

Reconciling data on the trends and abundance of North Atlantic humpback whales within a population modelling framework

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ABSTRACT

Populations of humpback whales (*Megaptera novaeangliae*) in the North Atlantic appear to have been increasing at least during the last few decades, following the cessation of substantial hunting almost 100 years ago. Several sources of data are available for these populations (survey and mark-recapture estimates of absolute and relative abundance, estimated catches, and estimates of the proportion of the animals on two feeding grounds that are from the West Indies breeding ground). These data were analysed using an age- and sex-structured population dynamics model that is spatially-explicit to the extent that abundance is tracked on five feeding and two breeding grounds. Several alternative hypotheses, including depensation and changes over time in carrying capacity, were captured within the model framework. Two scenarios form the focus of the analyses, based on alternative interpretations of the size of the breeding population off the Cape Verde Islands. The results of these analyses confirm the increase in the number of humpback whales in the North Atlantic, although it is not possible to determine the extent of such increases. Whether both the West Indies and Cape Verde Islands breeding stocks have increased depends on whether the estimate of abundance for the Cape Verde Islands population of approximately 100 animals is valid. Although many of the data sources can be reconciled given the model applied, some conflicts remain; resolution of these conflicts will require collection of additional data.

KEYWORDS: HUMPBACK WHALES; MODELLING; ATLANTIC OCEAN

INTRODUCTION

In the North Atlantic, the humpback whale (*Megaptera novaeangliae*) ranges from tropical waters north to the Arctic pack ice (e.g. Winn and Reichley, 1985). During winter, the majority of animals congregate in low latitude areas to mate and calve. The principal breeding/calving areas documented in recent times lie on offshore banks and off insular coasts on the Atlantic margins of the West Indies (Winn *et al.*, 1975; Whitehead, 1982; Smith *et al.*, 1999). Historically, humpback whales wintered further south along the Antillean arc through the Windward Islands (Winn *et al.*, 1975; Mitchell and Reeves, 1983; Reeves *et al.*, 2001) and around the Cape Verde Islands (CVI) in the eastern North Atlantic (Braham, 1984; Reeves *et al.*, 2002); they currently occur in low numbers in these regions. In spring, North Atlantic humpback whales migrate to several high-latitude feeding grounds, which they occupy during the summer and autumn (Smith *et al.*, 1999). Feeding grounds are located in the Gulf of Maine, off the eastern Canadian maritime provinces (Canada), along West Greenland, around Iceland (including Jan Mayen), and to the north of Norway (Fig. 1). However, 19th century whaling logbooks and some recent sighting surveys include summer sightings of humpback whales in the mid North Atlantic to the west of and on the Mid-Atlantic ridge, well away from present day known feeding grounds (Reeves *et al.*, 2004)

Humpback whales were apparently reduced to low levels throughout the North Atlantic by intensive hunting during the late 19th and early 20th centuries (Braham, 1984; Mitchell and Reeves, 1983; Winn and Reichley, 1985). Aboriginal subsistence whaling for a small number of humpback whales continued in West Greenland until 1985, the allowance was removed by the International Whaling Commission (IWC) because of uncertainties regarding regional abundance and stock structure (IWC, 1986). On Bequia (an island part of St Vincent and The Grenadines) in

the Windward Islands, a small aboriginal subsistence fishery continues today (IWC, 1994). The humpback whale is listed as 'endangered' by the Convention on International Trade in Endangered Flora and Fauna and as either 'endangered' or 'vulnerable' by various governments and international conservation organisations (Klinowska, 1991).

The reduction in catches led to an increase in population size at least in the western North Atlantic. Capture-recapture data provide the longest time-series of estimates of abundance for this component of the humpback whale population. These data suggest a rate of increase of 0.031 (SE=0.005) per annum over the 14-year period 1979-92 (Stevick *et al.*, 2003b). These estimates are, however, not the only data that relate to the abundance and population dynamics of humpback whales in the North Atlantic; data on relative and absolute abundance are also available for several of the feeding grounds (e.g. Larson and Hammond, 2004) and estimates of the proportion of the animals off Iceland and Norway that breed in the West Indies based on analyses of genetics data are also available (IWC, 2002; 2003).

Assessments of several whale stocks that have been the subject of intensive hunting have been conducted under the auspices of the Scientific Committee of the IWC. In general, these assessments have been based on a limited number of data sources (usually just catches and estimates of absolute abundance from surveys) and simple age-aggregated (e.g. humpback whales in the Southern Hemisphere – Johnston *et al.*, 2001; Johnston and Butterworth, 2002) or age-structured population dynamics models (e.g. bowhead whales in the Bering, Chukchi, and Beaufort Seas – Givens *et al.*, 1995; gray whales off the west coast of North America – Punt *et al.*, 2004). In contrast, there are several data sources for humpback whales in the North Atlantic and considerable uncertainty exists regarding some of the historical catches, the number of breeding grounds (at least two associated with the West Indies and CVI; IWC, 2002), and several feeding

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grounds. Furthermore, some of the data sources (e.g. the estimate of abundance for Iceland, the proportion of animals off Iceland that are not from the West Indies breeding stock, and the estimate of the size of population off the CVI) appear to be in conflict.

This paper attempts to reconcile the various data sources for North Atlantic humpback whales by developing a population dynamics model that is capable of representing several stocks simultaneously and that can include various hypotheses regarding the factors determining the population dynamics of these whales. The values for the parameters of this model are estimated either directly from sampled data or indirectly by fitting it to the available data sources to provide estimates of the pre-exploitation size of the population and how population size has changed over time, regionally and across the entire North Atlantic. The uncertainty associated with these estimates is examined by varying the assumptions of the model and by applying a bootstrap technique to estimate variance.

METHODS

Breeding and feeding grounds

The analyses of this paper assume that there are two breeding grounds (nominally 'West Indies' and 'CVI') and that each breeding ground consists of animals from five feeding grounds (Fig. 1); the possible mid-Atlantic ridge feeding ground (IWC, 2002) is ignored in this paper. Animals from more than one breeding ground may be found on the same feeding ground. The model considers the dynamics of each feeding ground – breeding ground combination (referred to here as a 'stock') separately although density-dependence is assumed to be a function of the total number of animals on a feeding ground. Some of these combinations may, of course, have no animals. Animals from the West Indies breeding ground are found on all five feeding grounds while animals from the CVI breeding ground have only been identified so far on the Norway and Iceland feeding grounds. There are therefore seven non-zero 'stocks' in the analyses of this paper.

Data available for assessment purposes

Catch data

Humpback whales have been taken in the North Atlantic since the 1600s in several fisheries operating throughout the area. Reeves and Smith (2002) describe the available

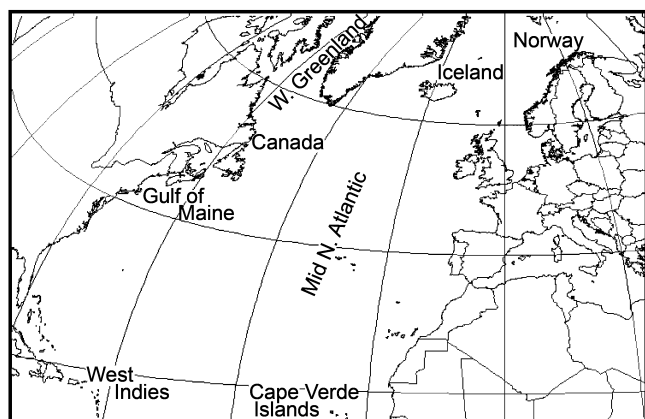


Fig. 1. Approximate location of five known present day feeding grounds (Gulf of Maine, Canada, W. Greenland, Iceland, and Norway), one possible feeding ground (Mid-N. Atlantic) and two breeding grounds (West Indies and CVI) used by humpback whales in the North Atlantic Ocean.

information on historical catches for each of 27 fisheries or sub-fisheries. While some of these fisheries were directed toward humpback whales, most targeted a wide range of baleen and toothed whales. Humpback whales were often not the first choice in these fisheries, but became increasingly targeted as the abundance of the more lucrative species declined and as catching technology improved.

Descriptions of humpback whale fishing operations have been published in a wide range of sources, and approximate locations and periods of operations for each fishery are generally known. Information on catches and landings ranges from: (1) detailed statistics for each animal reported to the Bureau of International Whaling Statistics in the 20th century; (2) to summary descriptions of commercial products shipped in various national and fishermen's reporting records; (3) to tabulations of landings from individual voyages in the 19th century; and (4) to irregular summaries and lists prepared for various reasons for earlier periods. These data were assembled by Smith and Reeves (2003b) into catches by feeding and breeding ground, separately for calves, non-calf females and non-calf males (Fig. 2).

The catches in Fig. 2 are known to be uncertain, so the sensitivity of the results from the model to this uncertainty is explored by considering scenarios regarding upper bounds for the historical catches. These scenarios are based on the sources of uncertainty identified by Smith and Reeves (2002; 2003a; b). None of the scenarios adjust the post-1880 catches because there is no evidence of deliberate misreporting or under-reporting for that period in the North Atlantic; however some of the catches in the early years (1880-1920) were unspecified to species and therefore the humpback whale component had to be estimated by proration.

Scenario A. This scenario considers the uncertainty introduced when it was necessary to interpolate annual landings between years because of incomplete data series. This involved replacing the baseline estimates of such catches by the highest levels reported for the surrounding years (see fig. 2 of Smith and Reeves, 2002), as this placed a reasonable upper bound on these catches.

Scenario B. This scenario considers the uncertainty associated with the estimated landings for the American non-mechanised pelagic fishery. These landings were based on reported whale oil returns (in barrels), assuming an average number of barrels from each whale, or were based on the average number of humpback whales landed per voyage. The catches by this fishery were set to upper bounds by increasing the annual landings estimates by twice the standard error of the estimates for the West Indies and the CVI sub-fisheries for the years 1865-86 (see table 4 of Smith and Reeves, 2003a).

Scenario C. This scenario considers the uncertainty associated with accounting for the numbers struck but lost. The loss factor for mechanised whaling was estimated to be 1.02 from detailed daily data from two North Pacific shore stations (Smith and Reeves, 2002). Here, a somewhat higher rate (1.06) based on fewer data from a North Atlantic land station is considered. For the American non-mechanised pelagic fishery, Smith and Reeves (2003a; b) followed Mitchell and Reeves (1983) by using a struck but lost correction factor of 1.85, or a proportion of struck animals landed of 0.54. Mitchell and Reeves (1983) developed this correction factor based on the inferred degree of injury. The catches shown in Fig. 2 are based on the assumption that all struck animals were in fact killed. Under this assumption, the voyage-specific proportions of struck animals that were

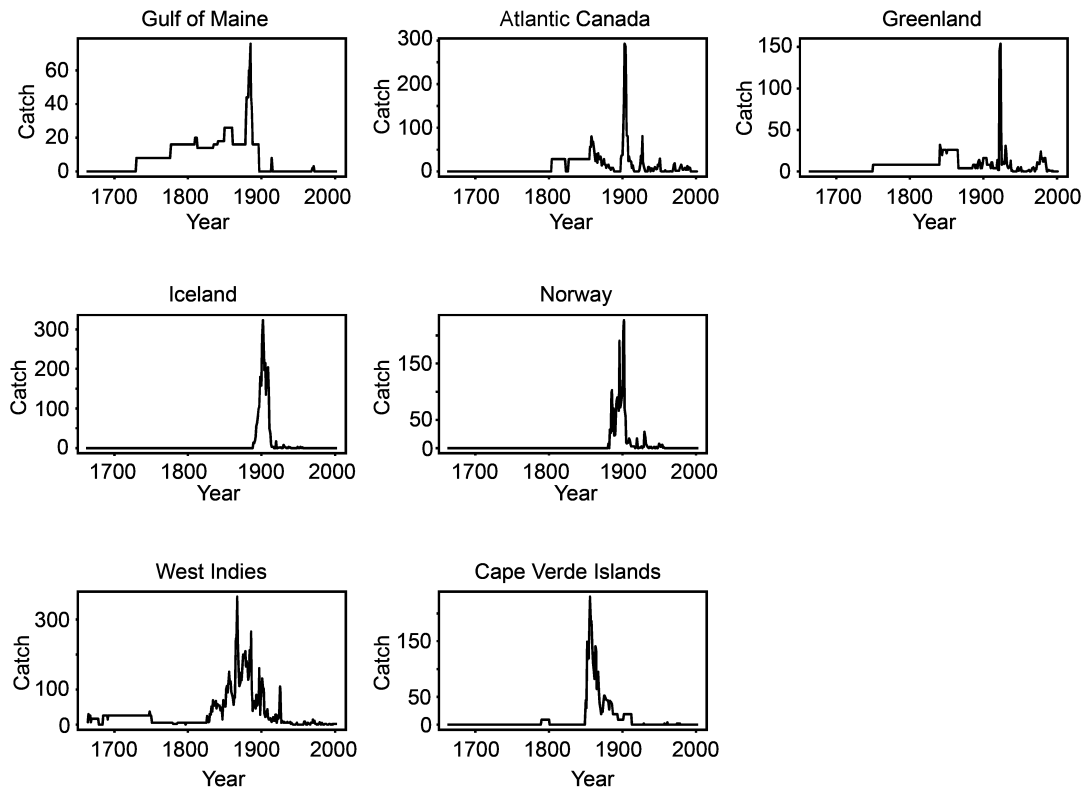


Fig. 2. The baseline catch series (aggregated over sex) by feeding and breeding ground.

landed ranged from 0.17 to 0.67 (mean 0.49, 95% CI 0.42-0.56). Scenario C is based on the next to smallest observed proportion landed (0.33), noting that the smallest observed proportion is 2.4 standard errors below the mean. This rate implies a proportion that is 62% of that originally used, with the corresponding correction factor now 3.0 (= 1/0.33). The factor of 1.5 for the remaining non-mechanised and transitional fisheries, which was based primarily on anecdotal information, was arbitrarily adjusted downwards by 62% as well.

Scenario D. This scenario accounts for the catches for the years prior to 1850 being based on substantially poorer data than those for the later years. It involves arbitrarily doubling the removals for the years prior to 1850.

Scenario E. This scenario combines the effects of scenarios A-D.

The removals for scenarios A-D were 11% to 46% higher than the baseline removals, and those for the multiple-factor scenario (E), 135% higher (Table 1). Scenarios C and E were used to explore the sensitivity of the model results to uncertainties regarding the estimates of the historical catches.

Table 1

Total removals of North Atlantic humpback whales as estimated by Smith and Reeves (2003a) and as calculated for sensitivity purposes under five scenarios.

Scenario	Total estimated removals (000s)	Increase over baseline	
		Number (000s)	%
Baseline	29		
A	33	4	11
B	33	4	11
C	43	14	46
D	37	8	25
E	69	40	135

Abundance indices and proportion data

Information on absolute and relative abundance is available from surveys and mark-recapture studies. Tables 2 and 3 list, respectively, the estimates of absolute and relative abundance used when estimating the values for the parameters of the model for the baseline analyses. The estimate for the CVI (99 animals; Table 2) was based on data collected during an ongoing study (Jann *et al.*, 2003). Preliminary photographic mark and recapture data for 2003 and 2004 collected around the two easternmost islands in the group (Sal and Boavista) were used to obtain this estimate. The estimate of 99 is the largest of several abundance estimates that could be derived from the available data. It was based on seven animals resighted from 18 and 41 animals sampled during the two years (Beatrice Jann and Frederick Wenzel, pers. comm.). The representativeness of this estimate for the entire breeding ground is unknown, and further studies are underway to evaluate this.

Published abundance estimates which were presented as ranges rather than point estimates with associated estimates of precision (e.g. Whitehead, 1982) or which did not include sufficient information to calculate coefficients of variation (e.g. Balcomb and Nichols, 1982; Winn *et al.*, 1975) are not included in Table 2. Furthermore, the abundance estimates for Newfoundland/Labrador obtained by Hay (1982) and for the Grand Banks obtained by Whitehead and Glass (1985) are not included in Table 2 because they are estimates for a subsection of a feeding area in the model.

Estimates of the proportion of animals off Iceland and Norway from the West Indies breeding stock (0.60, SE=0.050 and 0.13, SE=0.057, respectively) are available from genetics studies (IWC, 2002).

Estimates of the rate of increase for humpback whales in the Gulf of Maine feeding ground are available based on demographic models (e.g. Barlow and Clapham, 1997; Clapham *et al.*, 2003). These estimates were not used, however, because some of the quantities used in their

Table 2

The estimates of absolute abundance for North Atlantic humpback whales used in the baseline analyses of this paper.

Breeding ground		Feeding ground	
Year	Estimate (CV)	Year	Estimate (CV)
West Indies¹		Gulf of Maine²	
1979	7,260 (0.16)	1992	652 (0.29)
1979	6,918 (0.15)	1999	902 (0.41)
1980	9,439 (0.22)	West Greenland³	
1980	8,119 (0.20)	1988	357 (0.16)
1981	7,234 (0.18)	1989	355 (0.12)
1981	9,695 (0.19)	1990	566 (0.42)
1982	8,864 (0.15)	1991	376 (0.19)
1982	7,064 (0.10)	1992	348 (0.12)
1983	7,603 (0.12)	Iceland⁴	
1983	7,309 (0.13)	1995	7,900 (0.22)
1984	9,200 (0.18)	Norway⁵	
1984	9,948 (0.29)	1995	1,210 (0.255)
1985	10,310 (0.31)		
1985	8,100 (0.36)		
1986	11,185 (0.39)		
1986	9,083 (0.36)		
1987	10,297 (0.32)		
1987	11,144 (0.25)		
1988	12,582 (0.25)		
1992	10,752 (0.07)		
Cape Verde Islands⁶			
2001	99 (0.23)		

¹Stevick *et al.* (2003b); ²Clapham *et al.* (2003); ³Larson and Hammond (2004); ⁴Pike *et al.* (2002); ⁵Øien (2003); ⁶calculated based on unpublished mark-recapture data from 2003 and 2004 courtesy of Beatrice Jann and Frederick Wenzel, with assistance of Philip Hammond and Peter Stevick.

Table 3

The estimates of relative abundance for North Atlantic humpback whales on their feeding grounds used in the baseline analyses of this paper.

Year	Estimate (CV)	Year	Estimate
Gulf of Maine¹		Iceland³	
1978	122	1970	0.11
1979	171	1971	0.37
1980	188	1972	0.25
1981	211	1973	0.31
1982	238	1974	0.64
1983	281	1976	0.16
1984	380	1977	0.59
1985	448	1978	0.63
Canada/Newfoundland¹		1979	0.66
1978	3,222	1980	0.54
1979	2,423	1981	0.88
1982	1,903	1982	1.01
West Greenland¹		1983	0.33
1981	183	1984	1.20
1982	239	1985	0.87
Norway²		1986	1.34
1988	1,126	1987	1.93
1989	698	1988	1.83

¹Katona and Beard (1990); ²Øien (2003); ³Sigurjónsson and Gunnlaugsson (1990).

calculation such as age-specific survival rates and the fraction mature at age were also used when fitting the population dynamics model.

Model formulation

The population dynamics model (Appendix A) is density-dependent, age- and sex-structured, and allows for multiple feeding and breeding grounds. Apart from the ability to deal with spatial structure, this model also generalises the model used conventionally as the basis for assessments of baleen whale populations by the IWC Scientific Committee (BALEEN II; de la Mare, 1989; Punt, 1999) by allowing:

- density-dependence (which is assumed to impact fecundity/infant survival, and to be functionally related to the size of the 1+ component of the population) to be governed by either a Pella-Tomlinson or a Ricker-like function (Equations A.2a and A.2b);
- depensation to occur at low population size if density-dependence is governed by a Ricker-like function (Equation A.2b);
- carrying capacity to vary over time (the scenarios considered in this paper assume a linear change in carrying capacity which started in 1910); and
- the values for the resilience parameter and for the extent of change in carrying capacity to depend on feeding ground or be independent of feeding ground.

Another difference between the population dynamics model in Appendix A and the BALEEN II model is that the population is not divided into 'recruited' and 'unrecruited' components. However, given the assumption of uniform selectivity on animals aged one and older on which this paper is based, this difference has no impact on the results because the two treatments of recruitment are identical.

Several other variants of the population dynamics model were examined on an exploratory basis (e.g. allowing a time-lag in the density-dependence term, allowing density-dependence to depend on stock or breeding ground rather than on feeding ground, allowing for density-dependent movement between feeding and breeding grounds, and allowing for 'inertial dynamics' (Witting, 2003)). The results of these variants either showed little difference from those presented, or suggested that the factor considered led to much poorer fits, so results for these exploratory analyses are not presented here.

Parameter estimation

The parameters of the population dynamics model can be divided into those whose values are estimable directly from data and those whose values are determined by maximising the likelihood function (see Appendix B for the contributions of the various data sources to the negative of the logarithm of the likelihood function and Table 4 for a full list of the parameters of the population dynamics model).

Table 4

The estimable parameters of the population dynamics model for the model variant which estimates the greatest number of parameters. The number of parameters is based on seven stocks.

Symbol	Description	No. parameters
$K_{1664}^{j,1+}$	Carrying capacity of stock j in 1664	7
$K_{2001}^{j,1+} / K_{1910}^{j,1+}$	Change in carrying capacity for stock j from 1910-2001*	5
A^j	Resilience parameter for stock j *	5
β	Extent of depensation	1
Total		18

*Same for all stocks in each feeding ground.

Table 5 lists the values for the parameters that are determined from information not included in the likelihood function. Two sets of estimates for the proportion of females by age that have reached parturition are listed in Table 5. Both sets of estimates are based on the ratio of known-age (and frequently observed) females in the Gulf of Maine feeding ground that are known to have given birth prior to the age concerned. One set of estimates is based on a period

(1979-92) when the humpback population in the Gulf of Maine was increasing rapidly while the other data set is based on a longer period (1979-2004). Most of the analyses of this paper are based on the larger data set, but sensitivity is explored using the smaller data set. This is because the estimates based on the longer period may reflect the consequences of the Gulf of Maine component of the population starting to approach its (current) carrying capacity.

Table 5

Values for model parameters that are fixed based on auxiliary information.

Age	Survival, S_a^1	Fraction 'mature', M_a^2	
		1979-92 ($n=19$)	1979-2004 ($n=53$)
0	0.875	0	0
1	0.96	0	0
2	0.96	0	0
3	0.96	0	0
4	0.96	0	0
5	0.96	0.29	0.14
6	0.96	0.67	0.29
7	0.96	0.88	0.45
8	0.96	1	0.52
9	0.96	1	0.70
10	0.96	1	0.71
11	0.96	1	0.71
12	0.96	1	0.83
13+	0.96	1	1

¹Barlow and Clapham (1997); ²Jooke Robbins (Center for Coastal Studies, Provincetown, MA 02657, pers. comm.).

Alternative models, model selection and variance estimation

A large number of alternative models could be developed given the model structure (e.g. should carrying capacity change over time? if so how? and how should the change be expressed spatially?) and data set choices (e.g. should all of the data be used or only subsets?).

No attempt was made to conduct an exhaustive evaluation of all combinations of model structure and data set choice. Instead, two key data-related scenarios were constructed based on hypotheses concerning stock structure and each of these scenarios was analysed using 18 alternative models (see Table 6). These two scenarios arise from the conflict between the data on the proportion of the animals at the Iceland and Norway feeding grounds that breed in the West Indies and the estimates of absolute abundance for Iceland, Norway and the CVI. These data can (potentially) be reconciled by: (a) ignoring the CVI estimate of abundance when fitting the model (abbreviation 'No CVI Est'); and (b) ignoring the information on the proportion of animals at the Iceland and Norway feeding grounds that are from the West Indies breeding stock (abbreviation 'No Proportions').

The first data scenario captures the possibility that either there are breeding grounds in the North Atlantic additional to those in the West Indies and the CVI, or that the estimate of abundance for the CVI is severely negatively biased. The second data scenario captures the possibility that the proportion data are biased and/or imprecise because of spatially or seasonally unrepresentative sampling. For example, there are no genetic samples for the CVI breeding ground so the genetic make-up of this breeding ground had to be inferred from samples taken off Norway.

Model selection was conducted separately for the two data scenarios. This involved first fitting each model and checking the results for biological realism and then using AIC_c (Burnham and Anderson, 2002) to select among the remaining models. AIC_c is more appropriate than AIC in this

case owing to the low ratio of parameters to data points for some of the models. Note, however, that use of AIC_c is not truly valid because of the inclusion of a penalty on the extent of inter-feeding ground variability in the value of the resilience parameter (see Equation B.3).

A parametric bootstrap approach was used to quantify the uncertainty associated with the estimates of the model parameters. Each of the 500 bootstrap replicate data sets involved adding noise to the actual survey and proportion data based on either the pre-specified coefficients of variation (absolute abundance estimates), pre-specified standard deviations (proportion data), or estimated residual standard deviations (relative abundance indices). It was not possible to determine that all of the bootstrap replicates converged to the true minimum of the negative log-likelihood function. As each bootstrap replicate was started from the point estimates of the parameters corresponding to minimum of the negative log-likelihood based on the fit to the actual data, any convergence to a local minimum will tend to lead to the bootstrap procedure underestimating the actual extent of uncertainty.

RESULTS

Selection of the baseline model

Table 6 compares the 18 models for the two data-related scenarios using AIC_c . The model with the lowest AIC_c for the 'No CVI Est' scenario is the one in which density-dependence is governed by the Ricker-like function, K varies among stocks, the resilience parameter is the same for all stocks, there is no depensation, and carrying capacity changed after 1910 (but to the same extent for all stocks). This model achieved an AIC_c that was only slightly smaller than that for the model with the same specifications except that carrying capacity was independent of time. The fits of these two models differ by 3.7 log-likelihood units, but the penalty imposed by AIC_c on the ratio of the number of parameters to data points makes this difference less consequential than would AIC. The model with the lowest AIC_c for the 'No Proportions' scenario is that in which density-dependence is governed by the Ricker-like function, K varies among stocks, the resilience parameter is the same for all stocks, there is no depensation, and carrying capacity is time-invariant.

The models with the lowest AIC_c values differ from those corresponding to the lowest negative log-likelihoods (see the models indicated by asterisks in Table 6) because the improvement in fit gained by adding additional parameters is not warranted given the large number of parameters involved. These models consequently have a very large AIC_c .

Figs 3 and 4 show the fits of the two models with the lowest AIC_c values to the absolute and relative abundance indices. The vertical bars in Figs 3 and 4 are 95% confidence intervals for the data (the estimated residual standard deviations are used to compute the confidence intervals for the relative abundance indices).

The model is consistent with the estimates of absolute abundance for both data scenarios, although the results for the 'No CVI Est' scenario mimic the observed trend in abundance in the Gulf of Maine and in the West Indies better than those for 'No Proportions' scenario. However, the model-predicted rate of increase for the West Indies breeding ground over 1979-92 for the 'No CVI Est' scenario is only 1.2% per annum rather than the 3.1% per annum implied by the raw data, even though carrying capacity is estimated to have increased by almost 200% since 1910.

Table 6

Comparison among models based on AIC_c . The models with the lowest AIC_c for each data scenario are indicated using bold-underline typeface, and the models with the lowest negative log-likelihoods are indicated by asterisks. The column '# pars' lists the number of parameters (those of the population dynamics model as well as the q_s and σ_s for the relative abundance indices).

Density-dependence function	Area-specific A	Depensation	# pars	No CVI Est		No Proportions	
				AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
Constant carrying capacity							
Pella-Tomlinson	-	-	16	50.94	3.29	68.61	12.96
Pella-Tomlinson	Yes	-	20	77.48	29.83	96.56	40.91
Ricker-like	-	-	16	47.85	0.21	<u>55.65</u>	<u>0.00</u>
Ricker-like	Yes	-	20	74.22	26.57	84.18	28.53
Ricker-like	Yes	Yes	21	84.34	36.69	96.26	40.61
Ricker-like	-	Yes	17	52.95	5.30	60.92	5.27
Changing carrying capacity – area specific							
Pella-Tomlinson	-	-	21	67.34	19.69	78.43	22.78
Pella-Tomlinson	Yes	-	25	149.94*	102.29	187.15*	131.50
Ricker-like	-	-	21	67.60	19.95	93.23	37.57
Ricker-like	Yes	-	25	150.25	102.60	201.96	146.31
Ricker-like	Yes	Yes	26	196.69	149.05	274.46	218.81
Ricker-like	-	Yes	22	80.50	32.85	108.75	53.10
Changing carrying capacity – same change over all feeding grounds							
Pella-Tomlinson	-	-	17	55.92	8.27	67.09	11.44
Pella-Tomlinson	Yes	-	21	86.73	39.09	103.25	47.60
Ricker-like	-	-	17	<u>47.65</u>	<u>0.00</u>	59.48	3.83
Ricker-like	Yes	-	21	77.62	29.97	93.14	37.49
Ricker-like	Yes	Yes	22	81.45	33.81	108.62	52.96
Ricker-like	-	Yes	18	53.60	5.96	66.09	10.44

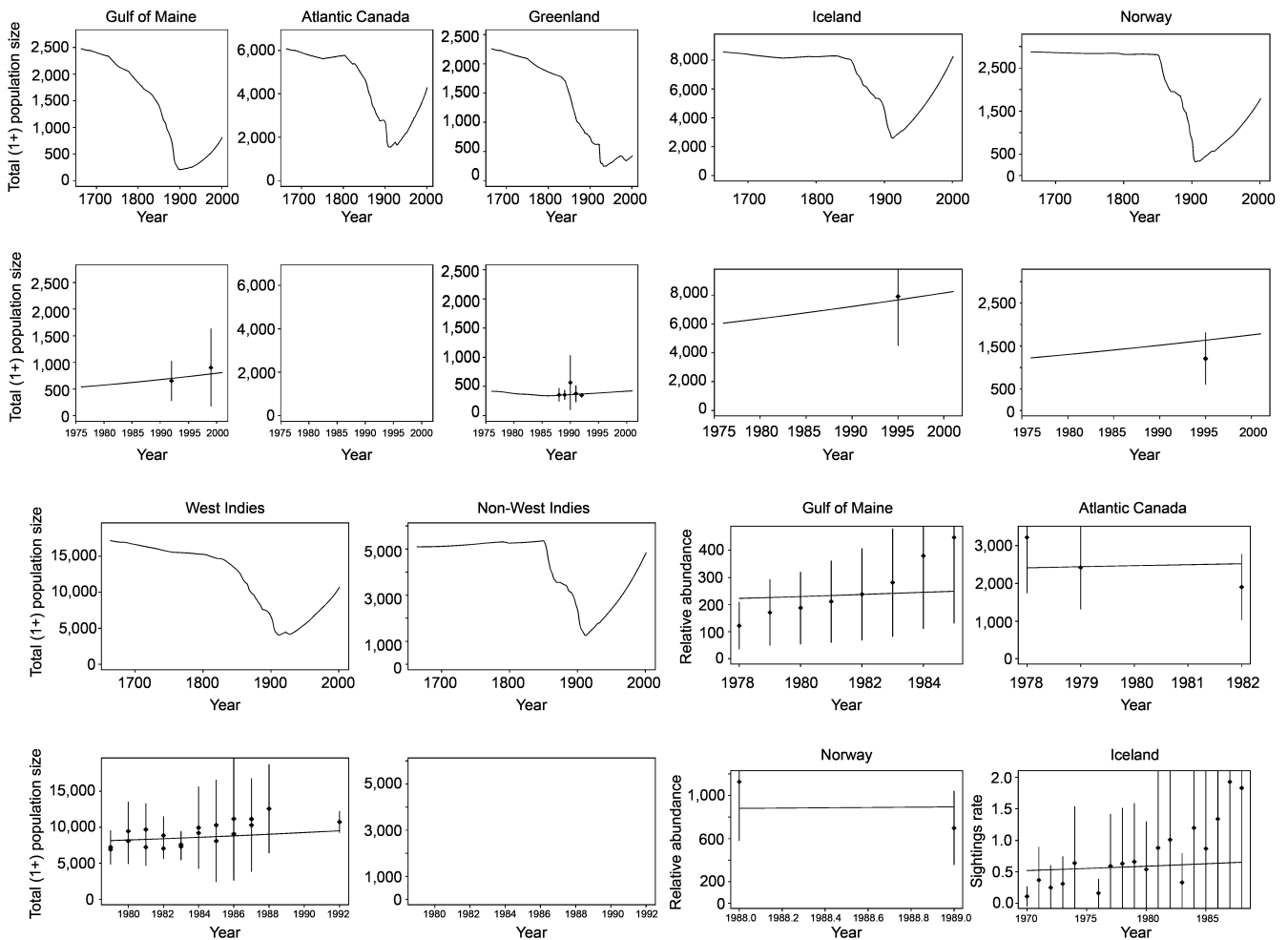


Fig. 3. Summary of the fit of the model with the lowest AIC_c to the 'No CVI Est' data-related scenario.

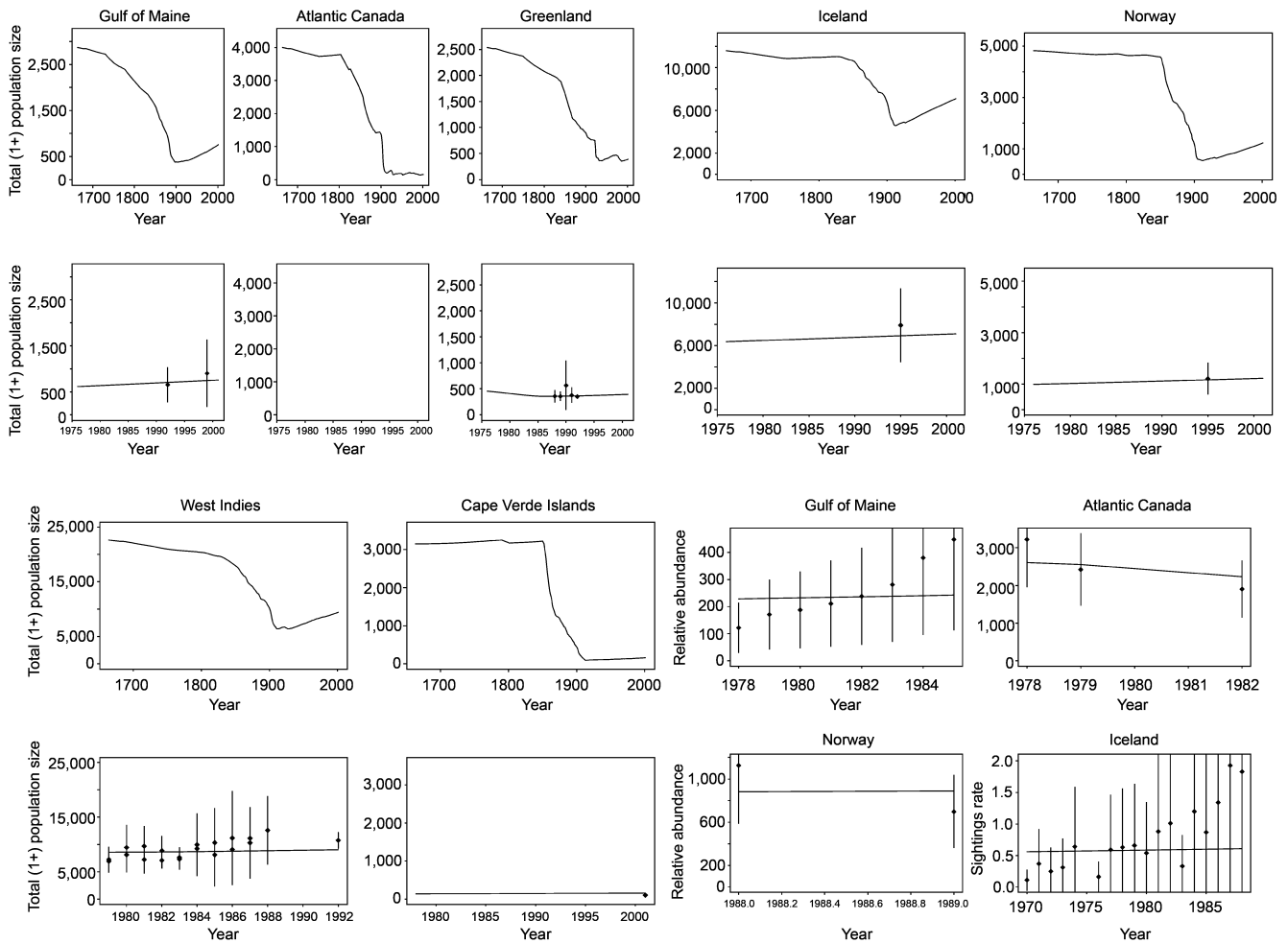


Fig. 4. Summary of the fit of the model with the lowest AIC_c to the ‘No Proportions’ data-related scenario.

Although better fits are possible with larger amounts of change in carrying capacity or by starting the change in carrying capacity more recently, these options were not pursued because the amount of change required in the first case appears biologically unrealistic and because in the latter case there is no information to support such differences. In any case, better fits occur when allowance is made for the carrying capacity for the Norway feeding ground to decline rather than increase over time. The reason for the inability to mimic the trend in the West Indies is primarily that, had the population been as productive as implied by the change over time in the estimates of abundance, it would have recovered to its carrying capacity many years ago.

Neither of the models in Figs 3 and 4 is capable of mimicking the relative abundance indices for the Gulf of Maine and Iceland. It is not really possible to comment on the fit to the relative abundance indices for Atlantic Canada and Norway given the low number of data points involved. The relative abundance indices for the Gulf of Maine are inconsistent with the absolute abundance estimates for the same area and, given that the coefficients of variation for the absolute abundance indices are pre-specified based on the extent of sampling error (Table 2) while the residual standard deviations for the relative abundance indices are estimated when fitting the model, the model chooses to mimic the estimates of absolute abundance.

Neither model is able to mimic the Icelandic relative abundance index based on sightings on whaling grounds to the west of Iceland. It is perhaps noteworthy that the rate at which this index increases from 1970-88 (11.4%) is

consistent with a trend in relative abundance from aerial surveys during 1986-2001 of 11.6% (Gunnlaugsson and Víkingsson, 2002).

The results for the two data-related scenarios differ markedly in terms of predicted abundance and trend. This is most evident for Atlantic Canada (for which there are no estimates of absolute abundance that could be included formally in the analyses) and the CVI. The current abundance for the latter area is close to 5,000 for the ‘No CVI Est’ scenario and only 100 for the ‘No Proportions’ scenario. This is perhaps not unexpected given that the ‘No Proportions’ scenario includes an estimate of absolute abundance of 99 for the CVI breeding ground. One consequence of the lower estimated abundance for the CVI is that almost all of the animals on the Norwegian and Icelandic feeding grounds must be West Indies animals. Given the constraint on the total abundance of the West Indies breeding population implied by the estimates of abundance for the West Indies, it follows that the population off Atlantic Canada must be fairly small.

The low estimates of abundance for Atlantic Canada in recent years from the ‘No Proportions’ scenario (Fig. 4) seem unrealistic given past survey effort in the area (Hay, 1982; Whitehead, 1982; Katona and Beard, 1990; Smith *et al.*, 1999; EC YoNAH, 2001; IWC, 2002). Estimates for sub-regions of Atlantic Canada range from a minimum of 738 (95% CI=235-1242) for eastern Newfoundland and southeastern Labrador from a line-transect survey in 1980 (Hay, 1982) to 3,236 (SE=484) for Newfoundland from a mark-recapture analysis for 1979 (Katona and Beard, 1990). The YoNAH project attempted to provide an overall

Table 7
Results of the sensitivity tests based on modifying some of the assumptions of the model/data set choices.

	West Indies			Non-West Indies			$-\ln L$
	N_{1664}^{1+}	N_{2001}^{1+}	K_{2001}^{1+}	N_{1664}^{1+}	N_{2001}^{1+}	K_{2001}^{1+}	
'No CVI Est' scenario							
Baseline	17,151	10,711	51,298	5,091	4,831	15,227	3.55
Alt Iceland ests	18,134	10,413	54,402	5,990	7,226	17,971	4.21
Alt West Indies ests	17,919	12,707	52,933	5,211	4,826	15,392	3.72
Alt cat-C	24,347	11,059	72,919	6,539	4,802	19,585	2.70
Alt cat-E	39,601	11,023	117,061	7,760	4,717	22,939	3.00
Alt rates	17,188	10,745	51,359	5,083	4,841	15,187	3.54
No rel abund	17,658	10,582	52,603	5,255	4,748	15,653	9.32
Alt Baseline							
Alt Iceland ests	17,965	9,627		5,519	4,306		6.21
Alt West Indies ests	19,643	9,355		6,886	6,215		7.45
Alt cat-C	18,872	11,384		5,656	4,406		6.58
Alt cat-E	24,772	10,030		6,794	4,366		4.95
Alt rates	39,034	10,383		7,737	4,365		4.53
No rel abund	18,155	9,636		5,557	4,296		6.18
	17,802	9,632		5,532	4,511		11.29
'No Proportions' scenario							
Baseline	22,647	9,444		3,152	160		9.36
Alt Iceland ests	21,185	9,645		3,067	173		12.17
Alt West Indies ests	25,199	11,100		3,203	147		9.06
Alt cat-C	37,036	9,136		5,521	217		14.56
Alt cat-E	56,082	9,251		7,485	225		14.54
Alt rates	20,133	9,746		2,985	186		9.72
No rel abund	23,766	9,360		3,178	149		14.14

estimate for Atlantic Canada, but found that sampling was highly variable spatially, not all areas of known concentration were sampled, and sampling intensity in sub-regions was variable relative to known prior densities. Stratifying the data into three regions within which effort was more consistent resulted in an estimate of 2,509 (CV=0.077), but the method of estimation ignored movement of individuals among strata. This estimate is also thought to suffer from significant negative bias due to spatial heterogeneity in sampling (EC YoNAH, 2001; IWC, 2002). Therefore, although the two data scenarios are examined further to capture uncertainty, the weight of qualitative evidence supports the 'No CVI Est' scenario.

Bootstrap quantification of uncertainty

Figs 5 and 6 show bootstrap median and 90% confidence intervals for 1+ population size by breeding ground (Fig. 5) and feeding ground (Fig. 6) for the two data-related scenarios. The model for each data-related scenario is that with the lowest AIC_c in Table 6. The estimates of 1+ population size for the West Indies breeding ground are precise in recent years, as are the estimates of population size for the CVI (non-West Indies) breeding ground for the 'No proportions' data scenario. This is perhaps not very surprising given that estimates of absolute abundance are available for these years. The estimates of population size are least precise for the Atlantic Canada feeding ground because there are no estimates of absolute abundance for this feeding ground, and its abundance is determined essentially by the difference between the number of whales estimated to be on the Gulf of Maine, West Greenland, Iceland and Norway feeding grounds and the total abundance of both breeding stocks.

Figs 7 and 8 show bootstrap median and 90% confidence intervals for 1+ population size for the four feeding grounds for which absolute abundance estimates are available and

for the West Indies breeding ground since 1970, along with the data points used to estimate the values for the model parameters. The results in Figs 7 and 8 confirm that the models are broadly comparable with the data used for fitting purposes. The results are, however, suggestive of an inability of the 'No Proportions' scenario to mimic the estimate of abundance for Iceland.

Sensitivity analyses

Table 7 lists the point estimates of population size by breeding stock in 1664 and 2001 for the models with the lowest AIC_c values (the baseline models) and for an alternate baseline model (time invariant carrying capacity) for the 'No CVI Est' data scenario ('Alt Baseline' in Table 7). An 'alternative baseline' model is considered in Table 7 because the baseline model does not provide a fit that is markedly better than this model. This table also lists the current (2001) carrying capacity for the baseline model for the data-related scenario in which the estimate of abundance for the CVI is ignored. Table 7 lists these quantities for a number of sensitivity tests.

- Alternative estimates of abundance for the Iceland feeding ground. The estimate of abundance for the Iceland feeding ground used in the baseline analyses (7,900) was selected by the Scientific Committee of the IWC. Alternative estimates of the abundance for the Iceland feeding ground exist (1995 – 22,305 (CV=0.59); 2001 – 14,259 (CV=0.50); Burt *et al.*, 2003) based on the NASS 95 and NASS 2001 surveys. This sensitivity test (abbreviation 'Alt Iceland ests') involves replacing the 7,900 estimate by these two estimates.
- Increased estimates of abundance for the West Indies. Stevick *et al.* (2003a) found that migration timing is influenced by feeding ground origin with animals from Greenland, Iceland, and Norway having later mean sighting dates in the West Indies. This raises the

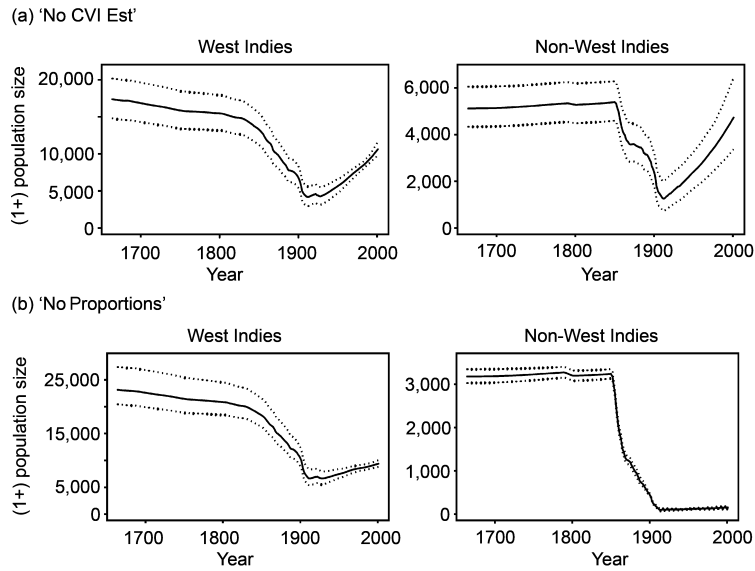


Fig. 5. Bootstrap median and 90% confidence intervals for the total (1+) population size by breeding ground.

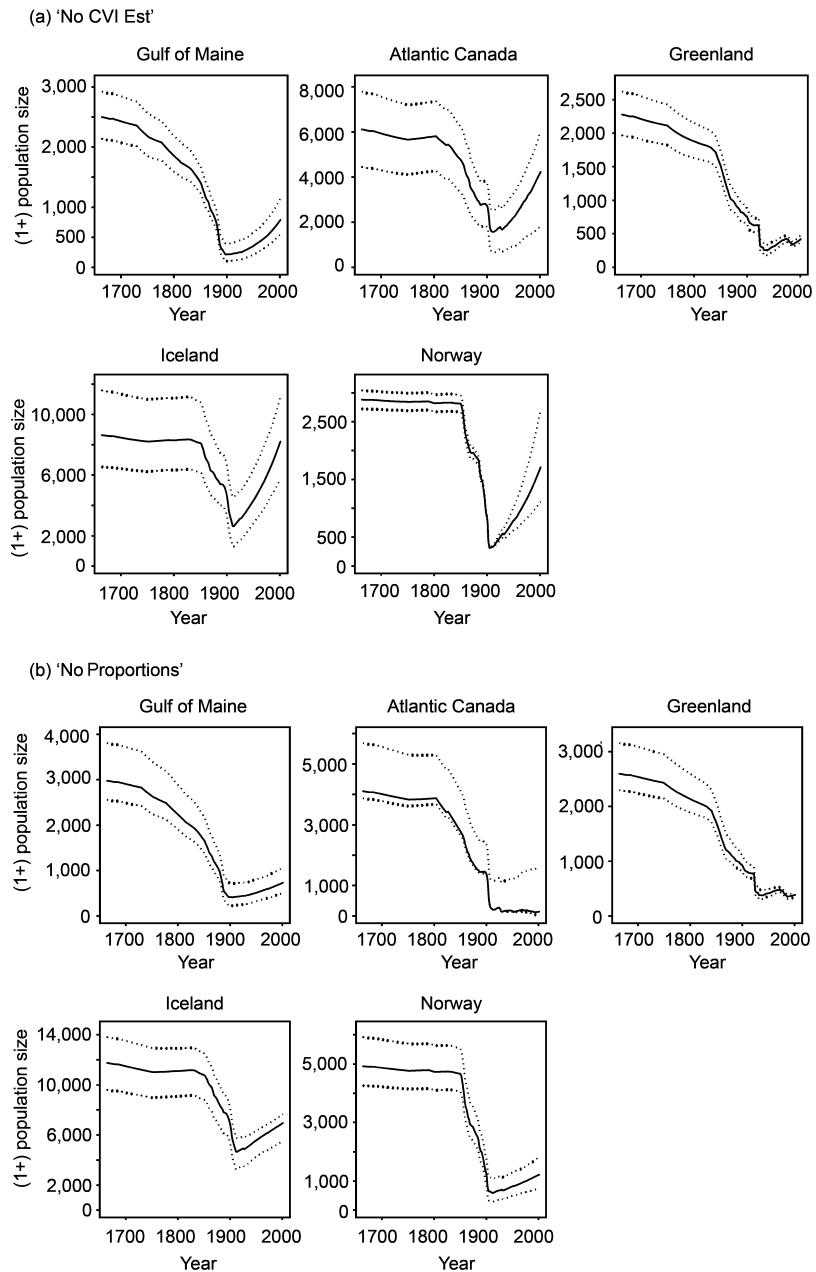


Fig. 6. Bootstrap median and 90% confidence intervals for the total (1+) population size by feeding ground.

possibility that animals from Iceland and Norway have a lower probability of capture in the West Indies because of a later arrival date and a zero probability of capture on the feeding grounds since these areas were not included in Stevick *et al.*'s (2003b) West Indies estimates. This possible heterogeneity in sampling probability would cause a negative bias in the West Indies abundance estimates. This sensitivity test (abbreviation 'Alt West Indies ests') involves increasing the estimates of abundance for the West Indies by 20%.

- (C) Alternative catch series. These sensitivity tests (abbreviations 'Alt cat-C' and 'Alt cat-E') involve replacing the baseline catch series (Fig. 2) by catch series C and E.
- (D) Alternative reproductive rates. This sensitivity test (abbreviation 'Alt rates') involves replacing the values for the age-specific proportion of females that have reached parturition by those based on the data collected during 1979-92 (Table 5).
- (E) Ignoring the relative abundance data. This sensitivity test (abbreviation 'No rel abund') involves dropping all of the relative abundance indices from the analysis and using only the absolute abundance and proportion data. The rationale for considering this sensitivity test is that the indices for the Gulf of Maine and those for Iceland are clearly in conflict with the remaining data.

Sensitivity is not explored to survival rates for animals age one and older because the estimate of 0.96 derived for the Gulf of Maine is virtually identical to that obtained by Larsen and Hammond (2004) for West Greenland (0.957, SE=0.028).

For the 'No CVI Est' scenario, replacing the abundance estimate of 7,900 for the Iceland feeding ground by the two alternative estimates (sensitivity test 'Alt Iceland ests' in Table 7) has relatively little impact on estimates of the size of the West Indies breeding stock, but does lead to an increase in the number of animals in the Iceland feeding ground, which in turn leads to an increase in the size of the non-West Indies breeding stock. It also leads to a reduction in the number of animals estimated to occur off Atlantic Canada (current abundance of 388 compared to 4,278 for the baseline analysis). In contrast to the situation for the 'No CVI Est' scenario, replacing the estimate of abundance for the Iceland feeding ground barely impacts the results for 'No Proportions' scenario'; the fit to the data simply deteriorates.

Increasing the abundance estimates for the West Indies by 20% (sensitivity test 'Alt West Indies ests' in Table 7) leads, as expected, to larger estimates of the pre-exploitation size and (particularly) the current size of the population. However, only for the 'No Proportions' scenario is the fit of the model to the data improved if the estimates of abundance are negatively biased by 20%.

The impact of increasing the historical catches (sensitivity tests 'Alt cat-C' and 'Alt cat-E' in Table 7) is, as expected, an increase to the pre-exploitation population size. Interestingly, the fit to the data (as quantified by the value of the negative log-likelihood) for the 'No CVI Est' scenario improves slightly when the historical catches are larger. Replacing the maturity at age estimates and dropping the relative abundance indices has only a small impact on the results.

The two baseline models imply similar pre-whaling abundances, 17,151 versus 22,647 for the West Indies population, and 5,091 and 3,152 for the Non-West Indies

population. However, carrying capacity is estimated to have increased by a factor of roughly three for the baseline model that allows for time-dependent carrying capacity. The estimated present depletion from pre-whaling abundance differs between the West Indies and Non-West Indies populations. In addition, the depletion of the Non-West Indies population is very sensitive to the data scenario, being 0.05 for the 'No Proportions' scenario, but 0.95 and 0.78 for the baseline and alternate baseline models for the 'No CVI Est' scenario. For this scenario, the depletion relative to the current estimates of carrying capacity for the baseline model is 0.21 and 0.32 for the two populations, respectively. The pre-whaling abundances for the two populations together range from 22,000 to 26,000 animals for the two baseline models.

DISCUSSION

The results of the analyses of this paper confirm the increase in the number of humpback whales in the North Atlantic. Whether both the West Indies and CVI breeding stocks have increased depends on whether the estimate of abundance for the CVI of approximately 100 is a valid estimate of the current size of this stock. The West Indies breeding stock is estimated to be approaching, but still well below its historical and current carrying capacities and continued increases in abundance of this stock are likely.

The analyses in this paper are based on a model that is spatially-explicit in that it considers seven 'stocks', two breeding grounds and five feeding grounds. Most of the recent assessments of marine mammal populations (e.g. Givens *et al.*, 1995; Johnston and Butterworth, 2002; Punt *et al.*, 2004) are based on the assumption that the population being assessed is a single homogeneous unit. Johnston *et al.* (2001) account for stock mixing by allocating catches by proration in areas where multiple stocks are found and then conducting assessments for each stock separately using a single-stock assessment technique. This approach will, however, be biased if the abundance of the stocks concerned is not changing at the same rate over time. Spatially-explicit models are the basis for the operating models used to evaluate the performance of variants of the IWC's Revised Management Procedure for the North Atlantic, Southern Hemisphere and North Pacific minke whales (IWC, 1993; 2004), although only in the last case has a population dynamics model been formally fitted to the available data.

A more complex model was necessary to reconcile the data for humpback whales in the North Atlantic because of this species' complex spatial and population structure. It is not clear whether the need for a complicated spatially-structured model reflects the uniqueness of the spatial and population structure of North Atlantic humpback whales or whether there is, as yet, insufficient information for other marine mammal species to determine that similarly complicated models are needed for these species as well. It is possible that models such as those considered in this paper will become the norm for assessments of marine mammal species once there is improved information on movement patterns.

Most of the data sources for North Atlantic humpback whales are broadly consistent once allowance is made for feeding ground differences in such factors as carrying capacity changes since 1910 (Figs 3 and 4). However, some of the data sources are in conflict, as reflected by the selection of two baseline models. Thus, depending on the model, either there are substantially more humpback whales

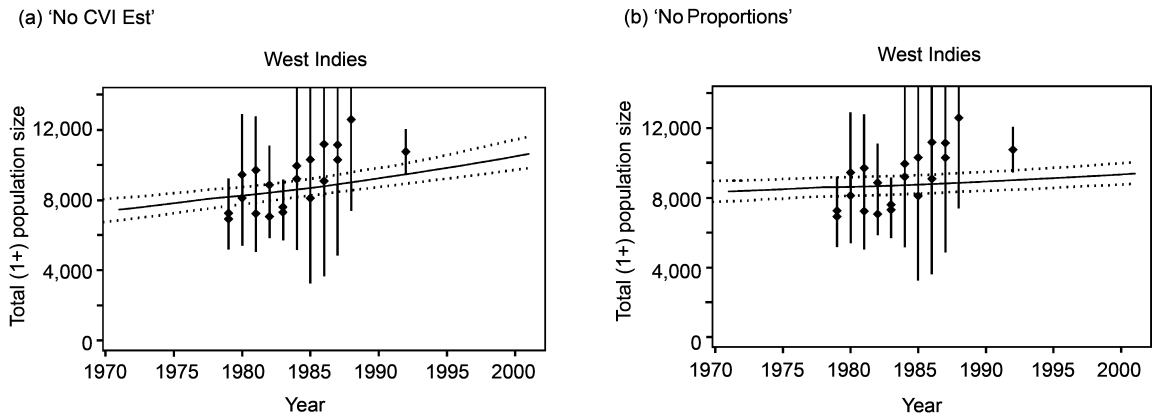


Fig. 7. Bootstrap median and 90% confidence intervals for the total (1+) population size for the West Indies breeding ground (1970-2001) and the data points used when fitting the model.

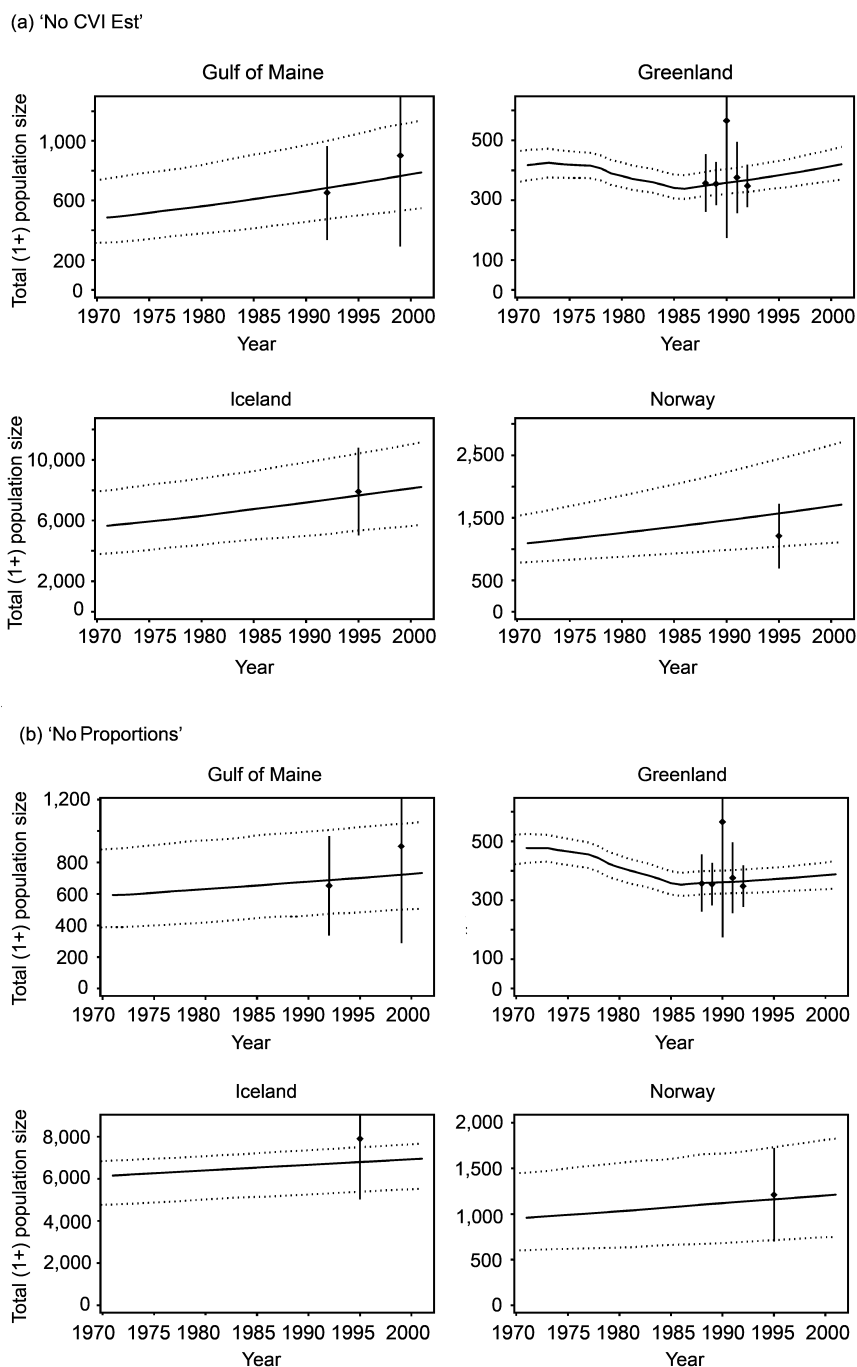


Fig. 8. Bootstrap median and 90% confidence intervals for the total (1+) population size by feeding ground (1970-2001) and the data points used when fitting the model.

using the CVI breeding area or other non-West Indies areas, or more animals that use the eastern North Atlantic feeding grounds also use the West Indies breeding ground than is suggested by the available data. Additional genetics and photographic samples from both the CVI and the eastern North Atlantic would help resolve this uncertainty.

The large differences in the estimated depletion of the CVI population between the two baseline models is related to the time-dependent carrying capacity allowed in the model. The large estimated increase in carrying capacity over the last century implies a much lower degree of depletion for the CVI population from its pre-whaling abundance. The possible causes of such implied ecosystem changes are not clear, although there has been substantial depletion of several whale and fish species in portions of the North Atlantic over the last century. As expected, the pre-whaling abundance estimates for both populations together for the several models considered were below the 'notional upper limit' (present abundance plus total catches; Holt, 2004). For all models considered, including those that explored the upper bounds on estimated catches, total pre-whaling abundance (Table 7) was substantially below the estimate of average abundance over evolutionary time scales of approximately 240,000 reported by Roman and Palumbi (2003) and criticised in IWC (2005, pp.32-4).

Even the best fitting models, however, fail to closely fit some of the data. For example, although the trend in abundance for the West Indies breeding ground is at least partially mimicked, the trend in the relative abundance for the Iceland feeding ground cannot be replicated. One possible explanation for these apparent inconsistencies is that there are more than two populations of humpback whales in the North Atlantic. For example, there may be a third stock of humpback whales in the North Atlantic, perhaps one that migrates between Iceland and Norway, a possibility suggested by winter observations of full term fetuses in northern Norway by Ingebrigtsen (1929) and by winter acoustic observations by Clark (IWC, 2002, p.232). Such a population would be consistent with observations of humpback whales in Icelandic waters throughout the winter (Gisli Víkingsson, pers. comm.). In such a case, the proportion of non-West Indies breeding animals in the Iceland and Norway feeding grounds data used when fitting the model would relate to the CVI breeding population and this putative third stock. From a modelling context, it would then be possible to include the proportion data and the CVI abundance simultaneously in the model. Preliminary explorations of such a model were encouraging, but the fits obtained were not as good as for the two stock model. This is because, although the three-stock model resolves the inconsistency between the estimates for the CVI and the proportion data, it cannot resolve problems such as the inability to mimic the trend in the estimates of abundance for the West Indies breeding ground. Further information on population structure in the eastern North Atlantic may help resolve this uncertainty.

Alternatively, it is possible that the abundance indices from Iceland pertain to only part of the whales using the Iceland feeding area. For instance, the Icelandic index was derived from fishing vessels operating to the west of Iceland, while recent abundance surveys have identified dense and variable aggregations to the north and east. Thus, long term shifts in distribution may have been occurring, perhaps related to fluctuating abundance of prey (Holst *et al.*, 2002). Further examination of the geographic distribution of both the historic catch data and the fisheries sighting data may shed light on this.

ACKNOWLEDGEMENTS

Support for AEP was provided by NOAA/NMFS and the IWC. This research was guided by the sub-committee on the Comprehensive Assessment of North Atlantic Humpback Whales. We would like to express our thanks to the members of that sub-committee and others who supplied suggestions for hypotheses to consider during the modelling. We thank Elizabeth Josephson for assistance with Fig. 1, and Beatrice Jann and Frederick Wenzel for sharing their unpublished data so that this analysis could be completed. Phillip Clapham and an anonymous reviewer are thanked for their comments on an earlier draft of this manuscript. The views expressed herein are those of the authors and do not reflect the views of the National Oceanic and Atmospheric Administration, University of Washington or any of their sub-agencies.

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Date received: July 2005

Date accepted: February 2006

Appendix A : The Population Dynamics Model

Basic dynamics

The dynamics of ‘stock’ j are governed by the equation:

$$N_{y+1,a}^{j,s} = \begin{cases} N_{y+1,0}^{j,s} & \text{if } a = 0 \\ N_{y,0}^{j,s} (1 - \sum_k P_j^k F_y^{F,k,0}) & \\ (1 - \sum_k Q_j^k F_y^{B,k,0}) S_0^j & \text{if } a = 1 \\ N_{y,a-1}^{j,s} (1 - \sum_k P_j^k F_y^{F,k,s,1+}) & \\ (1 - \sum_k Q_j^k F_y^{B,k,s,1+}) S_{a-1}^j & \text{if } 2 \leq a < x \\ (N_{y,x-1}^{j,s} + N_{y,x}^{j,s}) (1 - \sum_k P_j^k F_y^{F,k,s,1+}) & \\ (1 - \sum_k Q_j^k F_y^{B,k,s,1+}) S_x^j & \text{if } a = x \end{cases} \quad (\text{A.1})$$

where

$N_{y,a}^{j,s}$ is the number of animals of sex s and age a in ‘stock’ j at the start of year y ,
 S_a^j is the survival rate (from natural causes) for animals of age a in ‘stock’ j ,
 $F_y^{F,k,0}$ is the exploitation rate on calves on feeding ground k during year y ,
 $F_y^{B,k,0}$ is the exploitation rate on calves on breeding ground k during year y ,
 $F_y^{F,k,s,1+}$ is the exploitation rate on fully-selected animals of sex s on feeding ground k during year y ,
 $F_y^{B,k,s,1+}$ is the exploitation rate on fully-selected animals of sex s on breeding ground k during year y ,
 P_j^k is the proportion of animals from ‘stock’ j that is found on feeding ground k ,
 Q_j^k is the proportion of animals from ‘stock’ j that is found on breeding ground k , and
 x is the oldest considered (treated as a plus-group).

The oldest age, x , is taken to be the 14+ age class because fecundity, the probability of being recruited and the survival rate from natural causes is independent of age for ages greater than thirteen (see Table 5).

Births

The equation that determines the number of calves of sex s born to ‘stock’ j at the start of year y depends on the number of animals of ‘stock’ j that have reached the age-at-first-parturition, the number of animals aged 1 and older on each feeding ground, the form of the stock-recruitment relation (Ricker or Pella-Tomlinson), and whether there is depensation:

$$N_{y,0}^{j,s} = \delta f_0^j \tilde{N}_y^j \begin{cases} \sum_k P_j^k \{1 + A^k [1 - (\bar{N}_y^k / \bar{K}_y^k)^z]\} & (\text{A.2a}) \\ \sum_k P_j^k \exp(\ell n A^k [1 - \beta \bar{N}_y^k / \bar{K}_y^k]) \times \\ \sum_k [1 - \bar{N}_y^k / \bar{K}_y^k] & (\text{A.2b}) \end{cases}$$

where

\tilde{N}_y^j is the number of mature females in ‘stock’ j at the start of year y :

$$\tilde{N}_y^j = \sum_a M_a N_{y,a}^{j,f} \quad (\text{A.3})$$

M_a is the fraction of females of age a that are ‘mature’ (i.e., have reached the age-at-first-parturition),
 f_0^j is the birth rate at pre-exploitation equilibrium for ‘stock’ j ,
 $N_y^{j,1+}$ is the number of 1+ animals in ‘stock’ j at the start of year y :

$$N_y^{j,1+} = \sum_s \sum_{a \geq 1} N_{y,a}^{j,s} \quad (\text{A.4})$$

$K_y^{j,1+}$ is the carrying capacity of ‘stock’ j during year y (in terms of the number of 1+ animals),
 \bar{N}_y^k is the number of 1+ animals on feeding ground k at the start of year y :

$$\bar{N}_y^k = \sum_j P_j^k N_y^{j,1+} \quad (\text{A.5})$$

\bar{K}_y^j is the carrying capacity of feeding ground k during year y (in terms of the number of 1+ animals),

A^j is the ‘resilience’ parameter for ‘stock’ j ,
 δ is the sex ratio at birth (assumed to be 50:50 – Smith *et al.*, 1999),
 β is the parameter that determines the extent of depensation, and
 z is the ‘degree of compensation’ parameter (assumed to be 2.39 for the analyses of this paper).

Catches and exploitation rates

Catches are available for calves and non-calves (by sex) and separately for the feeding and breeding grounds. The exploitation rates during year y for ‘stock’ j are determined using the equations:

$$F_y^{F,k,0} = \frac{C_y^{F,k,0}}{\sum_j P_j^k \sum_s N_{y,0}^{j,s}} \quad (\text{A.6a})$$

$$F_y^{B,k,0} = \frac{C_y^{B,k,0}}{\sum_j Q_j^k \sum_s N_{y,0}^{j,s} (1 - \sum_l P_j^l F_y^{F,l,0})}$$

$$F_y^{F,k,s,1+} = \frac{C_y^{F,k,s,1+}}{\sum_j P_j^k \sum_{a \geq 1} N_{y,a}^{j,s}} \quad (\text{A.6b})$$

$$F_y^{B,k,s,1+} = \frac{C_y^{B,k,s,1+}}{\sum_j Q_j^k \sum_{a \geq 1} N_{y,a}^{j,s} (1 - \sum_l P_j^l F_y^{F,l,s,1+})}$$

where

$C_y^{F,j,0}$ is the catch of calves during year y on feeding ground j ,
 $C_y^{B,j,0}$ is the catch of calves during year y on breeding ground j ,
 $C_y^{F,j,s,1+}$ is the catch of non-calves of sex s during year y on feeding ground j , and
 $C_y^{B,j,s,1+}$ is the catch of non-calves of sex s during year y on breeding ground j .

Initial conditions

The initial conditions (1664) correspond to a population at its pre-exploitation equilibrium size.

Appendix B : The Likelihood Function

Three sources of data (estimates of absolute abundance, relative abundance indices, and estimates of the proportion of the animals on a given feeding ground that are from the West Indies breeding ground) are available to determine the values for the ‘free’ parameters of the model.

Absolute abundance estimates

The contribution of the data for each of the absolute abundance indices to the negative of the logarithm of the likelihood function (ignoring constants) is given by:

$$-\ln L = \sum_y \left\{ \ln \sigma_y^{S,j} + \frac{(\ln S_y^j - \ln \hat{S}_y^j)^2}{2(\sigma_y^{S,j})^2} \right\} \quad (B.1)$$

where

- S_y^j is the (observed) estimate of (1+) abundance for year y and area (a breeding or feeding ground, depending on the index concerned) j ,
- \hat{S}_y^j is the model-estimate of the number of 1+ animals in area j at the start of year y , and
- $\sigma_y^{S,j}$ is the observed standard deviation of S_y^j .

Relative abundance estimates

The contribution of the data for each of the relative abundance indices to the negative of the logarithm of likelihood function is given by:

$$-\ln L = \sum_y \left\{ \ln \sigma^S + \frac{(\ln S_y^j - \ln [q^S \hat{S}_y^j])^2}{2(\sigma^S)^2} \right\} \quad (B.2)$$

where

- S_y^j is the relative abundance index for year y and area j ,
- \hat{S}_y^j is the model-estimate of the number of 1+ animals in area j at the start of year y ,
- q^S is the coefficient that relates the abundance indices to 1+ abundance, and
- σ^S is the standard deviation of S_y^j .

The values for q^S and σ^S are treated as estimable parameters when fitting the model.

Estimates of the fraction of West Indies animals

The estimate of the fraction of West Indies animals on feeding ground j is assumed to be normally distributed about the corresponding model prediction.

Penalty on the resilience parameters

If the resilience parameter is assumed to depend on feeding ground, the following term is added to the objective function minimised to find the values for the model parameters to constrain the extent to which resilience can differ among ‘stocks’/feeding grounds:

$$\frac{1}{2CV_A^2} \sum_j (\ln A^j - \ln \bar{A})^2 \quad (B.3)$$

where

- CV_A is the inter-feeding ground coefficient of variation for the resilience parameter (assumed to be 0.2 for the calculations of this paper), and
- $\ln \bar{A}$ is the average of the $\ln A^j$ s.

