Abundance and demographic parameters of humpback whales from the Gulf of Maine, and stock definition relative to the Scotian Shelf

Phil Clapham*, Jay Barlow+, Moriah Bessinger#, Tim Cole*, David Mattila#, Richard Pace*, Debra Palka*, Jooke Robbins# and Rosemary Seton¥

Contact e-mail: pclapham@whsun1.wh.whoi.edu

ABSTRACT

The Gulf of Maine is one of the principal summer feeding grounds for humpback whales (*Megaptera novaeangliae*) in the North Atlantic, and was one focus of effort in an ocean-basin-wide study known as the Years of the North Atlantic Humpback (YoNAH) project. Data from that project and from subsequent surveys were used to assess stock boundaries, abundance and demographic parameters for Gulf of Maine humpbacks. Surveys on the Scotian Shelf in the summers of 1998 and 1999 produced the first substantial dataset of identified individual humpbacks observed in this region, which lies between the well-studied areas of the Gulf of Maine and Newfoundland. The results gave a match rate of approximately 27% (14 of 52 individuals) between the Scotian Shelf and the Gulf of Maine, with evidence that many of the matched whales were transient in the Gulf of Maine; there were no matches to any other location in the North Atlantic. These data suggest that the range of most whales from the Gulf of Maine usually does not extend as far east as the Scotian Shelf or Newfoundland. Only one whale was observed on the Scotian Shelf in both the 1998 and 1999 surveys, and another seen in 1998 had also been sighted there in 1994. This low inter-annual match rate suggests that the abundance of humpback whales on the Scotian Shelf is larger than previously recognised. Three different but overlapping estimates of abundance for the Gulf of Maine population were calculated. Mark-recapture data from 1992/93 gave an estimate of abundance of 652 (CV = 0.29); however, this estimate is likely biased because of heterogeneity in sampling and in animal distribution. Photo-id data also provided a minimum population estimate of 497 humpbacks known to be alive in 1997; this estimate is also likely to be negatively biased because of heterogeneity. Finally, line-transect surveys conducted in 1999 yielded estimates of 816 (CV = 0.45) or 902 humpback whales (CV = 0.41, including a portion of the eastern Scotian Shelf stratum); these transect-based estimates are more consistent with the number of humpbacks (1,273, including dead animals) in the current photo-id catalogue for the Gulf of Maine. Overall, the size of the Gulf of Maine population is likely to be in the high hundreds, but no more precise estimate can be calculated at this time. The growth rate for the Gulf of Maine population was estimated using an interbirth interval method using data from 1992-2000. The estimate was either 1.00 (for a calf survival rate of 0.51) or 1.04 (for a calf survival rate of 0.875). Although confidence limits are not available (because maturation parameters could not be estimated), both estimates of population growth rate are outside the 95% confidence intervals of the previous estimate of 1.065 for the period 1979-1991 (Barlow and Clapham, 1997). It is unclear whether this apparent decline is an artefact resulting from a shift in distribution or is a real phenomenon; if the latter, it may be related to known high mortality among young-of-the-year whales in the waters of the US mid-Atlantic states. However, calf survival appears to have increased since 1996, presumably accompanied by an increase in population growth.

KEYWORDS: HUMPBACK WHALE; NORTH ATLANTIC; ABUNDANCE; STOCK DEFINITION; POPULATION GROWTH; PHOTO-IDENTIFICATION

INTRODUCTION

Humpback whales return each spring to the waters of the Gulf of Maine, which is one of several major summer feeding areas in the North Atlantic (Katona and Beard, 1990). This population has been extensively studied through continual photo-identification (photo-id) work since the 1970s (Clapham *et al.*, 1993). It was also one focus of a large-scale multinational study, the Years of the North Atlantic Humpback (YONAH) project, in 1992 and 1993 (see Smith *et al.*, 1999).

Previously, the North Atlantic humpback whale population was treated as a single stock for management purposes under the US Marine Mammal Protection Act (Waring *et al.*, 1999). Indeed, earlier genetic analyses (Palsbøll *et al.*, 1995), based upon relatively small sample sizes, had failed to discriminate among the four western North Atlantic feeding areas of Greenland, Newfoundland/Labrador, the Gulf of St Lawrence and the Gulf of Maine. However, genetic analyses often reflect a timescale that extends well beyond that commonly used by managers. Accordingly, the decision was made by the US National Marine Fisheries Service (NMFS) to reclassify the Gulf of Maine as a separate feeding stock for the most recent NMFS marine mammal Stock Assessment Report (Waring *et al.*, 2000). This decision was based upon the strong fidelity by individual whales to this region, and the attendant assumption that, were this sub-population extirpated, repopulation by immigration from adjacent areas would not occur on any reasonable management timescale. This reclassification has subsequently been supported by new genetic analysis based upon a much larger collection of samples than those utilised by Palsbøll *et al.* (1995). These analyses have found significant differences in mtDNA haplotype frequencies of the four western feeding areas, including the Gulf of Maine (Larsen *et al.*, 1996; Palsbøll *et al.*, in prep.).

Photo-id data gathered by the YoNAH project in the Gulf of Maine have been supplemented by information from annual directed cruises, primarily by the Center for Coastal Studies. However, these surveys were focused solely on areas within the geographic Gulf of Maine. Consequently, with the exception of long-distance photographic comparisons to catalogues from other feeding grounds (e.g.

* *Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA.*
+ *Southwest Fisheries Science Center, Box 271, La Jolla, CA 92037, USA.*
# *Center for Coastal Studies, Box 1036, Provincetown, MA 02657, USA.*
¥ *College of the Atlantic, Bar Harbor, ME 04609, USA.*

Newfoundland), the resulting data could not be used to determine the extent to which the range of Gulf of Maine whales extends beyond this region. Resolution of this question is important to the issue of the 'boundary' of this stock.

Here, photo-id data from directed cruises to the Scotian Shelf in 1998 and 1999 were used to address the question of the population identity of humpback whales found in that region. Both mark-recapture and line-transect data were used to estimate abundance for the Gulf of Maine feeding stock, and to provide updated estimates for selected population parameters.

MATERIALS AND METHODS

Photo-identification

During the summers of 1998 and 1999, the Northeast Fisheries Science Center (NEFSC) conducted surveys for humpback whales on the Scotian Shelf, which is the area of continental shelf between the southern coast of Nova Scotia and the deeper offshore waters of the North Atlantic (Fig. 1). The 1998 survey covered an area from Roseway Basin to Emerald Basin and Western Bank, with the easternmost extent of sampling at approximately 62°W. The 1999 cruise repeated this coverage, but also surveyed further north and east as far as French Bank (approximately 44°45'N, 61°00'W). The objective of these surveys was to establish the occurrence and population identity of the animals found in this region, which lies between the well-studied populations of the Gulf of Maine and Newfoundland. Additional observations of humpback whales were made in areas within the Gulf of Maine, notably Georges Bank and the Bay of Fundy. Where possible, photographs were taken of the ventral fluke pattern and of the dorsal fin, both of which can be reliably used to identify individual humpback whales (Katona and Whitehead, 1981; Hammond *et al.*, 1990).

Photographs from both surveys were compared to a large regional catalogue of 1,273 humpback whales from the Gulf of Maine, maintained by the Center for Coastal Studies (CCS), Massachusetts. This catalogue is based upon annual directed cruises throughout the Gulf of Maine, and near-daily whalewatching-based data collection in one area (Massachusetts Bay). The geographic coverage of the collection is shown in Fig. 2. Scotian Shelf photographs from the 1998 and 1999 surveys were also compared to the North Atlantic Humpback Whale Catalogue (NAHWC), which is maintained by the College of the Atlantic, Maine. The NAHWC contains fluke photographs of 5,431 individuals from all over the North Atlantic, from the West Indies to the Arctic. With the exception of those photos taken in the Gulf of Maine, comparisons were not made to the separate collection of photos from the YoNAH project.

Since the primary goal of this work was to evaluate exchange with the Gulf of Maine, photographs were first evaluated as to their likelihood of being successfully matched. Photographs that were deemed unlikely to be matched on the basis of quality were eliminated from further consideration. In some cases, experienced matchers were able to recognise the Scotian Shelf animals and subsequently

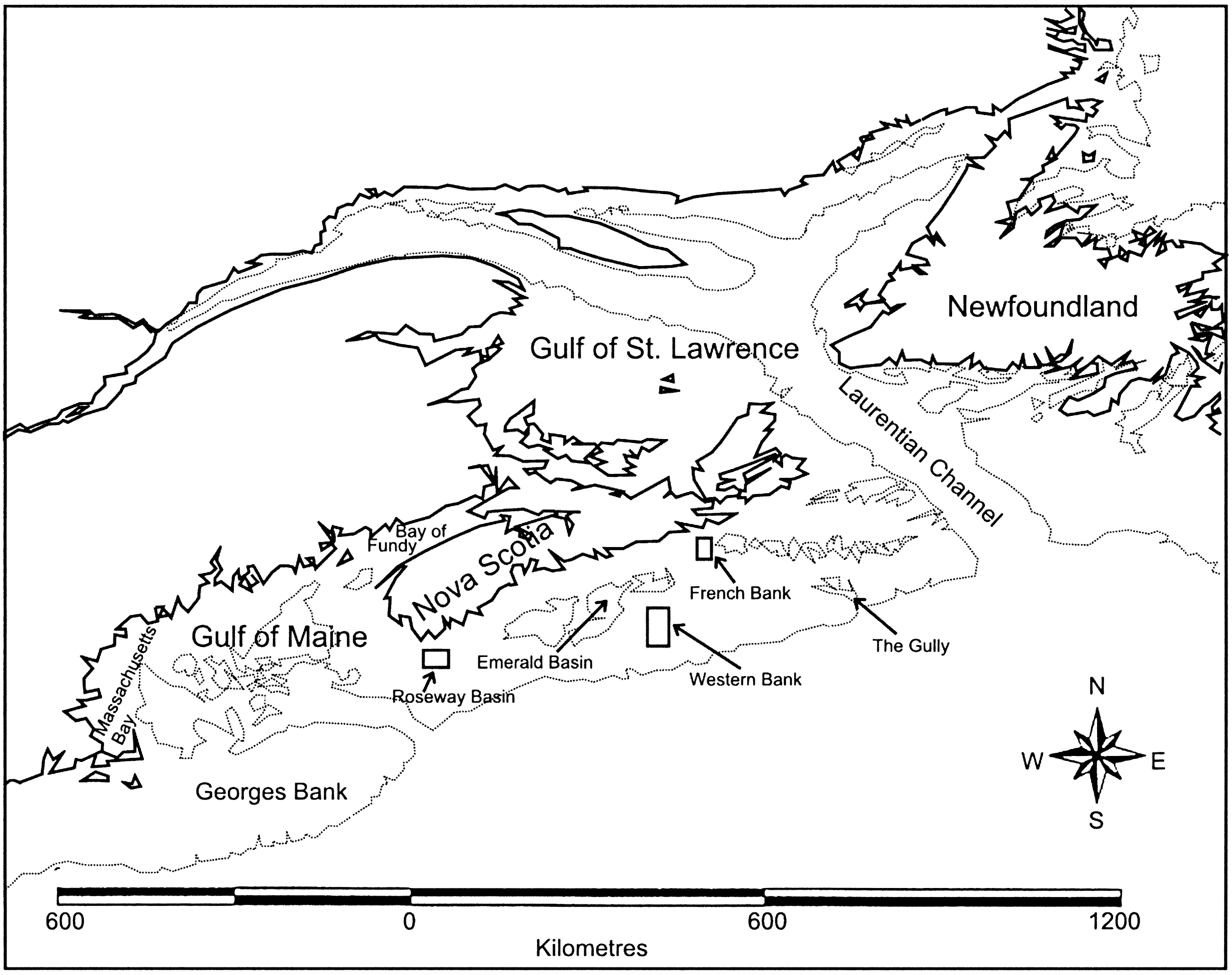

Fig. 1. Major locations mentioned in text. The depth contour shown is the 100m isobath.

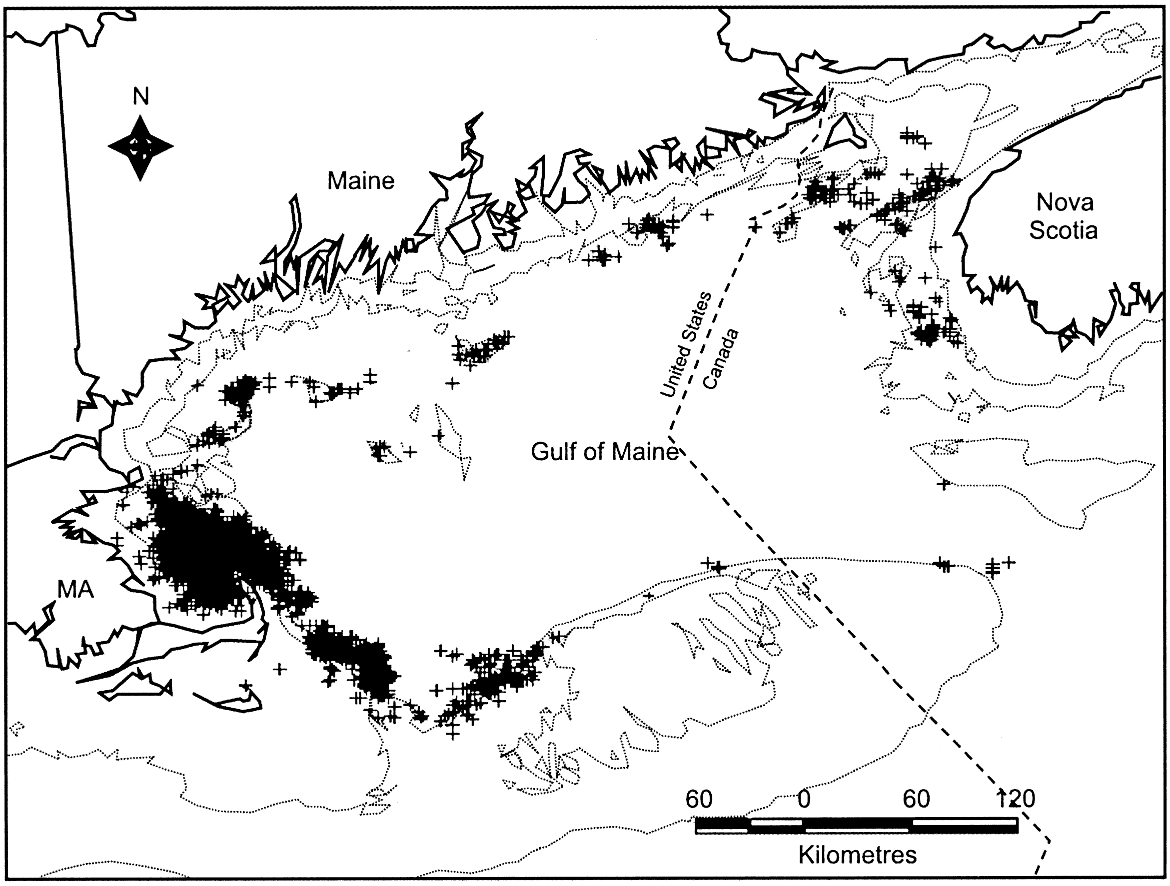

Fig. 2. Geographic coverage of the Center for Coastal Studies' Gulf of Maine humpback whale catalogue. Points represent locations of identified individual whales.

confirm those identifications against catalogue photographs. Otherwise, the matching process for each animal began with available fluke documentation. Fluke photographs were first matched against a sub-section of the catalogue containing whales with a similar pigmentation pattern. In addition to the pattern, the matching process considered the shape of the trailing edge and the presence of specific marks or injuries. If the first matching attempt was unsuccessful, the fluke was run through the entire catalogue at least twice, relying heavily on the shape of the trailing edge. This was intended to reduce the likelihood that a match was missed due to an age- or injury-related change in pigmentation. When available, CCS used dorsal fin documentation to validate or reject potential fluke matches.

When an individual was not successfully matched to the Gulf of Maine catalogue by its flukes, or if no fluke photos were available, matching was performed using any available dorsal fin photographs. As in the case of flukes, dorsal fins were first run through the section of the dorsal fin catalogue that contained similar morphology. Prominent or distinctive dorsal fin scarring was taken into consideration, as was distinctive lateral body scarring, the shape of the hump immediately preceding the dorsal (if present), the peaked ridges on the peduncle (if present). If a match was not made in the first round of matching, the images were run through the entire dorsal fin catalogue at least one more time.

Virtually every animal in the Gulf of Maine catalogue is double-marked (i.e. photos exist of both flukes and dorsal fin), and thus duplicate identifications were not a problem in this analysis. However, dorsal fins were not used in comparisons to the NAHWC.

Population composition

All matches to the Gulf of Maine, regardless of photo quality or coverage, were considered when examining the composition of whales using the Scotian Shelf. Life history information available for catalogued Gulf of Maine whales includes the year born (or first year seen), sex, maternal lineage and (for mature females) calving history. Sexes of Gulf of Maine humpback whales are based on molecular analysis of a tissue sample (Palsbøll *et al.*, 1992; Bérubé and Palsbøll, 1996a; b), a photograph of the genital slit (Glockner, 1983) or, in the case of females, documentation of at least one calf. The Gulf of Maine catalogue presently contains 385 known females and 287 known males. While the sex ratio of the overall population is parity (Clapham *et al.*, 1995), the additional sexing opportunity for females has produced a bias towards females (1.3:1) in the catalogue.

The exact age is presently known for 421 animals catalogued in the Gulf of Maine during their first year of life. For animals without a known year of birth, a minimum age was assigned by assuming that the whale was at least 1 year old the first year it was sighted. Female humpback whales in the Gulf of Maine have been shown to reach sexual maturity at the average age of five years (Clapham, 1992), a figure which corresponds well with findings for both male and female humpback whales in the Southern Hemisphere (Chittleborough, 1965). Consequently, juvenile whales were assumed to be those that were first catalogued as calves and were less than five years old in the year of interest. Whales were considered to be sexually mature if they were known to be at least five years old or were first sampled as an independent whale at least four years prior. A maturational class of 'unknown' was assigned to whales without a known year of birth that were first catalogued less than four years prior to the year of interest.

Abundance estimation

Three approaches to estimating abundance for Gulf of Maine humpback whales were employed: mark-recapture estimates; minimum population size; and line-transect estimates.

Mark-recapture estimates

During the YoNAH project, photo-identification surveys were conducted around the Gulf of Maine in the summers of 1992 and 1993 using methodology described by Smith *et al.* (1999). These surveys involved intensive effort and broad geographic coverage of the region over a relatively short time frame and are thus assumed to be less subject to heterogeneity than other available datasets. Accordingly, abundance was estimated with Chapman's modification of the Petersen method (Seber, 1982) using mark-recapture data from the YoNAH surveys.

Minimum population estimate

The second approach used photo-identification data to establish the minimum number of humpback whales known to be alive in a particular year, 1997. This was accomplished by determining the number of identified individuals seen either in that year, or in both a previous and subsequent year. A similar calculation was also made for 1992, which would be contemporaneous with the YoNAH estimate noted above.

Line-transect estimates

In the third approach, data were used from a 28 July to 31 August 1999 line-transect sighting survey conducted by a ship and aeroplane covering waters from the Gulf of Maine and Georges Bank to the mouth of the Gulf of St Lawrence. The ship (*R/V Abel-J*) surveyed 2,563km of track lines in an area of 30,298km^2; the aeroplane (a De Havilland Twin Otter) surveyed 5,649km of track lines in an area of 195,103km^2 (Fig. 3). Shipboard data were collected by naked eye by two independent teams of three observers, while travelling at about 10 knots. This allowed the estimation of $g(0)$, the probability of detecting a group on the track line (e.g. Palka, 1995). Data collected included sighting, effort and environmental data. Sightings data included time, bearing and distance to the initial position of the group, species composition of the group, best, high and low estimate of group size, behaviour, sighting cue and swim direction. Effort data included location of the ship (recorded every minute), ship's speed and course, and identification of person at each sighting station. Environmental data included water temperature, wind speed, Beaufort sea state, visibility, direction of sun, and magnitude of glare. Shipboard data were analysed using the modified direct duplicate method (Palka, 1995) that corrects for $g(0)$. This method involves first using standard line transect estimation methods (Buckland *et al.*, 1993) to estimate the uncorrected abundance of animals within a stratum for each team and for duplicate sightings, sightings seen by both teams. Then these three abundance estimates were used in mark-recapture methods to estimate a corrected abundance (Palka, 1995). Aerial data were collected by one team of three observers while travelling at 110 knots at 600 feet above the sea surface. Two observers used side bubble windows to clearly see the track line below the plane and to also see the horizon; the third observer used a belly window that allowed good visibility within about 25° of the track line. The types of data collected were similar to that collected for the ship. Aerial data were analysed using standard line transect methods (Palka, 2000), not corrected for $g(0)$. The effect of not correcting for $g(0)$ for the aerial data is that the abundance estimates for these areas are negatively biased.

Demographic parameter estimation

Demographic parameters of Gulf of Maine humpback whales were estimated from photo-id mark-recapture data using the interbirth-interval method (Barlow and Clapham, 1997) to estimate reproductive rates (birth intervals and maturation ages), and a modified Jolly-Seber approach (Buckland, 1980) to estimate non-calf survival rates. These demographic parameters are then used to estimate population growth rate (λ), with standard error calculated using a Monte Carlo approach (Barlow and Clapham, 1997). Results using photo-id data collected by CCS over the period 1992-2000 are compared to previously published results from the 1979-1991 time period. The CCS data derive from both intensive whalewatching cruise effort and directed research cruises.

RESULTS

Photo-identification

Photo-identification Exchange rates

Plots of humpback whale sightings from the 1998 and 1999 NEFSC surveys are shown in Fig. 4. A total of 88 individual humpback whales was photographed (with photos of matchable quality) on the two surveys. Of these, 52 individuals were recorded on the Scotian Shelf and 36 in the Gulf of Maine region (including Georges Bank and the Bay of Fundy).

All 36 individuals (100%) photographed within the Gulf of Maine were successfully matched to the Gulf of Maine catalogue. By contrast, the overall match rate between the Scotian Shelf and the Gulf of Maine was 27% (14 of 52 Scotian Shelf individuals from both years). To examine whether match rate declined with distance from the Gulf of Maine, the Scotian Shelf survey area was arbitrarily divided into two portions: northern (French Bank) and southern (all other areas). Comparable rates of exchange were obtained from the southern (26%, $n = 10$ of 38 whales) and northern (27%, $n = 4$ of 15 whales) portions, despite the additional distance of nearly 100 n.miles. One individual was observed in both southern and northern areas.

Comparisons of the 52 NEFSC Scotian Shelf whales to the NAHWC revealed no matches to any feeding area other than the Gulf of Maine. Only one of the individuals seen on the Scotian Shelf in 1998 was resighted there in 1999, despite the geographic overlap of effort in those two years. One other whale observed on the Scotian Shelf in the 1998 NEFSC survey had previously been photographed there (near the area known as the Gully) by Memorial University staff in 1994.

Gulf of Maine sighting histories

Three of the 14 Scotian Shelf whales matched to the Gulf of Maine were male, two were female and nine were of unknown sex (Table 1). At least 71% (10 of 14) were reproductively mature at the time they were documented on the Scotian Shelf. One whale was known to be a yearling and three were of unknown age class.

None of the individuals sighted on the Scotian Shelf had extensive Gulf of Maine sighting histories, although the yearling was born to a well-known Gulf of Maine whale.

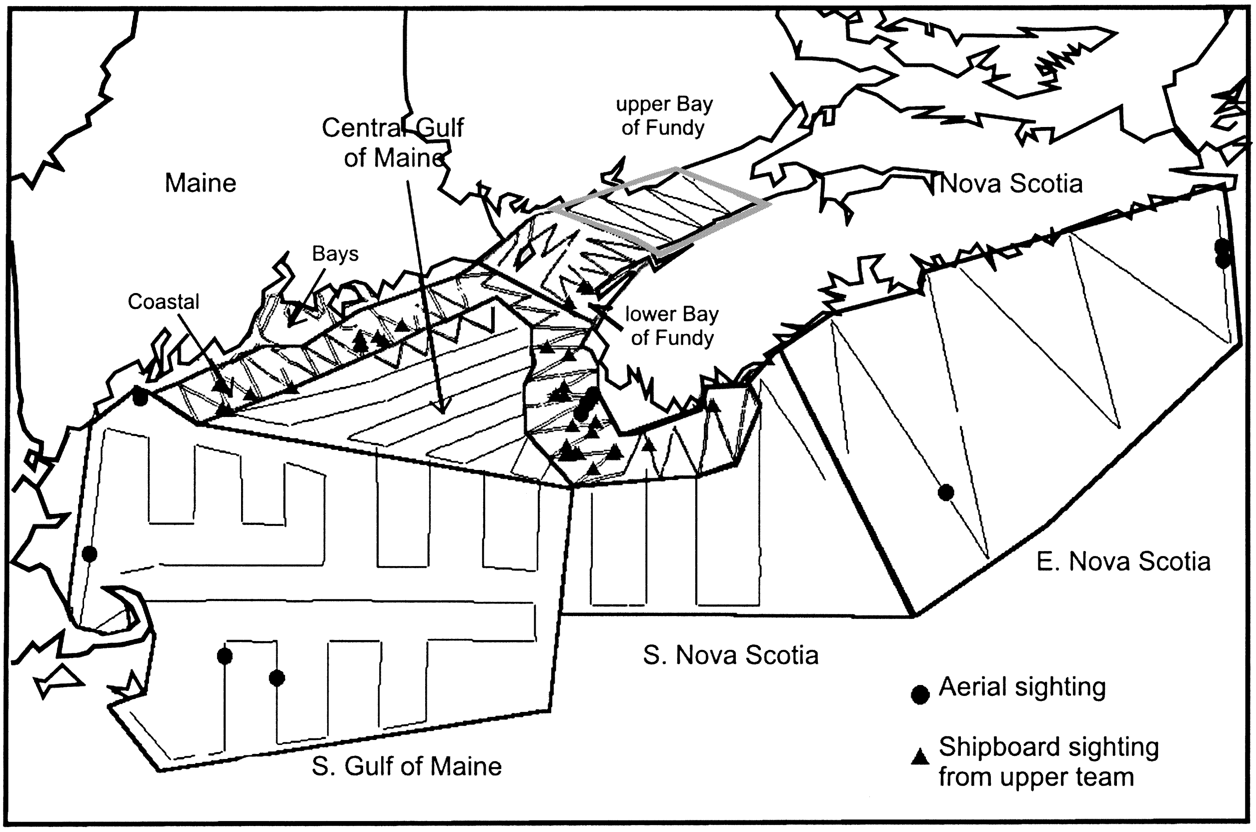

Fig. 3. Survey strata and locations of humpback whales observed from NEFSC shipboard and aerial line-transect cruises, 28 July to 31 August 1999.

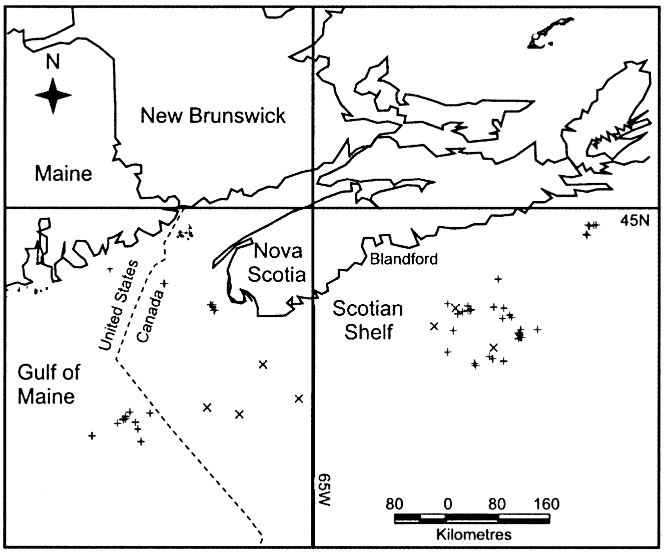

Fig. 4. Locations of humpback whales photo-identified by NEFSC in 1998 and 1999 (+), and catches of humpback whales from the whaling station at Blandford, Nova Scotia (x). Catch data from Mitchell (1973).

None were documented in more than three years (mean = 1.64 years, $n = 14$) and, with one exception, annual return occurred exclusively in consecutive years.

Only four of the matched Scotian Shelf whales have been recorded in the Gulf of Maine in recent years (including 2002). The yearling was first sighted as a calf in the Massachusetts Bay area one year prior to its Scotian Shelf sighting. It was sighted as a calf on nine separate days in the spring and autumn months of 1997 (April, May and September). 'Bedlamer', a recently catalogued individual of unknown age and sex, was the only individual in the Scotian Shelf sample that was also sighted within the geographic Gulf of Maine during the same year. Sightings took place in the Massachusetts Bay area on four days between 4 May and 23 June 1998. Bedlamer was also seen in Massachusetts Bay during the spring of 1999 (one year after having been seen on the Scotian Shelf), and again in 2002. One additional individual was seen in the Bay of Fundy two years after being seen on the Scotian Shelf. That animal had no previous sighting history in the Gulf of Maine.

Gulf of Maine sightings of these animals took place between April and October, which corresponds to the period of greatest sampling effort. Only eight of all Gulf of Maine sightings took place in the peak of the summer (June through August). A small number of the sightings ($n = 4$) were in the northern or eastern part of the region. When individuals were seen in more than one year, they tended to be documented during the same time period each year.

Abundance

Mark-recapture estimate

Data on individual whales identified during the 1992 and 1993 YoNAH research cruises gave an estimate of 652 (CV = 0.29) non-calf humpback whales in 1992.

Minimum population estimate

Using data from the CCS Gulf of Maine catalogue, the minimum number of humpback whales known to be alive in 1997 was 497. The equivalent estimate for 1992 (contemporaneous with the YoNAH mark-recapture estimate above) was 501.

Line-transect estimate

Results of the line-transect survey are summarised in Table 2. Excluding the Scotian Shelf survey blocks yielded an estimate of 816 humpbacks (CV = 0.45). An alternative calculation which included 25% of the eastern Scotian Shelf

Table 1

Life histories of Scotian Shelf whales matched to the Gulf of Maine.

Whale identity and life history					Gulf of Maine sighting history[2]			
Working no.	Name	Sex	First year	Min. age on Scotian shelf[1]	Years seen	Days seen	Most recent	Seasons[3]
NEFSC98-08	Bedlamer	U	1997	2	3	5	2002	SM
NEFSC98-14	Etcetera	U	1984	15	1	6	1984	SM
NEFSC98-20	Islet	M	1986	13	1	1	1986	M
NEFSC98-26	Chapin	U	1989	10	1	1	1989	S
NEFSC99-28	Antennae	M	1993	6	1	1	1993	M
NEFSC98-32	Charmer	U	1997	1[E]	1	9	1997	SA
NEFSC98-34	Tines	U	2000	U	1	2	2000	A
NEFSC99-05	Slide	F	1988	12	3	10	1991	S
NEFSC99-07	Minos	F	1988	12	1[4]	1[4]	1988	?
NEFSC99-08	(unnamed)	U	2000	1	1	1	2000	M
NEFSC99-36	River	U	1992	8	2	3	1993	S
NEFSC99-47	Camel	M	1980	20	2	2	1994	M
NEFSC99-48	Massachusetts	U	1990	10	3[4]	3[4]	2002	M
NEFSC99-65	Ping	U	1994	6	2	3	1994	MA

[1]E = exact age; all other ages are minimum ages. U = unknown.
[2]Due to individual-level habitat preferences and variable sampling effort across the Gulf of Maine, the seasonal habitat use patterns shown here are not necessarily comparable among individuals.
[3]Season codes: S = Spring (April-May); M = Summer (June-August); A = Autumn (September-November).
[4]Identification photographs were contributed to CCS by other institutions. While the individual was present in the Gulf of Maine on at least one day, no additional information is available in the CCS database.

stratum (to accommodate the approximate exchange rate of whales from the Gulf of Maine to this region) gave an estimate of 902 whales (CV = 0.41).

Demographic parameters

For the period 1992-2000, the female non-calf survival rate was estimated to be 0.950 (SE = 0.011). This estimate is slightly lower, but not statistically different from the estimate of 0.960 (SE = 0.008) for period 1979-1991 (Barlow and Clapham, 1997).

For 1992-2000, birth interval probabilities (the probability of giving birth x years after a prior birth, conditional on not having given birth during the intervening period) were estimated as 0.0357, 0.579, 0.608, 0.806 and 1.000 (for post-parturition years of 1-5, respectively). The mean birth interval implied by these estimates and the above survival

Table 2

Line transect estimates of humpback whale abundance in the Gulf of Maine/Scotian shelf region based on a shipboard and aerial survey conducted 28 July to 31 August 1999. For the shipboard data, the upper line is from the data collected by the upper team and the lower line is from the lower team. No. groups is the number of groups (n); n/L is the encounter rate, number of groups (n) divided by the length of track line (L); CV is coefficient of variation; ESW is effective strip width, measured in metres; $g(0)$ is the probability of detecting a group on the track line. Methods described in Palka (2000).

Stratum[1]	No. groups (n)	CV(n/L)	Mean group size(s)	CV(s)	ESW (in m)	CV(ESW)	$g(0)$[2]	CV($g(0)$)[2]	Animal density (/km²)	Abundance (N)	CV(N)
Coastal	34	0.33	1047	0.07	1104	0.25	0.45	0.28	0.0294	643	0.54
	37	0.34	1.49	0.09	1464	0.13	0.37	0.27			
Lower BOF	3	0.80	1.33	0.13	1104	0.25	0.31	0.48	0.0070	43	0.87
	3	0.80	1.33	0.13	1464	0.13	0.23	0.61			
South GoM	1	0.92	1	0	150	0.16	1	-	0.0016	130	0.96
East NS	2	0.97	1	0	150	0.16	1	-	0.0056	342	0.72
Total									**0.0051**	**1,158**	**0.38**
Sub-total I[3]									0.0063	816	0.45
Sub-total II[4]									0.0047	902	0.41

[1]All strata and the platform that surveyed them are listed below. If a stratum is not specified in the table, no humpback whales were detected there. The Total is for all strata (below), so the density for strata not specified in the table is assumed to be zero.

Ship strata:
Coastal — Coastal Gulf of Maine
Lower BOF — Lower Bay of Fundy
Bays — Maine Bays

Plane strata:
Upper BOF — Upper Bay of Fundy
Central GoM — Central Gulf of Maine
South GoM — Southern Gulf of Maine
South NS — Southern Nova Scotian shelf
East NS — Eastern Nova Scotian shelf

[2]$g(0)$ for aerial surveys was assumed to be one, and its CV undefined; thus resulting in negatively biased abundance estimates.
[3]Sub-total I stratum covers the habitat of the Gulf of Maine humpback stock, the sum of the coastal, lower BOF, Bays, Central GoM and South GoM strata. (Area of this sub-stratum is 129,808 km²).
[4]Sub-total II stratum covers the habitat of the Gulf of Maine humpback stock, the sum of the coastal, lower BOF, Bays, Central GoM, South GoM and 25% of east NS stratum. (Area of this sub-stratum is 191,158 km²).

rate is 2.56 years, slightly greater than the mean birth interval estimated by Barlow and Clapham (1997) for the time period 1979-1991 (2.38 years).

Attempts to estimate age-at-maturation parameters for the 1992-2000 time period were thwarted by small sample size of individuals observed from birth until the age of maturation. In large part, this appears to be due to a very low calf survival rate during the period of 1992-1995; of the 18 calves that were first observed during this time period, only 2 (11%) were seen again in a subsequent year. In comparison, 83% of the calves seen in 1979-1991 were observed again in a subsequent year, and 70% of calves recorded in the 1996-1998 period were resighted.

In previous analyses (Barlow and Clapham, 1997), calf survival rate was estimated as an average between the minimum estimate (83% that were known to survive) and the maximum likely value (92%, estimated as the square of the non-calf survival rate). For the period 1992-2000, the difference between the minimum estimate and maximum estimates of calf survival (51% vs 90%) is too large to ignore, and averaging these estimates is inappropriate. In this paper, population growth rates are estimated using calf survival rates as either 0.51 (observed number surviving) or as 0.875 (estimated from the period 1979-1991).

Since age-at-maturation could not be derived directly from the 1992-2000 photo-id data, population growth rate was calculated using age-at-maturation parameters that were estimated from 1979-1991 (Barlow and Clapham, 1997). Using these values, the intrinsic rate of population growth (λ) was estimated as 1.00 (for calf survival rate of 0.51) or 1.04 (for calf survival rate of 0.875). Although confidence limits are not available for the latter estimates (because maturation parameters could not be estimated), both recent estimates of population growth rate are outside the 95% confidence intervals (+/- 2 SE) of the previous estimate of 1.065. Differences are due to slightly lower non-calf survival rates and longer calving intervals, and (in the case of λ = 1.00) a much lower estimate of calf survival rate.

DISCUSSION

Gulf of Maine stock definition

Exchange with the Scotian Shelf

The matching results presented here indicate that approximately a quarter of the individuals on the Scotian Shelf had sighting histories in the Gulf of Maine. However, this should be considered a minimum value, as individuals cannot be excluded from the Gulf of Maine because they were not matched to the catalogue. Despite the fact that CCS performs sampling throughout the region, sighting effort in the Massachusetts Bay area has been substantially higher than in other locations. Individuals that consistently use other areas of the Gulf of Maine, particularly during the spring or autumn, would have been less likely to be sighted and catalogued.

Gulf of Maine sighting histories provided few additional data with which to understand the composition of the Scotian Shelf population. Most notable was the fact that a high percentage of matched Scotian Shelf whales were mature animals. However, that may simply be due to the fact that there have been more opportunities to sample older animals in the Gulf of Maine.

There are several potential explanations for the fact that some individuals exhibited Gulf of Maine and Scotian Shelf sighting histories. For example, the primary foraging range of some individuals may overlap both regions. In that event, one might expect to see evidence that animals had moved between areas within and between feeding seasons. One might further anticipate sightings to have occurred preferentially in the northern or eastern portions of the Gulf of Maine, which are the areas closest to the Scotian Shelf. Finally, Gulf of Maine sightings would likely have occurred during the peak of the season, when the sighting effort was highest throughout the Gulf of Maine. As described above, one individual was seen in both regions during the same year and was also documented in the Gulf of Maine both prior to and after its Scotian Shelf sighting. However, all of the Gulf of Maine sightings of that individual were limited to the early part of the feeding season. The majority of Gulf of Maine sightings took place outside the peak of the summer (April, May, September or October) and few were in the northern or eastern part of the region. CCS effort is biased towards the western Gulf of Maine; however, with one exception Scotian Shelf whales were also not represented among unknown whales contributed to CCS from whalewatching-based data collection programmes out of Brier Island (on the eastern side of the Bay of Fundy in southwestern Nova Scotia). Furthermore, NEFSC sampling performed at the geographic extremes of the Gulf of Maine resulted in 100% rates of exchange. Thus, while one cannot eliminate the possibility that the primary feeding range of some individuals consistently overlaps the Gulf of Maine and the Scotian Shelf, that hypothesis does not clearly explain the data available.

Alternatively, individuals from one area may have permanently shifted their distribution to the adjacent habitat. Unfortunately, because of the timing of the Scotian Shelf sampling, this study can only examine whether Gulf of Maine whales relocated to the Scotian Shelf, and not vice versa.

Finally, some individuals may transit the Gulf of Maine on their way to or from their summer feeding ground, whether the final destination is the Scotian Shelf, or another Canadian feeding habitat. Transient use of the Gulf of Maine would explain the limited number of documented sightings and the concentration of those sightings in the early and late portions of the feeding season. Individuals using the Gulf of Maine in this way could be sighted both prior to and after sightings in other regions. However, if it exists, this practice does not appear to be a long-term habit of any particular individual. Furthermore, it does not explain the fact that a few sightings have occurred during the peak summer months. Of the hypotheses presented, it seems most likely that the observed exchange is primarily due to animals transiting the Gulf of Maine *en route* to the Scotian Shelf or more distant Canadian habitats. However, it is also likely that the primary foraging range of some individuals includes both areas.

Boundaries of the Gulf of Maine stock

It is clearly not meaningful to attempt to place strict geographic boundaries on this (or probably any other) population of whales. However, the situation with the Gulf of Maine humpback whale population can be broadly characterised as one of isolation by distance: the further one gets from the Gulf of Maine, the lower the probability of finding Gulf of Maine whales. The observed match rate between the Gulf of Maine and other major feeding areas of the North Atlantic is quite low: for example, of 1,082 Gulf of Maine humpbacks compared to other North Atlantic regions through the end of 2000, only 12 (1.1%) were also recorded off Newfoundland, and 22 (2.0%) in the Gulf of St Lawrence (J. Allen, unpublished data). This undoubtedly reflects the strong maternally directed fidelity which characterises humpback whale feeding stocks in this and some other oceans.

The situation becomes somewhat more complex when we consider the coastal waters south of the geographic Gulf of Maine, notably those of the US mid-Atlantic coast states (New Jersey to North Carolina). Humpback whales have been observed with increased frequency in this region over the past decade, principally during the winter months. Barco *et al.* (2002) compared fluke photos of 40 live or dead humpback whales from the mid-Atlantic states region to both the Gulf of Maine catalogue and the NAHWC. Of 21 live whales, 9 (43%) matched to the Gulf of Maine, 4 (19%) to Newfoundland and 1 (5%) to the Gulf of St Lawrence. Of 19 dead humpbacks, 6 (32%) were known Gulf of Maine whales.

Although the population composition of the US mid-Atlantic coast states region appears to be dominated by Gulf of Maine whales, lack of recent photographic effort in Newfoundland and the Gulf of St Lawrence make it likely that the observed match rates under-represent the true presence of Canadian whales in the region. Barco *et al.* (2002) suggested that the mid-Atlantic coast states area primarily represents a supplemental winter feeding ground, which is used by humpbacks for more than one purpose. It remains to be seen whether the mixing there of whales from different feeding areas is (as current data suggest) exclusively a winter phenomenon. Humpback whales appear to be much less common in the region in summer, and to date the only matches from that season have been Gulf of Maine whales.

Taking all the data together, we suggest that the Gulf of Maine population contains some whales whose summer foraging range extends to the Scotian Shelf, but rarely beyond; and that in summer a small number of individuals from this stock range south as far as the US mid-Atlantic states.

Abundance

It is difficult to assess the reliability of the mark-recapture estimate provided here (652, CV = 0.15). Heterogeneity of capture rates will negatively bias population size estimates from capture-recapture models (Hammond, 1990), and differences in fluking behaviour and individual distinctiveness are recognised sources of capture heterogeneity in humpback whale photo-id studies (Perkins *et al.*, 1985). Variation in geographic distribution of survey coverage, when combined with the apparent fidelity of individual whales to sub-areas of the Gulf of Maine or subtle shifts in the distribution of whales among years inevitably introduces individual capture heterogeneity into resighting histories. Longer capture histories (eight years) have been analysed for humpbacks in the Gulf of Maine and these data indicated a strong transient effect. Analyses of additional data (longer capture histories and surveys of wider geographic coverage) suggested that some marked individuals might not be present within the Gulf of Maine during the capture period of a given year. In the analysis of more than two capture periods this is equivalent to temporary emigration or transients; either violates assumptions of mark-recapture models and would positively bias local-area population estimates in a two-sample estimate such as ours (Williams *et al.*, 2002). Heterogeneity and underestimation are suspected to be the greater issue here, but because a combination of violations almost certainly exists in these data (heterogeneity, transients and temporary emigration) the resultant estimate is of unknown reliability.

Two sources of bias result in underestimated line-transect abundance estimates: perception and availability bias. There are no factors that would result in a significant overestimate. Perception bias and availability bias due to short dives were accounted for in the estimate of $g(0)$ for the shipboard portion of the estimate, which was approximately 25% of the study area and the commonly believed higher density area. However, $g(0)$ was not estimated for the aerial portion. On feeding grounds, such as in this study area, humpback whales generally have short dives: 57% of humpback whale dives in Frederick Sound, Alaska were less than 2.8 minutes in duration and only 18% surpassed 6.0 minutes (Dolphin, 1987). Since the ship travels approximately 1,853m in 6.0 minutes, it is likely that most, although not all, humpback whales were available to be seen from the ship. This is not true from the plane, since the plane travels about 3,400m in one minute. The estimates of $g(0)$ for the shipboard teams were in the range of 0.25-0.6, depending on the area (Table 2). The effect of this is that the uncorrected shipboard density estimate was doubled to quadrupled (depending on the area) due to corrections for perception and availability (short dives) biases. Humpback whales that dived, on average, for more than 0.5 minutes were probably not available to be seen by the plane, and so $g(0)$ for the plane would be much less than that for the ship. Thus, estimates from the plane are more negatively biased than the ship's estimates. The magnitude of this bias is related to the proportion of humpback whales unavailable to be seen by the two platforms and the relative difference in the true density of humpback whales in the areas surveyed by the ship versus plane. The overall effect of these factors is that the reported line-transect abundance estimate is negatively biased to an unknown degree.

Although the mark recapture point estimate is relatively precise (CV of 0.15), the interval estimate overlaps with the minimum population estimate of 501 whales for the same period; the latter figure is likely to be negatively biased, again because of heterogeneity of sampling. The line-transect estimate of 816 (CV = 0.45) also overlaps with both the mark-recapture and minimum population estimates. However, given that the rate of exchange between the Gulf of Maine and the Scotian Shelf is not zero, the alternative line-transect estimate (902 whales, CV = 0.41) may be more appropriate. Both of the line-transect estimates are more consistent with the number of individual humpback whales identified in the Gulf of Maine (currently 1,273 whales, including dead animals).

Overall, it seems reasonable to suggest that the size of the Gulf of Maine humpback whale population is in the high hundreds, but that provision of a more precise estimate is not possible at this time. Dedicated surveys to estimate abundance, with a sampling design that takes heterogeneity issues into account, should be conducted in the future.

Demographic parameters

Barlow and Clapham (1997) applied the same interbirth interval model used here to photographic mark-recapture data and estimated the population growth rate of the Gulf of Maine humpback whale stock at 6.5% (CV = 0.012). Maximum net productivity is unknown for this population, although a theoretical maximum for any humpback population can be calculated using known values for biological parameters (Brandao *et al.*, 2000; Clapham *et al.*, 2001). For the Gulf of Maine, data supplied by Barlow and Clapham (1997) and Clapham *et al.* (1995) give values of 0.96 for survival rate, six years as mean age at first parturition, 0.5 as the proportion of females, and 0.42 for annual pregnancy rate. From this, a maximum population growth rate of 7.2% is obtained according to the method described by Brandão *et al.* (2000). This suggests that the observed rate of 6.5% for the period 1979-91 (Barlow and Clapham, 1997) was close to the maximum for this stock.

The new population growth rate estimates of either zero (for calf survival rate of 0.51) or 4% (for calf survival rate of 0.875) are notably different from Barlow and Clapham's (1997) earlier estimate of λ. Accordingly, it may be the case that population growth slowed or even stopped in the period since the previous study. A statistically based method of estimating calf survival rates is clearly needed to account for varying sighting effort and success in different years; nonetheless, this change in apparent calf survival rates in the early 1990s is not likely to be a statistical artefact.

Most of the decline appears to be the result of a reduction in calf survival rates between 1992 and 1995; however, reduced adult female survival and increased interbirth intervals may also have contributed to the apparent decline. The possibility that the apparent reduction in calf survival is related to a shift in distribution cannot be rejected; indeed, such a shift occurred during exactly the period in which survival rates declined. It is possible that this shift resulted in calves born in those years imprinting on (and thus subsequently returning to) areas other than those in which intensive sampling occurs.

On the other hand, if the decline in calf survival is real it is possible that it is partly related to the known high mortality rate of young whales off the mid-Atlantic coast states of the US. Of 48 humpback whale mortalities there between 1990 and 2000 for which length data exist, 39 (81.2%) were estimated to be first-year whales (Barco *et al.*, 2002). Of 19 stranded whales for which fluke photographs were available, six (32%) matched to the Gulf of Maine; there were no matches to other areas. Given the apparent predominance of Gulf of Maine whales in this region, it is possible that the impact of these mortalities is reflected in the low calf survival estimates given above.

Whatever the cause, it appears that calf survival returned to near-previous levels beginning in 1996, and it is likely that population growth is now comparable to that observed between 1979 and 1991. Additional years of photo-id effort will be needed to estimate the current rate of growth for this population.

Additional analytical research is needed to properly model the observed variability in survival rates and birth rates. The methods used here (and developed for the 1979-91 time period) are more appropriate for estimating demographic rates that are relatively constant (as was observed in the earlier time period). A method of modelling annual changes or trends in survival and birth rates might allow better insight into how population growth changes in response to environmental conditions and increasing intra-specific competition as the population approaches carrying capacity.

Status of Scotian Shelf humpback whales

The whaling station at Blandford, Nova Scotia killed a small number of humpback whales on the Scotian Shelf between 1969 and 1971 (Mitchell, 1973). The southern area of NEFSC Scotian Shelf sampling corresponds with one of the areas in which animals were taken (Fig. 4). The plotted positions of the remaining catches place them at the mouth of the Gulf of Maine. Based on the results reported here, it is likely that some of the animals caught were from the Gulf of Maine.

The paucity of any year-to-year matches ($n = 1$) among the 52 individual humpback whales identified on the Scotian Shelf in 1998/99 suggests that the population in this area is considerably larger than previously recognised. Additional observations from a NEFSC dedicated survey in 2002 (P. Clapham, unpublished data) show that humpbacks occur along much of the Scotian Shelf, at least as far north as the waters east of the Laurentian Channel; this suggests an essentially continuous distribution from the Gulf of Maine to Newfoundland. Line-transect data from the July/August 1999 NEFSC survey gave an estimate of 342 humpback whales ($CV = 0.72$) for the eastern Scotian Shelf survey block. However, this estimate is imprecise and further survey work is required.

The absence of matches between the Scotian Shelf and other North Atlantic feeding grounds (except the Gulf of Maine) implies that the former region is host to a large number of whales that have not previously been sampled elsewhere. However, the match rate could have been artificially depressed by the low sampling effort in other areas of Atlantic Canada (Newfoundland and the Gulf of St Lawrence) in the last decade. Whatever the case, it is clear that a systematic photo-identification survey of the entire Scotian Shelf should be conducted to clarify the status and habitat use of humpback whales in this largely unstudied region of the North Atlantic.

ACKNOWLEDGMENTS

We thank Richard Merrick, Fred Serchuk and two anonymous referees for their helpful reviews of this manuscript. Appreciation for matching assistance is due to Judy Allen of the North Atlantic Humpback Whale Catalogue at College of the Atlantic, Bar Harbor, Maine. We thank the Cetacean Research Unit (Gloucester, Massachusetts), and Shelley Barnaby (Brier Island, Nova Scotia) for additional sighting data on matched whales. Finally, we are grateful to the captains, crew and scientists on board the NOAA Ship *Delaware II* for their assistance during the fieldwork for this study.

REFERENCES

Barco, S.G., McLellan, W.A., Allen, J.M., Asmutis-Silvia, R.A., Mallon-Day, R., Meacher, E.M., Pabst, D.A., Robbins, J., Seton, R.E., Swingle, W.M., Weinrich, M.T. and Clapham, P.J. 2002. Population identity of humpback whales (*Megaptera novaengliae*) in the waters of the US mid-Atlantic states. *J. Cetacean Res. Manage.* 4(2):135-41.

Barlow, J. and Clapham, P.J. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology* 78(2):535-46.

Bérubé, M. and Palsbøll, P.J. 1996a. Erratum of 'Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers'. *Mol. Ecol.* 5:602.

Bérubé, M. and Palsbøll, P.J. 1996b. Identification of sex in cetaceans by multiplexing three ZFX and ZFY specific primers. *Mol. Ecol.* 5:283-7.

Brandao, A., Butterworth, D.S. and Brown, M.R. 2000. Report of the Scientific Committee. Annex G. Report of the Sub-Committee on the Comprehensive Assessment of Other Whale Stocks. Appendix 8. Maximum possible humpback whale increase rates as a function of biological parameter values. *J. Cetacean Res. Manage. (Suppl.)* 2:192-3.

Buckland, S.T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. *Biometrics* 36:419-35.

Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, New York and London. xii+446pp.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshwater Res.* 16:33-128.

Clapham, P.J. 1992. Age at attainment of sexual maturity in humpback whales, *Megaptera novaeangliae*. *Can. J. Zool.* 70(7):1470-2.
Clapham, P.J., Baraff, L.S., Carlson, C.A., Christian, M.A., Mattila, D.K., Mayo, C.A., Murphy, M.A. and Pittman, S. 1993. Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine. *Can. J. Zool.* 71(2):440-3.
Clapham, P.J., Bérubé, M. and Mattila, D.K. 1995. Sex ratio of the Gulf of Maine humpback whale population. *Mar. Mammal Sci.* 11(2):227-31.
Clapham, P., Robbins, J., Brown, M., Wade, P. and Findlay, K. 2001. Report of the Scientific Committee. Annex G. Report of the Sub-Committee on the Comprehensive Assessment of Whale Stocks – In-depth Assessments. Appendix 5. A note on plausible rates of population growth in humpback whales. *J. Cetacean Res. Manage. (Suppl.)* 3:196-7.
Dolphin, W.F. 1987. Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. *Can. J. Zool.* 65:354-62.
Glockner, D.A. 1983. Determining the sex of humpback whales in their natural environment. pp. 447-64. *In:* R. Payne (ed.) *Communication and Behavior of Whales*. AAAS Selected Symposium 76. Westview Press, Boulder, Colorado. xii+643pp.
Hammond, P.S. 1990. Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. *Rep. int. Whal. Commn* (special issue) 12:135-9.
Hammond, P.S., Mizroch, S.A. and Donovan, G.P. (eds.). 1990. *Report of the International Whaling Commission (Special Issue 12). Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters*. International Whaling Commission, Cambridge, UK. [vi]+440pp.
Katona, S.K. and Beard, J.A. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep. int. Whal. Commn* (special issue) 12:295-305.
Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Rec.* 20:439-44.
Larsen, A.H., Sigurjonsson, J., Oien, N., Vikingsson, G. and Palsbøll, P.J. 1996. Population genetic analysis of mitochondrial and nuclear genetic loci in skin biopsies collected from central and northeastern North Atlantic humpback whales (*Megaptera novaeangliae*): population identity and migratory destinations. *Proc. R. Soc. Lond. Ser. B.* 263:1611-8.
Mitchell, E. 1973. Report of the Scientific Committee, Annex M. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations, 1969-1971. *Rep. int. Whal. Commn* 23:138-54.
Palka, D. 1995. Abundance estimate of the Gulf of Maine harbour porpoise. *Rep. int. Whal. Commn* (special issue) 16:27-50.
Palka, D. 2000. Abundance of the Gulf of Maine/Bay of Fundy harbor porpoise based on shipboard and aerial surveys during 1999. NOAA/NMFS/NEFSC Ref. Doc. 00-07 (unpublished). 29pp. [Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026].
Palsbøll, P.J., Vader, A., Bakke, I. and El-Gewely, M.R. 1992. Determination of gender in cetaceans by the polymerase chain reaction. *Can. J. Zool.* 70:2166-70.
Palsbøll, P.J., Clapham, P.J., Mattila, D.K., Larsen, F., Sears, R., Siegismund, H.R., Sigurjónsson, J., Vasquez, O. and Arctander, P. 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behavior on population structure. *Mar. Ecol. Prog. Ser.* 116:1-10.
Perkins, J.S., Balcomb, K.C., Nichols, G., Hall, A.T., Smultea, M. and Thumser, N. 1985. Status of the West Greenland humpback whale feeding aggregation, 1981-1983. *Rep. int. Whal. Commn* 35:379-83.
Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd Edn. Charles Griffin and Company Ltd., London. i-xvii+654pp.
Smith, T.D., Allen, J., Clapham, P.J., Hammond, P.S., Katona, S., Larsen, F., Lien, J., Mattila, D., Palsbøll, P.J., Sigurjónsson, J., Stevick, P.T. and Øien, N. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Mar. Mammal Sci.* 15(1):1-32.
Waring, G.T., Palka, D.L., Clapham, P.J., Swartz, S., Rossman, M.C., Cole, T.V.N., Bisack, K.D. and Hansen, L.J. 1999. US Atlantic marine mammal stock assessments – 1998. NOAA Technical Memorandum NMFS-NE 116. pp.151-59. [Available from: *http://www.nmfs.gov*].
Waring, G.T., Quintal, J.M. and Swartz, S.L. 2000. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2000. NOAA Technical Memorandum NMFS-NE 162. 303pp. [Available from: *http://www.nmfs.gov*].
Williams, B.K., Nichols, J.D. and Conroy, M.J. 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA. 815pp.

Date received: 8 March 2002.
Date accepted: 22 October 2002.