend, 1935; Scarff, 1986a; 1991). Areas of concentration included Japan, the Okhotsk Sea, the Kurils, Kamchatka, the Aleutians and southeastern Bering Sea (Bristol Bay Ground), and the Northwest Ground.

The data summarised here generally confirm this distribution. In the western North Pacific, right whales have been observed in significant numbers within the last forty years in areas known to be historically important. In particular, the Okhotsk Sea has consistently had significant numbers of sightings, the most during the 1990s; it is clear that this region, and the adjacent Kuril Islands and Kamchatka coast, represent a major feeding ground for the species. Furthermore, a concentration of Japanese sightings in the Bering Sea, loosely centered around 55°N, 170°W, suggests that this region was an important summer habitat for eastern North Pacific right whales. Small numbers of right whales have been sighted east of this area in recent years (1998-1999) during dedicated vessel and aerial surveys (LeDuc *et al.*, 2000). A detailed Geographic Information Systems analysis of all data presented here is in preparation.

The current rarity of right whales in previously populous parts of the eastern North Pacific is testament to the extreme damage done by whaling. Nowhere is the contrast between past and present abundance more striking than on the Northwest Ground. Scammon (1874) noted that right whales were there 'scattered... as far as the eye can discern from the

Table 3.1

Commercial and scientific catches of right whales in the western North Pacific since 1900.

Date	Latitude	Longitude	Location	No.	Source	Nation	Remarks
1911-1948			Kuril Is, S Hokkaido and	113	Omura, 1986	Japan	
			NE Honshu	26			
			S Honshu and E Kyushu	8			
			Bonin Is	8			
			Okhotsk Sea	4			
			W Kyushu	1			
			Coast of Korea				
Feb. 1921	28°00'N	129°24'E	Amami Is, Japan	1	Miyazaki and Nakayama, 1989	Japan	47ft - stranding?
1924-1925			Off Kamchatka	2	Tomilin, 1957	Norway	Factory ship *Kommandøren I*
1932-1946			WN Pacific and Bering Sea	9	Zenkovich, 1955	USSR	Factory ship *Aleut*
Aug. 1940			Bering Sea	1	Terry, 1950	Japan	Factory ship *Tonan maru*
10-11 Jun. 1941	48°N	158-159°E	SE of Kamchatka	2	Matsuura and Maeda, 1942; Omura, 1958	Japan	Factory ship *Tonan maru*. 58ft female, 45ft male
1941			Off Kamchatka	1	Terry, 1950	Japan	Factory ship *Tonan maru*
17 May 1955	45°08'N	149°46'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 18.3m female
1 Jun. 1955	46°23'N	152°34'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 17m male
19 Jun. 1955	47°01'N	150°25'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 16.3m female
13 Jul. 1955	49°44'N	157°17'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 17.1m male
22 Jul. 1955	49°34'N	156°35'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 17.4m female
22 Jul. 1955	49°42'N	154°31'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 19m male
10 Aug. 1955	50°47'N	155°21'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 16.6m male
10 Aug. 1955	50°22'N	155°12'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 16.6m male
11 Aug. 1955	51°05'N	155°51'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 11.4m female
28 Aug. 1955	50°00'N	154°25'E	Kuril Is	1	Klumov, 1962	USSR	Scientific research take; 17.8m female
May-Jun. 1956	38-42°N	143-149°E	Off eastern Japan	2	Omura, 1957	Japan	Scientific research take; 12.4m male, 12.6m female
Late 1950's			Off Paramushir I., Kuril Is	?	Yablokov, 1994	USSR	Number unknown, but Yablokov had 'anatomical materials' from right whales taken at this time.
1967			Off SE Sakhalin I., Okhotsk Sea	126	Doroshenko, 2000	USSR	Illegal pelagic whaling
1967			Olyutorskiy Bay, Kamchatka	1	Doroshenko, 2000	USSR	
20/25 Jul. 1968	48°N	145-146°E	Southeastern Sakhalin I., Okhotsk Sea	2	Omura *et al.,* 1969	Japan	Scientific research take; 15.2m male, 12.6m female
1971			Northern Kuril Is	10	Doroshenko, 2000	USSR	Illegal pelagic whaling
Jan. 1973			Haiyang I., Yellow Sea	2	Wang, 1978	China	18m female, 12.8m male. In Dailan Museum of Natural History
Mid-Oct. 1974			Sea of Japan	1	Park, 1987	Korea	'Approx 64ft'. Taken by whaling ship *Je 3 Deyahng*
Dec. 1977			SE Haiyang I., Yellow Sea	1	Wang, 1988	China	17.1m female with 4.99m foetus

Table 3.2

Commercial and scientific catches of right whales in the eastern North Pacific since 1900.

Date	Latitude	Longitude	Location	No.	Source	Nation	Remarks
1911-1938			Gulf of Alaska, SE. Bering Sea and off British Columbia	28	Tomilin, 1957 Reeves *et al.,* 1985 Brueggeman *et al.,* 1986 Kellogg, 1931	USA Canada	Years and total of 28 taken from Tomilin; others give fewer animals over shorter period. See text.
9 Apr. 1924	37°40'N	124°W	Off Farallon Is, California	1	Gilmore, 1956	USA	Moss Landing whaling station log says 40ft female, empty stomach.
May 1951			Off British Columbia	1	Pike and McAskie, 1969	Canada	'accident'
1961	55°54'N	153°07'W	South of Kodiak I., Alaska	1	Omura *et al.,* 1969	Japan	Scientific research take
1961	55°54'N	153°08'W	South of Kodiak I., Alaska	1	Omura *et al.,* 1969	Japan	
1961	55°53'N	153°06'W	South of Kodiak I., Alaska	1	Omura *et al.,* 1969	Japan	
1962	53°42'N	171°17'W	SE Bering Sea (north of Aleutians)	1	Omura *et al.,* 1969	Japan	Scientific research take; TK on factory ship
1962	54°30'N	170°22'W	SE Bering Sea (north of Aleutians)	1	Omura *et al.,* 1969	Japan	
1962	54°18'N	170°21'W	SE Bering Sea (north of Aleutians)	1	Omura *et al.,* 1969	Japan	
1963	53°52'N	172°46'W	SE Bering Sea (north of Aleutians)	1	Omura *et al.,* 1969	Japan	Scientific research take
1963	54°04'N	172°35'W	SE Bering Sea (north of Aleutians)		Omura *et al.,* 1969	Japan	
1963	54°03'W	172°50'W	SE Bering Sea (north of Aleutians)		Omura *et al.,* 1969	Japan	
1963			Gulf of Alaska	141	Doroshenko, 2000	USSR	Illegal pelagic whaling
1 Jun. 1964	57°20'N	150°00'W	Gulf of Alaska, E of Kodiak I.	1*	IWC database	USSR	Infraction. Factory ship *Dalnij Vostok*. 13.8m male
1964			Gulf of Alaska	87	Doroshenko, 2000	USSR	Illegal pelagic whaling
1964			SE Bering Sea	113	Doroshenko, 2000	USSR	Illegal pelagic whaling
1965			Gulf of Alaska	20	Doroshenko, 2000	USSR	Illegal pelagic whaling
1966			Gulf of Alaska	3	Doroshenko, 2000	USSR	Illegal pelagic whaling
1967			SE Bering Sea	8	Doroshenko, 2000	USSR	Illegal pelagic whaling

* This whale is not included in the total count as it is considered part of the 87 whales illegally taken in the Gulf of Alaska in 1964.

masthead'. Remarkably few right whales have been observed in these waters in the past thirty-five years despite often extensive effort in the form of dedicated marine mammal surveys.

It has been suggested by several researchers that the current paucity of sightings from waters off the west coast of North America is due to overexploitation (e.g. Gaskin, 1987). However, Scarff (1986a; 1991) makes a convincing case that right whales were never common in this region. Although some records are available from Washington state, there is little evidence that right whales were regularly taken by local aboriginal peoples. Relatively few right whales were observed or killed by whalers on this coast in even the early years of the fishery (Townsend, 1935; Scarff, 1986a; Mitchell and Reeves, 2001). Furthermore, as Scarff (pers. comm.) points out, there is not a single record of a calf, either at sea or stranded, from this region (this is not the case for the western North Pacific).

Migratory movement, breeding and calving

The seasonal migratory movement of right whales in the North Pacific has been a topic of debate for many years. In general, one observes a northward movement to high latitudes in spring, and a similar southward trend in autumn (although there is considerably less information for the latter period). However, right whales are found across a broad latitudinal range during both seasons, suggesting a staggered migration (Scarff, 1991).

A more fundamental question relates to the location of breeding and calving grounds. In the western North Pacific, various areas have been proposed, including the Ryukyu Islands (Omura, 1986), the Yellow Sea (Tomilin, 1957), the Sea of Japan (Omura, 1986), and offshore waters far from land (Scarff, 1991). There are no recent reports of right whales around Taiwan, although Townsend (1935) plotted a small number of catches in the Taiwan Strait. The Bonin Islands have also been proposed as a wintering area (Omura, 1958); the three recent sighting records from this area, all made in April, are of interest in this regard, although Scarff (1991) notes that Maury recorded few right whales in this area despite reasonable search effort in late winter. Overall, mid-winter sightings and seasonal movements in spring and autumn give various degrees of support to all of the above suggestions, but the general paucity of records from winter make a definitive assessment impossible.

There is very little information on where right whales from the eastern North Pacific spend their winters. The 14 sightings (of a total of 15 animals) from California and Baja California this century exhibit seasonality: with the exception of one September record, all occurred between February and May. While this could be viewed as a remnant population continuing to follow traditional routes to or from an unknown wintering area off the west coast, the historical data do not support the idea that this region ever contained major habitats for right whales at any time of year. Based upon some autumn and spring records in mid-ocean in Maury's compilations, Scarff (1991) argues for more rigorous examination of the possibility that the animals which summered along the high-latitude margins on the eastern North Pacific wintered and calved in mid-ocean waters far offshore. Others have suggested that right whales on both sides of the North Pacific calve (or once calved) in embayments, as occurs in the North Atlantic and in southern right whales (*Eubalaena australis*). However, no such bay has been identified. Furthermore, in areas where coastal calving or nursing takes place (e.g. western North Atlantic, Kraus *et al.*, 1986; Argentina, Payne, 1986), not all females appear to use these habitats, and some may calve offshore. Since the advantage of coastal calving is not clear, there is currently no good reason to suppose that right whales would not give birth and perhaps mate far from land.

Fig. 1. North Pacific right whale taken in the southeastern Bering Sea (Bristol Bay Grounds) in 1964 and being processed on board the USSR factory ship the *Vladivostok*. Courtesy of A.A. Berzin.

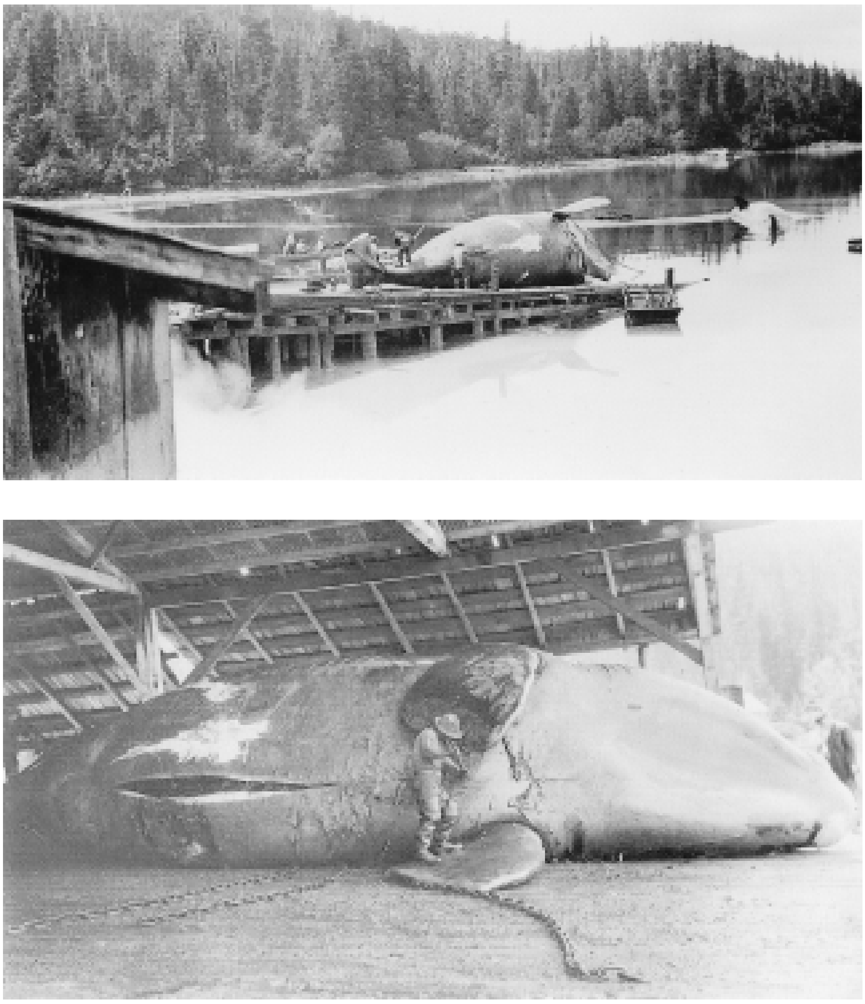

Fig. 2. North Pacific right whale landed on 25 June 1929 at Rose Harbour, northern end of Kunghit Island, Queen Charlotte Islands, Canada. Courtesy of J. Storrie via J. Goddard and the Maritime Museum of British Columbia, Victoria, BC, Canada.

Fig. 3. North Pacific right whale found stranded 14 November 1999 on the west coast of Kamchatka, Russia. Courtesy of V.S. Nikulin.

Table 4

Strandings and entanglements of North Pacific right whales since 1900.

Date	Latitude	Longitude	Location	Source	Remarks
1902			Hamiyashima, Amami I., Japan	Miyazaki and Nakayama, 1989	Stranded
14 Nov. 1916			Santa Cruz I., California	Woodhouse and Strickley, 1982	Stranded
Dec. 1939			Lundskii Bay, Sakhalin I.	Tomilin, 1957	Stranded *ca* 9m
1976			Bering I. (Commander Is)	Ivashin and Vertjankin, 1987	Stranded female
15 Apr. 1977	34°40’N	138°45’E	Kumomi, Izu Peninsula Japan	Yamamoto and Hiruta, 1978	Stranded 11.5m male
1980			Bering I. (Commander Is)	A.M. Burdin, pers. comm.	Stranded?
15 Mar. 1984			Bering I. (Commander Is)	A.M. Burdin, pers. comm.	Stranded male
25 Jul. 1984			Medny I. (Commander Is)	A.M. Burdin, pers. comm.	Stranded?
16 Oct. 1989			Pacific coast of C Lopatka, Kamchatka	Kornev, 1994	Stranded 12.15m male, entangled in gillnet
25 Jun. 1991			Medny I. (Commander Is)	A.M. Burdin, pers. comm.	Stranded, size and sex unknown
29 Mar. 1997			Cape Lopatka, Kamchatka	V.S. Nikulin, pers.comm.	Stranded, *ca* 14m
Summer 1998			Shumshu I. , Kuril Is	S.I. Kornev, pers. comm.	Stranded, size and sex unknown
14 Nov. 1999			West coast of Kamchatka	V.S. Nikulin, pers. comm.	Stranded, 12.6m male

Note: On 27 Jan 1995 a right whale skull was unearthed at a beach development 2 miles north of Crescent City, California (41°46’N, 124°15’W). Its date of burial and the animal's cause of death were unknown (J. Cordaro, pers. comm.)

Stock separation

The question of whether two or more stocks of right whales exist in the North Pacific remains open. Townsend’s (1935) charts show a largely discontinuous distribution of right whales across high latitudes, with few catches in the mid-Pacific region. This has been used by a number of authors as evidence of the existence of two discrete populations (e.g. Klumov, 1962). However, Scarff (1991) noted that Maury’s charts showed a relatively continuous distribution across the Pacific, including a surprisingly high (relative to effort) incidence of sightings in mid-ocean. Scarff maintained that the gaps in Townsend’s charts result from a lack of searching effort in the regions concerned, and that the relatively low number of catches from the central Aleutians region was due to the whalers’ concentration on known high-density areas elsewhere.

Twentieth century sightings support the two-stock hypothesis. The fact that the right whale populations in the eastern and western North Pacific appear to have distinct catch and recovery histories also supports the idea that at least two stocks exist, at least with regard to feeding ground divisions. The eastern population was clearly the more intensively whaled, and this is reflected in the fact that fewer animals exist there today than in the west. This difference in post-exploitation abundance represents some evidence in favour of the two-stock hypothesis. However, the extent of exchange between the two populations in high latitudes, and whether the different feeding stocks mix on a common breeding ground offshore, is unknown. This could be addressed with molecular genetic analyses using both mitochondrial and microsatellite DNA, although finding and sampling a sufficient number of whales (notably in the east) would be a major obstacle to such a study.

A second question relates to possible subdivision within the western North Pacific. Both Klumov (1962) and Omura (1986) believed that the right whales which summer in the Okhotsk Sea represent a discrete population which winters in the Sea of Japan and perhaps the East China Sea. However, right whales today in the Sea of Japan appear to have been almost extirpated. Omura (1986) believed that a second, ‘Pacific’, stock migrates up the east coast of Japan, possibly from breeding grounds in the Ryukyu Islands, and summers in the Kurils and the Bering Sea. Although we find it difficult to accept that animals found in such close proximity to one another (notably in the Kurils and Okhotsk Sea) could represent discrete stocks, we can offer no new data to this debate.

Extent of illegal catches

In order to address the question of the present status of North Pacific right whales, the extent of illegal hunting by the Soviet Union must be examined. Three known episodes can be identified: factory ship whaling in the Okhotsk Sea and the Northwest Ground/southeastern Bering Sea, and a land-based operation in the Kurils. Based upon the evidence presented below, it seems probable that many of the Soviet 'sightings' of right whales in these areas are in fact whales that were killed.

Southeastern Bering Sea/Northwest Ground/eastern North Pacific

As noted above, there is considerable confusion concerning exactly where the Soviets observed 200 right whales in 1963, and whether this uncharacteristically large number can be considered accurate. However, the more significant issue concerns whether these sightings (wherever they were made), and others reported in 1958-64 by Berzin and Rovnin (1966), actually represent catches. It should be noted that the Soviet catches in the southeastern Bering Sea and in the Gulf of Alaska in 1964 totalled 200 right whales (Doroshenko, 2000). A.A. Berzin (pers. comm. to RLB) reported that two sister ships built specifically for the North Pacific (the *Vladivostok* and the *Dalniy Vostok*) killed about 200 right whales in the eastern North Pacific in 1964.

The Soviet catch of 372 right whales during the 1960s must have represented a large proportion, probably the majority, of the remaining eastern North Pacific population. If so, one would expect to see this depletion reflected in data from subsequent years. This appears to be the case. In addition to the Soviet sightings of several hundred animals in 1958-64 (Berzin and Rovnin, 1966), analysis of Japanese whalecatcher observations from 1954 to 1957 show more than a hundred sightings of right whales in the eastern Aleutians and southeastern Bering Sea in the months of June and July, including approximately 60 in July of 1956 alone (Omura, 1958, fig. 1). Overall, between 1941 and 1964 there were 598 sightings of right whales east of 180° (including a midpoint total of 330 for Berzin and Rovnin, 1966, and ignoring the 200 from Berzin and Doroshenko, 1982); this is an average of 24.9 whales per year. These records contrast sharply with the results of surveys conducted in later years: from 1965 to 1999, only 82 sightings were reported for the entire eastern North Pacific, or 2.3 per year. This number includes the results of extensive Japanese surveys conducted over a 27-year period from 1965 to 1991, including in the previously quite populous eastern Aleutians and southeastern Bering Sea. Even if *all* of the sightings reported by Berzin and Rovnin (1966) were false, a major decline is still evident.

As early as the mid-1970s, Gilmore (1978) suggested that illegal catches were made on the Northwest Ground. However, information to support his suspicion was not available until very recently and emerged in part because of the present review. In conclusion, it is clear that the Soviet takes inflicted severe damage on the remaining eastern North Pacific population.

Kuril Islands/Okhotsk Sea

Yablokov (1994) stated that 'hundreds' of right whales (including bowheads) were taken in the Okhotsk Sea in the 1960s, and also mentions whaling of undetermined extent from Paramushir Island in the Kurils prior to the late 1950s (this whaling was in addition to the scientific research take of ten animals reported by Klumov, 1962). Since Paramushir was just one of several whaling stations that began operations in the Kurils in 1948, it is possible that the 1950s takes were also extensive.

Available data show that the take of right whales in this region was indeed substantial. As in the eastern North Pacific, the sighting data for this area reveal a pattern of relative abundance followed by apparent decline. In just three summers (1955-57), 244 right whale sightings were reported by Soviet whaling vessels in the Kurils alone (Klumov, 1962), although the actual number of whales or of the rate of duplicate sightings involved is unknown. In the years that followed, there were only two substantial reports of right whales in the Okhotsk Sea region: one of 70 animals off eastern Sakhalin in 1967 (Berzin and Vladimirov, 1989) and another of 40-45 northeast of Kashevarov Bank in 1974. In 1967, 126 right whales were killed by Soviet commercial whaling operations off the southeastern end of Sakhalin Island (Doroshenko, 2000). In July 1968, the Japanese killed two right whales in the same area under a research whaling permit (Omura *et al.*, 1969). By contrast, between 1975 and 1991, only nine animals were recorded in the region by either Soviet or Japanese surveys, although 34 were observed in the summer of 1992 and 11 in the summer of 1999. Although the trend is less marked than in the eastern North Pacific, the general decline in sightings after the 1960s suggests that a significant proportion of the right whales of the Okhotsk Sea region were killed during one or more periods of illegal whaling by the USSR. How many of the various Soviet sightings (including the 244 reported from the 1950s by Klumov) may represent catches is unclear, and no original data appear to exist from this period.

Present status

Regrettably, none of the published estimates of abundance relating to North Pacific right whales can be regarded as reliable. Even the indices of abundance calculated from extensive Japanese sighting surveys (e.g. Ohsumi and Wada, 1974) suffer from the inevitable problems of high variance that accompany extrapolations from very few observations over a wide area. Other estimates appear to be little more than conjecture based upon general patterns of sightings: examples include '300-500' for the North Pacific (Berzin and Yablokov, 1978), 100-200 for the North Pacific (Braham and Rice, 1984) and 150-200 for the Okhotsk Sea (Berzin and Vladimirov, 1989, citing Berzin, 1982), or 800 and 900 for the Okhotsk Sea (Vladimirov, 1994 and Vladimirov, 2000, respectively). However, no quantitative data exist to confirm any of these estimates. The most refined preliminary estimate for the Okhotsk Sea is 900 whales (Miyashita and Kato, 1998), but the confidence interval for this estimate (404-2,108) is large. The only thing common to all of the estimates, whether regional or basin-wide, is that they are low: all agree that the North Pacific right whale is not numerous anywhere within its historic range.

The data summarised here clearly support this view. The relative paucity of sightings virtually everywhere in the 20th century, and the pattern of apparent decline observed after the 1960s, all point to a situation in which remnant populations may have been slowly recovering from intensive whaling, only to be devastated by illegal Soviet catches. In the western North Pacific, Soviet catches nullified any increases that occurred during the 20th century. Although quantitative analysis is impossible, recent sightings suggest that this population may number at least in the low hundreds and may therefore be large enough to survive. By contrast, sightings of right whales in the eastern North Pacific are today exceedingly rare; this is true despite the often intensive search effort that has occurred in many potential right whale habitats as a result of offshore oil and gas development, and recent dedicated surveys. Overall, the situation in the North

Pacific closely parallels that with the North Atlantic right whale. The eastern North Atlantic stock was greatly reduced by protracted whaling; it appears likely that the remaining animals were then virtually extirpated by a burst of Norwegian catches at the turn of the 20th century (Collet, 1909; Brown, 1986). A remnant population numbering approximately 300 animals remains in the western North Atlantic (IWC, 2001a).

It is not clear what the future holds for the right whale in the North Pacific. It is possible that the western population is large enough that, given sufficient time and protection, it will recover. However, one should note that no increase has been apparent in a population of similar size in the western North Atlantic despite six decades of protection, although this population is known to suffer a high mortality rate from anthropogenic factors such as entanglements and vessel collisions (Kraus, 1990; Clapham *et al.*, 1999; IWC, 2001a). Entanglements in fishing gear may represent a significant problem for the western population of North Pacific right whales, particularly given the present operation of Japanese salmon driftnet fisheries within the Russian EEZ inside the Okhotsk Sea.

The prognosis for the eastern North Pacific population is poor. This population is one of the most endangered populations of whales in the world and is also one of the most poorly studied (Clapham *et al.*, 1999). A long-term monitoring programme is needed to better understand the conservation status of this population and to determine if it may be affected by any negative human interactions that require mitigation. This is especially needed because these whales are long lived, delay breeding, have a long reproductive cycle and have a small current population. Long-term monitoring will also allow better determination of the range of the summer feeding grounds in the eastern North Pacific. It is hoped that the increases reported in southern right whale populations, which were also heavily exploited during the 19th century and then again by USSR whaling operations (during the late 1950s and 1960s) in the Southern Hemisphere (Tormosov *et al.*, 1998), will be repeated by the right whale population in the eastern North Pacific.

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A note on recent surveys for right whales in the southeastern Bering Sea

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ABSTRACT

Research vessel and aerial platforms were used between 1997 and 2000 to collect genetic and photographic data from a small population of right whales that summers in the southeastern Bering Sea. Totals of 11 and six unique individuals were identified using photographic and genetic methods, respectively. Single matches between years occurred using both methods, and all genetic samples turned out to be from male whales. Long-term research is needed to estimate the size of this population and to determine what threats the whales may be facing.

KEYWORDS: NORTH PACIFIC RIGHT WHALE; SURVEY-AERIAL; SURVEY-VESSEL; GENETICS; PHOTO-IDENTIFICATION

INTRODUCTION

Brownell *et al.* (2001) review 20th century records of North Pacific right whales (*Eubalaena japonica*). There are thought to be at least two populations of this species, one in the western Pacific and the other in the east. The latter is one of the most endangered baleen whale populations in the world (Clapham *et al.*, 1999). Until recently, the unpredictable nature and low number of right whale sightings in the eastern North Pacific has precluded any attempts at directed research on their status and biology. However, the discovery of a small number of animals that regularly occur in the southeastern Bering Sea (Goddard and Rugh, 1998; Tynan, 1998) has allowed us to initiate a research program aimed at characterising the remnants of this once-abundant population. This note presents the initial findings using biopsy samples and vertical aerial photographs that have been collected from these whales.

SIGHTINGS

Ship surveys

Tynan (1998) reported that on 20 July 1997, a group of at least five right whales (only three individuals were genetically identified from six biopsy samples; details given below) was sighted during a cetacean survey from the R/V *Miller Freeman* in the southeastern Bering Sea (57°08'N, 162°50'W). Based on this sighting and other opportunistic sightings during the 1990s in the southeastern Bering Sea (see Goddard and Rugh, 1998), the Southwest Fisheries Science Center (SWFSC) initiated a research program directed at right whales in this area using aerial (1998, 1999 and 2000) and vessel (1999 only) platforms. The locations of all right whales sighted during this research are presented in Fig. 1. During the July 1999 cruise conducted from the US Coast Guard vessel *Sweetbrier,* there were four sightings (total five whales). Biopsy samples were collected during both the 1997 and 1999 shipboard sightings (six and five samples, respectively).

Aerial surveys

Aerial surveys of the southeastern Bering Sea were conducted during July of 1998, 1999 and 2000 (methods given in Perryman *et al.*, 1999). In 1998, there were three sightings of single right whales and a single sighting of a pair. In 1999, a single right whale was seen from the air in addition to the five whales mentioned above for the concurrent vessel survey. In 2000, there were five sightings (total 13 animals). Whenever conditions allowed, vertical aerial photographs were taken of right whales with a 127mm format image motion compensated reconnaissance camera. As each photograph was taken, a data acquisition system recorded time, position and a radar altimeter reading.

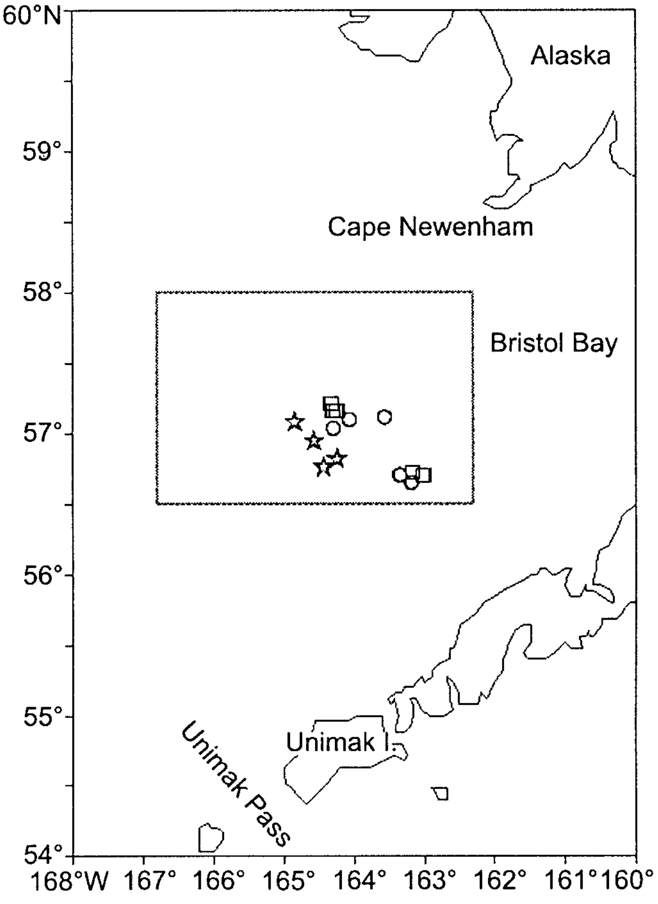

Fig. 1. Observations of right whales in the southeastern Bering Sea. Key: ☆ = 1998 right whale sightings (4 sightings totalling 5 whales); ○ = 1999 sightings (5 sightings totalling 6 whales); □ = 2000 sightings (5 sightings totalling 13 whales). Box represents boundaries of area surveyed by ship and aircraft.

Altimetry data were calibrated by comparing recorded altitude readings with altitude calculated from aerial photographs of known-sized targets. Individual right whales were identified by callosity patterns on their rostra and added to the catalogue established and maintained at the SWFSC, a catalogue that also includes photographs from past opportunistic sightings from the eastern Pacific. Whenever possible, body lengths were calculated from the vertical aerial photographs.

GENETIC ANALYSES

DNA was extracted from all samples at the SWFSC, using standard protocols. A 400bp region of the mitchondrial control region was amplified and sequenced; some (1997 samples only) of these data were published in Rosenbaum *et al.* (2000) as part of a study of worldwide right whale genetic variation. In addition to the sequence data, each sample was typed for 15 microsatellite loci (Table 1).

Table 1

Microsatellite markers used in this study. Although primer pairs for each marker were as given in the cited papers, reaction conditions were altered for this study; details are available from the authors.

Microsatellite marker	Reference
EV1, EV5, EV14, EV30, EV37, EV94	Valsecchi and Amos (1996)
GATA028, GATA053, GATA098, GATA417	Palsbøll *et al.* (1997)
DlrFCB5, DlrFCB17	Buchanan *et al.* (1996)
GT023, GT101	Bérubé *et al.* (2000)
SW19	Richard *et al.* (1996)

Of the 15 markers, two (GATA053 and EV30) were monomorphic and only two alleles were represented in each of four other markers (GT023, EV5, EV14 and EV94). There was one marker (GATA417) with three alleles, three (EV1, GATA098 and EV37) with four alleles, four (GT101, SW19, GATA028 and DlrFCB17) with five and one (DlrFCB5) with six.

The sex of each individual was determined by co-amplification of segments of the X- and Y-chromosome-linked zinc-finger gene with a segment of the Y-chromosome-specific SRY gene[1]. In this method, amplification of the zinc-finger segments acts as a positive control for the PCR conditions, with successful amplification of the SRY segment serving as an indicator of the male genotype.

On the basis of the genotypes, it was found that a number of individuals had been sampled more than once: the six samples from 1997 represented three individuals (one animal was sampled twice and another three times) and the five samples from 1999 represented four individuals. In addition, one of the animals was sampled in both years, bringing the total number of individuals represented by the 11 samples to six. Rosenbaum *et al.* (2000) reported a sample size of five for North Pacific tissue samples from 1997. This was the number of individuals originally inferred to be represented by the six samples from 1997 (instead of three as reported here). This discrepancy resulted from premature conclusions drawn from preliminary microsatellite data by the SWFSC and provided to Rosenbaum *et al.* The analysis and results presented in Rosenbaum *et al.* (2000) are not affected by this change in sample size. As reported in Rosenbaum *et al.* (2000), the sample set contained two mitochondrial haplotypes. One haplotype occurred in a single individual (the three duplicate samples from 1997) and another in all other individuals, including all of the 1999 samples.

All of the sampled individuals were male.

PHOTOGRAPHIC STUDIES

Of all the whales photographed, there were three each from 1998 and 1999 and seven from 2000 for which the photographs were adequate for individual identification. Amongst these, the only resighting was a single individual seen in all three years. Thus a total of 11 individuals could be added to the photo-identification catalogue.

Body lengths from 12 animals were determined from the vertical aerial photographs. This total differs from the number of individuals added to the catalogue because some of the identified animals could not be accurately measured due to the position of their bodies in the photographs whilst some of the animals that could be measured could not be individually identified because poor lighting or water obscured their callosity patterns. The total lengths of the 12 whales ranged from 14.7 to 17.6m. Based on the examination of 23 North Pacific right whales, Omura *et al.* (1983) and Klumov (1962) estimated that females and males can be sexually mature after about 15m in total length. Therefore, regardless of sex, all the right whales we measured may have been sexually mature except perhaps the three smallest ones (14.7, 15.1 and 15.2m).

DISCUSSION

The results of the present study do little to alleviate concerns about eastern North Pacific right whales. Even with these limited data, the population is clearly the most endangered in US waters. The sightings were clustered within a relatively small section of our survey area (Fig. 1), in spite of the cumulative search effort of over 15,400km of aerial tracklines and over 1,400km of vessel tracklines across that area. The fact that there were instances of genetic and photographic resampling of individuals between years even with such small datasets supports the idea that the population is critically small (Brownell *et al.*, 2001). In addition, the detection of only two haplotypes may mean that genetic diversity has already been severely compromised. Of particular concern is that all of the biopsied individuals from both years were male; barring geographic segregation by sex on the summering grounds (or some behavioural characteristic of males that makes them easier to biopsy) - this raises the possibility that females are few or lacking.

However, any inferences must be tempered by a consideration of the limitations of the data. The number of individuals for which the sex has been determined is only about half of the minimum number of individuals determined from the catalogue, which itself is not a complete representation of the population in the Bering Sea (new individuals still comprised all but one of the photographs taken in 2000). Furthermore, eastern North Pacific right whales seen south of the Bering Sea for which there are adequate photographs (at least four animals) can be reliably ruled out as matches to those photographed in the Bering Sea.

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[1] Rosenberg, A. and Mesnick, S.L. Unpublished. Protocol for the determination of gender. Contact author RGL.

The small sample size makes it premature to make any other inferences about the characteristics of this population, such as levels of heterozygosity or the degree of relatedness among individuals. Similarly, a reliable population estimate based on mark-recapture is not possible with so few samples. Such questions can only be addressed by the continuation of biopsy and photographic efforts until an adequate collection has been built up. However, the present genetic results do suggest that there is sufficient variability to establish a catalogue of individual whales based on DNA fingerprints, a valuable complement to the photo-ID catalogue. Obviously, there is also a dire need for other information about North Pacific right whales. For example, their abundance in the southeastern Bering Sea cannot be reliably estimated from the present data, their seasonal movements and distribution are almost completely unknown and potential anthropogenic threats to their survival are yet to be determined.

ACKNOWLEDGEMENTS

The collection of biopsy samples from right whales in the southeast Bering Sea in 1997 was supported by a grant to C. Tynan by the Office of Protected Resources, NOAA, Recover Protected Species Program. All other research discussed here was supported by grants from the same agency to the SWFSC. We would also like to acknowledge the cooperation and skill of the command and crews of the R/V *Miller Freeman* and the USCGC *Sweetbrier* during the 1997 and 1999 survey cruises, respectively. Aerial surveys were conducted with the services of Commander Northwest Ltd., and were successful largely due to the abilities of the pilot, Dave Weintraub. We would like to thank the numerous shipboard and aerial observers and scientists who gathered all the data. One in particular deserves special mention: Bob Pitman, who collected all the biopsies discussed here and was indispensable in the field.

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A note on an automated system for matching the callosity patterns on aerial photographs of southern right whales[1]

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ABSTRACT

Photographs showing the callosity patterns of southern right whales (*Eubalaena australis*) are currently compared by eye to identify individuals and monitor their occurrence within certain areas. This paper describes software designed to reduce the number of by eye comparisons required to maintain each of the existing local photo-identification catalogues. The software is used to extract, from each photograph, a viewpoint-independent description of the shape and location of each callosity which generates a parallel catalogue of extracts. This is then compared with the description extracted from each new photograph to generate a list of similarity scores and thus highlight likely matches. The software can also be used to compare the different catalogues of extracts with each other. Using a test set of 67 photographs of 23 whales taken from 1974 to 1986, the software reduced the number of by eye comparisons required to identify all individuals by 93% when compared with a purely random search.

KEYWORDS: PHOTO-ID; SOUTHERN HEMISPHERE; RIGHT WHALE

INTRODUCTION

A study of the feasibility of automated matching for right whale photographs, commissioned by the International Whaling Commission, was completed in 1990 (Lovell and Hiby, 1989). In 1997, the International Fund for Animal Welfare provided funds to update and install such a system for routine use in management of a photo-identification catalogue. A catalogue of aerial photographs of southern right whales near Península Valdés, Argentina, has been maintained at the Whale Conservation Institute (WCI) in Salt Lake City, Utah, since 1971. It holds photographs taken from 1970 to 1990, with those taken since 1991 awaiting entry. The automated system was installed at the WCI in October 1997 and is being used to bring the catalogue up to date. Inter-year similarity scores for photographs of the 1,077 individuals already identified will, in time, provide an extensive performance test for the new system. Currently, the only available test data consists of a sample of photographs of 23 whales taken over the period 1974 to 1986. Brief results are presented below, along with an outline of the system as installed at the WCI.

The most important features permitting individual identification of southern right whales in the WCI and other catalogues (at the University of Pretoria, for example) are the shape and locations of 'callosities', which are patches of thickened cornified epidermis on the top and side of the head. The callosities are grey but are usually covered by dense populations of cyamids that make them look white in contrast to the black skin. Fig. 1 (reproduced from Payne *et al.*, 1983) shows a typical distribution of callosities. The 'bonnet', 'coaming' and 'eyebrows' are always present but the shape of the bonnet and the number and location of the 'rostral islands' and 'lip patches' vary; this allows most individuals to be distinguished and given individual identification numbers.

The automated system makes use of the variation in shape, number and location of callosities on the rostrum and lips. The objective is not to replace visual comparison of the callosity patterns but to suggest the order in which the existing library be searched for matches to a new photograph, or to eliminate from the search those photographs in the library that cannot possibly be potential matches of the new one. The method used is to extract from each new photograph a simplified map of the callosity pattern; this is used to generate similarity scores with extracts from photographs already in the catalogue. The list

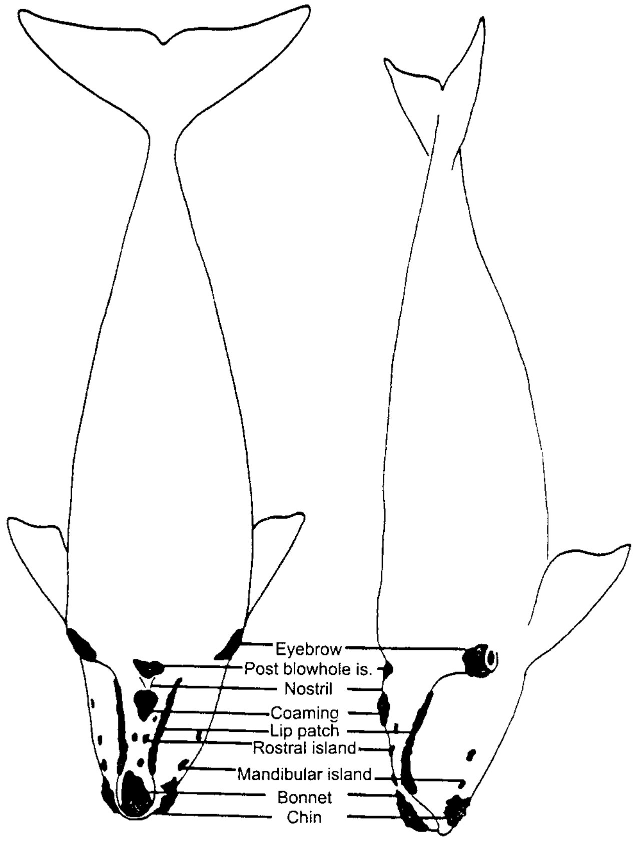

Fig. 1. Typical distribution of right whale callosities (reproduced from Payne *et al.*, 1983)

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[1] Presented to the IWC Scientific Committee as SC/M98/RW38.

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of scores is then used to order the search and/or eliminate the least likely photographs. Thus, two main programs are required, one to extract the map in such a way that the result does not depend on the viewpoint of the camera, the other to calculate the similarity scores.

DESCRIPTION OF THE SYSTEM

The first program was adapted from that developed for grey seal pelage patterns (Hiby and Lovell, 1990), which has been used since 1991 to monitor local grey seal populations in the North, Baltic and Irish Seas. A three-dimensional (3D) surface model of the head is used which allows for differences in viewpoint. Each new photograph is scanned into a computer and the digital image displayed on a monitor. The 3D surface model is superimposed on the image, the orientation and scaling of the model being matched to that of the whale in the photograph by identifying four points on the image with the mouse cursor. The points used are at the front margin of the bonnet, the rear margin of the coaming and the upper margin of the eyebrow callosities. Because those points have specific 3D locations on the model, their screen locations should define the required rotations and scaling. The distribution of callosities over the surface of the rostrum and lips is then extracted from the region of the image underlying the appropriate section of the 3D model. Fig. 2 shows the bonnet, coaming and eyebrow points marked on the image, the 'best-fit' projections of the corresponding 3D model points and the resulting orientation of the surface model section.

The distribution of callosities is sampled using a raster scan over the model section, so the spacing of the corresponding sample points on the screen varies with the shape of the model surface, being more closely spaced in areas where the surface meets the camera axis at an oblique angle. The resulting extract is a matrix of sample points with each point classified as 'callosity' or 'skin' depending on the value of the image at the location corresponding to that point in the raster scan.

In the grey seal system there is no pre-processing of the digital image before the pelage pattern is sampled; the right whale system, however, requires an operator to interpret the callosity patterns before sampling. This is because areas of pale skin, water splashes and highlights can be easily confused with the callosity patterns, which are themselves variable in appearance due to the growth of cyamids. It would not be sufficiently reliable to have the computer classify pixels as 'callosity' or 'skin' purely on the basis of, say, brightness as compared with a base value. To overcome this problem, the operator is asked to identify samples of callosity and skin from the digital image, which the program then uses to generate a discriminant function based on the colour, saturation and intensity of each pixel in the samples. That function is then used to classify all the remaining pixels in the image, giving an orange shade to those classified as 'callosity' to allow the operator to see the extent of the callosity regions identified. If necessary, the operator can then use the mouse cursor to extend or reduce those regions. Finally, the operator identifies which of the callosities lie along the lip margins so that the entire image is classified

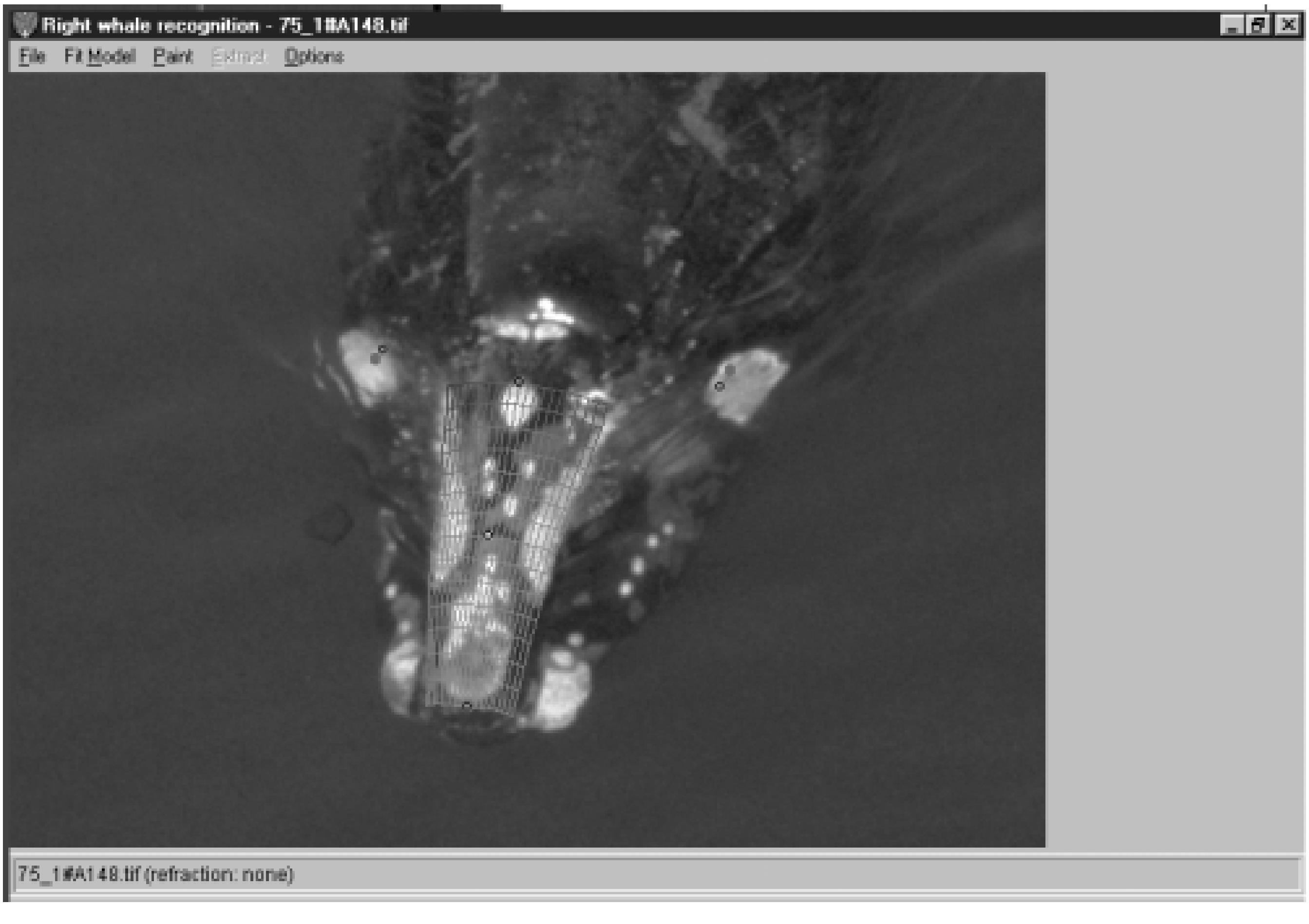


Fig. 2. An aerial photograph of a right whale, taken off Peninsula Valdes in Argentina, displayed on a monitor screen with a section of the 3D surface model superimposed over the rostrum and lip margins. The four dots on the bonnet, coaming and eyebrow callosities are the points marked on the image to define the rotation and scaling of the model required to match its orientation and size to that of the whale in the photograph.

into areas of rostral callosity, lip callosity and skin. Areas of uncertainty can also be highlighted using the mouse cursor. Finally, as the raster scan is performed, any areas obscured by the height of the callosities and the angle of the rostrum to the camera axis are automatically identified as additional areas of uncertainty. Thus, three further types of area are added to the description of the callosity pattern, i.e. possible rostral callosity, possible lip callosity and possible callosity of either type.

This process can take several minutes to complete for each new photograph entered into the catalogue. However, it is only performed once for each photograph. A manual search of a catalogue would require each pattern to be re-interpreted when comparing every pair of photographs, this effort increasing as the square of the number of entries. The key to this digital system is the capture of the operator's best efforts at interpretation; the potential performance of the system is therefore dependant on the skill and experience of the operator.

The second program is designed to calculate similarity scores for any pair of pattern extracts. The 'similarity score' is a measure of total distance from each sample point on the margin of each contiguous region of definite callosity on one extract, to the nearest point of definite or possible callosity of the same type (rostral or lip) on the other extract. The sum distance over all sample points is minimised with respect to the length of the second extract and its rotation about an 'origin' corresponding to the location of the coaming. These distortions can bring regions of definite or possible callosity on the second extract closer to points of definite callosity on the first one. The most similar extracts are thus those with the smallest sum distance score; the minimisation with respect to length and rotation counteracts any increase in the sum distance resulting from a poor fit of the 3D model. The coaming was chosen as the origin because its location on the photograph is the least affected by camera axis orientation and refraction by waves. Because some callosity patterns are sparser than others, all scores are standardised with respect to the distribution of scores across all extracts in the library. The worse (i.e. larger) of the two resulting standardised distance scores is chosen because, if two extracts are from the same whale, the distance score between them will be small when compared with the distance score each would achieve with extracts in the catalogue from other whales.

'Areas of uncertainty' highlighted by the operator or identified automatically by the program are considered as regions of 'possible callosity' during the comparison and therefore tend to reduce the size of the distance score. The measure used does not match pairs of photographs where one member has no callosities in the region of the rostrum or lip margins where the other member has one or more definite callosities. Even a small callosity may give rise to quite a large distance score if the other extract has no definite or possible callosities in or near that location. The measure is weighted in this way because although the exact size and shape of each callosity might be difficult to determine, callosities should not be completely invisible on an acceptable photograph.

The system uses filenames to record decisions about which photographs are of the same whales and stores the summary statistics used to derive standardised scores within the extract files themselves. This allows it to be used with catalogues that have been established over a number of years, where the results of visual comparisons and associated data already form an extensive database. The filename system can exist in parallel to such a database and hence avoids the need to reorganise the original catalogue. A set of *Microsoft Excel* modules has been written to facilitate the selection and editing of filenames, and to display the images of the pairings from which the high-scoring extracts were obtained.

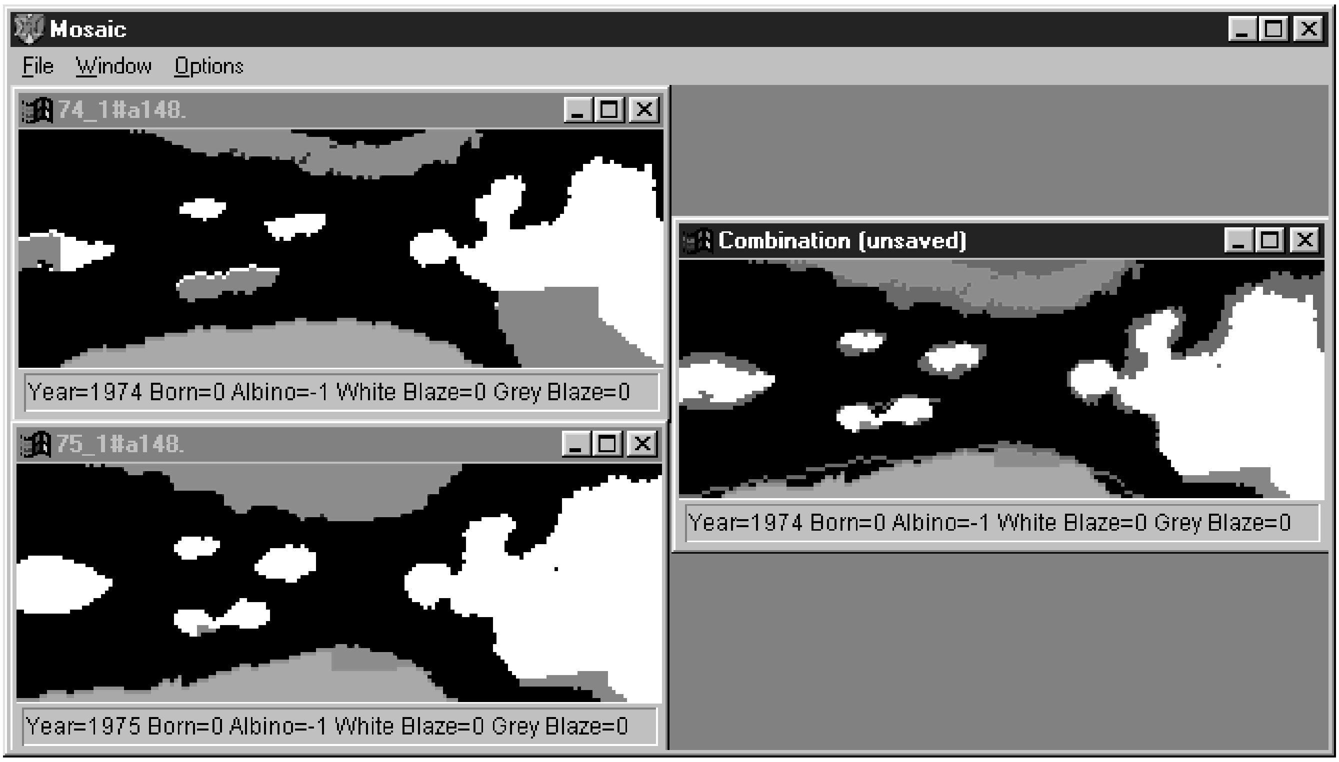
The extracts are initially stored as files in a 'pending' directory and then automatically compared, either singly or in batches, to each extract file in a 'library' directory. The standardised distance scores are stored, in ascending order, in result files, one for each selected pending file. Following automated comparison, the selected pending files are moved to the library. The digital images from which the extracts with the best scores were obtained can then be displayed next to the image corresponding to the pending file, to confirm or reject a match. Extract files are assigned unique names (based on whatever system was used to identify the photograph) but the filename can also be extended using an individual identification or 'whale' number. The name of each extract thus identifies which photograph it came from and which whale was in that photograph. Initially, the whale number may be a temporary number used to identify photographs of the same whale in the pending batch, but when a match is confirmed the whale number part of the pending filename is edited to that of the library one. Furthermore, if two files in the library with different whale numbers are found to represent the same whale (because both match to the same pending file) the whale number part of the later filename is edited to that of the earlier one. Thus, the capture history of a given whale is represented in the sequence of filenames.

The whale number part of the filename is also used to collate the similarity scores. In order to minimise the risk of missing a match, different images of the same whale are allowed to build up in the library. When a new file in the pending directory is compared with the library, only the maximum similarity score for each group of library files having the same whale number is chosen for storage in the results file. This avoids the operator having to make visual comparisons with each photograph of a set already known to be of the same whale.

TRAINING AND TESTING

In regular use, the files selected from the pending directory will be for unidentified whales. However, where a backlog of photographs of identified whales is to be entered, as in the case of the WCI catalogue, the filenames for the files in the pending directory will already have established whale number extensions. In that case the similarity scores for any files from the same whale already transferred to the library will be highlighted in red in the results. The performance of the system can thus be monitored during entry of the backlog and any problems, e.g. in interpretation of the patterns before sampling, can be identified.

The system also allows extracts to be displayed for visual comparison (Fig. 3). This allows problems with low-scoring pairs from the same whale to be identified, for example, one or more small callosities might have been missed. The code used to display the extracts also allows two or more extracts to be combined into a new representation. This option is provided for instances where a sequence of photographs may reveal the callosity pattern over the entire rostrum and lip margins, but where on each individual photograph part of the area is obscured. A mosaic of the partial patterns can then be constructed and may be more informative than the collection of partial samples would be. For example, a sample from a different whale might score quite well against each of the partial samples individually but score badly against the



Year=1974 Born=0 Albino=-1 White Blaze=0 Grey Blaze=0

Year=1975 Born=0 Albino=-1 White Blaze=0 Grey Blaze=0

Year=1974 Born=0 Albino=-1 White Blaze=0 Grey Blaze=0

Fig. 3. Extracts from photographs of whale number 148 taken in 1974 and 1975 are displayed for visual comparison, to the left of the screen. The coaming and bonnet callosities are to the left and right of the extracts. The 1975 extract shows three definite rostral callosities whereas in the 1974 extract two of the three have been marked as ‘definite’ and one as ‘possible’. This may be because the operator was uncertain whether a pale area was a callosity or another feature such as a scar or highlight due to the oblique angle of the photograph. The program automatically marks as ‘possible’ those regions where the extent of the callosity ‘footprint’ on the rostral surface is uncertain because it is hidden by the height of the callosity. Regions of the bonnet, coaming and right lip callosities have been marked in the same way. The extract to the right of the figure shows that different extracts can be combined if the resulting extract provides a better representation of the callosity distribution.

mosaic because of the relative positions of the callosities over the whole area. To facilitate correct orientation for the components of the mosaic the operator can identify any distinctive feature visible on all photographs in the sequence. When the 3D model has been orientated to the first photograph in the sequence the screen location of that feature is marked. The 3D location for that feature is then added to the locations of the bonnet, coaming and eyebrow callosities and used to aid orientation of the 3D model to the subsequent photographs of the sequence.

The similarity scores generated by the system can be used in different ways. Where most new photographs are of whales that will probably not be represented in the catalogue, it may be best to inspect only those library photographs which achieve a similarity score above a set threshold level. The distribution of scores between matching photographs in the backlog can be used to assess the risk that none of the extracts from matching library photographs will exceed the threshold score. Similarly, the distribution of scores between photographs of different whales will show what proportion fall below the threshold and will therefore not require comparison by eye. Alternatively, if the proportion of ‘new’ whales among each batch of new photographs is generally small, as is the case in the WCI catalogue, it may be better to search the entire library visually, in the order of descending similarity scores, instead of imposing a threshold. The likely saving offered by the system in this instance is then given by the mean ranking of similarity scores for pattern pairs from the same whale. The results for the small sample of test photographs mentioned in the introduction are presented below in this format.

RESULTS

A sample of 67 colour transparencies was selected by the WCI showing 23 whales over the period 1974-86. Each whale was present in two or three of the years. The sample was selected to represent the range of problems encountered in interpreting the callosity patterns so the average photographic quality over the sample was less good than over the catalogue as a whole. A pattern sample was selected from each photograph, the resulting files copied to the pending and library directories and all the pending files compared, in a single batch, with the library. With the 67 library files collated into the 23 animal groups and the pattern pairs inspected in descending order of similarity score, a total of 54 potential matches had to be eliminated by eye before all the matching whales were located. Had the files been inspected in random order the expected number eliminated by eye would have totalled 67 × 23/2, i.e. 771. Thus, about 93% of the matching effort was eliminated by using the automated system to order the potential matches, as compared with a purely random search. The calculation of random search effort is intended only to provide a convenient baseline - actual catalogue searches are never performed in a totally random order because some classification by type is used when patterns are stored in the catalogue.

The histogram (Fig. 4) shows that when the library files were not collated, so that similarity scores were returned for each sample pair, a number of same-whale pairs achieved poor similarity scores. The results indicate that for whales represented by a single pattern sample in the library, the reduction in search effort provided by the system would be only around 75%. Visual comparison of the low-scoring sample pairs showed that, in every case, the problem was misinterpretation of the callosity pattern, resulting in one or more callosities being missed for one member of the pair. The number of errors would clearly have been reduced if the patterns had been interpreted by someone with more experience of looking at right whale callosities but it is not possible to say by how much. It should be possible to provide a better estimate once the backlog of WCI photographs has been entered into the library and each pairing subjected to comparison.

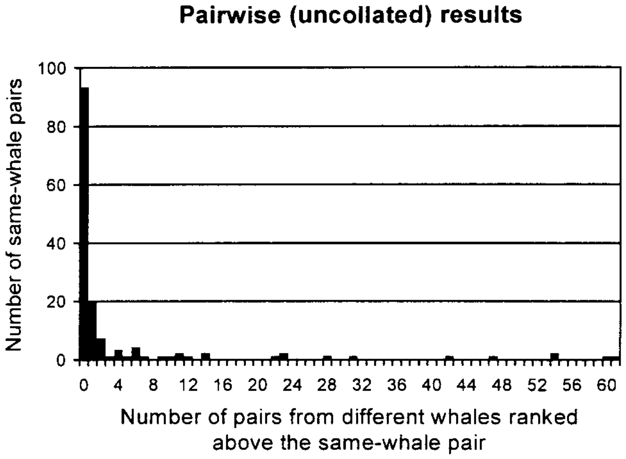


Fig. 4. The frequency distribution for the number of non-matching extract pairs ranked above each matching pair by the software designed to generate pair-wise similarity scores.

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A note on a prototype system for simple computer-assisted matching of individually identified southern right whales, *Eubalaena australis*

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ABSTRACT

A system using computer assistance in the matching of the callosity patterns of individual southern right whales is described. When provided with a digitised representation of an individual whale's callosity pattern, the prototype system produces a hierarchical output of the most similar patterns in the database with relatively high accuracy. A trial database of binary images of the callosity patterns of 165 individually identified southern right whales was created. A further two replicates each of nine different individual whales within the trial database, were then created by two different operators, producing a test set of 18 images. A software program, utilising a pattern recognition algorithm and incorporating a mouse driven user interface, was developed so that when provided with a binary bitmap of an individual whale from the test set, the program compares it against a trial database of previously saved bitmaps and produces a hierarchical output of the most similar whales, or nearest 'matches'. For 15 of the 18 test images (83%), the system returned the correct whale as the top match out of the 165 in the trial database. For the remaining three test images the correct whale was the second, sixth and sixteenth ranked whale in the trial database containing 165 whales. The program was successful in reducing the number of individuals required for manual comparison to a small percentage of the total catalogue, with a high degree of accuracy, and with a significant associated time saving. It is envisaged that the final matching will continue to be done visually by an experienced operator using the original photographs. Further refinement of the system with the aim of streamlining and simplifying the input process and incorporating partial pattern recognition is intended.

KEYWORDS: SOUTHERN RIGHT WHALE; PHOTO-IDENTIFICATION; TECHNIQUES

INTRODUCTION

Southern right whales, *Eubalaena australis*, were the first whale species to be commercially hunted off Australia. Over 26,000 were killed in Australian and New Zealand waters, the majority between 1830 and 1850, shortly after which the industry collapsed (Dawbin, 1986). The species received international protection in 1935, at which time it was rare throughout its range. The species' recovery from such over-exploitation has been slow; the first published record of right whales visiting the Australian coastline this century is of a female and calf pair near Albany, Western Australia, in 1955 (Chittleborough, 1956). Recent evidence of large numbers of southern right whales killed long after their supposed protection (Yablokov, 1994; Tormosov *et al.*, 1998) may explain why it has only been in the last 20 or so years that any significant recovery has been noted (Bannister, 1990; Best, 1990; Payne *et al.*, 1990).

The current Australian population is thought to number around 1,000 individuals. The southern right whale is a listed species under Australian Endangered Species legislation and monitoring of the population wintering off southern Australia is a high priority for Australian Government conservation authorities (e.g. Bannister *et al.*, 1996).

Right whales possess callosities on the top of their heads; these thickened, raised areas of skin, often infested by whale lice, are whitish-grey in colour. The number, shape and pattern of these callosities are highly variable, unique to each individual and undergo only minor changes with time (Payne *et al.*, 1983). They provide an ideal natural marking system that has been successfully exploited using photographic-identification in several long-term studies of this species (e.g. Bannister, 1990; Payne *et al.*, 1990; Best, 1994). The ability to recognise individual whales within the population is critical to many aspects of research on this species and photographic catalogues can provide information on the life histories of individual whales, including movements, reproductive intervals, association patterns and age at first parturition (e.g. Hammond *et al.*, 1990).

Comparisons and matching of photographs within these catalogues has usually been done by eye – an extremely time consuming and labour intensive task; as the number of catalogued whales increases, the time spent confirming the presence or absence of a 'new' whale in the catalogue can be great. This paper describes an approach to develop a computer-assisted matching process for right whales. Computers have been used to assist with the cataloguing and matching of individuals in studies of several cetacean species, including fluke pigmentation patterns in humpback whales, *Megaptera novaeangliae* (Mizroch *et al.*, 1990), fluke margins of sperm whales, *Physeter macrocephalus* (Whitehead, 1990), and for dorsal fin comparisons in bottlenose dolphins, *Tursiops truncatus* (e.g. Defran *et al.*, 1990). A different approach for right whales is discussed by Hiby and Lovell (2001).

METHODS AND MATERIALS

Identification photographs of the dorsal surface of the head of individual southern right whales used in the development of this system were obtained from the catalogue held by one of the authors (SRB). This catalogue, which currently comprises over 450 identifiable non-calf individuals, has been generated during a long-term study of the ecology and behaviour of this species centred on the Head of the Great Australian Bight in South Australia (Burnell and Bryden,

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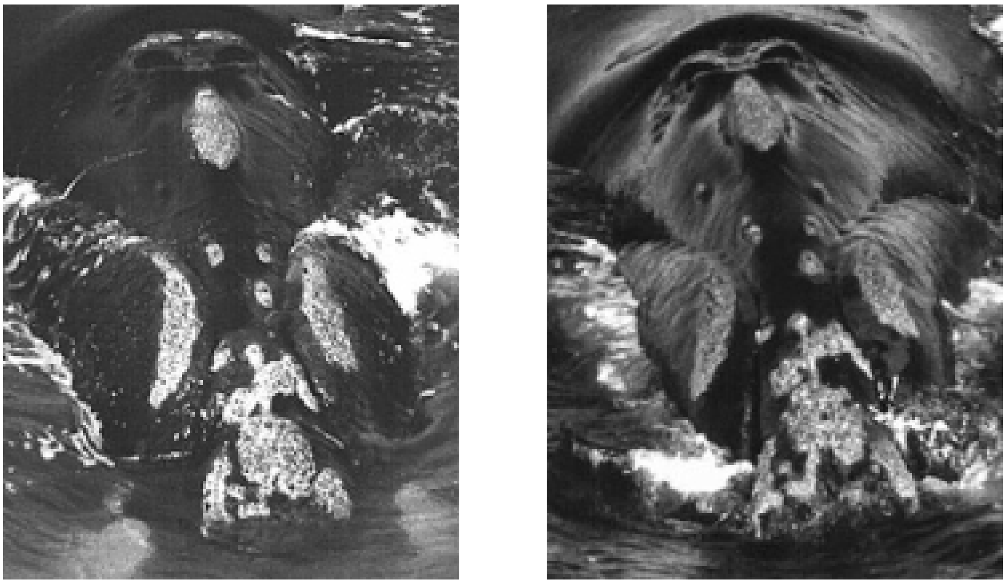

Fig. 1. Two photographs of the same right whale taken five years apart (1992 and 1997), with the unique callosity pattern easily discernible.

1997; Burnell, 2001). All photographs used during the development of this system were 35mm colour transparencies. Fig. 1 shows two representative photographs from the catalogue of the same right whale taken five years apart (1992 and 1997), with the callosity pattern easily discernible.

A two-dimensional template of the dorsal view of the jawline and blowholes of a southern right whale was developed from a large selection of photographs of the heads of right whales taken from most orientations, and refined with the benefit of several thousands of hours observation of living right whales. Using an 18 × 12 inch digitising tablet connected to a personal computer running AutoCAD™ ver.11.1 (Autodesk Inc) the template was digitised. All subsequent data entry was made onto it.

For each of 165 individual whales within the catalogue at the time of the trial in 1994, a range of the best available photographs from the catalogue were collated and viewed together on a light box. Using these photographs, a sketch of the unique callosity pattern of each individual was made onto the template. Using photographs from many different orientations enables an operator experienced in right whale cataloguing to make an accurate representation of the true callosity pattern. Each sketch was entered by tracing it with a digitising pointer, hatching the callosity areas and saving the result as an individual AutoCAD™ drawing file. These drawing files were then converted to 8-bit binary bitmaps using CorelDRAW™ software.

Of the 165 whales digitised and termed the trial database, three whales were randomly chosen by ID numbers from each of the three sighting years (1991, 1992 and 1993) of the catalogue's history. Two different operators with little or no right whale matching experience made duplicate sketches of these nine whales using the same set of photographs available to the original operator and the same standard template. This was done with no access to the original trial database image and no assistance from the original operator aside from a familiarisation with the standard template and a short briefing on the techniques required. This process provided two replicates each of a subset of nine of the whales in the trial database, termed the test set. All three operators were asked to ensure that the total time from first viewing the slides to the completion of the sketch did not exceed 15 minutes.

The matching algorithm was written in C++ in a 32-bit environment and involves multiple-pass connector/component scans of the image to identify individual features (groups of callosities) which are then compared for number, area, size and shape of pixel clusters (callosities) within each feature. This provides two distinct matching areas; general feature information and specific cluster information. The final score given to each whale is an aggregate of the similarity scores for all clusters adjusted for the weighting given to different features. Different search stringency criteria are incorporated and the lip callosities (grey in Fig. 2), due to their increased temporal variability, can have their relative weighting reduced in comparisons. The whales in the database are then ranked according to their similarity score with the test image and displayed. The operator can then visually scroll through the images before checking the original photographs to confirm the match.

RESULTS

In 15 of the 18 test cases (83.3%), the computer-aided matching system placed the correct whale in the trial database of 165 sketches as the top match with the test image sketched by a different operator. In the three other test cases, the system placed the correct whale as the second, sixth and sixteenth most likely match within the database of 165 animals. The time taken by the program to compare a pattern against the trial database and rank by similarity score is less than 0.1 seconds.

Fig. 2 shows the mouse-driven graphic interface of the system. The pattern being searched for lies alongside (on the right) of the catalogue of 165 whale images in the trial database. The example given shows two different whales, i.e. not a match.

DISCUSSION

When provided with a digitised representation of each individual whale's callosity pattern, the system produces a hierarchical output of the most similar patterns in the database with relatively high accuracy.

An experienced right whale matcher has previously estimated that the time taken to compare each whale against

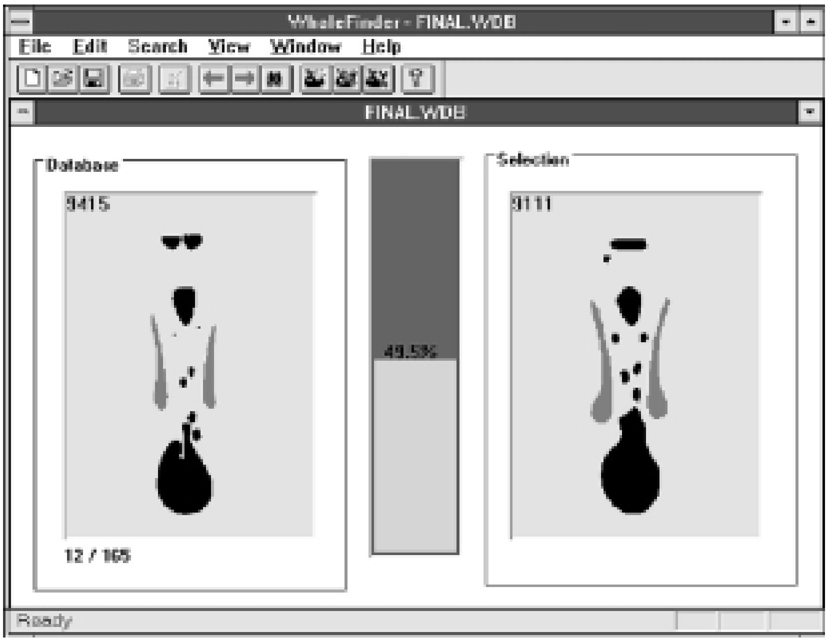

Fig. 2. The graphic interface of the computer matching system for identified individual right whales developed during this study. Different search stringency criteria are incorporated, and the lip callosities (shaded gray), due to their increased temporal variability, can have their weighting reduced.

a catalogue of around 800 animals may take three hours (Rowntree, in Hammond *et al.*, 1990). The computer-assisted matching program described here has the potential to reduce the number of individual whales required for manual comparison to a small percentage of the total catalogue, with a high degree of accuracy and with a significant associated time saving.

In the trial carried out, the two sketches that returned the worst result (matched sixth and sixteenth) were of the same whale. Both operators who drew the test images had trouble discerning the delineation of individual 'island'[1] callosities on the whales rostrum as there were several such 'islands' very close together. The more experienced matcher who made the sketch for the database had identified these as individual islands but both trial operators joined several of these islands together in their sketches. With some simple rules regarding how patterns are entered, such problems associated with operator interpretation can and have been easily overcome. It is intended that the final matching will continue to be done visually by an experienced operator using the original photographs.

The prototype system described here was a first attempt undertaken in 1994 using the identification catalogue as it stood at that time as the trial database. Since that time, further development of the system using more recent technology has streamlined the process of data entry and decreased the time taken to input a sketch, although the system itself has not changed significantly. It is hoped that the system can be refined and adapted to work with partial patterns (such as one side of the head) and applied to other right whale catalogues where photographs from various orientations are obtained (e.g. the Northwest Atlantic catalogue). This trial was intended to test a prototype algorithm and the effect of inter-operator variability on matching success. It is described here as a system that shows some promise and has been useful in our work. A more extensive trial with the aim of increasing the number of individuals tested and using different photographs of new sighting events against the whole catalogue is planned.

The system described does not directly scan and manipulate photographic data and requires an operator to represent the photographic data in the form of a binary sketch. We believe that substantial problems remain with fully automated pattern recognition systems, and to date, the ability of such systems to correctly and adequately extract the pertinent information from scanned photographic images without considerable operator input has not been demonstrated. Further, the output from any computer-assisted system for matching individual animals will always require an experienced researcher to compare the photographs and confirm or refute the match. Given this scenario, and the relatively small number of potential users of such a system for right whales, we believe that in some situations the use of a simple, robust and effective system, that requires the operator to generate the image, may have greater accuracy and ultimately be more efficient than a more complex and automated system where a computer attempts to extract the information directly from a photograph. This will be particularly true of situations where parts of the pattern being extracted are frequently obscured, as is the case with white water and whale lice on right whales.

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[1] The term 'island' is used to define the small callosity entities found on right whales that do not have specific names or positions and are highly variable between individuals.

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Ultrasonic measurement of blubber thickness in right whales

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ABSTRACT

The right whale population in the northwestern Atlantic appears to face the risk of extinction: ship and fishing gear trauma are significant mortality factors, but calving rates are also depressed compared to southern right whales. A major factor in calving success in many species is body condition. Knowledge of the dynamics of body condition is also important in studies of juvenile and sub-adult growth and seasonal changes in adults. This paper describes a method to assess body condition in live right whales. To characterise the acoustic properties of the blubber/muscle interface we first studied samples of Atlantic white-sided dolphin and right whale in the laboratory. Tissue heterogeneity was examined grossly and in histological sections. Acoustic echoes were strong from the sub-dermal connective tissue sheath(s). Echo strengths did not appear to vary with lipid content. We then used a 0.5MHz ultrasound transducer on a cantilevered 12m pole to touch the back of surfacing right whales briefly. Multiple laboratory and field measurements on individual animals suggest repeated measures of blubber thickness at a single location are reasonably consistent. Data will be normalised to both sampling position on the body and to length of the animal, estimated by mensuration from stereo video images of the animal during sampling. In this way, using a long-term consistent database of blubber thickness measurements, and catalogued reproductive histories from on-going photographic identification studies, we plan to assess the significance of changing body condition in right whale population dynamics.

KEYWORDS: NORTH ATLANTIC RIGHT WHALE; NUTRITION; REPRODUCTION; ULTRASOUND TECHNIQUES

INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) was estimated to have numbered 12,000-15,000 individuals in 1530 in the northwestern Atlantic (Gaskin, 1991). In spite of the absence of significant reported whaling mortality in the past 150 years, the total population today is only 300 individuals, of which about half are sexually mature (IWC, 2001). In the early 1990s, the population growth rate was estimated at 2.5% per annum (Knowlton *et al.*, 1994), although a more recent analysis suggests that the population is now decreasing (Caswell *et al.*, 1999).

By contrast, the south Atlantic populations of the southern right whale (*Eubalaena australis*) have increase rates of 7.3% (Best and Underhill, 1998) and 7.5% (Payne *et al.*, 1990), respectively. Table 1 comprises the status of the northwestern and southeastern Atlantic populations. Two major mortality factors in the northwestern Atlantic are known to be ship strikes and gear entanglement. Evidence of both is commonly seen in scars on survivors and carcasses following these events (IWC, 2001). However, this mortality is not sufficient to explain that the reproductive rate in the North Atlantic is only about half of that in the South Atlantic. Only 38% of the mature females are known to be reproductively successful in the NW Atlantic population (Brown *et al.*, 1994). Therefore there must also be a failure in calf production in addition to shipping and entanglement deaths. Calving rate is influenced by the ability to conceive and to carry foetuses to birth. Both these parameters could be affected by a number of factors including inbreeding, disease, toxic chemical exposure and inadequate nutrition associated with prey availability and other complex habitat quality interactions (IWC, 2001). In rodents and humans, fertility is impacted by an insufficiency or an excess of body fat (Marshall and Hammond, 1926; Frisch, 1984; Thomas, 1990).

In order to test the hypothesis that body condition is predictive of reproductive success, or investigate other relationships between body condition and population dynamics, a reliable non-destructive method for measuring body condition in right whales is required. Ultrasound has been used in the past to measure blubber thickness in restrained marine mammals (Gales and Burton, 1987). The approach is based upon the knowledge that tissue heterogeneity can cause attenuation and reflection of sound waves (Bamber and Hill, 1979; Gammell *et al.*, 1979; McClements and Povey, 1992). Tissue interfaces, such as between fat and connective tissue show strong reflectivity. Sound also attenuates to a greater extent with higher lipid content (Gammell *et al.*, 1979). In this study we first established the acoustic properties of a series of Atlantic white-sided dolphin (*Lagenorhynchus acutus*) blubber samples and a single North Atlantic right whale sample in the laboratory, and then applied this knowledge to North Atlantic right whales at sea.

Table 1

Summary of population status for northwest and southeast Atlantic right whales.

	Northwest Atlantic (Caswell *et al.* 1999, Kraus *et al.*, 2001)	Southeast Atlantic
Population growth rate (%)	Negative to 2.5	7.3 (1979-96) (Best and Underhill, 1998)
Reproductive rate (%)	4.5	Unknown
Calving interval (y)	3.7 (recent increase to >5)	3.1 (Best *et al.*, 2001)
Mortality rate	2.0%	Low

METHODS

Ultrasound

An acoustic system[1] was used that has been applied to a diverse range of non-destructive thickness testing in steel, power generation and livestock industries. It has a broad

[1] Epoch, 111 Model 2300, Panametrics Inc., 221 Crescent St, Waltham MA 02154, USA.

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range of adjustable parameters: pulse strength can be set at 100, 200 and 400V; the receiving gain can be adjusted from 0-100dB; damping can be set at 50, 150 and 400 ohms; and filtration can be standard or high pass. The display on the unit shows an x-y plot of wave-form pattern, with depth (timebase) range being calculated from selected transmission velocity, with adjustable zero offset. The system samples at a rate of 30Hz. The wave-form can be full, half and unrectified. Other parameters are also adjustable, but are less relevant to the application described here. The unit has a bi-directional serial port. A wide range of transducers is available, with the lowest frequency transducer being 0.5MHz. The instrument can be powered with an external 12V supply, or can be supplied with internal 6 or 12V lead acid batteries. In this study, three transducers were used: 0.5, 1.0 and 2.2MHz (Panametrics Catalog Nos A301S, A303S, and A304S respectively).

Data acquisition and analysis

Real time data recording for this unit was developed as a custom PC software package by Upper Cape Systems[2]. The recording program uses a serial communications link with the *Epoch* 111 ultrasound system. It sends commands and receives responses and data through the COM1 or COM2 port. It gives interactive control of parameters such as gain, velocity and time-base, real time capture, display and recording of wave-forms at 2Hz, recording directory selection and time-stamped records. Acoustic parameters in use during the recording are also displayed. Data are automatically stored in sub-directories labelled by Julian day. Initiation of a recording session opens a new file, which closes on the stop command. Files are labelled by start time. Each data frame is labelled with date and time of data acquisition. This software is used with a 200MHz laptop with 2GB hard-drive, and internal zip drive for data backup, using Microsoft Windows NT 4.0 as the operating system. Files are manually backed-up to an internal 100MB zip drive after each recording period. Data playback was also developed by Upper Cape Systems. This program allows selection of files, and playback of filed records as single frame, or at an adjustable continuous rate. Specific time points in the file can be selected.

Laboratory studies

White-sided dolphin

Samples of skin, blubber and superficial muscle were collected from ten white-sided dolphins, which were excised after a mass stranding on Cape Cod in January 1998. The 5 × 5 × 5cm samples were taken lateral to the dorsal fin and frozen at -10°C until thawed for analysis. The time elapsed from death to sampling ranged from 6 to 24 hours. Sub-samples were fixed in 10% buffered formalin, embedded in paraffin, sectioned at 5μm and stained with haematoxylin and eosin and Masson's trichrome (Luna, 1968). Sections were examined histologically. Lipid was extracted from thawed blubber samples according to the method of Folch (1957) as modified by Iverson (1988) and Smith *et al.* (1997).

North Atlantic right whale

A 5 × 5 × 15cm core of skin, blubber and muscle from a North Atlantic right whale (No. 2220), necropsied at Wellfleet MA on 9 March 1996, was stored frozen at –20°C. For ultrasound testing, the sample was thawed and suspended inside a plastic bag in a water bath at 37°C. A 3cm collar of styrofoam surrounded the core, such that the upper 3cm of the core was above the water level. The skin surface was covered with ice. In this way the thermal gradient, and hence oil phase, presumed to exist *in vivo* between the body and ambient sea water was approximately simulated.

Transducer deployment systems at sea with right whales

The transducer was hinged on the end of one of two pole systems: (1) a hand-held carbon fibre pole 5.4m in length, 2cm in diameter, with a wall thickness of 3mm[3]; (2) a cantilevered pole system (Fig. 1). For the latter, two 6.5m carbon fibre sailboat spars[4] were sleeved into one another with a 1m overlap, to achieve a total length of 12m. The inner pole was a 5.8kg cylinder of 64mm outside diameter with a 2.5mm wall thickness. The outer pole was a 6.8kg tapered spar, with an outer diameter where it sleeves into the inner pole of 59mm, decreasing to 35mm at the outer tip. Wall thickness averaged 2mm. The two sections of the pole were disassembled for travel to the study area. The 12m pole slides in and out through a pivot point consisting of a plastic block with a hole bored to accommodate the pole. This pivot can swivel up and down as well as rotate, allowing full control of the pole tip by movement of the inboard pole end. The pivot was mounted on a bowsprit set at 45 degrees to port of the midline of the boat. The inboard end of the pole carried an 11.9kg solid stainless steel handle, which also acted as a counterweight. The ultrasound transducer on the outer pole end was rigidly flush-mounted in a 7mm thick, 22cm diameter clear plastic (*Lexan*) disc. The disc was hinged on the pole end with the axis of the hinge being perpendicular to the long axis of the pole and parallel to the water. Thus, as the disc was laid on the whale's back, the transducer settled flat on the animal, irrespective of pole angle. The operator rotated the pole axis to ensure a flat landing laterally. The coaxial cable from the transducer was inserted down the length of the pole. The length of this cable had to exceed twice the length of the pole to allow retraction of the pole, whilst maintaining connection with the recording unit under the foredeck. This permitted disinfection of the probe with alcohol and a sterile swab and application of ultrasound gel between animals. Stereo video cameras were mounted on a 2m mast on the pivot point to allow time-coded video recording of the probing event to facilitate interpretation of ultrasound recordings and subsequent mensuration of the image to estimate body length. Details of these methods will be reported elsewhere. In this study, the position of the transducer on the back of the animal is reported as an estimate of the probe position in terms of a percentage of the distance from the blowhole to the fluke notch after review of available video tape frames.

Platform

The vessel for this operation had the following features: a rigid foredeck, suitable for mounting the bowsprit; an open well aft of the foredeck allowing the pole operator to swing the pole end as needed; an upper steering and observation deck; and adequate stability to support the weight of the pole when deployed laterally. The vessel was a 7.5m, deep-vee centre console hull[5] with a 330HP Mercruiser inboard outboard. A crew of four was deployed as follows: the pole operator; a 35mm still photographer for photo-ID images; an

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[2] 29 Prince Henry Drive, Falmouth MA 02536, USA.

[3] Fiberspar, 2380 Cranberry Highway, Wareham MA, USA.

[4] Composite Engineering, Baker Ave, Concord MA, USA.

[5] Surfhunter, Atlantic Boats, 2820 Cranberry Highway, Wareham MA, USA.

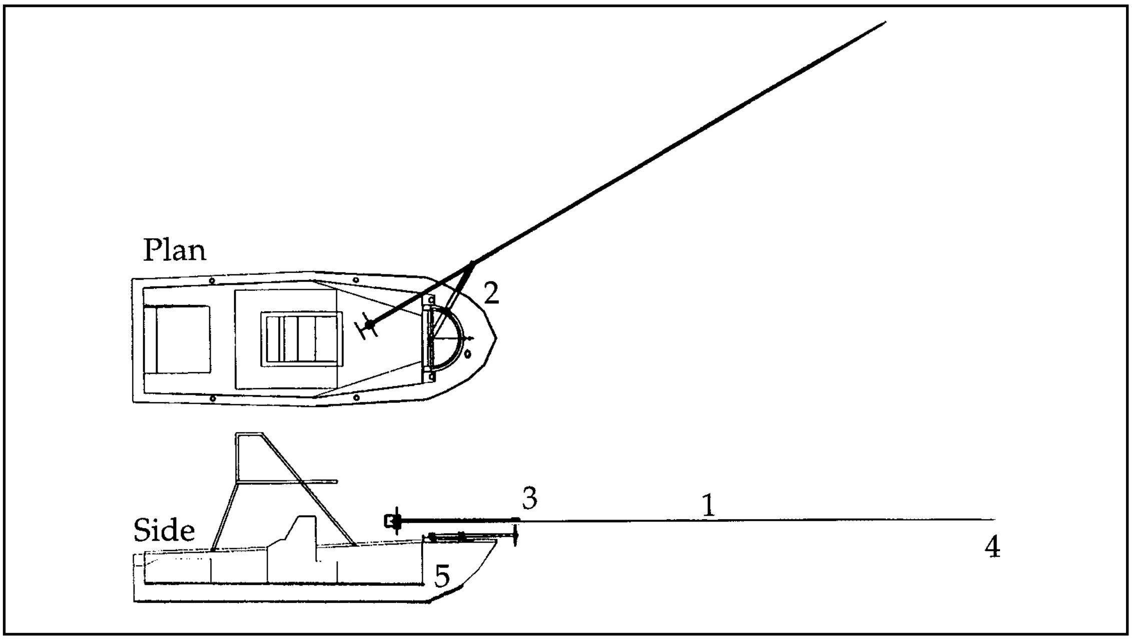

Fig. 1. Apparatus used to lay the ultrasound probe flat on the back of a right whale. Pole (1) is cantilevered off a laterally mounted bowsprit (2). The pole slides in and out, and rotates, through a vertically adjustable pivot (3) that is mounted on the bowsprit tip. The pole operator stands in front of the steering console, swinging the pole tip to meet the whale. The ultrasound transducer head, embedded in a 22cm diameter Lexan landing disc, is hinged on the pole tip (4). The data cable runs down the inside of the pole to a data recording system housed in a waterproof Pelican case stowed under the foredeck (5). A pair of stereo video cameras are mounted on the pivot (3) to record the location of the probe on the animal, and allow body length estimation.

observer to sketch callosity patterns, to take additional 35mm photographs and observe whale movement dynamics; and the helmsman.

Photo ID

Routine 35mm photographs of each animal were taken, optimally of left and right head, dorsal and ventral flukes and other markings. Photographs were then compared with the North West Atlantic right whale catalogue at the New England Aquarium to ascertain catalogue number and reproductive history of animals studied.

RESULTS

Laboratory analysis

Histological analysis of the white-sided dolphin tissues showed two connective tissue layers previously described (Pabst, 1990) collectively as the subdermal connective tissue sheath (SDS) between the blubber and muscle layers. The second connective tissue layer interdigitated with the muscle tissue (Fig. 2). Smaller bands were observed between the two major layers. The second layer was more uniform and substantial than the first. Masson Trichrome staining showed the connective tissue sheaths to consist primarily of collagen. The available parameters on the *Epoch* system were empirically adjusted to maximise the echo strength at the subdermal connective sheath layers. This resulted in the use of a pulse strength of 400V, a receiving gain of 60dB, damping at 400 ohms and high pass filtration. Acoustically the epidermis/dermis junction, and the two major layers of subdermal connective sheath gave strong peaks at all the frequencies used (Fig. 3). The distance (mean±SD in mm) measured between skin surface and lower subdermal sheath was 24.1±0.2 measured with a ruler on the cut edge, *vs* 24.8±0.2 measured acoustically in samples from eight different animals. It was observed that small changes in transducer orientation resulted in variable peak heights, but not position. Lipid content (mean % wet weight ±SD) was 59.0±7.3. Echo strength in the blubber layer did not appear to vary with lipid content. A series of studies (data not shown), using 0.5, 1.0 and 2.25MHz transducers, were run to compare echo strength, sound attenuation and transmission velocity with lipid content. No relationships were apparent.

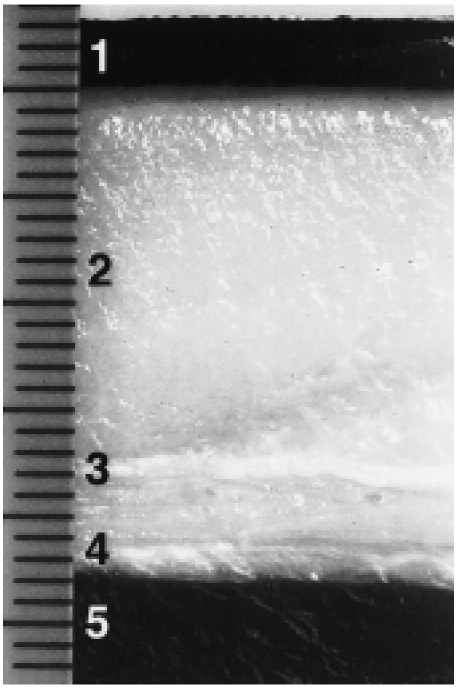

Fig. 2. Photograph of a slice of white-sided dolphin skin (1), blubber (2), upper (3) and lower (4) subdermal connective sheaths, and muscle (5). Scale marker: small division = 1mm.

The right whale skin, blubber and muscle core described above was examined visually and with the *Panametrics* system (Fig. 4). Fig. 4A shows a photograph of the slice

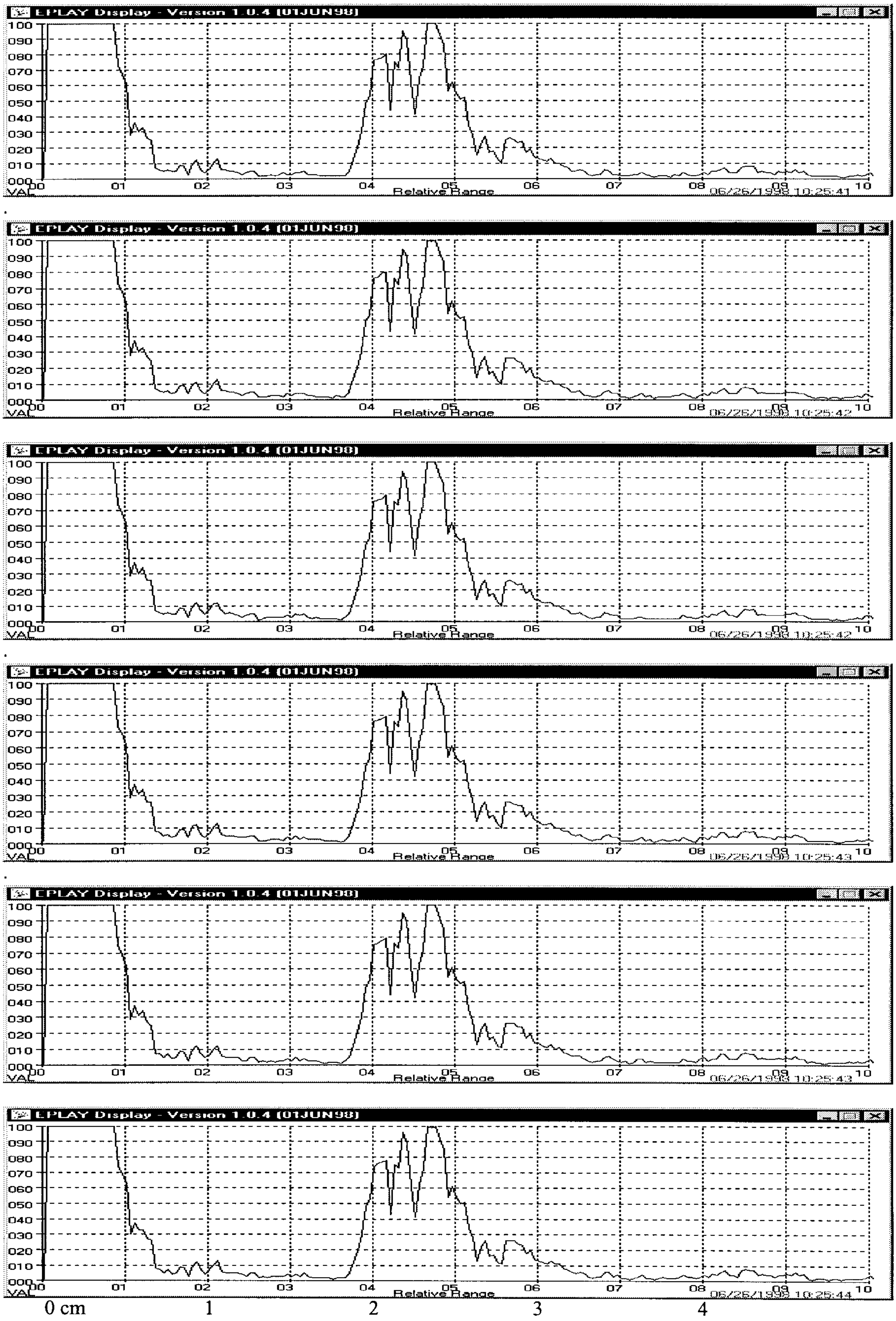

Fig. 3. A series of echoes from a single location on a sample of white-sided dolphin blubber and muscle. 1.0MHz. Vertical bars at 5mm spacing, assuming a velocity of 1,770ms^{-1}.

examined. The lower, more vascularised portion of blubber, (pink in life, grey in the image) overlay an upper and lower connective tissue sheath, which in turn overlay the skeletal muscle. In preliminary trials (data not shown) it was established that the optimum transducer frequency for this blubber thickness for the Epoch system was 0.5MHz. This choice was made on peak strength, and reproducibility. Fig. 4B shows a representative trace of this slice. Strong peaks were observed at both sheath layers (9.7 and 11.2cm respectively). The system was calibrated to assume 1,770 ms^{-1} transmission velocity. This was used as it gave an accurate acoustic measurement of what was measured

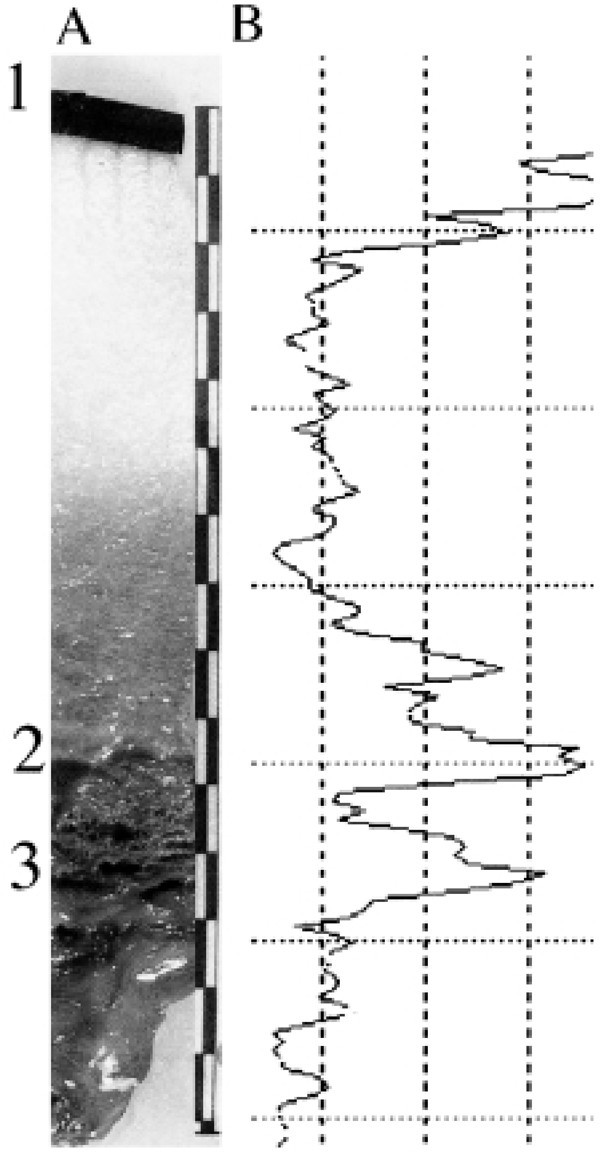

Fig. 4 A: Photograph of a cross-section of blubber and muscle from a North Atlantic right whale, catalogue No. 2220, from the necropsy at Wellfleet MA, March 9 1996. (1) Epidermis. (2) Superficial subdermal connective tissue sheath. (3) Deep subdermal connective tissue sheath. B: 0.5MHz echograph of the same sample. Strong signal strength is evident at both (2) and (3). Centimetre scale in centre.

physically for the two sheath layers (9.5 and 11.1cm respectively). Similar transmission velocities are reported for other oils (McIntire, 1991).

Field deployment

Results with the 5.4m hand-held pole were occasionally excellent, but in general the pole proved to be too short to allow successful approaches. The 12m cantilevered pole was first deployed with multiple outriggers and guy wires. It proved to be unwieldy and hard to operate. In August 1997, the 12m pole was again deployed in the Bay of Fundy, Canada, but without outriggers or guy wires (Fig. 1). The loss of rigidity was more than compensated for by the enhanced manoeuverability. The resultant approaches and 'touches' with an ultrasound probe are listed in Table 2. At this time the *Panametrics* system had not been acquired. Ultrasound data, from another system used for that field period are not shown here as the system then in use proved to yield poor quality data. An 'approach' was defined as an encounter within 30 feet of the surfaced whale and moving with it. The best approaches occurred in dense concentrations of whales: 10-20 whales or more surfacing or logging at less than half a mile apart. Usually the closest animal just surfacing from a long dive or logging at the surface was chosen for an approach. The most productive approaches were those when the vessel slowly idled, without changing engine speed, towards the animal in a sector 90-135 degrees from the anterior/posterior axis of the animal moving in the same direction as the animal (Fig. 5).

Table 2

Summary of field events during approaches of northern right whales for blubber thickness measurements in the Bay of Fundy.

Date (Aug. 1997)	Sea state	Visibility (n.miles)	No. Id'd	No. approaches	No. touched	No. probe touches
3	0	2-4	33	29	17	19
4	2	10-15	54	38	11	15
6	0-3	15	52	32	22	26
8	1-3	2-10	33	19	14	15
10	1-2	10-15	44	30	26	39
13	0-1	15	51	38	31	46
Totals			267	186	121	160

Fig. 5 The optimum orientation for approaching surfacing right whale to apply an ultrasound probe. The vessel is behind and to the side of the surfacing whale. The image shows the pole end with the transducer laying on the back of a northern right whale just after the blowholes have submerged at right.

The *Epoch* 111 system was first deployed in the field in February 1998 in Cape Cod Bay, MA, USA. In this habitat whales are generally hard to approach and are scarce. One animal was approached three times during an afternoon. The results are shown in Fig. 6. Fig. 7 shows a selection of traces over a 7 second interval from a second individual. Data are summarised in Table 3 (p. 308). The major peaks at 18-23cm in depth represent echoes from the usually bilaminar subdermal connective tissue sheath. A larger dataset from ongoing deployments of this system will be reported elsewhere.

DISCUSSION

This paper reports a functional system to measure blubber thickness at sea in right whales, after obtaining laboratory data from blubber/muscle samples from nine white-sided

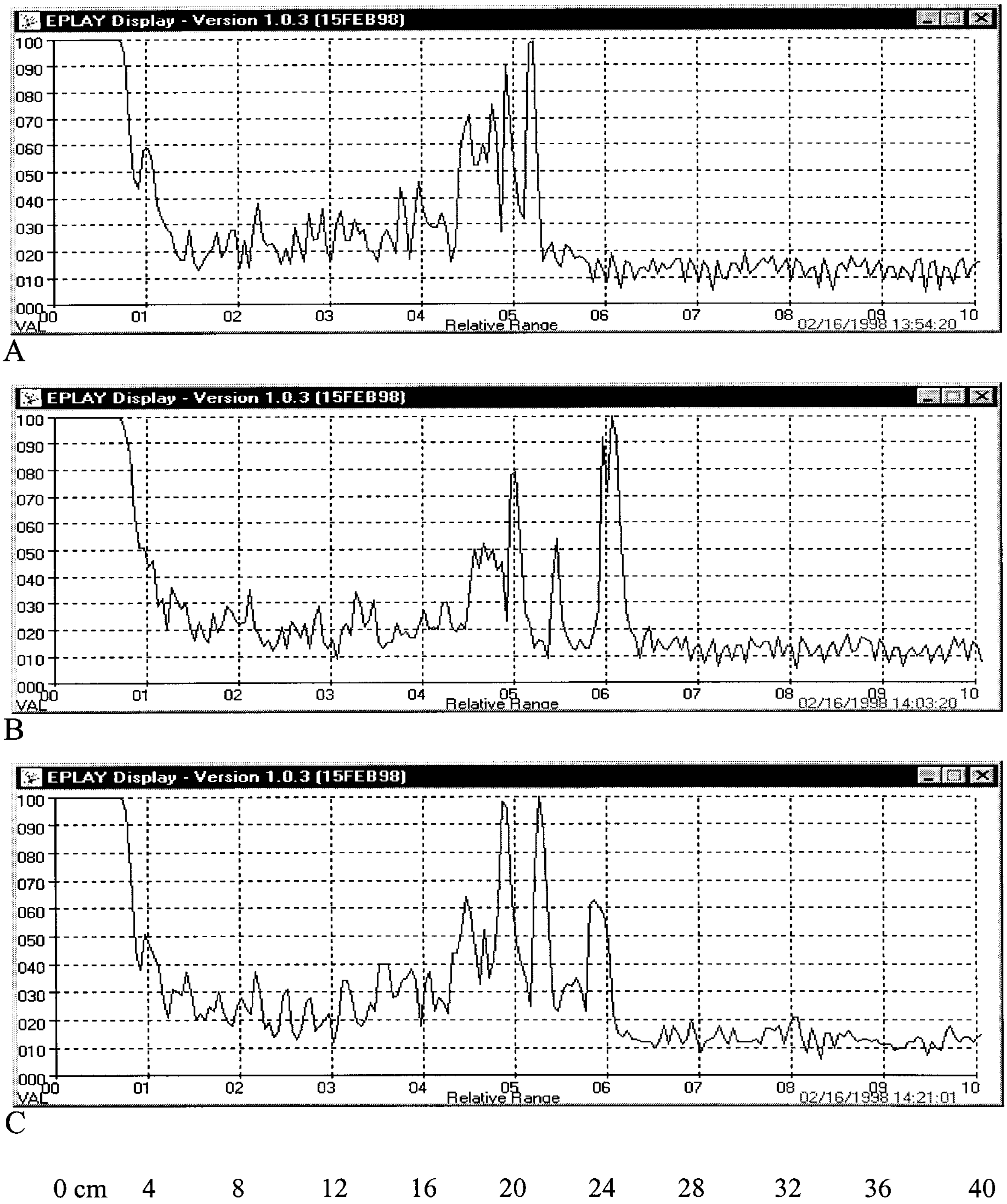

Fig. 6. Ultrasonographs through dorsal skin and blubber from a single North Atlantic right whale, (Field ID 'F'), during three separate approaches on 16 February 1998. For each, approach time (hh.min.sec) and position (deg. min. latitude N, longitude W) are given: A: 13:54:20, 41° 51.8 70° 10.4, B: 14:03:20, 41° 51.6 70° 10.7, C: 14:21:01, 41° 51.9, 70° 10.8. Vertical bars at 40mm spacing, assuming a velocity of 1,770ms^{-1}. 0.5MHz transducer frequency. Strong peaks from the upper and lower subdermal connective tissue sheaths are evident at 18-20cm and 21-24cm respectively.

dolphins and one right whale. The data suggest that such measurements accurately reflect echoes from the bilaminar subdermal connective tissue sheath found at the blubber-muscle interface in both species. The minor difference (0.7mm on average) in measurement compared with the ruler and acoustic measures in the white-sided dolphins occurred within the accuracy one could expect to obtain with a ruler.

Equally, one cannot expect an acoustic accuracy greater than 3.5mm at the sound velocity in use (1,770ms^{-1}). The repeatability of these measurements in the field in right whales was in part confirmed by the data shown in Fig. 6. Before these echograms can be used objectively to measure blubber thickness in the field, a statistical approach to waveform analysis will have to be developed. Such data will then have to be analysed in the context of acoustic maps of the dorsal region of right whales obtained either at necropsy, or from entangled animals prior to release. Such analysis will then test the validity of one or a few point measures in predicting general body condition in individual animals. The value of the eventual approach for testing the hypothesis that blubber thickness dynamics predict reproductive success can only be assessed once a substantially larger, multi-year dataset is in hand and appropriately analysed. In the final

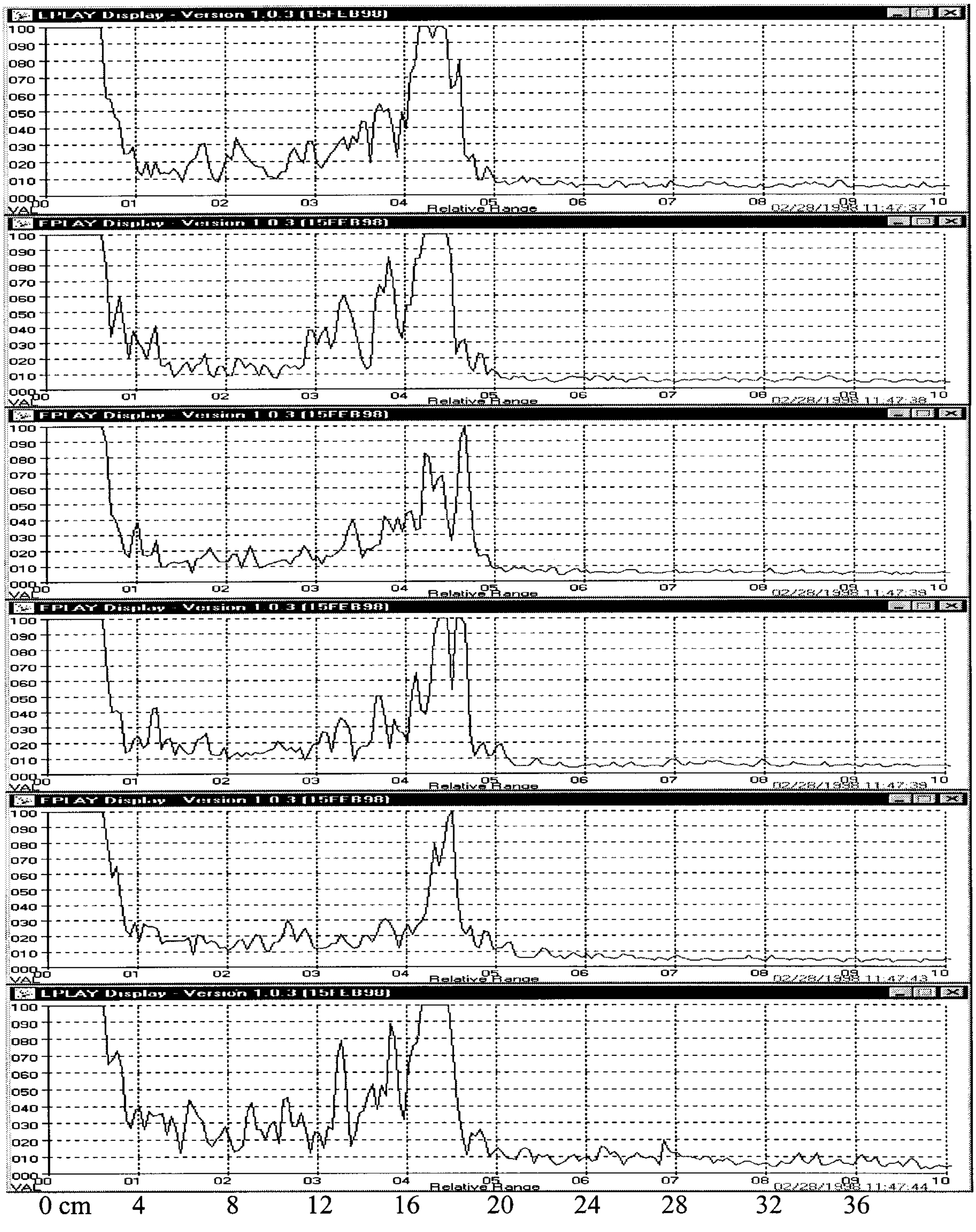

Fig. 7. Ultrasonographs obtained during a seven second period from a single North Atlantic right whale, Field ID ‘F’, 28 February 1998, Cape Cod Bay, MA, USA. Frequency = 0.5MHz, Gain = 60dB. Vertical bars spaced at 40mm assuming a velocity of 1,770ms^{-1}. 0.5MHz transducer frequency. Subdermal connective tissue sheath peaks are evident at 17-19cm depth.

section we discuss relevant literature, the problems apparent with the approach described here, and the manipulations these and future data will have to be subjected to before the necessary comparisons can be made.

In fin and sei whales it has been found that the dorsal posterior part of the body is a major site for lipid storage in both blubber and muscle (Lockyer *et al.*, 1985). These authors suggested that this part of the body was the best area for condition estimates, and that body girth should be estimated at the mid-point of the body. A related study showed that increased body fatness correlated with increased food abundance and fecundity (Lockyer *et al.*, 1985).

Blubber thickness data in right whale literature is sparse (Thompson, 1928; Matthews, 1938; Omura *et al.*, 1969). Unpublished data are also available for necropsied animals sampled from the USA in the past 10 years (Kraus *et al.*, pers. comm. and unpublished data). These data will be used to build a numerical model of the dorsal blubber coat layer of northern right whales. This model will allow the standardisation of the data described here in terms of the position on the animal at which the measurement was made, on the basis of the video record. This same video record will also allow normalisation of the data in terms of body length, using available techniques for body length estimation from

Table 3

Measurements of blubber thickness from individually identified North Atlantic right whales in Cape Cod Bay in February 1998.

Date (Feb. 1998)	Catalogue no.	Thickness (cm)	Estimated position of touch (% distance from blowhole to fluke notch)	No. echographs
10	1407	19	34	1
16	1503	12	31	3
16	1039	22	34	2
16	1039	20	34	4
16	1039	23	44	3
16	1039	19	25	4
20	2614	14	28	4
20	2614	18	44	1
28	1709	17	44	4
28	1709	16	31	3

head images (Whitehead and Payne, 1981). Once a standardised condition index has been established it will then be possible to investigate the relationship between condition and reproductive success for the individual animals recognised photographically.

Limitations to data quantity and quality reflect field and technical variables. The system has been deployed in two locations. In Cape Cod Bay, the animals are in water depths of 40m or less and are often sub-surface skim feeding. The duration of surface intervals are short and the number of breaths per surfacing few. They appear to need little recuperation before the next dive. In contrast, animals in the Bay of Fundy are in depths of 200m, often bottom feeding as evidenced by mud on their heads and have prolonged multiple breath surfacings where they are often resting at the surface. Right whale behaviour in the latter habitat is much more conducive to successful deployment of the system described. Current effort is thus focusing on the Bay of Fundy to generate a dataset with multiple measures of blubber thickness from individual animals. The aim is to develop a set of data that will rank individuals for body condition and compare those with the reproductive success of the same individuals.

Technical limitations in this study included both acoustic and data processing. One issue concerns the variability of quality in acoustic coupling achieved when contact is actually made. This variable affects echo strength but not time of return. Therefore, as long as the characteristic sharp tall peak of the lower subdermal sheath is detectable, we believe that the data quality is acceptable. Data processing limitations of the system reflect primarily the sampling rate of the serial port link to the laptop. This could be augmented if the necessary hardware and software developments for parallel port data retrieval were instituted.

Data interpretation may be complicated by the physical and chemical properties of blubber. If blubber is not sufficiently elastic to contract as muscle mass and hence sub-blubber body circumference decreases, it is possible that a leaner muscle mass may actually lead to an increased blubber thickness. Properties of blubber in this regard need to be experimentally evaluated. Studies of captive animals would be of value. Furthermore, changes in the lipid and/or collagen content of blubber could change the echo characteristics. Comparison of the lipid content and blubber echo strength in the dolphin samples did not show any change in echo strength with lipid content. This may reflect the small range in lipid content in the samples available. It may also suggest, in dolphin blubber at least, that lipid content affects echo strength and position less than structural interfaces. Finally, a comparison of the acoustic properties of blubber in live *vs* dead animals must be made.

In summary, the method described here may have genuine utility in addressing the question of the role of body condition in right whale fecundity. That utility will depend on the ability to employ this tool consistently and persistently over the next 4-6 years, with appropriate objective data analysis. An additional benefit of this development is the necessary engineering and fabrication of a pole system that can contact the backs of right whales in an unobtrusive manner for any appropriate purpose.

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Keyword index

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