Estimates of the current global population size and historical trajectory for sperm whales

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ABSTRACT: Assessments of sperm whale *Physeter macrocephalus* abundance based on invalid analyses of whaling data are common in the literature. Modern visual surveys have produced population estimates for a total of 24% of the sperm whale's global habitat. I corrected these assessments for whales missed on the track line and then used 3 methods to scale up to a global population. Scaling using habitat area, plots of 19th century catches and primary production produced consistent global population estimates of about 360 000 whales (CV = 0.36). This is approximately 20% of the numbers reproduced in current literature from invalid whaling-based estimates. A population model, based on that used by the International Whaling Commission's Scientific Committee, and which considers uncertainty in population parameters and catch data, was used to estimate population trajectories. Results suggest that pre-whaling numbers were about 1 110 000 whales (95% CI: 672 000 to 1 512 000), and that the population was about 71% (95% CI: 52 to 100%) of its original level in 1880 as open-boat whaling drew to a close and about 32% (95% CI: 19 to 62%) of its original level in 1999, 10 yr after the end of large-scale hunting. Thus, widely held views about the status of sperm whale populations need considerable revision.

KEY WORDS: Sperm whale · *Physeter* · Population · Depletion · Whaling

INTRODUCTION

The sperm whale *Physeter macrocephalus*, the largest of the odontocetes or toothed whales, is a deep diver found over almost all deep (>1000 m) ice-free waters of the globe (Rice 1989). Because of its size, wide distribution, and presumed numbers it is thought to be an important element in mesopelagic ecosystems (e.g. Clarke 1977, Katona & Whitehead 1988). The sperm whale has been the subject of 2 large-scale and economically significant periods of hunting (Starbuck 1878, Tønnessen & Johnsen 1982; Fig. 1). 'Open-boat' whaling for sperm whales which began in 1712, peaked in about 1830, and continued into the 1920s, was one of the foremost industries of the late 18th and early 19th centuries. 'Modern' whalers with engine-powered whaling vessels, harpoon guns and other technological aids, first attacked sperm whales in the early 20th century, although sperm whales were not a major target until the 1950s. Modern sperm whaling was particularly intense during the 1960s after the decline of most baleen whale populations. However, due to the International Whaling Commission's moratorium on commercial whaling and for other reasons, sperm whaling had virtually ended by 1988.

Despite great commercial and scientific interest in the species, there has been no valid population estimate, globally or for any ocean basin. Thus we have no real concept of the effects of the hunts on sperm whale populations.

In the late 1970s and early 1980s the Scientific Committee of the International Whaling Commission, with the hope of better managing exploitation, put considerable effort into assessing sperm whale populations. Initially, the Committee used catch-per-unit-effort methods (e.g. Ohsumi 1980). However, there were many problems when applying these techniques to modern
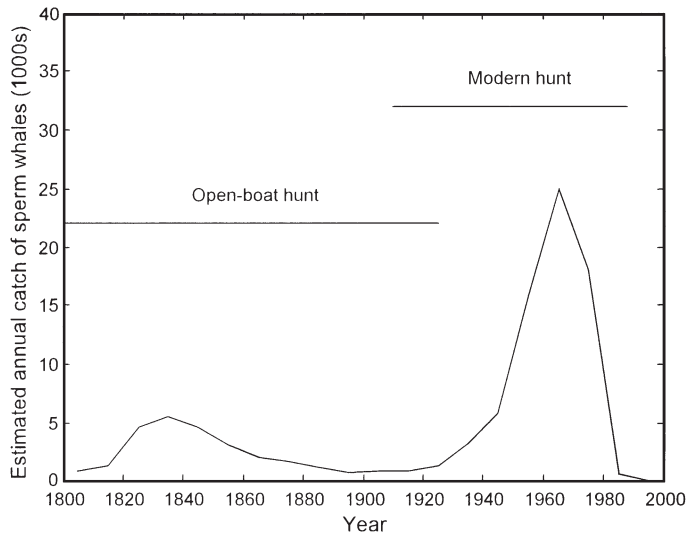
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Fig. 1. *Physeter macrocephalus.* Sperm whale catches from 1800 to 1999 (from Best 1983 and FAO Fisheries Department, Fishery Information, Data and Statistics Unit. FISHSTAT Plus: Universal software for fishery statistical time series. Version 2.3. 2000). The open-boat hunt began in 1712 and catches from it may be under-estimated here (Best 1983)

sperm whaling data, including recruitment and mortality (Cooke 1986), temporal trends in the practice of whaling (Horwood 1980, Smith 1980), whale movements (Cooke 1986), grouping of whales (Allen 1980), multiple-species hunts, and falsification of data (Zemsky et al. 1995). Consequently, assessment of sperm whale populations by catch-per-unit-effort methodology was virtually discontinued in the early 1980's (Tillman & Breiwick 1983).

Attention then turned to complex age-specific, and especially length-specific, techniques (e.g. Cooke & de la Mare 1983), in which changes in length or age distributions indicated the degree of depletion of the stock. Although less problematic than catch-per-unit-effort methods, some difficulties persisted. These included falsified data (Best 1989) and movements of the whales (Cooke 1986, Whitehead 2000). There were also new challenges such as the need for accurate aging (for age-specific methods) or an accurate age-length key (for length-specific methods). After a few years of hard work, it became apparent that these techniques were also unable to give reliable estimates (Cooke 1986), and with the decline of the sperm whaling industry the Scientific Committee of the International Whaling Commission turned their attention elsewhere.

Unfortunately, despite the acknowledgments by those involved in these assessments (e.g. Cooke 1986), invalid estimates of sperm whale populations using catch- per-unit-effort or length-specific methods made their way into reviews of sperm whale biology (e.g. Gosho et al. 1984, Rice 1989). From there, these esti-

mates propagated into more general literature (e.g. Evans 1987, Berta & Sumich 1999, Bowen & Siniff 1999). Reports of current global population sizes of about 1.5 to 2 million whales, constituting 65 to 85% of the original populations, (Evans 1987, Berta & Sumich 1999, Bowen & Siniff 1999) which originated in the catch-per-unit-effort or length-specific methods of the Scientific Committee of the International Whaling Commission are of very questionable validity.

In recent years, the abundance of sperm whale populations have been estimated over scales of less than an ocean basin using 3 principal techniques: mark-recapture techniques applied to photographic identifications (e.g. Childerhouse et al. 1995, Whitehead et al. 1997), acoustic censuses (e.g. Leaper et al. 1992, Davis & Fargion 1996, Barlow & Taylor 1998), and visual censuses from ships or aircraft (Table 1). Although mark-recapture analyses of photoidentifications and acoustic censuses have considerable promise for estimating sperm whale abundance, they have only been used occasionally, and the great majority of reasonably valid sperm whale population estimates come from visual censuses. Visual censuses of cetaceans and other animals pose a number of methodological challenges, but, fortunately, there is a standard and well-developed methodology (Buckland et al. 1993) which is generally used. The principal remaining difficulty with most of the estimates of sperm whale populations is that they have not been corrected for the whales not counted because they were underwater as the censusing ship or aircraft passed. The probability that an animal on the transect line is sighted, referred to as $g(0)$, is usually assumed to be 1. Due to their long dives (Papastavrou et al. 1989, Watkins et al. 2002), this is plainly false for sperm whales.

Here I use available visual censuses for sperm whales, make a correction for $g(0)$, and then extrapolate to a global population estimate. I try to scale up from the areas that have been surveyed to the global sperm whale habitat using 3 alternative assumptions: that sperm whale densities are similar in areas that have and have not been surveyed; that sperm whale density in any area is roughly proportional to the number of whales killed in the area by open-boat whalers (see Whitehead & Jaquet 1996 for a justification of this); or that sperm whale density in any area is roughly proportional to primary productivity. The latter is justified by the transfer of energy up the food chain, so that, over large spatial and temporal scales, regions with higher primary production generally possess more sperm whales (Gulland 1974, Jaquet 1996, Jaquet et al. 1996). This global estimate of current sperm whale abundance is then used, together with other information on the population biology of the whales and estimates of removals by whalers, to pro-

Table 1. *Physeter macrocephalus.* Estimates of sperm whale population size from ship (SS) and aerial (AS) surveys, estimates corrected for $g(0)$ (the proportion of whales on the survey line which are counted), the number of plots on Townsend's (1935) charts in each survey area, and the estimated chlorophyll mass (in tonnes) in the first meter of water over each study area. Study areas are shown in Fig. 2

Area		Uncorrected estimate		Estimate $g(0)$ corrected		Area (1000 km²)	Density: (whales per 1000 km²)	Town-send's plots	Chlorophyll[a] (t in first m)	(whales t⁻¹)	Source
		n	CV	n	CV						
1. Northeast Atlantic	SS	5231	0.3	6013	0.32	1226	4.9	0	–	–	Christensen et al. (1992)
2. Iceland-Faeroes	SS	1542	0.2	1772	0.18	2309	0.77	0	1079	1.64	Gunnlaugsson & Sigurjónsson (1990)
3. US east coast	SS	4702	0.4	5405	0.37	317	17.04	210	212	25.49	National Marine Fisheries Service (2000b)
4. Northern Gulf of Mexico	SS-AS	530	0.3	609	0.32	258	2.36	32	117	5.21	National Marine Fisheries Service (1995)
5. Antarctic (S of 60° S)	SS	10500	0.2	12069	0.17	18548	0.65	0	4258	2.83	International Whaling Commission (2001)
6. Eastern tropical Pacific	SS	22666	0.2	26053	0.24	19148	1.36	5083	3657	7.12	Wade & Gerrodette (1993)
7. Eastern temperate North Pacific	SS	20880	0.5	24000	0.46	7786	3.08	154	912	26.32	Barlow & Taylor (1998)
8. Hawaii	AS	66	0.6	76	0.57	81	0.94	30	6	12.64	National Marine Fisheries Service (2000a)
9. Western North Pacific	SS	25816	0.1	29674	0.14	25681	1.16	1896	4923	6.03	Kato & Miyashita (2000), using only primary sightings
All surveyed areas				105671	0.13	75354	1.40	7405	14085	7.50	
Total globe						316620		21336	54992		

[a] The boundary of the study area for the northeast Atlantic is survey is not available and so the chlorophyll cannot be estimated for this area

duce plausible trajectories of global sperm whale populations since the start of commercial whaling in 1712.

MATERIALS AND METHODS

Estimation of current global sperm whale population size. The 9 estimates of sperm whale population size of which I am aware that result from either ship or aerial visual surveys are listed in Table 1. Estimates superseded by later work with increased sampling effort in the same area or better methodology applied to the same data are excluded. The surveyed areas, which have virtually no overlap, are shown in Fig. 2. Together the surveys cover 75.4×10^6 km², about 24 % of the surface of the ocean which is greater than 1000 m deep and less than 70° latitude (i.e. excluding the frozen Arctic Ocean), primary sperm whale habitat (Rice 1989). All the surveys, except 2 of the smallest, were from ships rather than aircraft.

Most survey assessments did not correct for $g(0)$, the whales missed because they were under water when the surveyors passed. Even where corrections were applied, the uncorrected values are given in the third column of Table 1. Of the surveys which did correct for $g(0)$, the best supported correction is that of Barlow & Taylor (1998), who used a methodology which incorporates the radial distribution of detection distances and the diving behavior of the whales. Thus, I have used their estimate of $g(0) = 0.87$ (CV = 0.09) to correct all the estimates of sperm whale abundance in Table 1. Barlow & Taylor (1998) consider that their estimate of $g(0)$ is not fully justified for their own survey, and it is likely to be even less valid for the other surveys. It is almost certainly too large for the aerial surveys, as the faster travel of the observers will lead to a greater proportion of diving whales being missed, biasing these estimates downwards. However, the aerial surveys only represent 0.1 % of the ocean area covered by the surveys listed in Table 1 and Barlow & Taylor's (1998) estimate of $g(0)$ is the best available. CVs for the $g(0)$-corrected estimates, given in Table 1, were calculated by combining the CV of the uncorrected abundance estimate (Column 4 of Table 1) and the CV of the estimate of $g(0)$:

$$\mathrm{CV}(n_i) = \sqrt{\mathrm{CV}(n_i')^2 + \mathrm{CV}(g(0))^2} \qquad (1)$$

where n_i' is the uncorrected population estimate for area i, and n_i is the corrected population estimate for area i.
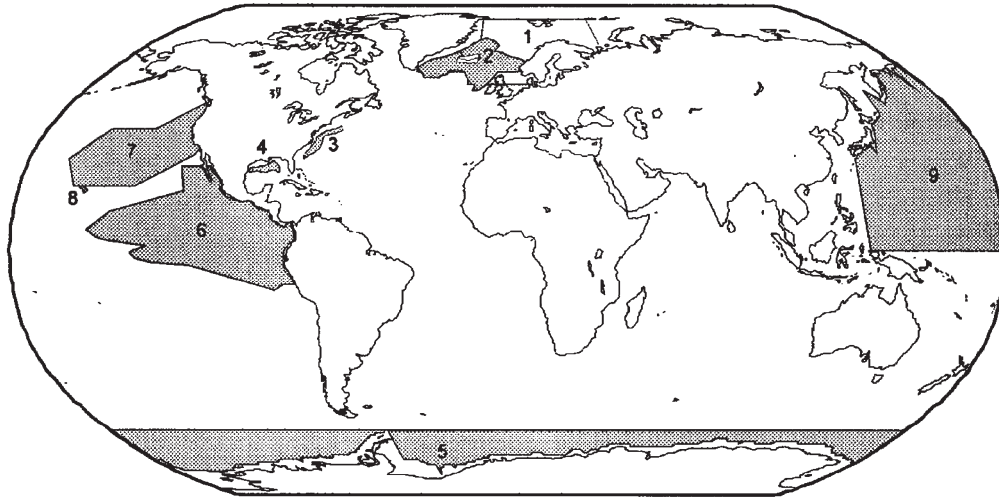
Fig. 2. Study areas for which there is a sperm whale population estimate from ship or aerial surveys (listed in Table 1). The boundary of the survey area in the northeast Atlantic off Norway is not available so its rough location is indicated by a line. Studies are labeled by numbers as in Table 1

Densities (whales per 1000 km^2) could then be calculated for each survey area using the $g(0)$-corrected estimates. An estimate of the population size in all the surveyed areas combined, n_T, was then obtained by summing the $g(0)$-corrected estimates for each survey area:

$$n_T = \sum n_i \qquad (2)$$

The CVs for the corrected population estimates were combined to produce a CV for the estimate for all areas:

$$CV(n_T) = \sqrt{\frac{\sum (CV(n_i)n_i)^2}{\sum n_i}} \qquad (3)$$

This population estimate for the surveyed areas combined was then extrapolated to the global habitat of the sperm whale using 3 techniques:

(1) Scaling by area. In this I assume that the ocean areas (>1000 m deep and <70° N) not covered by the surveys have the same average density of sperm whales as those that were surveyed.

(2) Scaling by catches marked in Townsend's (1935) charts of the positions in which 19th century US whalers made their kills of sperm whales. This assumes that the current density of sperm whales in any area is proportional to the number of days on which catches were made in any area as represented on the charts. Whitehead & Jaquet's (1996) simulations suggest that this should be approximately true. The total number of sperm whale plots on Townsend's (1935) charts, 21 336, is from Best (1983).

(3) Scaling by primary productivity. Sperm whale abundance seems related, over broad scales, to primary productivity (Jaquet et al. 1996). The estimated surface chlorophyll (tonnes per meter depth) was calculated for each of the study areas and for all the oceans suitable for sperm whales (>1000 m deep, and south of 70° N) using estimates of chlorophyll mass at the surface per meter depth by NOAA (www.nodc.noaa.gov/ocs/data_woa.html).

Global estimates of sperm whale populations were then:

$$N = n_T \frac{X}{\sum x_i} \qquad (4)$$

where x_i is the amount of the scaling factor (area, plots on Townsend's charts, or chlorophyll) in survey area i, and X is the amount in all sperm whale habitat. Coefficients of variation for N were calculated from:

$$CV(N) = \sqrt{CV(n_T)^2 + CV(n_i/x_i)^2} \qquad (5)$$

No coefficient of variation for N could be calculated for extrapolation method (2), as some of the survey areas at high latitudes had no plots on Townsend's charts. Thus, $x_i = 0$ and $n_i/x_i = \infty$, rendering $CV(n_i/x_i)$ meaningless.

Population trajectory. A simple population model, based on the approach used by the Scientific Committee of the International Whaling Commission (International Whaling Commission 1982), was used to examine possible trajectories of the global sperm whale population following the start of commercial whaling in 1712.

The model considers 2 areas, the Atlantic and Pacific/Indian Oceans, between which there is assumed to be little interchange. This seems to be true for females, although possibly not for all males (Lyrholm et al.

1999). This division is made because commercial sperm whaling started in the Atlantic about 85 yr before it progressed into the other 2 oceans but the profile of exploitation was likely quite similar in the Pacific and Indian Oceans (Wray & Martin 1983).

There are usable catch data available from 1800 to 1999 (Fig. 1), although these may be biased downwards in some cases (Best 1983, Zemsky et al. 1995). However, there is a gap between 1712, when commercial sperm whaling started in the Atlantic, and 1800, when hunting was beginning to move into the Pacific and Indian Oceans.

In year y, let $n(A,y)$ be the population of sperm whales in the Atlantic Ocean, and $n(P,y)$ the population in the Pacific and Indian Oceans, so that $n(.,y)$ is the global population [$n(.,y) = n(A,y) + n(P,y)$]. If p_A is the proportion of the global sperm whale population in the Atlantic before whaling, q_A gives the relative depletion of Atlantic population in 1800, $c(y)$ is the reported global catch of sperm whales in year y (as in Fig. 1), and $d(y) \times c(y)$ the actual catch (so that d corrects for underreporting), then:

$$n(A, 1800) = p_A \times (1 - q_A) \times n(.,1712)$$
$$n(P, 1800) = (1 - p_A) \times n(.,1712)$$
(6)

and for $y > 1800$:

$$n(A,y) = \left[N(A,y-1) - d(y) \times c(y) \times \frac{n(A,y-1)}{n(.,y-1)} \right] \times$$
$$\left[1 + r \times \left(1 - \frac{n(A,y-1)}{p_A \times n(.,1712)} \right)^{1+b} \right]$$

$$n(P,y) = \left[N(P,y-1) - d(y) \times c(y) \times \frac{n(P,y-1)}{n(.,y-1)} \right] \times$$
$$\left[1 + r \times \left(1 - \frac{n(P,y-1)}{(1-p_A) \times n(.,1712)} \right)^{1+b} \right]$$
(7)

where r is the maximum potential rate of increase of sperm whale populations, and b the density-dependent exponent, which describes how rates of increase vary with relative population size. The actual rate of increase at any population size n is given by $r \times [1 - n/n(0)]^{1+b}$, where $n(0)$ is the population size before exploitation ($p_A \times n(.,1712)$ and $(1-p_A) \times n(.,1712)$ for the Atlantic and Pacific/Indian Oceans).

For any choice of population and exploitation parameters [$n(.,1712)$, p_A, r, b, {d}, q_A] a population trajectory can be calculated, giving a current population size, $n(.,1999)$. In practice, there is information on the population in 1999, from the first part of this paper, but not in 1712. Thus for any set of the other parameters, and a value of $n(.,1999)$, an estimate of $n(.,1712)$ was found (using the 'fmins' function of MATLAB5.3) so that the trajectory reached $n(.,1999)$ in 1999. If no trajectory using the other randomly selected parameters

reached the chosen $n(.,1999)$, then the parameters were discarded and a new set chosen. Consequently, for a set of [$n(.,1999)$, p_A, r, b, {d}, q_A], the model produces a trajectory and value of $n(.,1712)$ from which degrees of depletion and other measures can be calculated.

There is considerable uncertainty about most of the input parameters for this model. Thus it was run with both the 'best' parameters, and sets of parameters chosen from within a 'reasonable range' using the uniform distribution, unless noted. These were:

Proportion of sperm whales in Atlantic before modern whaling: best $p_A = 33\%$; reasonable range 25 to 40% (as 25% of waters >1000 m deep are in the Atlantic; 33% of surface chlorophyll in Atlantic; and 33% of plots on Townsend's charts in Atlantic; Best 1983).

Reduction in Atlantic population 1712 to 1799: best $q_A = 33\%$; reasonable range 10 to 55%. There is little information on this, but many whalers certainly perceived that the Atlantic sperm whales were substantially depleted when they moved operations into the other oceans in about 1800 (e.g. Starbuck 1878).

Maximum rate of increase: best $r = 1.1\%$; reasonable range 0.7 to 1.5%. The population parameters used by the International Whaling Commission (1982) suggest $r = 0.9\%$ for a population with stable age distribution, but these include very uncertain, and probably overestimated, mortality rates, and no changes with age in either fecundity or adult mortality. It may be more realistic to use the well-established mortality schedule of killer whales (*Orcinus orca*; Olesiuk et al. 1990) and an age-specific pregnancy rate taken from the data presented by Best et al. (1984; pregnancy rate for mature females = $0.257 - 0.0038 \times$ Age in years), in which case the annual rate of increase with stable age distribution is 1.1% yr^{-1}.

Density-dependent exponent: best $b = 1.4$ (International Whaling Commission 1982); reasonable values chosen randomly from {0, 0.5, 1.4, 6, 100}, as there is no empirical data on its real value.

Correction for open-boat catch: There are a number of reasons why the estimates of open-boat catch shown in Fig. 1, which were calculated from oil production, may be underestimates, including catches by non-US and British whalers, whales caught but not processed, and wrecked whaling ships, but the scale of this underestimate is unclear (Best 1983). Thus the catches from 1800 to 1910 are corrected by a factor of $d = 1.5$ (reasonable range 1.1 to 3.0).

Correction for modern catch: There are also inaccuracies of reporting in the modern hunt (Zemsky et al. 1995, Kasuya 1999). Figures presented by Zemsky (1995) suggest under-reporting by at least 16% in Soviet Antarctic pelagic whaling for sperm whales. It is

not clear whether such levels were common in other modern sperm whaling operations, and in some circumstances there may have been over-reporting (e.g. Kasuya 1999). Thus the catches from 1910 to 2000 are uncorrected ($d = 1.0$) but a reasonable range for d during this period was taken to be 0.9 to 1.2.

Population in 1999: best $n(.,1999) = 360\,000$, reasonable range chosen from normal distribution with mean $360\,000$ and CV = 0.36, from the earlier part of this paper.

From each run of the model, 3 trajectory measures were calculated: the pre-exploitation level [$n(.,1712)$], and the relative levels of the population in 1880 and 1999 [$n(.,1880)/n(.,1712)$, $n(.,1999)/n(.,1712)$]. By discarding the 25 lowest and 25 highest values of each measure from the 1000 random runs, approximate 95% confidence intervals were obtained. Sensitivities were calculated by correlating each input parameter with the 3 output measures.

RESULTS

Densities

The estimated mean density of sperm whales in the surveyed areas was 1.4×10^{-3} whales km^{-2} (CV = 0.13), but there was considerable variation in sperm whale density between areas, ranging from a high in the western North Atlantic between the edge of the continental

Fig. 3. *Physeter macrocephalus.* Estimated population trajectories for the global sperm whale population from 1700 to 1999. The upper plot shows the trajectory calculated from my best estimate of the population and model parameters, the lower plot shows 20 trajectories calculated using randomly chosen parameters within reasonable ranges. The period from 1712 to 1800 is dashed as information about this time period is very limited

shelf and the Gulf Stream of 17×10^{-3} whales km^{-2} to a low in the Antarctic of 0.65×10^{-3} whales km^{-2}.

Abundance

There were an estimated total of 105 670 sperm whales (CV = 0.13) in the surveyed areas combined. These were extrapolated into global population estimates as follows:

(1) $N = 452\,000$ sperm whales (CV = 0.53), scaling by area;

(2) $N = 304\,500$ sperm whales, scaling by plots on Townsend's charts;

(3) $N = 361\,400$ sperm whales (CV = 0.36), scaling by primary production.

It is encouraging that the 3 estimates are fairly similar with overlapping CVs. Of the 3, that obtained by scaling from primary productivity (3) appears the most precise as it has the lowest CV. This is indicated by the smallest variation among study areas in the density columns of Table 1. It is also intermediate between the other estimates.

Trajectory

The reconstructed trajectory of the global sperm whale population from 1700 to 1999 using the 'best' estimates of the population parameters is shown in the upper part of Fig. 3. As an indication of uncertainty in this reconstruction, 20 runs using randomly selected parameters from within reasonable ranges are displayed beneath. There is clearly much uncertainty in how global sperm whale populations have risen and fallen with whaling pressure. However, some generalities do emerge.

The initial population size seems to have been about 1 110 000 whales (approximate 95% confidence interval 672 000 to 1 512 000; Table 2). The open-boat hunt appears to have reduced the population to about 71% of its original value (approximate 95% confidence interval 52 to 100%) of its original level in 1880. The population seems to have recovered somewhat from 1870 to 1940 with diminished catches, but, except in a few runs, did not approach its unexploited level. Modern whaling's severity is clearly shown by the trajectories with populations declining dramatically from 1945 to 1975. The model also indicates that the decline in sperm whaling in the late 1970s came just in time to prevent severe overexploitation. The
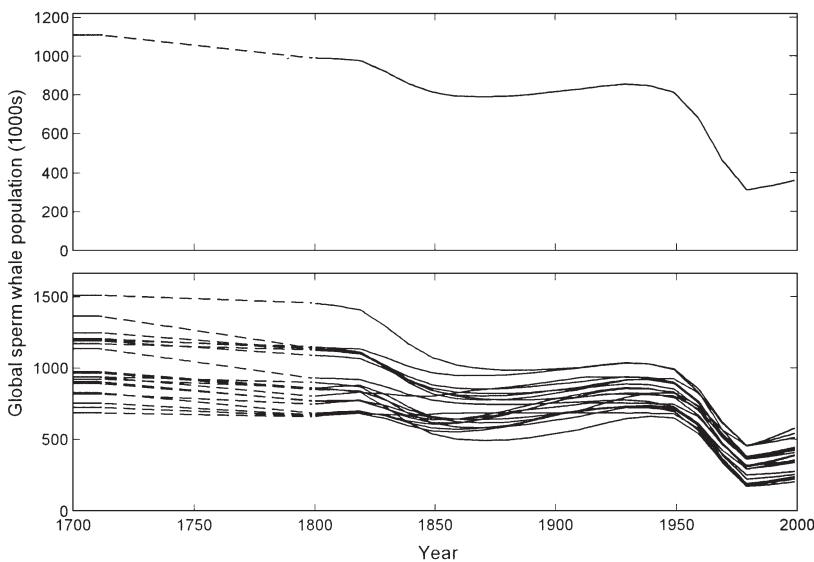
model suggests that the current population is about 32% of its pre-whaling value (approximate 95% confidence interval 19 to 62%). Using the current population estimates from scaling by area or Townsend's (1935) charts, rather than productivity, gives similar estimates of these population measures (Table 2).

The results of the sensitivity analysis (shown in Table 3) suggest that more accurate estimates of initial population will require better estimates of the maximum rate of increase, the density-dependent exponent, and the current population size. The estimate of depletion in 1880 is most dependent on the correction for the open-boat catches and the density-dependent exponent. The estimate of current depletion largely depends on current population size and the density-dependent exponent. In contrast, the input values of the proportion of sperm whales in the Atlantic in 1712, the reduction in the Atlantic population by 1800 and the correction for misreporting the modern catch have relatively little impact on the output measures. Overall then, improving the current population estimate will also give us a better idea of the historical trajectory of sperm whale populations, although to calculate an accurate trajectory of the global sperm whale population we also need more information on population parameters and 19th century catch rates.

Table 2. *Physeter macrocephalus.* Summary of results on global sperm whale population sizes from running population trajectory model. Approximate 95% confidence intervals ($n(.,1999)$ from scaling by productivity) from 1000 runs of model with randomly determined input parameters

Measure	Current population calculated using scaling by:		
	Productivity (95% CI)	Area	Townsend's (1935) charts
Initial population	1 110 000 (672 000 to 1 512 000)	1 184 000	1 067 000
Relative size in 1880	71% (52 to 100%)	73%	70%
Relative size in 1999	32% (19 to 62%)	38%	29%

Table 3. *Physeter macrocephalus.* Sensitivities of output measures from trajectory model to input parameters as indicated by the correlation between input parameters and output measures

Output measures:	Initial population	Relative level, 1880	Relative level, 1999
Input parameters:			
Proportion in Atlantic	0.06	−0.07	0.00
Reduction in Atlantic by 1800	0.06	−0.27	−0.04
Maximum rate of increase	−0.39	0.14	0.24
Density-dependent exponent	−0.54	0.43	0.43
Correction for open-boat catch	0.24	−0.7	−0.10
Correction for modern catch	0.26	0.15	−0.16
Population in 1999	0.37	0.19	0.72

DISCUSSION

Current population size

The global sperm whale population estimates calculated here should have more credibility than previous ones, as most sources of uncertainty are explicitly incorporated in the methodology used to analyze the original surveys, and scaling them up to a global estimate. However there are some potential biases and errors which were not fully considered in the model. As a consequence the global estimates may be more imprecise than is suggested by the calculated CVs. These include the estimate of $g(0)$ and calculation of mean group size in the original surveys (Barlow & Taylor 1998).

To assess the potential for error in $g(0)$, consider the behavior of sperm whales. According to a range of sources (summarized by Whitehead 2003), sperm whales socialize about 25% of the time at the surface, and during the remainder of the 75% spent foraging dive for roughly 37.5 min with about 7.5 min at the surface. Thus, if t min is the time period for which a sperm whale at the surface on the track line of the survey vessel is visible, then an estimate for $g(0)$ is:

$$g(0) = 0.25 + \frac{0.75(7.5 + 2t)}{37.5} = 0.4 + 0.04t \qquad (8)$$

As survey ships travel at about 18 km h^{-1} and can see sperm whales to about 3.6 km, $t = 12$ min and $g(0) = 0.88$, almost exactly Barlow & Taylor's estimate. In an extreme case, the ship might travel at 25 km h^{-1} and see sperm whales to about 2.5 km, so $t = 6$ min and $g(0) = 0.64$, which is only just outside 2 CVs of Barlow & Taylor's estimate of $g(0)$. Therefore Barlow & Taylor's estimate of the precision of their $g(0)$ is not unreasonable. Thus I suspect that additional error and biases from this and other unaccounted sources are reasonably small compared with the estimated CV in the global population estimate of 0.36.

This CV itself is somewhat disappointingly large, principally the result of imperfect scaling up from the surveyed areas to the global habitat of the sperm whale. This is indicated by the wide variation in densities of sperm whales and numbers per tonne of chlorophyll in Table 1. None of the 3 scaling measures that I

have used predict sperm whale abundance particularly well. If a better scaling factor could be found, we would have a more precise global estimate.

Nonetheless, this current estimate of 360 000 whales is considerably more valid than those that currently pervade the literature, for which precision and bias have not been able to be assessed. It appears that these estimates, in the range of 2 million or so whales worldwide (Evans 1987, Berta & Sumich 1999), are optimistically large by a factor of about 5. Consequently, ecological studies which require an estimate of global sperm whale numbers (e.g. Clarke 1977) need revision.

Trajectory

I have tried to incorporate uncertainty about the population biology and exploitation history of the sperm whale by the random choice of input parameters into the population model. However this is still a simplistic model and several potentially important factors are omitted.

One of the most important is geographical population structure. Although sperm whale populations show remarkably little population structure genetically (Lyrholm & Gyllensten 1998) or in most other aspects of their biology (Dufault et al. 1999), hunting was not uniform across sperm whale habitat during the periods of exploitation. Thus there will have been relatively exploited and unexploited parts of the population with different rates of increase. The effects of averaging over sub-populations with different degrees of depletion will vary with the density-dependent response of the population (represented in the model used here by *b*). To provide an idea of the potential significance of such structuring on global population dynamics, I divided each of the 2 areas, Atlantic and Pacific/Indian oceans, into 2 separate equal-sized sub-populations, one of which was exploited first, with exploitation of the second not beginning until the first had been eliminated. Using the best estimates of the input parameters of the model the outputs were: population in 1712 of 1 267 000 (rather than 1 110 000 in the original runs with fully mixed populations in each ocean area), a population in 1999 of 28% of the initial value (rather than 32%) and a population in 1880 of 74% (rather than 71%). Thus, under this rather extreme scenario of population subdivision, outputs were little affected, indicating that the assumption of homogeneous exploitation of each ocean population does not critically affect the results of the modeling.

Other simplifications include a lack of explicit age structure in the population model, and the effects of whaling on social structure, and thus on the fitness of whales not killed (e.g. Botkin et al. 1980). These are most likely to be important in the consideration of modern whaling which was both more selective and more severe in its impact than the open-boat hunt. Together with other modern anthropogenic influences, such as fisheries by-catch (Haase & Félix 1994), chemical pollution (Law et al. 1996, Nielsen et al. 2000) and noise, this may mean that the apparent recovery over the last 20 yr indicated in the trajectories of Fig. 3 may be optimistic.

The results of the model indicate that pre-whaling population levels were about one million, much less than the numbers of 2 to 3 million indicated elsewhere (e.g. Rice 1989). They also suggest that the current population is about 32% of the pre-whaling level and so considerably more depleted than the 65 to 85% levels which are reported elsewhere (Evans 1987, Berta & Sumich 1999).

The trajectories suggest that the open-boat hunt did not have a very substantial effect on the global population, reducing it by perhaps 0 to 50% by 1880 (Table 2). This seems to conflict with reports of the 19th Century open-boat whalers that sperm whales were becoming substantially scarcer (e.g. Melville 1851), and reductions in sighting rates of about 60% from 1830 to 1850 off both the Galápagos Islands and in the northwest Pacific (Tillman & Breiwick 1983, Whitehead 1995). The discrepancy between the severe drop in the sighting rates of the whalers over this period and the results of the model may be at least partially explained if the whales changed their schooling behavior or distribution as exploitation progressed, or if there were refuges, such as unavailable or undiscovered grounds, where the whales were fairly free from the whalers.

Future prospects

While this analysis shows that estimates of sperm whale current and historical abundance found in the literature are seriously inaccurate, there is still much uncertainty about population levels. As indicated by the sensitivity analysis, a more precise estimate of current numbers would also improve the historical trajectory. One way to increase precision would be to find a more effective scaling factor, but this may not be possible. Alternatively, precision would be improved by increasing the proportion of sperm whale habitat for which estimates are available. Acoustic censuses for this vocal species hold great promise (Leaper et al. 1992, Davis & Fargion 1996, Barlow & Taylor 1998), and it may be possible to automate acoustic censuses from ships of opportunity, thus providing wide coverage with relatively little cost, and so resulting in much more precise estimates of abundance for this species.

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