Separating southern blue whale subspecies based on length frequencies of sexually mature females

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When sexually mature, Antarctic (true) blue whales are substantially longer than pygmy blue whales. To estimate the proportions of these two subspecies in various regions, Bayesian mixture models were fitted to catch length frequencies of sexually mature females. The extent of rounding to 5-ft intervals was also estimated. Antarctic blue whales dominated (99.2%) pelagic catches south of 52°S, while pygmy blue whales dominated (99.9%) north of 52°S and in 35°–180°E. South of 60°S only 0.7% (95% credibility interval 0.5–1.0%) were pygmy blue whales, lower than the 7% upper bound currently assumed. Shore-based catches from SW Africa and those before 1937 from South Georgia and the South Shetlands were estimated to contain 90–92% Antarctic blue whales. Actual proportions were probably higher, but these data show evidence of rounding (up to 19% of records), poor length estimation methods and other problems. The mean length of sexually mature female Chilean blue whales (77.1 ft, 23.5 m) was intermediate between pygmy (68.9 ft, 21.0 m) and Antarctic blue whales (83.4–86.3 ft, 25.4–26.6 m). A good fit to these data was obtained only by assuming that the Chilean whales are a separate subspecies or distinctive population. This finding is also consistent with their discrete distribution, and genetic and call type differences compared to Antarctic and pygmy blue whales.

INTRODUCTION

Two recognized subspecies of blue whales are present in the Southern Hemisphere and northern Indian Ocean: Antarctic (or true) blue whales (*Balaenoptera musculus intermedia*) and pygmy blue whales (*B. m. brevicauda*). Pygmy blue whales have a shorter maximum length[5]: 24.1 m (79 ft) vs. > 30 m (99 ft), shorter mean length at sexual maturity: 19.2 m (63 ft) vs. 23.7 m (77–78 ft), relatively shorter baleen plates and a proportionately shorter tail region (Mackintosh and Wheeler 1929, Ichihara 1966). The subspecies differ somewhat genetically (LeDuc *et al*. in press, Conway 2005) and inhabit different regions in the austral summer: Antarctic blue whales remain largely south of 55°S while pygmy blue whales are generally found north of 55°S (Ichihara 1966, Kato *et al*. 1995). Acoustic detections throughout the Antarctic are similar and are assumed to arise from Antarctic blue whales, but calls of pygmy blue whales in other Southern Hemisphere regions differ both from the Antarctic-type calls and from each other (Ljungblad *et al*. 1998, Stafford *et al*. 1999, Širović *et al*. 2004, Stafford *et al*. 2004, Rankin *et al*. 2005, McDonald *et al*. 2006).

The status of the two subspecies is also different. Antarctic blue whales are estimated to have been numerous prior to exploitation (202,000–311,000) but whaling reduced their numbers to 150–840 in the early 1970s before they increased to 860–2900 by 1996, just 0.3–1.3% of their original abundance (Branch *et al*. 2004). The past and present status of pygmy blue whales is poorly known, but an estimated 424 (CV = 0.42) inhabited the Madagascar Plateau (25–35°S, 40–45°E) in 1996 (Best *et al*. 2003). In the International Whaling Commission (IWC) catch database, 373 catches were taken in the survey region and time period (7–29 December), but an additional 842 were taken outside this region during the same time period, and at least 12,618 were caught in total (Branch *et al*. 2004). Thus the survey estimate likely applies to only a small fraction of the total population. Despite the limited survey coverage compared to the overall pygmy blue whale distribution, this 1996 abundance estimate is 3.0% of the total known pygmy blue whale catch. In contrast, the 1996 abundance estimate for the entire Antarctic blue whale population is only 0.5% of their total catch (Branch *et al*. 2004), suggesting that pygmy blue whales are not as depleted as Antarctic blue whales.

Calculations of the current status of these two subspecies assume that historical catches and recent sightings in Antarctic waters are Antarctic blue whales, while those in more northern areas are pygmy blue whales. To better quantify their relative status, historical catches and abundance estimates need to be separated by subspecies. Although the two subspecies can be readily separated when caught, this occurred rarely because 96% of blue whale catches in the Southern Hemisphere and northern Indian Ocean (IWC catch database, C. Allison pers. comm.) were taken prior to the recognition of pygmy blue whales as a subspecies in the early 1960s (Ichihara 1961, 1963, 1966). Even after the formal recognition of pygmy blue whales, blue whale catches were not always recorded to subspecies. Current estimates of abundance are similarly problematic because it is difficult to identify sightings to subspecies. Available abundance estimates from the IDCR/SOWER (International Decade of Cetacean Research / Southern Ocean Whale and Ecosystem Research) and JARPA (Japanese Whale

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[5]Most catch lengths were recorded in whole English feet (0.3048 m), and hence many anomalies in the data due to rounding and legal minimum catch lengths are tied to measurements in feet. As a result the analyses and general discussion are based on feet, but metric conversions are included where relevant.

Research Program under Special Permit in the Antarctic) programs are therefore assumed to apply to Antarctic blue whales based on latitude (south of 60°S), while recognizing that they could include some pygmy blue whales (Branch and Butterworth 2001, Branch and Rademeyer 2003, Matsuoka *et al*. 2006).

Previous efforts to separate Southern Hemisphere blue whales by subspecies have relied on at-sea identification, genetics, acoustics, ovarian corpora, and length frequency distributions. Estimates of the proportion of pygmy blue whales in the Antarctic during the austral summer are generally small. Based on dorsal hump type this proportion was 2.3% (1 out of 43), while 6.9% (4 out of 58) were tadpole-shaped (an assumed pygmy blue whale character) and not torpedo-shaped (an assumed Antarctic blue whale character) (Kato *et al*. 2002); however, it is not known whether these characters uniquely separate the two subspecies. Based on these analyses, the IWC currently assumes up to 7% of blue whales in the Antarctic are pygmy blue whales (IWC 2003).

Genetic analyses are promising but the sample sizes available to date are small and the actual genetic sequences of each subspecies are not known. Bayesian analyses of mitochondrial DNA have provided a minimum estimate for the proportion of pygmy blue whales in the Antarctic of 2.2% (1 out of 47) (LeDuc *et al*. in press). Additionally, an analysis of nuclear DNA introns (204 samples, 24 Antarctic region) found a significant separation ($P < 0.001$) between Antarctic and southern Indian Ocean samples (Conway 2005).

Acoustic recordings throughout the Antarctic returned the same type of call and have not yet included any putative pygmy blue whale sounds (Ljungblad *et al*. 1998, Širović *et al*. 2004, Stafford *et al*. 2004, Rankin *et al*. 2005, McDonald *et al*. 2006).

Several analyses of catch length frequencies have been conducted, and offer promise because of large sample size and broad geographic coverage. Short pregnant females (< 72 ft, 21.9 m) are almost certainly pygmy blue whales while all those longer than the 79.5 ft maximum pygmy blue whale length should be Antarctic blue whales; the key question is how to deal with intermediate length (72–79 ft) whales. Branch (2006) used the accumulation of corpora in ovaries with age to distinguish between pygmy (high corpora counts) and Antarctic blue whales (low or zero counts) at intermediate lengths, and applied a mixture model to estimate that 0.4% of blue whales in the Antarctic region were pygmy blue whales. However, as the 95% confidence interval for this estimate (0.0–1.1%) included zero, the data did not exclude the possibility that there were no pygmy blue whales in the Antarctic region.

Length data are more numerous than ovarian corpora data but on their own offer less ability to discriminate between the subspecies. For an initial analysis, Donovan (2000) assumed that pregnant or lactating females south of 60°S were pygmy blue whales if they were shorter than 75 ft (22.9 m), estimating that 1.99% were probable pygmy blue whales, but this estimate is based on the assumption that all short mature females are pygmy blue whales. In reality, some Antarctic blue whales probably become pregnant at lengths much shorter than their mean length at maturity of 77–78 ft (Mackintosh and Wheeler 1929, Mackintosh 1942). In any case, fixing this length at 75 ft also assumes that there are no 75–79 ft pygmy blue whales, which is clearly untrue (Ichihara 1966). Kato *et al*. (2000) took this analysis one step further by fitting two distributions to sexually mature female lengths: a normal distribution for the Antarctic region, and a truncated normal for pygmy blue whale catches. In Kato *et al*.'s analysis, only one whale out of 114 (0.9%) caught in the Antarctic was short enough to be considered a pygmy blue whale.

In this paper, we extend the analyses of Donovan (2000) and Kato *et al*. (2000) in the following ways: (1) the fixed cut-off length in Donovan (2000) is replaced by the assumption that observed length frequencies are a mixture of two normal distributions representing pygmy and Antarctic blue whales, (2) the percentage of records rounded to the nearest 5 ft interval is estimated in the model, (3) the database used in Kato *et al*. (2000) is expanded to include all recorded mature female catches, and (4) data are analyzed separately for pelagic and shore-based catches and are divided into different regions.

METHODS

Note that throughout this paper "mature" will refer to sexually mature (evidence of past or present ovulation) and not physically mature (vertebrae fused preventing further growth in length) whales.

Data

Whaling on Southern Hemisphere blue whales started in December 1904 and continued until the IWC ban in 1964, although illegal whaling by the USSR continued until the International Observer Scheme was implemented in 1973. The catch database used for blue whales caught in the Southern Hemisphere and northern Indian Ocean was provided by C. Allison (IWC). This database includes individual data for 311,948 blue whales caught between 1913 and 1973, about 83.6% of the estimated 362,879 caught (Branch *et al*. 2004). Length and sex were recorded for 306,929 individual whales; positions were recorded for 297,980 of these. The database includes data recovered from the illegal USSR whaling in the 1960s and early 1970s (Zemsky and Sazhinov 1982, Yablokov 1994, Mikhalev 1997) and from similar illegal operations by the *Olympic Challenger* during 1950/51–1955/56 (Anon. 1956, Barthelmess *et al*. 1997).

Immature Antarctic blue whales are similar in length to mature pygmy blue whales so that their lengths cannot be used to separate the two subspecies, but mature females have a much smaller overlap and are more useful for this purpose. The database records 33,299 mature females (22.7% of all females) under the following categories: pregnant (n = 32,949), ovulating (n = 16), lactating (n = 325), or combinations of these categories (n = 9). Most records were recorded in whole feet

(n = 31,024), but some were recorded in feet and inches (n = 115), and in meters (n = 2,160). All measurements were converted to feet because key features (specifically rounding) of much of the data are dependent on feet being the main unit of measurement. Measurements were then grouped into 1 ft length bins as follows: a whale of length x ft is in the l ft bin if $l - 0.5 \le x < l + 0.5$. Note that the IWC database records only two digits for whale length so that all whales > 99 ft are listed as 99 ft with a text note containing the reported length.

Potential data problems

A brief overview follows of potential problems affecting length measurements of mature females, including the use of Norwegian feet, incorrect measurement techniques, rounding and mis-recording of lengths, and deliberate misreporting of species. A more extensive overview is contained in Best (1989).

Norwegian feet and English feet

Some early measurements may have been recorded in Norwegian feet (0.314 m) and not English feet (0.3048 m). For example, in Risting (1928, pp. 115–118) lengths were reported in Norwegian feet for catches around South Georgia, the South Shetland Islands and the South Orkney Islands during 1920–25. Norwegian feet are about 3% longer than equivalent English feet values; thus a 77.5 ft blue whale could have been recorded as 75 Norwegian feet. There is no method of determining which measurement unit was used in the IWC catch database.

Measurement methods

The standard measurement for whales is to record the straight line distance from the tip of the snout to the notch between the flukes (Mackintosh and Wheeler 1929). The notch was used because the tips of the flukes themselves were usually cut off at sea to reduce carcass drift while the catcher boats pursued more whales. In practice, this measurement could be implemented in several ways depending on how the tape was placed and held taut, thus adding uncertainty to the distance recorded (Best 1989). Other possible measurement methods were biased in relation to the standard: Hinton (1915) measured from the tip of the lower jaw, recording lengths 2.35% (range 1.02–3.65%) longer than from the tip of the snout. Hinton also noted that some researchers measured along the curvature of the body instead of in a straight line, thus inflating length estimates. A further issue was that when factory ships were first introduced to the Antarctic, whales were processed alongside these vessels resulting in very uncertain length estimates compared to whales processed at a shore station or on the deck. Risting (1928) used alongside-length estimates to explain the high proportion of reported small pregnant blue whale females from the South Shetlands and South Orkneys compared to South Georgia.

Whale stretching, rounding and shrinking

In the 1937/38 season a minimum length of 70 ft was introduced and remained in effect until the ban on catching blue whales by the IWC in 1964. An interesting consequence was that many whales that were actually shorter than the legal minimum were "stretched" and reported as being 70 ft or slightly longer. Mature female Antarctic blue whales were not affected by this regulation, but stretching is apparent in catches of immature males and females, and for mature female pygmy blue whales caught by Japanese vessels—the number in each length class (0 at 60–69 ft, 52 at 70 ft, 53 at 71 ft) implies unrealistically that spotters could perfectly discriminate between 69 ft and 70 ft blue whales at sea. Whale "stretching" is well documented for other species and locations, e.g. sperm and fin whales caught at Durban (Best 1989). Large sperm whales at Durban were also sometimes "shrunk", i.e., reported lengths were shorter than actual lengths, probably to ensure that stretching small whales did not result in suspiciously low average product yields (Best 1989). During the 1960s and 1970s when the USSR was whaling illegally, they ignored the 70 ft minimum length regulation, but did stretch whales to 18.0 m (59 ft), with smaller than expected numbers between 16.5 and 18.0 m (Mikhalev 1996). Evidence for rounding (or estimating) to the nearest 5 ft interval is also common in the data before 1930 (Donovan 2000).

Species identification

Given their experience, it is unlikely that whalers would misidentify blue whales as one of the other species, but if the blue whale caught was shorter than the minimum length, there would be an incentive to record it as a fin whale to avoid any penalties (Donovan 2000). Additionally, when the Blue Whale Unit (BWU) system was introduced for pelagic catches in 1946, quotas were limited to a certain BWU quantity, with one blue whale being equivalent to two fin whales, 2.5 humpback whales, or six sei whales. Reporting a blue whale as a fin whale would therefore halve its contribution to the BWU quota and allow increased catches (Donovan 2000). It is not known to what extent these practices might have occurred. Land stations were unaffected by this incentive because they were outside the BWU system until well after the protection of blue whales.

Areas and time periods

For the analysis, catches were assigned to particular areas and time periods. Catches lacking positional information were excluded from individual categories. Three categories were examined: pelagic catches, shore stations, and a subset of the pelagic catches taken at the same time and place as the more recent IDCR/SOWER sighting surveys (i.e. SOWER-comparable, although this will be abbreviated as "SOWER" throughout). Regions with fewer than 10 mature females are excluded from the analyses, while regions with 10–35 records are plotted but not analyzed using the mixture model.

Pelagic catches were taken mainly in the Antarctic region and were divided into areas as shown in Figure 1. Note that the Pelagic Pygmy region extends from 52°S northwards to include the northern Indian Ocean and catches to the south of Madagascar. South of 60°S the catches were assigned to one of the six IWC Management Areas (Donovan 1991). The 52°S boundary represents the best division between catches of likely Antarctic and likely pygmy blue whales based on a degree-by-degree examination of length frequencies and the proportion of mature females longer than 79 ft. Most of the catches in the 52–60°S band were taken in the early austral summer months (October–November), and probably come from the same group of whales caught later in the summer south of 60°S when the ice edge is further south. Small numbers of pelagic catches were excluded if taken north of 60°S and west of 60°W, or north of 52°S and west of 0°. All region definitions were inclusive of the northern and western boundaries and exclusive of the southern and eastern boundaries; this is important since many catch locations were recorded only to the nearest degree.

To estimate the proportion of pygmy blue whales sighted during the recent IDCR/SOWER sightings surveys, a subset of the historical pelagic catches taken in the same months and regions was analyzed. The "SOWER" subset of the pelagic catches were all south of 60°S and divided into the six IWC Management Areas, but only those catches within the 29 December–12 February time period were included. These days correspond to the approximate average start and end of the IDCR/SOWER sighting surveys, thus providing the most appropriate estimates of the likely proportion of pygmy blue whales encountered by these sighting surveys. Note that the IDCR/SOWER surveys are sighting surveys only (not to be confused with whaling operations) and are more recent (1978/79–2005/06) than the historical catches in the Antarctic (largely 1904/05–1963/64). The "SOWER" subset of the historical catches is provided purely to allow abundance estimates from the IDCR/SOWER surveys to be separated into the two subspecies.

Shore station catches (Figure 2) from Saldanha Bay and Hangklip, South Africa, and Walvis Bay, Namibia, were included in the SW Africa grouping. All shore-station catches in Chile were grouped together. Shore-station catches in the sub-Antarctic and Antarctic region (Ross Sea, South Orkney Islands, and South Sandwich Islands) were generally included in the pelagic catches, except that those from South Georgia and the South Shetlands included higher fractions of small mature females, and were therefore analyzed separately. The following regions are excluded from the analyses because fewer than 10 mature females were recorded: Angola, Argentina, Australia, Brazil, Congo, Ecuador, Falklands Islands, Galapagos Islands, Mozambique, and Peru. Mature female data from SE Africa were not analyzed (n = 12); these data were all from Durban, South Africa.

The catch seasons in the individual catch database range from 1913/14 to 1972/73 (note that 1913/14 is shorthand for a austral summer catch season running from late 1913 to early 1914). These seasons are split into "early" and "late" periods to allow for changes in the data caused by the minimum length regulation introduced in the 1937/38 season. Shore station catches for Chile, SW Africa and SE Africa are not divided into early and late periods because the minimum length for these northerly shore stations was 65 ft (19.8 m), well below the modal length of mature female pygmy blue whales.

Shorter time periods could be used if exploitation or density-dependent effects systematically altered the mean length in the population. However, the mean length of mature females showed no consistent trend from the 1920s to the 1960s south of 60°S, likely because blue whales only continue growing in length for only a short fraction of their adult life between sexual maturity and physical maturity.

Mixture model

A mixture model assumes that the observed data are the sum of two or more distributions, in this case representing the two subspecies of blue whales. The variables to be estimated are the parameters describing each of the distributions and the parameters governing the relative weights (proportion of each subspecies) to assign to each of the distributions. A Bayesian estimation method is implemented for the mixture model in this paper. In the Bayesian framework, a prior distribution is assigned to each of the parameters and then the likelihood of the data for the mixture model is combined with the priors to obtain posterior distributions which reflect the probabilities associated with different values of the parameters.

For this mixture model we assumed that the mature length frequencies from pygmy blue whales and Antarctic blue whales were normally distributed, and that Antarctic blue whales were longer on average than pygmy blue whales. An observed length frequency can then be thought of as a mixture of these two normal distributions, comprising a proportion p of pygmy blue whales $\sim N(\mu_p, \sigma_p^2)$ and $1-p$ of Antarctic blue whales $\sim N(\mu_a, \sigma_a^2)$, so that the probability of recording a whale of length l rounded to the nearest 1 ft ($P_{1\text{ft}}$) is:

$$P_{1\text{ft}}(l-0.5 \le l < l+0.5) = p \int_{l-0.5}^{l+0.5} \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(\frac{-(l-\mu_p)^2}{2\sigma_p^2}\right) dl + (1-p) \int_{l-0.5}^{l+0.5} \frac{1}{\sqrt{2\pi\sigma_a^2}} \exp\left(\frac{-(l-\mu_a)^2}{2\sigma_a^2}\right) dl \quad (1)$$

For the shortest length group ($l_{\min} = 60$ ft) the integration is from $-\infty$ to $l_{\min}+0.5$, and for the longest length group ($l_{\max} = 99$ ft) the integration is from $l_{\max}-0.5$ to ∞, though for the parameter values to be considered these contributions are negligible. Note that the variance parameters σ_p^2 and σ_a^2 include both real variation and the effects of measurement error.

The observations show substantial evidence of rounding, with higher than expected frequencies at 70, 75, 80, 85 and 90 ft. For data rounded to the nearest 5 ft interval, *l*, the probability ($P_{5\text{ft}}$) of recording length *l* is:

$$P_{5\text{ft}}(l-2.5 \le l < l+2.5) = p\int_{l-2.5}^{l+2.5} \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(\frac{-(l-\mu_p)^2}{2\sigma_p^2}\right) dl + (1-p)\int_{l-2.5}^{l+2.5} \frac{1}{\sqrt{2\pi\sigma_a^2}} \exp\left(\frac{-(l-\mu_a)^2}{2\sigma_a^2}\right) dl \quad (2)$$

The predicted proportion recorded at each length is therefore a mixture model of $P_{1\text{ft}}$ and $P_{5\text{ft}}$ (each of which is in turn a mixture of Antarctic and pygmy blue whales), with a new parameter p_5 for the proportion of lengths rounded to the nearest 5 ft interval. This implicitly assumes that the rounded data were measured just as accurately, but were then rounded when recorded. If instead the rounded data were estimated with poorer precision than the unrounded data, the rounded lengths would have more spread than the unrounded lengths and the values of σ_p and σ_a in equation (2) would need to be increased.

The overall predicted proportions of whales of both subspecies at each length *l* are:

$$P_l(l-0.5 \le l < l+0.5) = \begin{cases} (1-p_5)P_{1\text{ft}}, & l \notin (60,65,...,95) \\ (1-p_5)P_{1\text{ft}} + p_5 P_{5\text{ft}}, & l \in (60,65,...,95) \end{cases} \quad (3)$$

In nearly all regions there were few mature females shorter than 71 ft, resulting in poor estimation of the values of μ_p and σ_p. To incorporate known information about these parameters, informative priors (in contrast to uninformative uniform priors) for these parameters were introduced into the Bayesian estimation process. The data used to develop these informative priors were from USSR catches (these ignored the minimum length regulations) of mature female blue whales in the Pelagic Pygmy region, excluding any that were longer than 79.5 ft. The prior standard deviations were obtained by dividing the data into groups and then applying the jackknife method (Efron 1982). This approach was used because of concerns that the pygmy blue whale samples might be drawn from a non-homogeneous distribution, so that treating them as completely independent might suggest greater precision of the estimates of the parameters of their length distribution than was actually the case. Jackknife analyses were conducted by area, season and expedition; as grouping by area demonstrated the greatest heterogeneity in estimates, the associated standard deviation estimates were used. For the grouping by area the USSR data in the Pelagic Pygmy region were divided by lines of 15° longitude between 30°E and 180°E and at 10°S latitudinally, and groups were excluded if there were fewer than 20 whales in any area. The jackknife formula for the variability around the quantity of interest is given by:

$$sd(Q) = \sqrt{\frac{n-1}{n}\sum_{g=1}^{n}\left(\hat{Q}_{-g} - Q_{(\cdot)}\right)^2}$$

where:

$n =$ the number of groups (4)

$\hat{Q}_{-g}$ = the estimate of Q obtained by omitting the data points associated with group g

$Q_{(\cdot)} =$ the mean of the $\hat{Q}_{-g}$'s.

In this formula, Q is the measurement (i.e. mean or standard deviation) for which the jackknife standard deviation is required. The resulting prior means are 68.9 ft for μ_p and 3.17 ft for σ_p, and the prior standard deviations from the jackknife analysis are 0.39 ft for μ_p and 0.077 ft for σ_p.

The mean and standard deviation of parameters were further restricted in accordance with the likely values for the respective subspecies based on USSR catches in pygmy blue whale regions (mean 68.9 ft, SD 3.2 ft), and catches in the six Antarctic regions (means 83.4–86.3 ft, standard deviations 3.6–4.9 ft). The restrictions on the standard deviation parameters were selected with robust estimation in mind; on the one hand outliers (possibly arising from errors in the recording of data) could otherwise lead to inappropriately large values, whereas on the other samples containing small numbers of one of the two species could otherwise give rise to anomalously small estimates.

The priors for the six model parameters were:

$$\mu_p \sim N(68.9, 0.39^2) \qquad 65 \le \mu_p \le 71$$
$$\sigma_p \sim N(3.17, 0.077^2) \qquad 2 \le \sigma_p \le 5$$
$$\mu_a \sim U[80, 90]$$
$$\sigma_a \sim U[2, 5]$$
$$p \sim U[0, 1]$$
$$p_5 \sim U[0, 1]$$

Note that since the informative priors on μ_p and σ_p are based on data from the Pelagic Pygmy region, uniform priors on these two parameters were imposed when the model was run for that region:

$$\mu_p \sim U[65, 71]$$
$$\sigma_p \sim U[2, 5]$$

We assume a multinomial likelihood with model-predicted proportions P_l at each length *l*, and observed numbers at each length, n_l, given by the data. Then the likelihood *L* and negative log likelihood NLL (the latter including the normally distributed informative priors on μ_p and σ_p) are given by:

$$L = \frac{n!}{\prod_l n_l!} \prod_l P_l^{n_l}, \qquad n = \sum_l n_l$$
$$\text{NLL} = -\sum_l n_l \ln P_l + \frac{(\mu_p - 68.9)^2}{0.39^2} + \frac{(\sigma_p - 3.17)^2}{0.077^2} \tag{5}$$

where NLL ignores a constant term whose value is independent of the estimable parameters.

Model best fits (the mode of the posterior distribution) were obtained by minimizing the NLL using AD Model Builder™ and double checked using Solver in Microsoft Excel. Posterior distributions were obtained by Markov Chain Monte Carlo (MCMC) methods as implemented in AD Model Builder™. In the MCMC approach, a chain of successive correlated draws performs a random walk through the parameter space. Given enough draws, this chain converges to the Bayesian posterior distribution. Evenly subsampling the chain at distant enough intervals removes the autocorrelation between successive draws. For these analyses, chains were run until subsamples of 1000 draws had autocorrelations smaller than 0.05 for all parameters. Chain lengths varied from 1 million to 400 million for each analysis. The median and 95% intervals were calculated from the subsampled draws. These 95% intervals are sometimes termed “credibility intervals”, “probability intervals” or “Bayesian intervals”; for brevity we refer to them as 95% intervals throughout.

Overall estimates of the proportion of pygmy blue whales

Overall estimates of *p* for pooled regions were obtained from a catch-weighted average for each group, combined over the early and late periods. Estimates were calculated for SOWER, pelagic Antarctic, Pelagic Pygmy, pelagic remainder, and shore stations. If p_i is the estimated pygmy blue whale proportion and C_i the total catch (all males and females) in region *i*, then the catch-weighted average $\bar{p}$ (for each MCMC draw) is:

$$\bar{p} = \frac{\sum_i p_i C_i}{\sum_i C_i} \tag{6}$$

Alternative model for Chilean population

Mature females from Chile were the only group poorly fit by the mixture model described above, essentially because the mode of the Chilean length distribution was between 71 and 80 ft. To test the hypothesis that Chilean blue whales come from a separate subspecies with a characteristic modal length, the mixture model was replaced with a single normal distribution with the mean restricted to 65–90 ft, and standard deviation restricted as before to 2–5 ft. The proportion of rounding to 5 ft intervals was also estimated, thus this alternative model had three parameters: μ_c, σ_c, and p_5:

$$P_l(l-0.5 \le l < l+0.5) = \begin{cases} (1-p_5)\displaystyle\int_{l-0.5}^{l+0.5} \frac{1}{\sqrt{2\pi\sigma_c^2}} \exp\left(\frac{-(l-\mu_c)^2}{2\sigma_c^2}\right) dl, & l \notin (60, 65, ..., 95) \\ (1-p_5)\displaystyle\int_{l-0.5}^{l+0.5} \frac{1}{\sqrt{2\pi\sigma_c^2}} \exp\left(\frac{-(l-\mu_c)^2}{2\sigma_c^2}\right) dl + p_5 \displaystyle\int_{l-2.5}^{l+2.5} \frac{1}{\sqrt{2\pi\sigma_c^2}} \exp\left(\frac{-(l-\mu_c)^2}{2\sigma_c^2}\right) dl, & l \in (60, 65, ..., 95) \end{cases}$$

To estimate the probability that the mean length of these blue whales overlaps with the bounds imposed on mean length for pygmy (65–71 ft) and Antarctic (80–90 ft) blue whales, an extra-long MCMC chain (100 million) was run to obtain 1 million draws.

Potential typographical errors

There are small percentages (around 1%) of short pregnant females (putative pygmy blue whales) in most regions. In this situation, typographical errors resulting in smaller lengths will often result in Antarctic blue whales being mis-classified as pygmy blue whales, increasing the apparent proportion of pygmy blue whales. However, as typographical errors resulting in larger lengths will seldom lead to mis-classification, thus errors can positively bias the estimated proportion of pygmy blue whales. To assess the possible impact of typographical errors, text notes in the IWC database for pregnant blue whales were examined for any indications of uncertainty in species identification, length, sex, or pregnancy status. Examples of common annotations included “Adult sex given as male (with foetus); coded as female” (n = 21), and “Records say x of the last y whales were pregnant but do not say which. Pregnancy details coded on a z ft one.” (n = 56). Of 497 pregnant blue whale records with annotations, 119 (0.36% of all mature females) were considered potentially problematic for the following reasons: species identification (n = 6), length (n = 13), sex (n = 35), and pregnancy status (n = 65). As a sensitivity test, these records were excluded and the analyses rerun.

RESULTS

Mixture model

The mixture model provided a good fit to data from all of the regions except Chile (Figures 3 and 4). Estimates of the model parameters are given in Table 1. Note that the posterior medians came close to the upper bound on the standard deviation for the Antarctic blue whale distribution on only three occasions (Pelagic West early, South Georgia early, South Shetlands early). All three cases came from earlier period data for which outliers were expected to be more likely.

Pelagic catches in regions south of 52°S were estimated to be almost entirely Antarctic blue whales, with mean estimates of p (the proportion of pygmy blue whales) ranging from 0.000 to 0.015, except for the Pelagic Area I (0.034) and Pelagic East (0.052) regions during the late period, although the sample size for Pelagic Area I was small (n = 79) and 95% interval was wide (0.005–0.103). Higher proportions might be expected from the Pelagic East region because it is directly south of the Pelagic Pygmy region (north of 52°S, east of 35°E) where catches were almost exclusively pygmy blue whales (p = 0.999, 95% intervals 0.994–1.000). The catches conducted at the same time of the year and region as the SOWER sighting surveys, were dominated by Antarctic blue whales, with posterior mode estimates of p below 0.023.

The model estimates that most of the early period South Georgia catches were Antarctic blue whales, but a sizeable proportion (0.104) was estimated to be pygmy blue whales, much higher than in the late period (0.019) and for surrounding pelagic catches. The higher early period estimate could be due to incorrect or inaccurate measurement methods, as outlined under “potential data problems” above, therefore the early period South Georgia data were examined by catch station to uncover any anomalies in lengths (Figure 5). While most catch stations included some mature females shorter than 75 ft, length frequencies differed greatly among catch stations. Some catch stations (e.g., #80 and #5200) rounded almost all records to the nearest 5 ft interval. There was a marked discrepancy between catch stations #150 and #160 which both operated from Stromness Harbor but in succeeding periods: 1913/14–1919/20 and 1920/21–1930/31 respectively. The modal length recorded for #0150 was 65–70 ft but for #0160 this was 80–85 ft (Figure 5).

Most South Shetland Islands catches (all early period) were estimated to be Antarctic blue whales (p = 0.083), but the proportion of pygmy blue whales was higher than for pelagic catches in the same region, possibly due to data problems in the early period. An examination of recorded lengths by catch station (Figure 6) revealed striking differences in length frequencies: modal lengths for mature females were less than 75 ft for some catch stations (#5300, #5411) but more than 85 ft for others (#220, #5210), and for still other catch stations, a high proportion of mature females were recorded as exactly 80 ft (#5140, #5360, #5370, #5390).

Off SW Africa most catches were estimated to be Antarctic blue whales (p = 0.077), but this also includes a sizeable proportion of pygmy blue whales. Sexual maturity was recorded for only a small number of blue whales: 63 out of 7,547. Most of the catches were recorded from Saldanha Bay (33°S 17°E) during 1913–1966, but four out of the six that were 76 ft or shorter were recorded by a single land station, #4570, in 1914 at Hangklip, Cape Agulhas (34°S 19°E) (Figure 7). Length frequencies of all males and females (regardless of maturity) from #4570 were 68–78 ft, differing from the 55–75 ft peak of immature blue whales taken at Saldanha Bay and in other years at Hangklip. When catches from the 1914 Hangklip season were excluded (reducing the sample from 63 to 56), the estimated proportion of pygmy blue whales was 0.037 (95% interval: 0.006–0.107).

Although the catch database included a large number of catches (2,489) off SE Africa (Durban), only 12 were recorded as mature females, four of which were 75 ft or shorter (65, 66, 72, 75 ft). Further analysis of the catches where maturity was not recorded revealed that the percentage of female blue whales longer than 79.5 ft decreased from 24.1% in 1920–31 to 9.4% in 1932–38 and 8.9% in 1946–66 (Figure 8). Male catches showed a similar pattern of decreasing percentages of > 79.5 ft whales: respectively 8.8%, 2.7% and 0.0% for the three time periods.

Although Chilean catches were estimated by the mixture model to be mostly Antarctic blue whales (p = 0.039), the model fit was poor (Figure 9). The estimated mean length of Antarctic blue whales was $\mu_a = 80.11$, near the lower bound specified (80 ft) and shorter than in any other region, an indication that the model was attempting to fit a distribution with true mean length between 71 ft and 80 ft.

In most cases the model estimated that some of the data were rounded to the nearest 5 ft interval. Highest estimates of the proportion of rounded data were for early period data: Pelagic V (0.169), SOWER V (0.244), South Georgia (0.143), and the South Shetlands (0.188); rounding was estimated to be lower (< 0.056) in the late period data for all regions.

Estimates of the overall proportions of pygmy blue whales weighted by catch are given in Table 2. For pelagic catches south of 60°S, 0.008 (95% interval 0.005–0.010) were estimated to be pygmy blue whales, and south of 52°S this proportion was 0.009 (95% interval 0.007–0.011). When the pelagic catches south of 60°S were restricted to the approximate period of the IDCR/SOWER surveys the estimate was 0.007 (95% interval 0.005–0.010). Shore-based catches had higher estimated proportions of pygmy blue whales, averaging 0.093 (95% interval 0.079–0.110).

Alternative model for Chilean population

The three-parameter single normal distribution model with $\mu_c = 77.09, \sigma_c = 3.92,$ and $p_5 = 0.040$ provided a far better fit to the Chilean data than the mixture model despite using three fewer parameters (Figure 9). The 95% intervals for mean length are (76.2; 78.0), and there is less than a 1 in 10^6 probability of the mean length lying outside (74.7; 79.6), thus these lengths are highly significantly different from both pygmy blue whales (upper bound 71 ft) and Antarctic blue whales (lower bound 80 ft). The mean length at sexual maturity for females in the Chilean population is longer than all but 1.3% of mature females in the Pelagic Pygmy region (99.9% pygmy blue whales), and shorter than all but 3.8% of mature females in Pelagic Areas I–VI (99.3% Antarctic blue whales).

Potential typographical errors

For nearly all of the regions there were no detectable differences in the estimated proportions of pygmy blue whales when the 119 problematic records were excluded. A small difference was found only for pelagic Area I late, for which there were few available records for mature whales (n = 79).

DISCUSSION

Historical catches and abundance estimates must be divided between pygmy and Antarctic blue whales to better assess the status of these two subspecies. Information from at-sea identification, genetics, acoustics, and ovarian corpora all consistently estimated low percentages of pygmy blue whales in the Antarctic, but these methods are currently limited by relatively small sample sizes and sparse coverage of the known geographical range of these subspecies. Analysis of mature female lengths has the advantage of using considerably more samples taken from a much broader geographic region than other methods.

One key assumption in this analysis is that the proportion of pygmy blue whales among mature females is representative of whales of all ages and both sexes. Sex ratios were generally even throughout all areas and time periods. In the IWC catch database, males slightly dominate (52.1%) both total catches and the fetal sex ratio (51.3%). For individual regions analyzed here (minimum 100 catches) the proportion of males among whales of all ages ranged from 37.0% to 59.1%, while 29 of the 35 regions had sex ratios within 5% of the overall mean. Although the sex ratio data do not suggest any violation of this key assumption, further work is needed on separation methods for immature and male blue whales. In some areas, immature blue whales comprised a higher proportion than in other areas, for example in SW Africa compared to the Antarctic (Mackintosh and Wheeler 1929). However, it seems unlikely that immature whales (especially suckling calves) from one subspecies would associate with adults from another subspecies. To separate males, the methods applied to ovarian corpora data (Branch 2006) could also be used on testes weight.

Pelagic catches in the Antarctic

The estimated proportion of pygmy blue whales south of 60°S in all catches (0.7%, 95% interval 0.005–0.010) is lower than previous estimates based on mature female lengths: 1.99% (Donovan 2000), and 0.9% (Kato *et al*. 2000). The mixture model used here is based on a very similar dataset to that used by Donovan (2000), but improves on his methodology by assuming that mature lengths are normally distributed instead of assuming that pygmy and Antarctic blue whales can be exactly divided at 75 ft. In addition, the mixture model explicitly incorporates measurement rounding to 5 ft intervals, thereby improving the model fit to the data. Kato *et al*. (2000) analyzed only 114 mature females in the Antarctic region, whereas this analysis was based on 18,646 mature females in the Antarctic alone.

This analysis address a major question surrounding the IDCR/SOWER (and JARPA) abundance estimates: what proportion should be assumed to be pygmy blue whales? An important finding is that only 0.7% (95% interval 0.5–1.0%) of these sightings should be assumed to be pygmy blue whales, a far lower value than the 7% upper bound currently assumed by the IWC (IWC 2003). This estimate is similar to the more accurate estimates of 0.4% (95% CI: 0.0–1.1%) from ovarian corpora (Branch 2006), but is based on a much larger and more widespread dataset. In combination with the corpora results, it seems that 1% would be a more reasonable upper bound of the proportion of pygmy blue whales in the Antarctic than 7%. Of course, the applicability of an estimate based on historical whaling (1913–1973) to sighting surveys in more recent years (1978–2006) rests on the assumption that the relative distribution of pygmy and Antarctic blue whales did not change between these time periods.

The results here could be used to create an historical catch series for southern blue whales for the pygmy and Antarctic blue whale subspecies. If these estimates correctly reflect the catch ratios, total catches of pygmy blue whales would increase somewhat from the most recent estimate of 12,618 (Branch *et al*. 2004), but would be dependent on what is assumed for South Georgia, the South Shetlands, and SW Africa, which are further discussed below.

South Georgia

For South Georgia, early period estimates (0.104) contrast with late period estimates (0.019) and with estimates from the surrounding Pelagic West region (early 0.015, late 0.002). A cursory examination of the data supports the high early period estimate—a high proportion (0.076) of mature females in the early South Georgia catches were 70 ft or shorter. But a more in-depth examination reveals substantial differences in length frequencies from one expedition to another. In particular, consistently high proportions of small recorded mature lengths at Stromness Harbor were followed by longer lengths from the catch season in which the station changed ownership. Hinton (1915) records a little known fact that explains this particular pattern: in the early years the equipment at some of the South Georgia land stations was designed to process humpback whales and was too small to handle large blue whales. Harpooners from some land stations consequently avoided the largest blue whales, resulting in length distributions that were skewed towards shorter blue whales.

There are other problems with the South Georgia data. There is clear evidence for rounding to the nearest 5 ft for some expeditions, and visual estimation of length instead of measurement from floating factories (Risting 1928), with the end result being a wider spread of length measurements than present in the real values. Additional culprits probably include the use of Norwegian feet instead of English feet (Risting 1928), incorrect species or maturity identification, and typographical errors.

South Shetland Islands

The estimated proportion from the South Shetland Islands (0.083) is also higher than expected from pelagic catches in the same region (early Pelagic II: 0.008). Again, there are striking inter-expedition differences in length frequencies, probably due to variation in length measurement methods. The high proportion of small pregnant blue whales at the South Shetlands was noted by Risting (1928), who ascribed this to poor length estimation on floating factories that processed whales alongside the vessel because whales were not laid out on a flat surface.

SW Africa

Estimates of the proportion of pygmy blue whales from SW Africa are higher than in the Antarctic regions (0.077), but this is primarily a consequence of anomalous lengths recorded from Hangklip in 1914. The Hangklip company went bankrupt at the end of 1914 and not all whales were recorded in that year (Best 1994), which may have some bearing on the anomalous lengths. Excluding this expedition, the estimated proportion is reduced to 0.037 with a 95% interval which almost includes zero (0.006–0.107). The lower value is in accord with Mackintosh and Wheeler (1929), who reported 24 morphometric measures for 537 South Georgia and 247 Saldanha Bay blue whales. They found that whales caught from these two regions were from the same population, i.e. Antarctic blue whales. Later, Ichihara (1966) made use of differences between the Mackintosh and Wheeler (1929) measurements and those from pygmy blue whales, to argue that pygmy blue whales were a separate subspecies.

Bannister and Grindley (1966) reported one definite and one possible pygmy blue whale at Saldanha Bay, but an examination of the original unpublished measurements (provided by P. B. Best) reveals some uncertainty about these identifications. Both whales were infested with high numbers of a baleen-infesting copepod, *Balaenophilus unisetus*, associated with the temperate water habitats preferred by pygmy blue whales. The larger of the two was a 72.75 ft immature female, about 5 ft longer than the longest known immature female pygmy blue whale (Branch 2006) and almost certainly an immature Antarctic blue whale. The other record was a 61.25 ft immature female with many developing follicles. The anus to fluke measurement (as a percent of total length) of the shorter female was 27.2%, closer to the mean for pygmy blue whales (26.15% vs. 29.55%) but within the ranges reported for both pygmy (21.7–30.4%) and Antarctic (26.6–30.3%) blue whales (Ichihara 1966). The shorter female had a length:breadth ratio of the longest baleen plate of 1.26, compared to means of 1.48 (range 1.08-1.93) for pygmy and 1.79 (range 1.26-2.33) for Antarctic blue whales (Ichihara 1966), just within the recorded range for both subspecies. Thus while the 61.25 ft female probably was a pygmy blue whale, the data do not conclusively show this.

In summary, available evidence from Mackintosh and Wheeler (1929) and the analyses in this paper suggests that 0.037 (95% interval 0.006–0.107) of the blue whales from SW Africa were pygmy blue whales.

SE Africa

For SE Africa (Durban) only 12 mature females were recorded. Not much can be inferred from such a small sample of mature females. However, many of the whales caught at Durban must have been Antarctic blue whales because of the 1,344 female blue whales for which maturity was not recorded, a substantial proportion were longer than the maximum pygmy blue whale length of 79.5 ft. This proportion decreased from 24.1% in 1920–31 to 9.4% in 1932–38, and to 8.9% in 1946–66 (IWC catch database). Similarly, when all males are examined regardless of maturity (n = 1,155), the proportions greater than 79.5 ft were 8.8%, 2.7% and 0.0% for the three time periods. Changes in catch-per-unit-effort at Durban also argue for the presence of Antarctic blue whales: this had declined by 1964 to a mere 2.8% of the level in 1920–28 (Best 2003). Changes in Antarctic blue whale numbers best reflect this decline: over the same period their abundance declined to 0.3% of their 1920s level (Branch *et al*. 2004), while pygmy blue whales probably did not decline as dramatically given the late development of whaling on that subspecies. On the other hand, some pygmy blue whales must have been present at Durban: half of the 12 mature females that were recorded were shorter than 77 ft, and one blue whale caught at Durban in 1963 was confirmed to be a pygmy blue whale (Gambell 1964). In conclusion, most initial catches were probably Antarctic blue whales although both pygmy and Antarctic blue whales were caught at Durban.

Chilean blue whales: a new subspecies?

Chilean blue whales are the only group that did not fit into the mixture model paradigm. Their modal length was outside the bounds placed on the lengths of the other subspecies and the Chilean length distribution showed no sign of bimodality as would be expected if these whales were a mixture of pygmy and Antarctic blue whales. A greatly improved fit to the data was obtained by assuming a single population of blue whales with a mean length of 77.1 ft, contrasting markedly with mean lengths of 83.4–86.3 ft for Antarctic blue whales and 68.9 ft for pygmy blue whales in other regions. More detailed measurements from Chilean blue whales are not available. Aguayo (1974) asserted that 10 pygmy blue whales were caught amongst 168 in 1965/66 and 1966/67 but provided no details; while a recent stranding was found to be more similar to an Antarctic blue whale than a pygmy blue whale (Van Waerebeek *et al*. 1997).

It thus seems appropriate to reconsider the hypothesis suggested by Clarke *et al*. (1978): that the Chilean blue whales are an as-yet undescribed subspecies, distinct from both Antarctic and pygmy blue whales. Before examining the evidence it is worth presenting working definitions of species, subspecies and populations, while accepting that taxonomic infighting surrounding these concepts is unlikely to be resolved soon. A *species* is a group of interbreeding individuals that is reproductively isolated from other such groups even if they share the same geographical range. A *subspecies* is a group of individuals from the same species that is geographically distinct, recognizably different (morphology, genetics or behavior) but could interbreed with another subspecies if they share the same habitat. A *population* is an assemblage of individuals from one species in a defined area. The evidence for Chilean blue whales being a subspecies is as follows:

One of the key characteristics separating pygmy and Antarctic blue whales is the length of mature females. The Chilean mature female length distribution is poorly explained by a mixture of the two subspecies. Only 1.3% of mature pygmy blue whales are longer, and only 3.8% of mature female Antarctic blue whales are shorter, than the mean length at sexual maturity for the Chilean population. Additionally, there is less than a 10^{-6} probability that the actual mean length of Chilean blue whales falls within the bounds on mean length for the other two subspecies.

There is a gap in the summer distribution of blue whales between the southernmost Chilean records at 44°S and the northernmost Antarctic catches at 64°S, and longitudinal gaps stretching to the western Pacific and southern Indian Ocean that separate them from pygmy blue whales (Branch *et al*. 2006). They therefore qualify as geographically separate from the other two subspecies in the Southern Hemisphere.

Acoustic recordings in May at 43°36'S 74°40'W reveal that Chilean blue whales make a unique call (Cummings and Thompson 1971) that has also been recorded from the Eastern Tropical Pacific (most frequently at 8°S 95°W) (Stafford *et al*. 1999), and this call type seems different from both the circum-Antarctic call type and from the various call types recorded from pygmy blue whale locations (Ljungblad *et al*. 1998, Širović *et al*. 2004, Stafford *et al*. 2004, Rankin *et al*. 2005, McDonald *et al*. 2006). However, additional acoustic recordings are needed to confirm this finding.

A genetic study of mitochondrial and nuclear DNA revealed a similar level of differentiation between the south-east Pacific Ocean (n = 28 from Chile, Ecuador and Peru), Indian Ocean (n = 36) and around the Antarctic (n = 47) (LeDuc *et al*. in press). A separate study based on nuclear DNA introns found a significant difference between south-east Pacific (Chile, n

= 26) and the Antarctic (*n* = 44) although only one Antarctic sample was from Area I, the area directly south of Chile (Conway 2005). The latter study, however, found no significant differences between samples from the south-east Pacific and the southern Indian Ocean (*n* = 22) or the south-east Pacific and the eastern tropical Pacific (California, Mexico, Ecuador, Peru, *n* = 135) (Conway 2005).

Both catches and sightings off Chile peak in the summer months when Antarctic blue whales are much further south (Hucke-Gaete *et al*. 2003).

Almost 12% of the females caught off Chile (regardless of maturity) were longer than the maximum recorded length of 79.5 ft for pygmy blue whales (IWC database).

Catches were too numerous in the 1960s to be Antarctic blue whales (Clarke *et al*. 1978): in 1964–66, 605 were caught at a time when Antarctic blue whales probably numbered less than 1,500 (Branch *et al*. 2004).

Chilean (south-east Pacific) blue whales are geographically distinct from the other Southern Hemisphere subspecies, and recognizably different in mean length, call type and genetics, and therefore potentially qualify as a separate subspecies. At a minimum, they should be managed and assessed separately.

Additional issues

This study has focused on Southern Hemisphere and northern Indian Ocean blue whales and has not addressed their relationship to northern blue whales, *B. m. musculus*, found in the North Atlantic and North Pacific. It is possible that Chilean blue whales are more closely related to the California/Mexico population of blue whales than to pygmy blue whales, although this is complicated by the finding that California/Mexican blue whales are more similar in total length and in the length of their tail region to pygmy blue whales, and are also about 2 m shorter than blue whales in the western and central North Pacific (Gilpatrick *et al*. 1997). Clearly a worldwide re-examination of blue whale length data is needed to separate known populations more clearly.

The results presented here obviously depend on the quality of the data included in the analyses. Known sources of bias have been discussed in the methods and include measurement units (Norwegian vs. English feet), different measurement methods, whale stretching, whale shrinking, rounding, and possible mis-recording of species identity. It is not possible to correct for most errors and biases given the data available, although the percentage of rounding to 5 ft intervals was estimated in the models used here, and entries in the database flagged as problematic did not influence the results when excluded.

These data problems tend to inflate the estimated proportion of pygmy blue whales because in all but one area (Pelagic Pygmy, containing 99.9% pygmy blue whales), Antarctic blue whales comprised >90% of the catches. Antarctic blue whale lengths that were incorrectly inflated by data problems would still be estimated to be Antarctic blue whales, but understated lengths might be incorrectly estimated to be pygmy blue whales. The overall effect would be to erroneously increase the estimated proportions of pygmy blue whales (except in the Pelagic Pygmy region). As a result, some regions estimated to include a small percentage of pygmy blue whales may actually contain none.

The mixture model could be extended to include additional distributions: a truncated normal distribution to account for whale stretching and minimum length regulations as used by Kato *et al*. (2000), a normal distribution with additional spread to account for less certain length estimates from whales measured alongside floating factory vessels as reported by Risting (1928), and a normal distribution offset by 0.971 to account for lengths measured in Norwegian feet and not English feet. However, it is doubtful that there is sufficient contrast in the data to estimate additional parameters beyond those already included in this paper. If ageing data were available, a reasonable extension would be to replace the normal distributions with length frequencies modeled as a mixture of length distributions for whales of different ages, as is common in length-based fisheries models. The problem is that very few age data are available for blue whales because the ear-plug ageing methodology (Purves 1955) was developed near the end of the period of whaling on blue whales—even a reliable age-length key for blue whales remains an elusive goal.

Conclusions

Despite recognized problems with the data, patterns are clear: blue whales in the study region are clearly separated geographically by subspecies. Pelagic catches everywhere were dominated (99.1%) by Antarctic blue whales, except in the Pelagic Pygmy region (east of 35°E, north of 52°S and including the northern Indian Ocean) where 99.9% of catches were pygmy blue whales. A major result obtained here is that at most 1.0% of the historical catches south of 60°S were pygmy blue whales, substantially less than the upper bound of 7% currently assumed by the IWC for recent sighting surveys (IWC 2003). Shore-based catches around South Georgia, the South Shetlands and off SW Africa probably comprised a similar majority (~99%) of Antarctic blue whales as is evident in the pelagic catches, but problems with rounding and length estimation likely resulted in point estimates of 90–93% Antarctic blue whales in these three areas. For Durban (SE Africa) although limited data were available, both subspecies were present. Finally, given the available evidence, Chilean blue whales may be a separate subspecies, and should at a minimum be managed and assessed separately from other populations.

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LITERATURE CITED

AGUAYO, L.A. 1974. Baleen whales off continental Chile. Pages 209–217 *in* W.E. Schevill, ed. The whale problem: a status report. Harvard University Press, Cambridge, Mass.

ANON. 1956. "Olympic Challenger" catch in relation to the provisions of the International Whaling Convention. Norsk Hvalfangst-Tidende 45(4):172–208.

BANNISTER, J.L., and J.R. GRINDLEY. 1966. Notes on *Balaenophilus unisetus* P.O.C. Aurivillius, 1879 and its occurrence in the southern hemisphere (Copepoda, Harpacticoida). Crustaceana 1966(3):296–302.

BARTHELMESS, K., K.-H. KOCK, and E. REUPKE. 1997. Validation of catch data of the *Olympic Challenger*'s whaling operations from 1950/51 to 1955/56. Report of the International Whaling Commission 47:937–940.

BEST, P.B. 1989. Some comments on the BIWS catch record data base. Report of the International Whaling Commission 39:363–369.

BEST, P.B. 1994. A review of the catch statistics for modern whaling in southern Africa, 1908-1930. Report of the International Whaling Commission 44:315–322.

BEST, P.B. 2003. How low did they go? An historical comparison of indices of abundance for some baleen whales on the Durban whaling ground. IWC Paper SC/55/SH18. 11 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.

BEST, P.B., R.A. RADEMEYER, C. BURTON, D. LJUNGBLAD, K. SEKIGUCHI, H. SHIMADA, D. THIELE, D. REEB, and D.S. BUTTERWORTH. 2003. The abundance of blue whales on the Madagascar Plateau, December 1996. Journal of Cetacean Research and Management 5:253–260.

BRANCH, T.A. 2006. Separating pygmy and Antarctic blue whales using ovarian corpora. IWC Paper SC/58/SH8. 17 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.

BRANCH, T.A., and D.S. BUTTERWORTH. 2001. Estimates of abundance south of 60ºS for cetacean species sighted frequently on the 1978/79 to 1997/98 IWC/IDCR-SOWER sighting surveys. Journal of Cetacean Research and Management 3:251–270.

BRANCH, T.A., K. MATSUOKA, and T. MIYASHITA. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science 20:726–754.

BRANCH, T.A., and R.A. RADEMEYER. 2003. Blue whale estimates from the IDCR-SOWER surveys: Updated comparisons including results from the 1998/99 to 2000/01 surveys. Report of the Scientific Committee, Annex G, Appendix 11. Journal of Cetacean Research and Management (Suppl.) 5:291–292.

BRANCH, T.A., D.M. PALACIOS, K.M. STAFFORD, C. ALLISON, J.L. BANNISTER, C.L.K. BURTON, P.C. GILL, K.C.S. JENNER, M.-N.M. JENNER, T. MIYASHITA, M.G. MORRICE, V.J. STURROCK, R.C. ANDERSON, A.N. BAKER, P.B. BEST, P. BORSA, S. CHILDERHOUSE, K.P. FINDLAY, A.D. ILANGAKOON, M. JOERGENSEN, B. KAHN, B. MAUGHAN, Y.A. MIKHALEV, OMAN WHALE AND DOLPHIN RESEARCH GROUP, D. THIELE, D. TORMOSOV, K. VAN WAEREBEEK, and R.M. WARNEKE. 2006. Past and present distribution of blue whales in the Southern Hemisphere and northern Indian Ocean. IWC Paper SC/58/SH16. 27 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.

CLARKE, C., A. AGUAYO, and S. BASULTO. 1978. Whale observation and whale marking off the coast of Chile in 1964. Scientific Reports of the Whales Research Institute 30:117–177.

CONWAY, C.A. 2005. Global population structure of blue whales, *Balaenoptera musculus ssp.*, based on nuclear genetic variation. PhD dissertation, University of California Davis. 106 pp.

CUMMINGS, W.C., and P.O. THOMPSON. 1971. Underwater sounds from the blue whale, *Balaenoptera musculus*. Journal of the Acoustical Society of America 50:1193–1198.

DONOVAN, G.P. 1991. A review of IWC stock boundaries. Report of the International Whaling Commission (Special Issue) 13:39–68.

DONOVAN, G.P. 2000. A note on the possible occurrence of pygmy blue whales (*Balaenoptera musculus brevicauda*) south of 60°S. IWC Paper SC/52/OS15. 15 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.

EFRON, B. 1982. The jackknife, the bootstrap and other resampling plans. Society for Industrial and Applied Mathematics, Princeton, NJ.

GAMBELL, R.G. 1964. A pygmy blue whale at Durban. Norsk Hvalfangst-Tidende 53:66–68.

GILPATRICK, J.W.J., W.L. PERRYMAN, R.L. BROWNELL Jr., M.S. LYNN, and M.L. DEANGELIS. 1997. Geographical variation in North Pacific and Southern Hemisphere blue whales (Balaenoptera musculus). IWC Paper SC/49/O9. 33 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.

HILBORN, R., and M. MANGEL. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.
HINTON, M.A.C. 1915. Appendix VII. Report on the papers left by the late Major Barrett-Hamilton relating to the whales of South Georgia. Pages 69–209 *in* Inter-departmental committee on whaling and the protection of whales. Colonial Office Misc. No. 298. Crown Agents for the Colonies, London.
HUCKE-GAETE, R., L.P. OSMAN, C.A. MORENO, K.P. FINDLAY, and D.K. LJUNGBLAD. 2003. Discovery of a blue whale feeding and nursing ground in southern Chile. Biology Letters 271:S170–S173.
ICHIHARA, T. 1961. Blue whales in the waters around Kerguelen Island. Norsk Hvalfangst-Tidende 50(1):1–20.
ICHIHARA, T. 1963. Identification of the pigmy blue whale in the Antarctic. Norsk Hvalfangst-Tidende 52(6):128–130.
ICHIHARA, T. 1966. The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. Pages 79–111 *in* K.S. Norris, ed. Whales, dolphins, and porpoises. University of California Press, Berkeley and Los Angeles.
IWC. 2003. Report of the Scientific Committee. Annexe G: Report of the sub-committee on stock assessment—in depth assessments. Journal of Cetacean Research and Management (Suppl.) 5:248–292.
KATO, H., T. MIYASHITA, and H. SHIMADA. 1995. Segregation of the two sub-species of the blue whale in the Southern Hemisphere. Report of the International Whaling Commission 45:273–283.
KATO, H., H. OKAMURA, A. NOMURA, and E. KOJIMA. 2000. Body length distribution and sexual maturity of southern blue whales, with special reference to sub-species separation. IWC Paper SC/52/OS4. 10 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.
KATO, H., Y. HONNO, H. YOSHIDA, E. KOJIMA, A. NOMURA, and H. OKAMURA. 2002. Further developments on morphological and behavioral key for sub-species discrimination of southern blue whales, analyses from data through 1995/96 to 2001/02 SOWER cruises. IWC Paper SC/54/IA8. 16 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.
LEDUC, R.G., A.E. DIZON, M. GOTO, L.A. PASTENE, H. KATO, S. NISHIWAKI and R.L. BROWNELL Jr. in press. Patterns of genetic variation in southern hemisphere blue whales, and the use of assignment test to detect mixing on the feeding grounds. Journal of Cetacean Research and Management.
LJUNGBLAD, D.K., C.W. CLARK, and H. SHIMADA. 1998. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded off Antarctica. Report of the International Whaling Commission 48:439–442.
MACKINTOSH, N.A. 1942. The southern stocks of whalebone whales. Discovery Reports 22:197–300.
MACKINTOSH, N.A., and J.F.G. WHEELER. 1929. Southern blue and fin whales. Discovery Reports 1:257–540.
MATSUOKA, K., T. HAKAMADA, H. KIWADA, H. MURASE, and S. NISHIWAKI. 2006. Distribution and abundance estimates of blue whales in the Antarctic Areas IIIE, IV, V and VIW (35°E–145°W) based on JARPA data. IWC Paper SC/58/SH7. 9pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.
MCDONALD, M.A., J.A. HILDEBRAND, and S.L. MESNICK. 2006. Biogeographic characterization of blue whale song worldwide: using song to identify populations. Journal of Cetacean Research and Management 8:55–65.
MIKHALEV, Y.A. 1996. Pygmy blue whales of the northern-western Indian Ocean. IWC Paper SC/48/SH30. 30 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.
MIKHALEV, Y.A. 1997. Additional information about the catches of Soviet whaling fleet *Sovetskaya Ukraina*. Report of the International Whaling Commission 47:147–150.
PURVES, P.E. 1955. The wax plug in the external auditory meatus of the Mysticeti. Discovery Reports 27:293–302.
RANKIN, S., D. LJUNGBLAD, C. CLARK, and H. KATO. 2005. Vocalisations of Antarctic blue whales, *Balaenoptera musculus intermedia*, recorded during the 2001/2002 and 2002/2003 IWC/SOWER circumpolar cruises, Area V, Antarctica. Journal of Cetacean Research and Management 7:13–20.
RISTING, S. 1928. Whales and whale foetuses: Statistics of catch and measurements collected from the Norwegian Whalers' Association 1922–25. Rapports et Procès-Verbaux des Réunions 50:1–122.
ŠIROVIĆ, A., J.A. HILDEBRAND, S.M. WIGGINS, M.A. MCDONALD, S.E. MOORE, and D. THIELE. 2004. Seasonality of blue and fin calls and the influence of sea ice in the Western Antarctic Peninsula. Deep-Sea Research II 51:2327–2344.
STAFFORD, K.M., S.L. NIEUKIRK, and C.G. FOX. 1999. Low-frequency whale sounds recorded on hydrophones moored in the eastern tropical Pacific. Journal of the Acoustical Society of America 106:3687–3698.
STAFFORD, K.M., D.R. BOHNENSTIEHL, M. TOLSTOY, E. CHAPP, D.K. MELLINGER, and S.E. MOORE. 2004. Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. Deep-Sea Research I 51:1337–1346.
VAN WAEREBEEK, K., L.A. PASTENE, J. ALFARO-SHIGUETO, J.L. BRITO, and D. MORA-PINTO. 1997. The status of the blue whale Balaenoptera musculus off the west coast of South America. IWC Paper SC/49/SH9. 10 pp. Available from the IWC, The Red House, 135 Station Road, Impington, Cambridge, UK CB4 9NP.
YABLOKOV, A.V. 1994. Validity of whaling data. Nature 367:108.
ZEMSKY, V.A., and E.G. SAZHINOV. 1982. Distribution and current abundance of pygmy blue whales. *in* V. A. Arsen'ev, editor. Marine Mammals. All-Union Research Institute of Marine Fisheries and Oceanography, Moscow [in Russian].

English translation by V.S. Gurevich, edited by M.A. Donahue and R.L. Brownell, Jr., Southwest Fisheries Science Center Administrative Report LJ-94-02, available from National Marine Mammal Laboratory, Seattle WA.

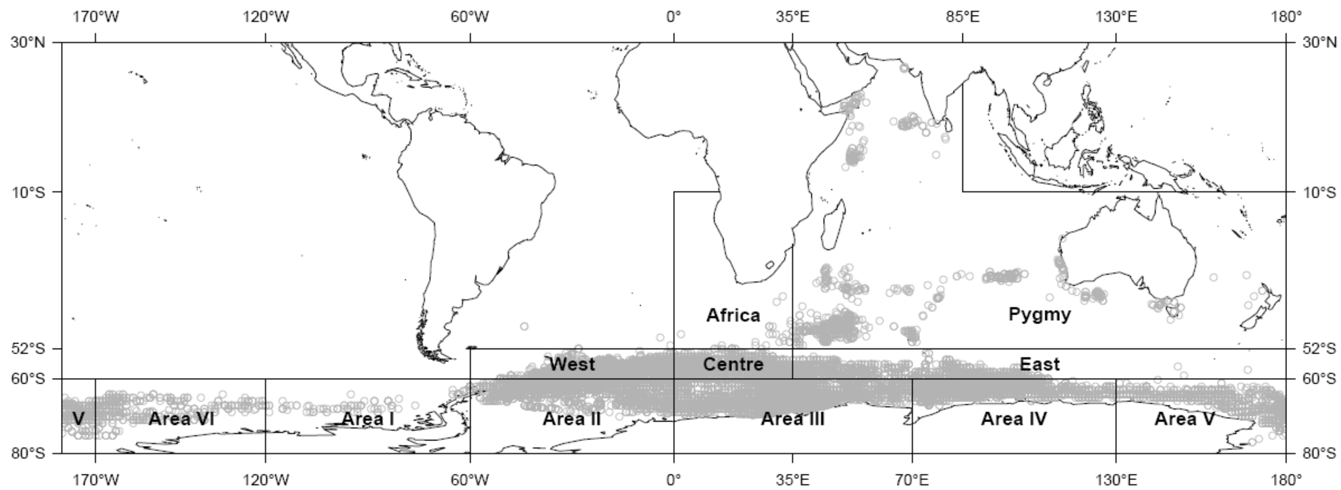

Figure 1. Locations of pelagic catches of pregnant blue whales (grey circles) and the pelagic regions chosen for analysis. In the Antarctic south of 60°S the regions correspond to these southerly components of the IWC Management Areas. Area V occurs on both sides of the map as it runs from 130°E to 170°W. Pelagic catches outside these regions were excluded from the analyses. The Pelagic Pygmy region extends from 52°S northwards to include the northern Indian Ocean and catches to the south of Madagascar.

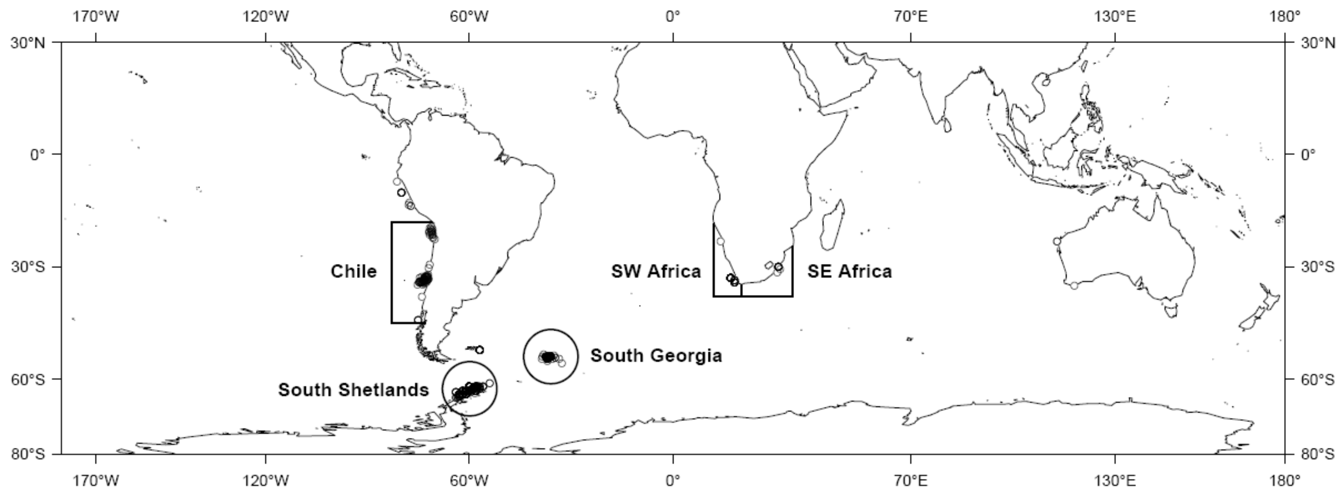

Figure 2. Catch positions of pregnant blue whales (circles) from land station. The regions chosen for analysis are enclosed inside bold lines. Land station catches outside these regions were excluded from the analyses.

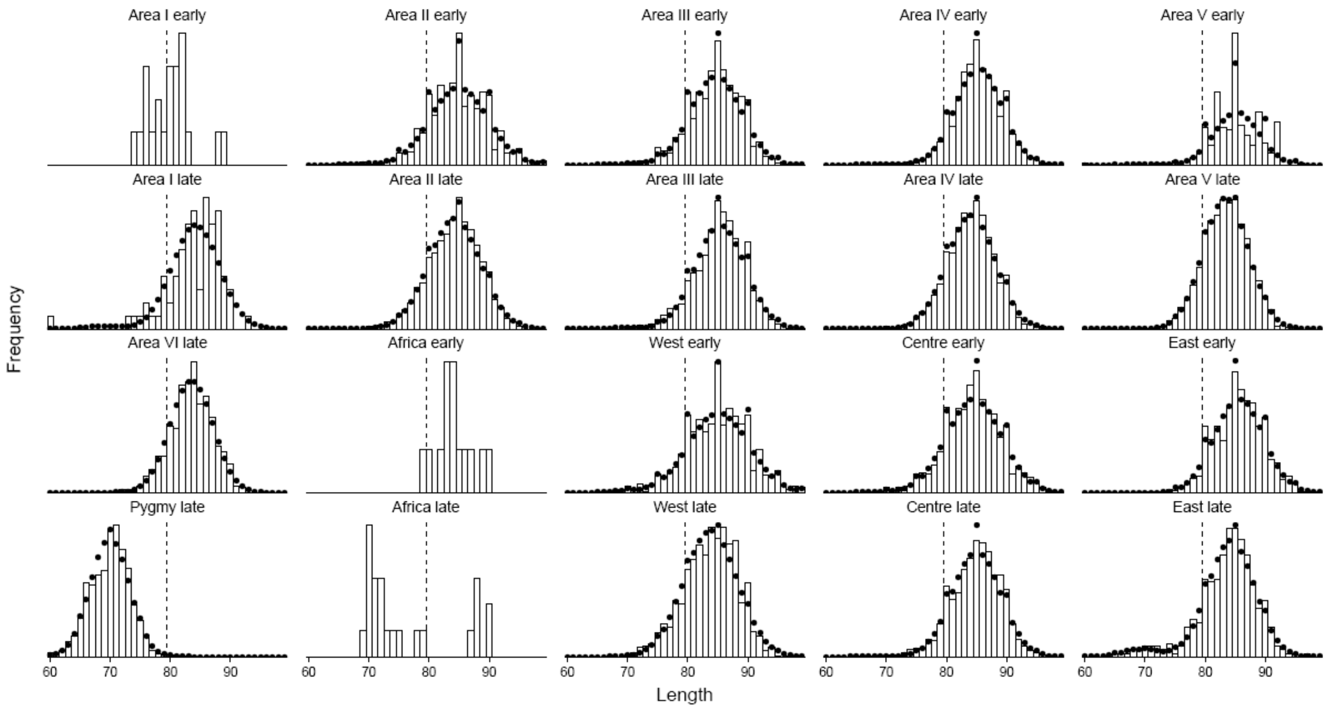

Figure 3. Length frequencies (bars) and mixture model estimates (posterior mode shown by solid circles) for sexually mature blue whale females in different pelagic regions. The early period is 1913/14–1936/37 and the late period is 1937/38–1972/73. A vertical dashed line indicates the 79.5 ft maximum pygmy blue whale length. In some panels the model estimates are higher at every 5 ft interval because of the high estimated proportion of 5-ft rounding in those areas. There are no model estimates for Pelagic Area I early and Pelagic Africa early and late because these groupings included fewer than 35 individuals, which was considered too few to yield reliable results.

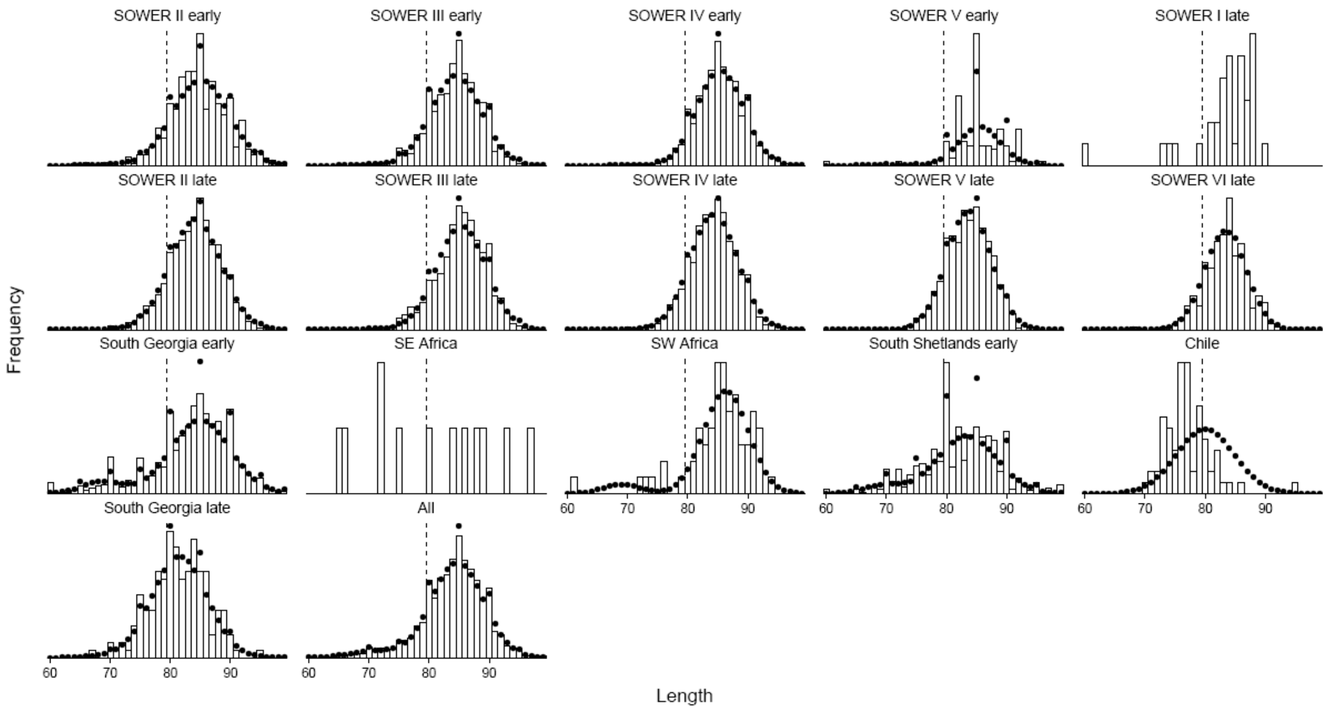

Figure 4. Length frequencies (bars) and mixture model estimates (posterior mode shown by solid circles) for sexually mature blue whale females caught in regions (south of 60°S) and days of the year (29 December–12 February) corresponding to those surveyed during the recent IDCR/SOWER sighting surveys, and for sexually mature blue whale females caught in the shore-based regions. The early period is 1913/14–1936/37 and the late period is 1937/38–1972/73. A vertical dashed line indicates the 79.5 ft maximum pygmy blue whale length. In some panels the model fits are higher at every 5 ft interval because the model estimates of the proportion of 5-ft rounding were high in those areas. There are no model estimates for SOWER I late and SE Africa because these groupings included fewer than 35 individuals, which was considered too few to yield reliable results.

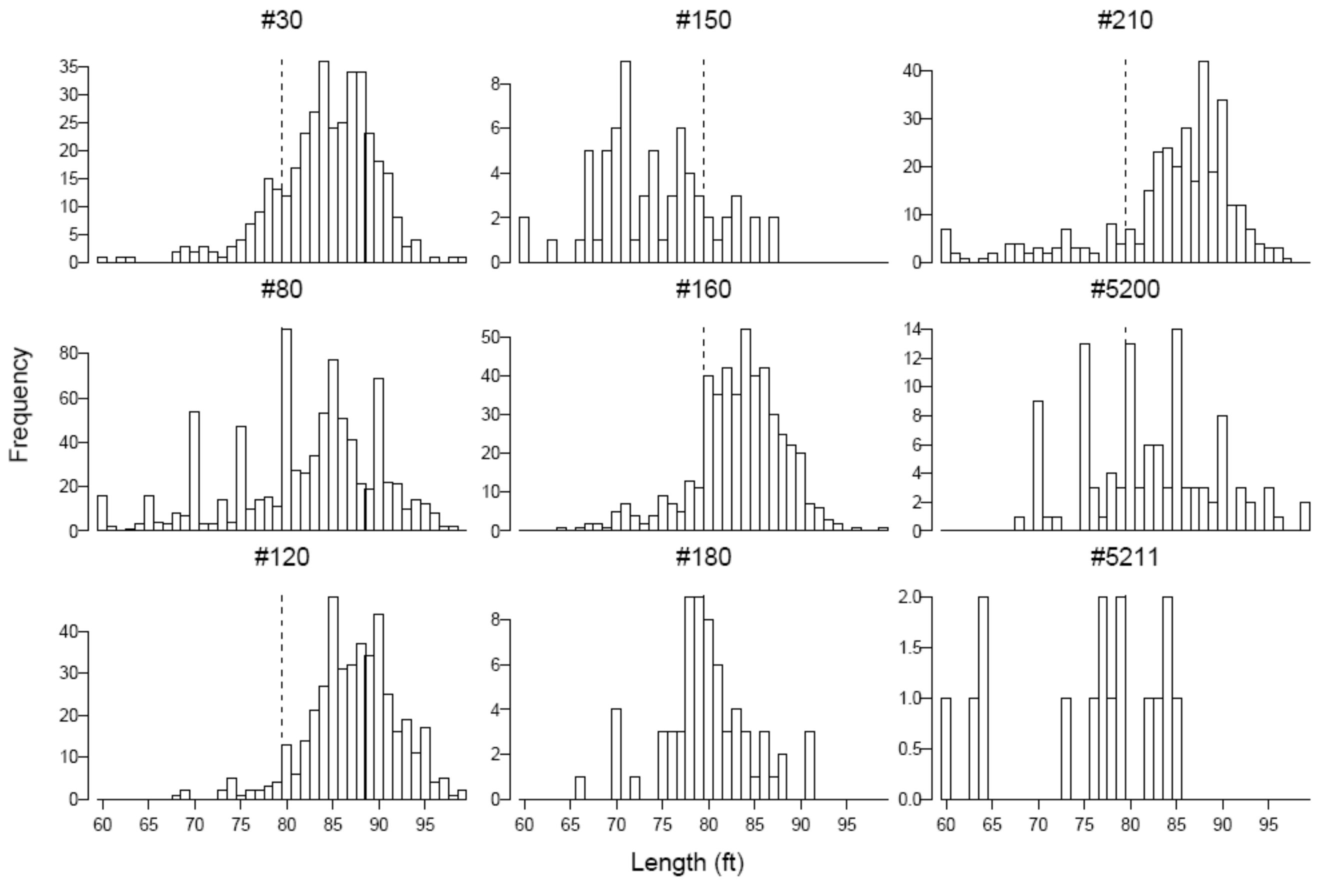

Figure 5. Length frequencies of blue whales recorded for each catch station operating out of South Georgia in the early period (1913/14–1936/37). A vertical dashed line indicates the 79.5 ft maximum pygmy blue whale length.

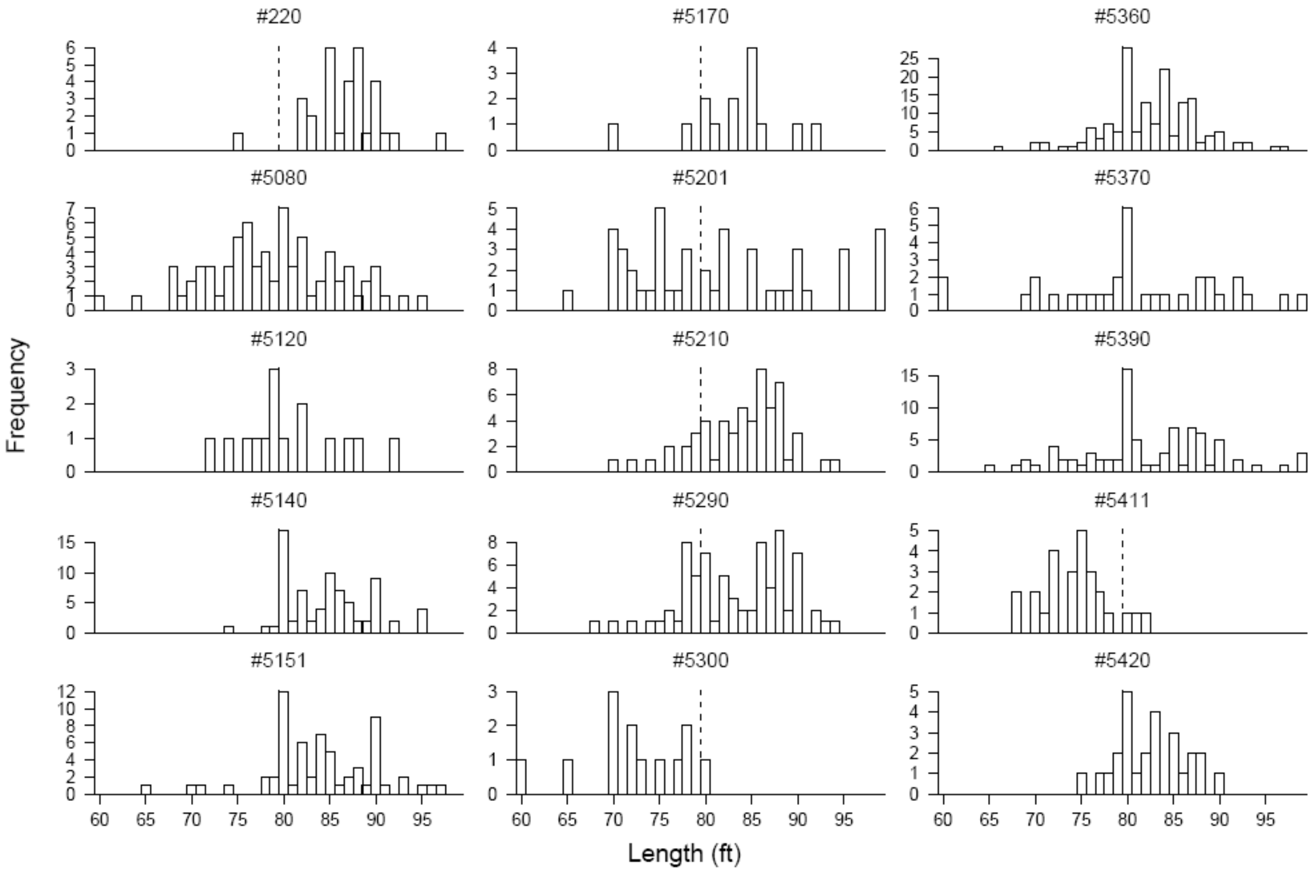

Figure 6. Length frequencies of mature females recorded by different catch stations in the South Shetlands (1917/1918–1930/31 seasons). A vertical dashed line indicates the 79.5 ft maximum pygmy blue whale length.

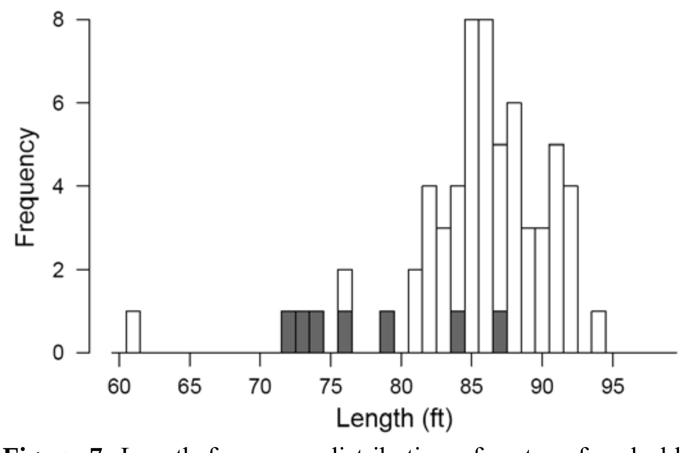

Figure 7. Length frequency distribution of mature female blue whales taken from SW Africa. Dark grey bars represent whales taken by expedition #4570 from Hangklip in 1914, while white bars represent whales taken in all other years from Saldanha Bay and Hangklip.

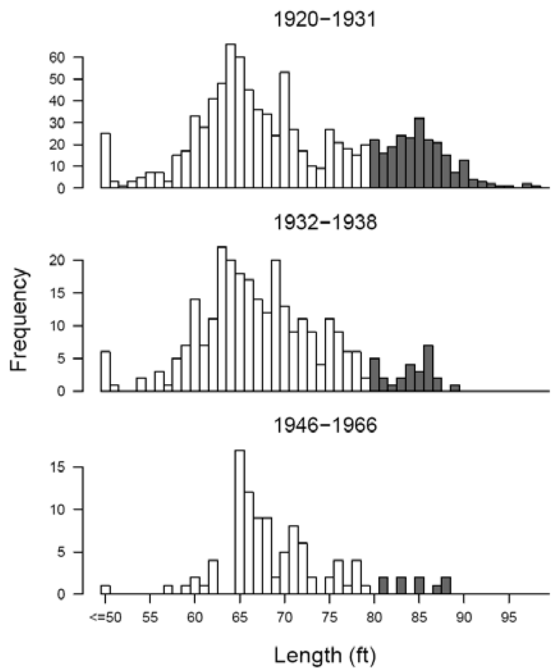

Figure 8. Length frequencies of all female blue whales (both mature and immature) taken at Durban, SE Africa, in different time periods. Dark gray bars represent whales longer than the maximum recorded for pygmy blue whales.

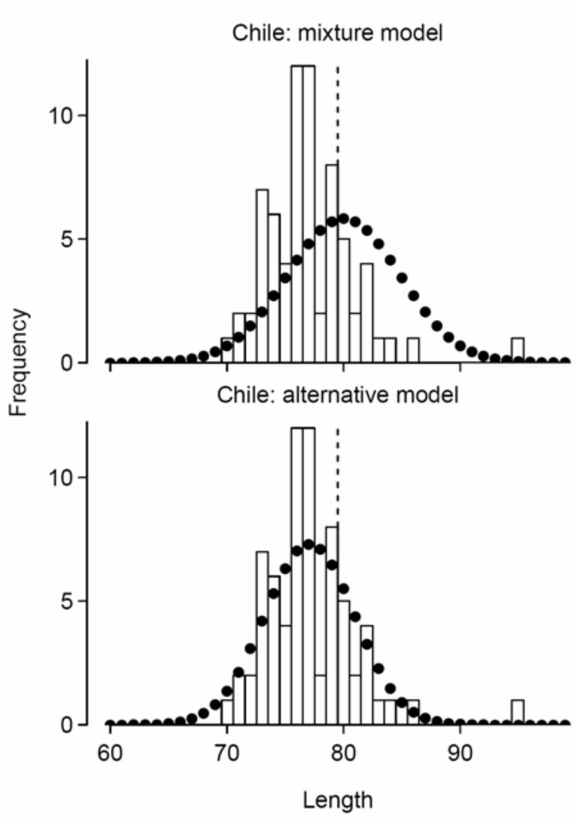

Figure 9. Chilean data for mature female blue whales and corresponding fits of the six-parameter mixture model (upper panel) and the alternative three parameter single normal model (lower panel). Means in the mixture model are constrained to ≤ 71 ft for pygmy blue whales and ≥ 80 ft for Antarctic blue whales, while in the alternative model the single mean is constrained to be within the 71–80 ft interval. The proportion of rounding to the nearest 5 ft interval is estimated to be zero for both models.

Table 1. Mixture model results for each region and time period, showing the sexually mature female catches, total catches, and posterior median estimates of the model parameters. The late period starts in 1937/38. The parameters are the proportion of pygmy blue whales (p) and associated 95% intervals, proportion of catches rounded to nearest 5 ft interval (p_5), mean length of pygmy blue whales (μ_p), standard deviation of pygmy blue whales (σ_p), mean length of Antarctic blue whales (μ_a), and standard deviation of Antarctic blue whales (σ_a).

Category	Region	Period	Mature ♀	Catch total	p (95% intervals)		p_5	μ_p	σ_p	μ_a	σ_a
Pelagic	I	Early	22	240	–	–	–	–	–	–	–
Pelagic	II	Early	1,191	12,597	0.008	(0.003; 0.016)	0.111	68.89	3.17	84.97	4.77
Pelagic	III	Early	3,149	28,874	0.011	(0.007; 0.018)	0.094	69.55	3.15	84.71	4.22
Pelagic	IV	Early	3,203	29,291	0.006	(0.003; 0.009)	0.073	69.30	3.18	85.34	3.88
Pelagic	V	Early	234	5,247	0.011	(0.002; 0.034)	0.169	68.84	3.19	85.20	3.71
Pelagic	VI	Early	0	1	–	–	–	–	–	–	–
Pelagic	I	Late	79	764	0.034	(0.005; 0.103)	0.026	68.83	3.19	84.31	3.92
Pelagic	II	Late	2,511	15,045	0.003	(0.000; 0.009)	0.035	69.13	3.17	84.23	4.31
Pelagic	III	Late	3,222	21,367	0.010	(0.006; 0.015)	0.056	69.59	3.17	85.40	4.15
Pelagic	IV	Late	3,240	22,084	0.004	(0.001; 0.008)	0.039	69.20	3.16	84.07	4.03
Pelagic	V	Late	1,252	9,476	0.001	(0.000; 0.005)	0.023	68.95	3.17	83.41	3.73
Pelagic	VI	Late	543	4,583	0.006	(0.001; 0.016)	0.015	68.99	3.17	83.54	3.54
Pelagic	Pygmy	Early	1	12	–	–	–	–	–	–	–
Pelagic	Africa	Early	14	97	–	–	–	–	–	–	–
Pelagic	West	Early	2,069	19,836	0.015	(0.009; 0.023)	0.118	69.26	3.16	85.17	4.96
Pelagic	Centre	Early	2,406	22,347	0.010	(0.005; 0.017)	0.081	69.17	3.16	84.56	4.61
Pelagic	East	Early	1,065	12,683	0.002	(0.000; 0.007)	0.083	68.97	3.17	85.60	4.04
Pelagic	Pygmy	Late	991	9,797	0.999	(0.994; 1.000)	0.021	69.93	3.24	83.69	3.43
Pelagic	Africa	Late	23	138	–	–	–	–	–	–	–
Pelagic	West	Late	1,503	8,611	0.002	(0.000; 0.009)	0.020	69.02	3.17	83.82	4.45
Pelagic	Centre	Late	1,442	10,727	0.005	(0.002; 0.011)	0.052	69.06	3.17	84.98	4.01
Pelagic	East	Late	458	3,380	0.052	(0.031; 0.075)	0.037	69.28	3.17	84.29	3.88
SOWER	I	Early	4	26	–	–	–	–	–	–	–
SOWER	II	Early	587	5,346	0.010	(0.003; 0.023)	0.077	68.80	3.17	85.02	4.71
SOWER	III	Early	1,620	14,534	0.010	(0.005; 0.018)	0.091	69.20	3.17	84.51	4.21
SOWER	IV	Early	1,627	14,738	0.004	(0.001; 0.010)	0.077	69.15	3.17	85.40	3.87
SOWER	V	Early	110	1,792	0.023	(0.005; 0.061)	0.244	68.82	3.18	85.54	3.55
SOWER	VI	Early	0	1	–	–	–	–	–	–	–
SOWER	I	Late	34	410	–	–	–	–	–	–	–
SOWER	II	Late	1,387	8,067	0.004	(0.000; 0.013)	0.040	69.10	3.17	84.14	4.28
SOWER	III	Late	1,549	10,548	0.008	(0.003; 0.014)	0.055	69.14	3.18	85.33	4.11
SOWER	IV	Late	1,726	11,319	0.004	(0.001; 0.010)	0.033	69.15	3.17	84.35	3.98
SOWER	V	Late	705	5,652	0.001	(0.000; 0.007)	0.039	68.92	3.17	83.72	3.68
SOWER	VI	Late	282	2,015	0.007	(0.001; 0.023)	0.028	68.91	3.17	83.40	3.45
Land stations	S Georgia	Early	2,710	31,939	0.104	(0.090; 0.119)	0.143	68.76	3.42	85.00	4.95
Land stations	S Georgia	Late	160	1,572	0.019	(0.001; 0.060)	0.078	68.96	3.17	81.58	4.51
Land stations	SE Africa	Early+late	12	2,489	–	–	–	–	–	–	–
Land stations	SW Africa	Early+late	63	7,547	0.077	(0.019; 0.169)	0.045	69.00	3.19	86.32	3.89
Land stations	SW Africa[1]	Early+late	56	7,504	0.037	(0.006; 0.107)	0.056	68.83	3.18	86.70	3.52
Land stations	S Shetland	Early	801	14,527	0.083	(0.060; 0.113)	0.188	69.42	3.20	83.44	4.97
Land stations	S Shetland	Late	0	0	–	–	–	–	–	–	–
Land stations	Chile	Early+late	71	2,270	0.039	(0.002; 0.156)	0.037	69.05	3.17	80.11	4.60

[1]SW Africa excluding catches from the 1914 Hangklip station.

Table 2. Posterior median estimates of pygmy blue whale catch, Antarctic blue whale catch and the catch-weighted estimate of the proportion of pygmy blue whales, $\overline{p}$, for each grouping of regions. The 95% intervals are given. "Total" catches include only those catches for which sex, length and geographic position were available.

Regions	Pygmy	95%	Antarctic	95%	$\overline{p}$	95%
Pelagic Antarctic (south of 60°S)	1,097	(800; 1,492)	148,231	(147,836; 148,528)	0.007	(0.005; 0.010)
Pelagic West, Centre, East (52–60°S, east of 60°W)	825	(618; 1,079)	76,759	(76,505; 76,966)	0.011	(0.008; 0.014)
Pelagic (south of 52°S)	1,918	(1,489; 2,478)	224,994	(224,434; 225,423)	0.008	(0.007; 0.011)
Pelagic Pygmy (north of 52°S, east of 35°E)	9,784	(9,739; 9,797)	13	(0; 58)	0.999	(0.994; 1.000)
"SOWER" total (subset of pelagic Antarctic)	524	(349; 751)	73,487	(73,260; 73,662)	0.007	(0.005; 0.010)
Shore-based South Georgia	3,344	(2,905; 3,831)	30,167	(29,680; 30,606)	0.100	(0.087; 0.114)
Shore-based South Shetlands	1,210	(874; 1,635)	13,317	(12,892; 13,653)	0.083	(0.060; 0.113)
Shore-based SW Africa	579	(143; 1,275)	6,968	(6,272; 7,404)	0.077	(0.019; 0.169)
All pelagic	11,695	(11,264; 12,261)	225,014	(224,448; 225,445)	0.049	(0.048; 0.052)
All shore-based	5,150	(4,377; 6,128)	50,435	(49,457; 51,208)	0.093	(0.079; 0.110)
All pelagic plus shore-based	16,849	(15,914; 18,022)	275,445	(274,272; 276,380)	0.058	(0.054; 0.062)