Separating pygmy and Antarctic blue whales using ovarian corpora

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ABSTRACT
Two Southern Hemisphere subspecies of blue whales exist: pygmy blue whales are shorter (≤ 79 ft, 24.2 m) and generally found north of 54°S in summer, while Antarctic (true) blue whales exceed 100 ft (30.5 m) and are found in more southerly waters. Abundance estimates of Antarctic blue whales rely on sightings south of 60°S but at-sea identification is difficult and these sightings may include some proportion of pygmy blue whales. Ovarian corpora (corpora lutea plus corpora albicantia) are permanent ovulation records that can be used to estimate this proportion. Pregnant females of the two subspecies may overlap at 72–79 ft (21.9–24.1 m), but pygmy blue whales at these lengths have high (> 4) corpora counts, contrasting with immature or newly mature Antarctic blue whales (0–3 corpora). Published papers yielded pairs of length-corpora data for 104 pygmy and 2,064 Antarctic region blue whales. The relationship between length and ovarian corpora counts is well fitted by logistic models (with negative binomial variability). A mixture model estimates that 0.4% (95% confidence interval 0.0–1.1%) of Antarctic region blue whales were pygmy blue whales, much lower than the "less than 7%" currently accepted by the IWC. If later ovarian corpora data (1947–51) are separately analysed, the estimated proportion is zero (95% CI = 0.0–0.5%), suggesting that the pygmy proportion in the Antarctic did not increase when Antarctic blue whales were greatly depleted. No support is found for Ichihara's suggestion that high (>7) ovarian corpora counts in 78–81 ft Antarctic region catches were pygmy blue whales. These whales are instead explained by natural variability in Antarctic blue whales. These methods could be applied to blue whale males through the analysis of testes weight, and may hold promise in separating catches of other species with diminutive forms such as fin and minke whales.

INTRODUCTION

There are two recognised subspecies of blue whales in the Southern Hemisphere: Antarctic (true) blue whales (*Balaenoptera musculus intermedia*) and pygmy blue whales (*B. m. brevicauda*). Pygmy blue whales are distinguished by their shorter maximum lengths (24.1 m vs. >30 m), shorter average length at sexual maturity (19.2 m vs. 23.7 m), relatively shorter baleen plates, and a relatively shorter tail region (Mackintosh and Wheeler 1929, Ichihara 1966). The two subspecies also differ somewhat genetically (LeDuc et al. 2003, Conway 2005), have distinctive acoustic calls (McDonald et al. in press), and inhabit geographically distinct regions in the austral summer, with Antarctic blue whales generally found south of 60°S and pygmy blue whales north of 54°S (Ichihara 1966, Kato et al. 1995). However, at-sea subspecies identification of sightings is difficult, although subspecies assignment can be made to a high degree of probability if close and prolonged examination is possible (Kato et al. 2001, Kato et al. 2002). For this reason, recent abundance estimates from the IDCR/SOWER and JARPA programmes are assumed to apply to Antarctic blue whales since the data are obtained from south of 60°S in the Antarctic (Branch and Butterworth 2001, Matsuoka et al. 2005). These sightings may contain a small proportion of pygmy blue whales, assumed by the IWC Scientific Committee to be no more than 7% (IWC 2003). The proportion of the two subspecies in historical catches is an open question. Pygmy blue whales were only identified and described in the early 1960s (Ichihara 1961, 1963, 1966), just before the ban on catching blue whales and thus the great majority of catches are not assigned to subspecies. Some of the catches in Antarctic waters may have been pygmy blue whales, conversely, some of the more northerly catches may have been Antarctic blue whales.

Estimates of the proportion of pygmy blue whales in Antarctic waters south of 55°S are largely reliant on historical data. Over this period pygmy blue whales have been depleted far less than Antarctic blue whales, with the result that this proportion may be much greater now than in historical times. Using this reasoning, LeDuc et al. (2001) suggest that as many as 32.1% of the blue whales in Antarctic waters may be pygmy blue whales. This hypothesis can be tested by estimating the proportion over different time periods. An increasing trend in estimates would provide support for this hypothesis.

Subspecies discrimination can be addressed using the IWC's catch database that contains the position, sex, length and pregnancy status of blue whales in the Southern Hemisphere. Mean length at sexual maturity for Antarctic blue whales is 23.7 m, therefore pregnant females shorter than this length are most likely to be pygmy blue whales, while the maximum length of pygmy blue whales is 24.1 m, thus whales longer than this should be Antarctic blue whales. In principle, length and pregnancy status should therefore be good determinants of subspecies. Donovan (2000) found that 1.99% of the pregnant or lactating females south of 60°S were smaller than 75 ft or 23 m[1], and considered these to be probable pygmy blue whales; and Kato et al. (2000) recorded one out of 114 (0.9%) pregnant blue whales to be smaller than 75 ft. However, while the

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[1] The majority of blue whale catches (and all the data used in this paper) were recorded in whole English feet (0.3048 m). Many features of the data are dependent on these whole units of measurement, and thus feet and metres are used interchangeably in this paper.

mean length at sexual maturity in Antarctic blue whales is 23.7 m (Mackintosh and Wheeler 1929, Mackintosh 1942), there is considerable individual variability, implying that these whales might have been short pregnant Antarctic blue whales and not pygmy blue whales. These analyses are also complicated because the database may contain errors in recording or measurement at similar levels to the estimated proportion of pygmy blue whales. Analyses of pregnant-female length distributions could be improved by assuming them to be a mixture of three distributions: (1) pygmy blue whales, (2) Antarctic blue whales, and (3) errors. This solution is currently being investigated (Branch, Mkango and Nasr, in prep.).

An alternative solution is to investigate the relationship between length and ovarian corpora in pregnant females. Corpora lutea are large conspicuous soft bodies formed in blue whale ovaries during pregnancy that afterwards diminish in size to become corpora albicantia (Mackintosh 1942). Many previous authors (e.g. Laurie 1937, Mackintosh 1942) have referred to both corpora lutea and corpora albicantia as "corpora lutea", but the term "ovarian corpora" is preferred here. Ovarian corpora are thought to provide a persistent record of lifetime ovulations in large whales (Mackintosh 1942), although at least in bottlenose dolphins there is evidence that they only record pregnancies (Brook et al. 2002). Whichever is true, sexually immature females have no ovarian corpora, while sexually mature (pygmy) blue whales accumulate ovarian corpora at about one every 2.5 years (Ohsumi 1979). Physical maturity (cessation of growth) in the Antarctic is reached at 11–12 ovarian corpora (Laurie 1937, Brinkmann 1948). These characteristics make ovarian corpora counts useful for blue whale subspecies discrimination, especially for those whales of intermediate length (72–79 ft, 21.9–24.1 m) that could either be short sexually mature Antarctic blue whales (with low corpora counts) or old pygmy blue whales (with high corpora counts). In this paper, ovarian corpora counts from published sources are examined to estimate the proportion of pygmy blue whales in the Antarctic catches, by assuming that Antarctic ovarian corpora counts are a combination of the distribution expected for Antarctic blue whales, and that expected for pygmy blue whales.

Previous authors have also noted this relationship and suggested that high corpora counts at small lengths indicate the presence of pygmy blue whales. Ichihara (1961) noted that Laurie (1937) found a number of ovaries from 78–81 ft (23.8–24.7 m) blue whales with high (7–29) ovarian corpora counts. Laurie had concluded these were in error, although these doubtful ovaries amounted to 4.3% of his total collection[2], but Ichihara (1961) suggested these were pygmy blue whales in Antarctic waters. Ichihara's hypothesis has the implications that: (1) many pygmy blue whales should be between 78 and 81 ft, (2) the proportion of doubtful ovarian corpora counts should decrease with increasing length as pygmy blue whales should be rarer at longer lengths, and (3) the geographic distribution of the doubtful ovaries should be in more northerly areas. These assertions are tested here.

METHODS

Data included and excluded

Ovarian corpora counts and corresponding lengths were obtained from published sources (Table 1). In most cases the data were read from figures in the papers but were also obtained from tables, text or appendices. Some papers were unsuitable for inclusion in the analysis as they only published selected data for particular lengths. Brinkmann (1948) and Mackintosh and Wheeler (1929) are excluded because they did not publish data for blue whales with zero ovarian corpora, although their non-zero records follow a similar distribution to those from other sources. Ruud and Jonsgård (1950) are also excluded since they only published data for selected whales (28 out of 653), including four females (0.6% of the total) each with a single corpus luteum and lengths of 65, 71, 74, 74 ft. The latter three were all taken by a single expedition (the *Suderøy*) in narrow geographical limits in Area III together with small mature males in the same region, suggestive of pygmy blue whales. Data for fin whales were also collected to see if the same relationship between length and ovarian corpora existed in other whale species.

Maximum recorded length for pygmy blue whales

The maximum recorded length for pygmy blue whales is required because it determines over what range of lengths the ovarian corpora data should be modeled as a mixture of pygmy and Antarctic blue whales, and also addresses questions about the problematic ovarian corpora in Laurie (1937). A literature review was conducted and the IWC catch database examined in the years and regions where Japanese and USSR fleets caught large numbers of pygmy blue whales.

Model fitting

Relationship between length and average ovarian corpora count

For a given length there will be an expected distribution of ovarian corpora counts. At small lengths, almost all whales are immature and have zero ovarian corpora counts. For lengths between sexual maturity and physical maturity, the mean ovarian corpora count will increase for every length step. At and above the mean length at physical maturity, nearly all whales have stopped growing and the mean ovarian corpora count will reach an asymptote. The 3-parameter logistic model provided a

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[2] The original data in Appendix II of this study (Laurie 1937) differs from the text. On page 245, 45 pairs of ovaries (4.3% of the 1058 whales with ovarian corpora and length data) are listed as being doubtful, but the appendix contains 58 ovaries (5.5% of the total) from blue whales with lengths 78–81 feet and greater than seven ovarian corpora. Ichihara (1961) states there are 45 pairs amounting to 6% of the total. Appendix II in Laurie (1937) itself contains a number of obvious typographical errors, e.g. one Antarctic catch at 28°S (serial #721), another with a ovarian corpora count of 111 (#581). The discrepancy in problematic ovaries (45 vs. 58) may thus be due to typographical errors in the Appendix.

good fit to the relationship between length and mean ovarian corpora count for pygmy and Antarctic blue whales and for fin whales:

$$\mu_L = \frac{C_{\max}}{1+\exp\left(-\ln 19 \cdot \frac{L-L_{50}}{L_{95}-L_{50}}\right)}$$

Where:

$C_{\max}$ is the asymptotic average ovarian corpora count at great lengths

L_{50} is the length at which the average ovarian corpora count is 50% of $C_{\max}$

L_{95} is the length at which the average ovarian corpora count is 95% of $C_{\max}$

μ_L is the average ovarian corpora count for whales of length L in ft

Distribution of ovarian corpora counts for a particular length

The logistic model provides estimates of the mean ovarian corpora count for a particular length, but it is also necessary to model the distribution of ovarian corpora counts around the mean. The data suggest that at shorter lengths this distribution is roughly negative exponential but at longer lengths it is more lognormal. The Poisson, lognormal, gamma and negative binomial distributions were tested but the negative binomial (equation 3.102 in Hilborn and Mangel 1997) provided a greatly superior fit to the available sets of data, and therefore the other distributions are not discussed further. The negative binomial has two parameters: the mean (μ_L as obtained from the logistic model) and the overdispersion parameter (n_L , one for each length), with the following properties:

$$P(X=x\,|\,L) = \frac{\Gamma(n_L+x)}{\Gamma(n_L)x!}\left(\frac{\mu_L}{n_L+\mu_L}\right)^x\left(\frac{n_L}{n_L+\mu_L}\right)^{n_L},$$

$$E[X\,|\,L]=\mu_L,\ \ \mathrm{var}[X\,|\,L]=\mu_L+\frac{\mu_L^2}{n_L}$$

where x is the number of ovarian corpora.

The overdispersion parameters are further reduced to a single parameter by assuming that variance at each length is a multiplicative factor *m* of the mean μ_L . The overdispersion parameters can therefore be rewritten as a function of *m* and μ_L :

$$\mathrm{var}(X)=\mu_L+\frac{\mu_L^2}{n_L}=\mu_L m, \qquad m>1$$

Hence $n_L = \dfrac{\mu_L}{m-1}$

Fitting to pygmy blue whale ovarian corpora data

Maximum likelihood estimates (MLEs) of the four parameters ($C_{\max}, L_{50}, L_{95}$ and m) are obtained for pygmy blue whales by minimizing the sum of the negative log-likelihood (NLLs) for the 104 pairs of length and ovarian corpora data (L_i, x_i) :

$$NLL=\sum_i\left[-\ln\Gamma(n_L+x_i)+\ln\Gamma(n_L)+\ln\Gamma(x_i+1)-x_i\ln\left(\frac{\mu_L}{n_L+\mu_L}\right)-n_L\ln\left(\frac{n_L}{n_L+\mu_L}\right)\right]$$

Fitting to ovarian corpora data from the Antarctic region

Whales from the Antarctic region that are ≤ 79 ft (the assumed maximum length of pygmy blue whales) are modelled as a mixture of two distributions, with a probability *p* of being pygmy blue whales and a probability $(1-p)$ of being Antarctic blue whales. For whales longer than 79 ft, all are assumed to come from the Antarctic blue whale distribution. Estimates for $C_{\max}, L_{50}, L_{95}$ and *m* for pygmy blue whales are fixed at the MLE values obtained from the pygmy blue whale data, but it is necessary to estimate *p* as well as the corresponding parameters $C'_{\max}, L'_{50}, L'_{95}$ and m' for Antarctic blue whales. The NLL to minimize for the $n'=2{,}064$ pairs of Antarctic region length and ovarian corpora data (L_i, x_i) is:

$$NLL = \sum_{i=1}^{n'} \begin{Bmatrix} -\ln\left[p\dfrac{\Gamma(n_L + x_i)}{\Gamma(n_L)x_i!}\left(\dfrac{\mu_L}{n_L+\mu_L}\right)^{x_i}\left(\dfrac{n_L}{n_L+\mu_L}\right)^{n_L} + (1-p)\dfrac{\Gamma(n'_L + x_i)}{\Gamma(n'_L)x_i!}\left(\dfrac{\mu'_L}{n'_L+\mu'_L}\right)^{x_i}\left(\dfrac{n'_L}{n'_L+\mu'_L}\right)^{n'_L}\right] & \text{for } L_i \le 79 \\ -\ln\left[\dfrac{\Gamma(n'_L + x_i)}{\Gamma(n'_L)x_i!}\left(\dfrac{\mu'_L}{n'_L+\mu'_L}\right)^{x_i}\left(\dfrac{n'_L}{n'_L+\mu'_L}\right)^{n'_L}\right] & \text{for } L_i > 79 \end{Bmatrix}$$

Where: $\mu'_L = \dfrac{C'_{\max}}{1+\exp\left(-\ln 19 \cdot \dfrac{L_i - L'_{50}}{L'_{95} - L'_{50}}\right)}$ and $n'_L = \dfrac{\mu'_L}{m'-1}$

The parameter p is the estimated proportion of pygmy blue whales only for the $n = 451$ blue whales that were ≤ 79 ft . The estimated proportion of pygmy blue whales among the $n' = 2,064$ whales of all lengths in the Antarctic region is:

$$p_{\text{pygmy}} = \frac{np}{n'}$$

Minimization methods
MLEs were obtained using AD Model Builder™ and double-checked using Solver in Excel. Reported results were those obtained in AD Model Builder™.

Sensitivity test for changing proportions over time
Data from the Antarctic region is divided roughly equally between two time periods: 1,058 came from 1934-36 (Laurie 1937), and 1,006 from 1947–51 (Nishiwaki and Hayashi 1950, Mizue and Murata 1951, Nishiwaki and Oye 1951, Ohno and Fujino 1952). According to the calculations in Branch et al. (2004), Antarctic blue whales had been depleted to 46% of pristine levels in 1935 and to 14% in 1949. During the same period, the pygmy blue whale population is thought to have remained nearly untouched. If the hypothesis of LeDuc et al. (2001) is correct, the estimated proportion of pygmy blue whales in the later period data should be 3.3 times higher than in the earlier period. To test this hypothesis, the data are divided into early and late periods and the proportion of pygmy blue whales in each set of data is estimated.

Laurie's problematic ovarian corpora
The geographic locations for ovarian corpora data in Laurie (1937) are plotted to detect any geographical patterns in the problematic ovarian corpora (length ≤ 81 ft, ovarian corpora > 7). A chi-square test was conducted to see if the geographic patterns deviated from that expected from random chance alone. The data were binned into latitude/longitude categories (68°S-60°S, 54°S–60°S) and (60°W–0°, 0°–60°E, 60°E–120°E), expected numbers of problematic ovarian corpora calculated (by multiplying the total number in each bin by the overall proportion of problematic ovarian corpora), and the chi-square test applied.

RESULTS

Ovarian corpora data
Data used in the analyses are contained in tables for Antarctic region blue whales (Table 2), Antarctic region blue whales from Laurie (1937) (Table 3), pygmy blue whales (Table 4), and fin whales (Table 5). Plots of ovarian corpora counts against length revealed two distinct clouds of points: one for pygmy blue whales and one from the Antarctic region (Figure 1). Between 68 and 73 ft all 70 pygmy blue whales had non-zero ovarian corpora counts, while only one out of 75 Antarctic region blue whales had non-zero counts. Between 74 and 77 ft, pygmy blue whales had 4–22 ovarian corpora (mean 9.1), while 152 out of 160 Antarctic region whales had 0–3 ovarian corpora (mean 1.0). For Antarctic catches at lengths 79 ft and longer there is a great range of ovarian corpora counts, and above 88 ft only one out of 337 Antarctic region blue whales had zero ovarian corpora. Only five out of 2,064 (0.2%) Antarctic catches had higher ovarian corpora counts than any pygmy blue whales of the same length or longer.

The shape of the relationship between length and ovarian corpora count in Antarctic region blue whales is similar to that for fin whales (Figure 2). Only 2 of 107 fin whales 62 ft or shorter had non-zero ovarian corpora counts, while fin whales of lengths 68 ft and greater had a great range of ovarian corpora counts, and only one of 72 ft or longer had zero ovarian corpora.

Maximum recorded length for pygmy blue whales
Ichihara (1966, p. 94) and Ichihara (1981) both reported the longest female caught by Japanese expeditions to be 24.1 m (79 ft), but Ichihara (1966, p. 109) also states that "no individual exceeding 24.4 m (80 ft) has been captured", presumably a

slight mistranslation of the previous fact. A posthumous publication of Ichihara's original data included a 24.2 m (79 ft 5 in) female (Omura 1984). A pygmy blue whale of 24.0 m (78 ft 9 in) is the only reported USSR catch out of 1,294 in the north-west Indian Ocean that exceeded 23.5 m (76 ft 5 in) (Mikhalev 1996, Mikhalev 2000).

The IWC database was examined for Japanese catches in 1959/60–1962/63 and USSR catches during 1962/63–1972/73 in the region and seasons in which nearly all pygmy blue whales were caught (north of 52°S, 35°E–180°E). Japanese catches included blue whales measuring 80 ft (24.4 m, *n*=3), 82 ft (25.0 m), 86 ft (26.2 m) and 89 ft (27.1 m). USSR catches included blue whales measuring 24.3 m (79 ft 8 in), 24.5 m (80 ft 5 in, *n*=2), and 25.7 ft (84 ft 4 in). All 10 of these catches were female, and none were identified in the database to subspecies level. There were 4,750 blue whales in this region with length measurements, of which 0.2% were greater than 79 ft.

In conclusion, the most likely maximum length for pygmy blue whales is 24.1–24.2 m (79 ft–79 ft 5 in). Data from the catch database suggests a small proportion (0.2%) in pygmy blue whale waters greater than this length but these could be Antarctic blue whales north of their usual distribution or typographical errors in position or length.

Model fitting

The logistic equation provided a good fit to the relationship between length and mean ovarian corpora count (Figure 3), and the negative exponential distribution also provided good fits to the distributions of ovarian corpora counts at each length for pygmy blue whales (Figure 4) and Antarctic region blue whales (Figure 5). The total NLL for the model fit was 6171.46.

Pygmy blue whales had a much smaller L_{50} and L_{95} than Antarctic blue whales (Table 6). In addition, the maximum average ovarian corpora count $C_{\max}$ was also lower (10.5 vs. 14.3), although the confidence intervals overlapped. Estimates for pygmy blue whales had much wider confidence intervals than the corresponding values for Antarctic blue whales, reflecting the smaller set of data available for pygmy blue whales. The model estimated that 1.8% of the Antarctic region blue whales 79 ft and shorter were pygmy blue whales, and that the overall proportion of pygmy blue whales (p_{pygmy}) in the Antarctic region was 0.4% (95% CI 0.0%–1.1%), i.e. not significantly different from zero. The results were sensitive to the assumed maximum pygmy blue whale length: if this was 78 ft, p_{pygmy} = 0.2%, if it was 80 ft, p_{pygmy} = 0.7%.

Sensitivity test for changing proportions over time

When the model is applied to the 1934–36 data, the estimated proportion of pygmy blue whales is 2.4%. However, these data contained only five records for whales shorter than 78 ft and thus there are few data from which to estimate the parameters of the logistic equation. When applied to the 1947–51 data, the mean estimate for p_{pygmy} is zero (95% CI = 0.0%–0.5%).

Laurie's problematic ovarian corpora

Problematic ovarian corpora were recorded from a wide range of locations, mirroring the distribution of all records (Figure 6). The observed numbers of problematic ovarian corpora were actually slightly lower than expected north of 60°S but the geographical distribution did not differ significantly from a random distribution ($\chi^2 = 4.91$, d.f.= 2, $P > 0.05$).

DISCUSSION

Proportion of pygmy blue whales in the Antarctic

Visual plots and statistical analyses of ovarian corpora counts demonstrate that only a very small proportion, if any, of the blue whales examined for ovarian corpora counts in the Antarctic were pygmy blue whales. The best estimate of this proportion is 0.4%, and is statistically indistinguishable from zero (95% CI = 0.0–1.1%). Two additional factors have not been taken into account in producing this estimate which would tend to further reduce this estimate. First, some of the apparently short Antarctic-region blue whales with high ovarian corpora counts may actually be typographical errors in either length, number of ovarian corpora, or species recorded (fin whales being of similar length to pygmy blue whales). Second, no account is taken in the model of the relative numbers of pygmy and Antarctic blue whales expected at different lengths. It seems reasonable that near the maximum pygmy blue whale lengths, the proportion of pygmy blue whales should decrease with increasing lengths, but in the data the opposite trend appears true.

This estimate of 0.4% improves on previous estimates of 1.99% (Donovan 2000) and 0.9% (Kato et al. 2000) based on pregnant length frequencies, because ovarian corpora allow for the detection of short Antarctic blue whales and of longer than average (>74 ft) pygmy blue whales in the catches. A minimum estimate of 2.2% (1 out of 46) was obtained from genetic analysis of part of the mitochondrial control region (LeDuc et al. 2003). An analysis of nuclear DNA introns (204 samples, 25 Antarctic region) was not intended to estimate this proportion but did find a significant separation ($P < 0.001$ based on net number of nucleotide differences) between southern Indian Ocean and Antarctic region samples (Conway 2005). At-sea identification of the morphology of living blue whales revealed estimates of 2.3% based on dorsal hump types (1 out of 43) and 6.9% based on the body being tadpole-shaped and not torpedo-shaped (4 out of 58) (Kato et al. 2002), but sample sizes were small and these characteristics are not unique to either subspecies. Finally, blue whale calls around the Antarctic are similar, while the distinctly different calls of putative pygmy blue whales have yet to be recorded in the Antarctic (Ljungblad et al. 1998, Širović et al. 2004, Stafford et al. 2004, Rankin et al. 2005).

It should be noted that available ovarian corpora counts are not representative of all parts of the Antarctic. The Japanese data from 1947–51 were in the region 100°E–165°W and south of 61°S, while Laurie's data from 1934–36 are taken from 55°W–105°E and south of 55°S. In addition, ovarian corpora data for pygmy blue whales come from only 104 whales. The analysis could be improved by the inclusion of additional data for pygmy blue whales from Japanese and USSR records, but these data exist only as archived records and could not be prepared in time for this meeting.

Changing proportions of pygmy blue whales over time?

The estimated proportion of pygmy blue whales in the Antarctic catches was 2.4% based on the 1934–36 data (but almost no data were available for whales smaller than 78 ft) and zero (95% CI 0.0–0.5%) for the 1947–51 data. If the proportion of pygmy blue whales in the Antarctic was increasing over time because of changes in the relative abundance of pygmy and Antarctic blue whales, this proportion should have been 3.3 times higher in the later period (and not zero) according to the hypothesis outlined in LeDuc et al. (2001). Although the data provide no support for this hypothesis, ovarian corpora for the two time periods were collected in different regions which complicates their comparability.

Laurie's problematic ovarian corpora

Available evidence argues against Ichihara's hypothesis that the problematic ovarian corpora in Laurie (1937) were pygmy blue whales. If true, the greatest proportion of problematic corpora counts would be for 78 ft blue whales, a lower proportion at 79 ft and a near-absence of problematic records for 80 and 81 ft whales (longer than the maximum pygmy blue whale length). The actual proportions for these lengths show the opposite pattern: 0.16, 0.34, 0.24, and 0.31 (calculated from Table 3). The problematic ovarian corpora are also randomly located geographically compared to the other data in Laurie (1937) with no evidence for a greater proportion in the northern areas (there was actually a greater proportion in the southern areas). Laurie's explanation that these problematic ovarian corpora were length measurement errors also seems unlikely given that problematic counts comprised a high proportion (26%) of the whales between 78–81 ft. The model used in this paper provided a good fit to the data at those lengths, and the data for Antarctic blue whales and fin whales show that high ovarian corpora counts are common over a wide range of lengths. It appears that there is considerable variability in the length at sexual maturity, followed by small annual length increases between sexual and physical maturity. Assuming that length at sexual maturity is approximately normally distributed, it would be expected that precocious sexually mature Antarctic blue whales may be seven or more feet shorter than the average of 77–78 ft (Mackintosh and Wheeler 1929), given that some Antarctic blue whales have not reached sexual maturity at lengths of 84 ft and 85 ft (Brinkmann 1948, Mizue and Murata 1951). In conclusion, the most parsimonious explanation is that Laurie's records were not in error but instead genuinely represent the variability in ovarian corpora at those lengths.

Broader applicability of methods

It is obvious that a variety of other historical biological data could also be used in a similar manner to distinguish between catches of pygmy and Antarctic blue whales. For example, testicular weight, ovarian weight and to a limited extent ear plug laminae were also recorded in historical catches, and these have the properties required for subspecies discrimination: low values for young and sexually immature whales and high values for old and sexually mature whales. Testes weight offers the additional advantage that it can be used to test what proportion of male pygmy blue whales were taken in the Antarctic, whereas ovarian corpora and pregnancy data apply only to females.

These methods might also be useful in identifying and discriminating between proposed diminutive subspecies in catches of other whales, such as pygmy fin whales (*B. physalus patachonica*) (Clarke 2004), dwarf killer whales (*Orcinus nanus*) (Mikhalev et al. 1981) and dwarf minke whales (*B. acutorostrata* sensu lato) (Best 1985, Arnold et al. 1987), and possibly also to discriminate between different forms, subspecies and species of Bryde's whale (*B. brydei*), Eden's whale (*B. edeni*) and Omura's whale (*B. omurai*) (Best 1977, Wada et al. 2003).

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Table 1. Sources of data consulted for the analyses. Data from Brinkmann (1948) and Mackintosh and Wheeler (1929) were excluded because they did not report the lengths of whales with zero ovarian corpora, and data from Ruud and Jonsgård (1950) were excluded because only a small and unrepresentative sample of the counts were reported.

Reference	Section	*n* blue	*n* fin	Data included	Subspecies	Notes
Brinkmann (1948)	Figure 9	295	561	No	Antarctic?	Data for whales with zero ovarian corpora not published, Norwegian fleets 1939/40
Gambell (1964)	Text	1	–	Yes	Pygmy	Durban, 21 September 1963
Ichihara (1961)	Table 3	28	–	Yes	Pygmy	Lengths 68-77 ft, from 1959/60
Ichihara (1966)	Table 11	32	–	No	Pygmy	All < 70 ft females, assumed repeated in Figure 12 (the next entry in this table)
Ichihara (1966)	Figure 12	75	–	Yes	Pygmy	Caption states n=76, may include some from Ichihara (1961); Japanese 1959/60–1962/63 (?)
Laurie (1937)	Appendix II	1,058	–	Yes	Antarctic?	Chosen whales were ≥ 78 ft; appendix enlarged from text but error-prone; Norwegian, British and Japanese fleets 1934/35–1935/36; length and lutea given for 1,058 of the 1,206 whales in appendix
Mackintosh and Wheeler (1929)	Figure 129	110	(–)	No	Antarctic?	Data for whales with zero ovarian corpora not published; 1925–27 from South Georgia and Saldanha Bay, South Africa
Mikhalev (2000)	Table 6	280	–	No	Pygmy	USSR 1963–1967; data not included in publication
Mizue and Murata (1951)	Figure 36, 37	258	437	Yes	Antarctic?	Japanese 1949/50
Nishiwaki and Hayashi (1950)	Figure 19, 20	371	344	Yes	Antarctic?	Japanese 1947/48
Nishiwaki and Oye (1951)	Figure 9a, 9b	238	520	Yes	Antarctic?	Japanese 1948/49
Ohno and Fujino (1952)	Figures 18A-D, 19C-E	139	929	Yes	Antarctic?	Japanese 1950/51
Ruud and Jonsgård (1950)	Table 2,5,8, p.37	28	–	No	Antarctic?	Only 28 out of 653 ovarian corpora counts published in paper; Norwegian fleets 1945/46–1947/48.

Table 2. Frequency of each combination of length (ft) and ovarian corpora (OC) count for blue whales recorded in all years in the Antarctic region.

OC \ ft	66	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	Total
0	1		10	11	21	32	32	30	34	19	38	27	22	9	9	7	3		1	6			1									313
1							1	3	7	3	17	18	25	10	6	8	4	4		3			1									110
2		1					1	1	4	5	19	16	21	21	17	8	4	7	4	1	2		2									134
3							2	1	3	6	11	11	17	13	16	9	6	4	4	1	2			2			2					110
4								2			6	4	7	15	17	18	12	8	7	6	2	3	2	1								110
5											1	6	6	7	10	10	18	8	8	8	3	3	1	3								92
6											2	4	8	7	10	15	8	13	8	4	6	2	4								1	92
7										1	3	1	6	9	13	14	9	8	14	7	3	4	2		1	2						97
8										1	4	1	1	1	8	12	13	7	12	5	9	3	4	2	2	1						86
9											2	1	9	8	10	2	12	9	13	10	3	7	5	1	1	2						95
10												1	5	2	5	12	5	16	14	11	5	2	6	2	2	1	1					90
11												1	5	8	4	4	9	4	13	4	5	2	5	5		2			1			72
12										1		2	4	5	7	5	3	7	12	10	5	8	6	1	2					1		79
13													2	3	7	9	9	11	12	4	5		3	1			2					68
14											1	1	2	2	3	5	4	5	6	8	3		6	1	2	1	1					51
15												3	3	3	2	2	3	7	9	4	4	2	4	1		1						48
16										1		1	1	4	3	5	6	4	2	3	6	5	2	3	4	2	1		1			54
17												2		1	4	6	4	4	9	3	3	5	4		1							46
18											2		3	1	2	1	4	8	2	7	9	4	2	4	1	1			1			52
19								1				4	1		1	2	2	5	5	5	1	5	2	2			1	2				39
20												1	2	2	2	5	2	3	3	3	2	5	3	5			1	1				40
21													1	4	4	2	3	1	7	4	2	2	3	1	1	1						36
22															1	2	1	4	1	4	4		2			1		1				21
23													1	1	1	3		3	4		3	3	4	2								25
24							1					1				1	2	4	4	2	2	3	1					1				22
25											1			1	1	1	1	2	1	6	1		1	1		2	1					20
26													1					3	2		2	1										9
27														1	1	3	1	4	1	2												13
28														1	1	1						1	1	1					1			7
29											1			1	1	1	2	1	1				1		1							10
30																	1		2	1					1							5
31														1		1	1		1	1	1											6
32																																0
33																2			1													3
34																																0
35																	1		1													2
36																	1															1
37																			1													1
38																		1														1
39																				1												1
40																			1													1
41																																0
42																																0
43												1							1													2
Total	1	1	10	11	21	32	37	38	48	37	108	107	153	141	166	176	154	165	187	134	93	70	78	39	19	17	10	5	4	1	1	2,064

Table 3. Frequency of each combination of length (ft) and ovarian corpora (OC) count for blue whales during 1934–36 (Laurie 1937). Blue whales 78 ft and longer are over-represented in the data because of the original sampling design.

OC \ ft	69	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	Total
0			1	1		20	10	17	5	7	4	2		1	6			1									75
1						5	6	15	5	5	5	2	3		3			1									50
2	1					6	3	9	9	6	4	2	6	4	1	1		2									54
3					1	2	1	8	7	6	5	6	3	2	1	2			2			2					48
4						2	1	3	5	6	6	6	4	3	3	2	3	2	1								47
5						1	4	4		4	5	11	4	7	5	2	2	1	3								53
6							1	3	4	2	5	4	8	6	4	5	2	4								1	49
7						1	1	2	3	5	9	5	6	11	1	3	3	2		1	2						55
8						2	1		1	3	4	7	4	6	5	7	3	4	2	2	1						52
9						2	1	6	5	7	2	7	7	9	6	3	7	5	1	1	2						71
10							1	1	1	3	6	1	11	10	6	4	2	5	1	2	1	1					56
11							1	2	3	4	3	5	4	10		4	1	4	5		2			1			49
12							2	2	2	2	1	2	4	7	6	3	6	6	1	2					1		47
13									1	3	5	5	7	11	4	3		2	1			2					44
14							1	1	1		2	2	1	2	4	1		5	1	2	1	1					25
15								2	1		1	3	3	3	3	4	1	3	1		1						26
16							1		2			3	2	2	3	5	4	2	3	4	2	1		1			35
17							1			3	3	4	4	7	2	2	4	4		1							35
18						1		2		1		2	5	2	6	7	4	2	2	1	1			1			37
19							4	1					3	2	4	1	4	2	2			1	2				26
20							1	1		1	3	1	2	1	1	1	3	3	4			1	1				24
21										2		1	1	6	3	2	2	3	1	1	1						23
22													3		3	4					1		1				12
23								1		1	1		3	3		2	1	3	1								16
24		1									1	2	3	2	2		3	1					1				16
25						1					1			1	4						2	1					10
26													1	1		2	1										5
27											3	1	4	1													9
28										1							1	1	1					1			5
29						1				1		1															3
30																											0
31																											0
32																											0
33														1													1
34																											0
Total	1	1	1	1	1	44	41	80	55	73	79	85	106	121	86	70	57	68	33	17	17	10	5	4	1	1	1,058

Table 4. Frequency of each combination of length (ft) and ovarian corpora (OC) count for **pygmy blue whales**.

OC \ ft	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	Total
0		1	1		1	1											4
1	1				1		1		1								4
2				2	1	2	2	1	3	1							12
3						2	1		2	1	1						7
4			1		2	1	2	1	1		2	1	1				12
5							2		2	1	2	3	1				11
6					1					2	1	2	3				9
7						1		1		1	1	1			1		6
8							1		1		3	3			1	1	10
9							1			1		2					4
10					1						1	1	1		1		5
11								1		1				1			3
12													1	1			2
13									1								1
14											1						1
15										1	1						2
16									1	2							3
17										1							1
18																	0
19											1						1
20									1								1
21																	0
22										1			1				2
23																	0
24										1	1						2
25																	0
26																	0
27																	0
28																	0
29											1						1
Total	1	1	2	2	7	7	10	4	13	14	16	13	8	2	3	1	104

Table 5. Frequency of each combination of length (ft) and ovarian corpora (OC) count for **fin whales**.

OC \ ft	55	56	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	Total
0	2	2	8	13	16	22	42	36	29	50	33	18	18	7	7	3							1		307
1								2	5	16	21	11	14	7	14	6	1		1						98
2								1	5	5	15	18	18	15	9	7	4	1	2						100
3							2		2	3	10	12	16	23	20	13	9	3	3	1					117
4								1	1	2	5	10	20	17	18	22	14	11	2	1					124
5										1	5	7	15	24	24	29	17	8	6	4	1				141
6											4	10	8	16	21	17	12	14	4	2	2				110
7											1	3	8	21	22	21	18	20	8	3	3			1	129
8												3	6	10	15	22	14	14	5	2	3	1			95
9											3	3	4	12	8	14	11	11	11	4	2		1		84
10										1		3	7	5	14	20	14	14	5	3	6				92
11											1	2	1	9	16	8	9	6	14	3	3	2			74
12												1	2	9	15	16	15	6	12	3	2	1			82
13									1			1	3	3	12	16	15	5	6	6	1	2			71
14													1	4	11	11	13	10	10	3	2		1		66
15											1	1	1	7	5	9	15	11	8	2	3				63
16													1	5	11	11	14	6	6	4	4		2		64
17											1			6	3	10	4	7	4	2	1				38
18														3	5	11	10	8	6	2					45
19												1	2	1	6	6	7	6	7	5	2				43
20													3	2	6	8	4	5	2	4	2	1			37
21													3	4	3	3	7	10	9		1	1			41
22															3	5		6	6	2	3	1			26
23													2		2	3	8	3	2	2	3	1		1	27
24													1	1	3	3	3	5	3	1	1				21
25													1	1		4	2	4	4	1	3	1			21
26														1	2	1	4	5	2	2	1	1			19
27												2			1	3	4	5	5		1				21
28															4	2	2	3	2	1	1	1			16
29													1	1	1	1	2	2	3		2				13
30													2	1	1		5	3	1	1					14
31															1				1						2
32													1					1	2						4
33															1				1		1				3
34															1	1	2			1					5
35														1				1	1						3
36																1	1								2
37														1		2		1							4
38																									0
39														1											1
40																1									1
41																		1							1
42																									0
43																		1		1					2
44																									0
45																									0
46																									0
47																									0
48																									0
49																	1								1
50																									0
51																									0
52														1											1
53																	1								1
Total	2	2	8	13	16	22	44	40	43	78	100	106	159	219	285	310	262	217	164	66	54	13	5	2	2,230

Table 6. Maximum likelihood estimates and 95% confidence intervals for each of the model parameters. Confidence intervals were obtained by likelihood profiling, and are the estimates for which the negative log likelihood is 1.92 units greater than that obtained for the MLE. P = pygmy blue whales, A = Antarctic blue whales.

Parameter	Symbol	MLE	95% CI
Asymptotic ovarian corpora at great lengths (P)	C_{max}	10.5	(8.3; 15.4)
Length (ft) where ovarian corpora are 50% of C_{max} (P)	L_{50}	68.0	(66.2; 73.5)
Length (ft) where ovarian corpora are 95% of C_{max} (P)	L_{95}	75.0	(71.0; 88.6)
Variance:mean for distribution of ovarian corpora (P)	m	3.09	(2.36; 4.51)
Asymptotic ovarian corpora at great lengths (A)	C'_{max}	14.3	(13.5; 15.2)
Length (ft) where ovarian corpora are 50% of C_{max} (A)	L'_{50}	81.5	(81.1; 81.9)
Length (ft) where ovarian corpora are 95% of C_{max} (A)	L'_{95}	87.6	(86.7; 88.7)
Variance:mean for distribution of ovarian corpora (A)	m'	4.98	(4.62; 5.37)
Pygmy blue proportion in Antarctic region (≤ 79 ft)	p	0.018	(0; 0.052)
Pygmy blue proportion in Antarctic region (all lengths)	p_{pygmy}	0.004	(0; 0.011)

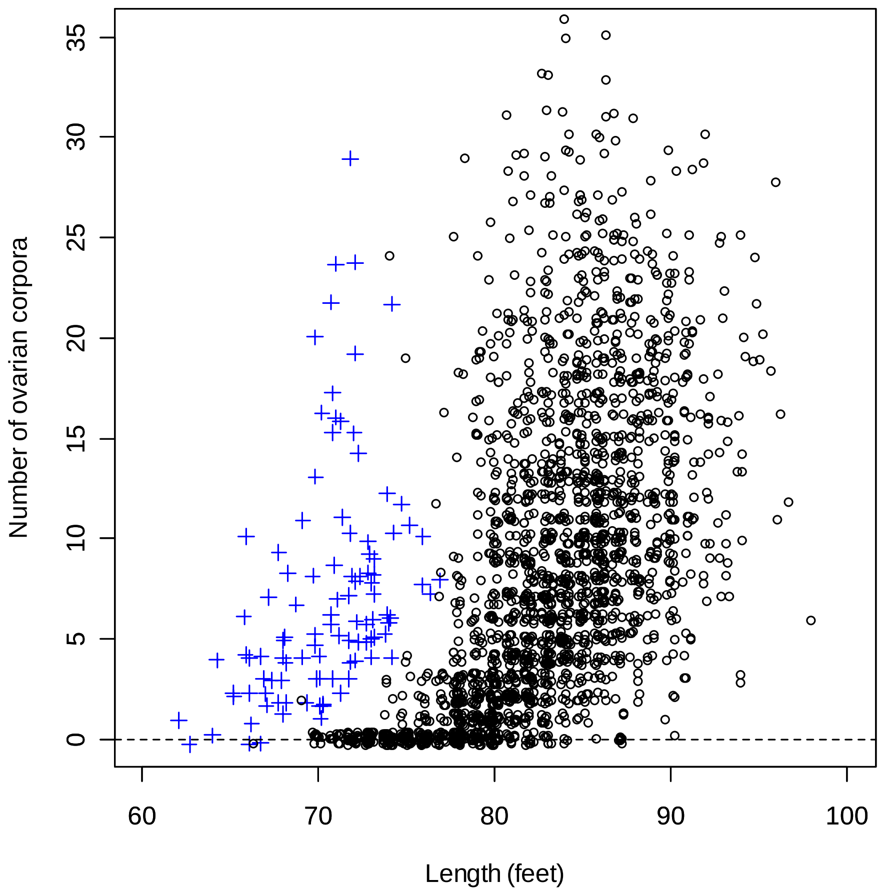

Figure 1. Relationship between length and ovarian corpora count for blue whale data. Ovarian corpora counts and length have been jittered by adding a uniform random number between -0.33 and 0.33 to their values to give an impression of the density of records at each position.

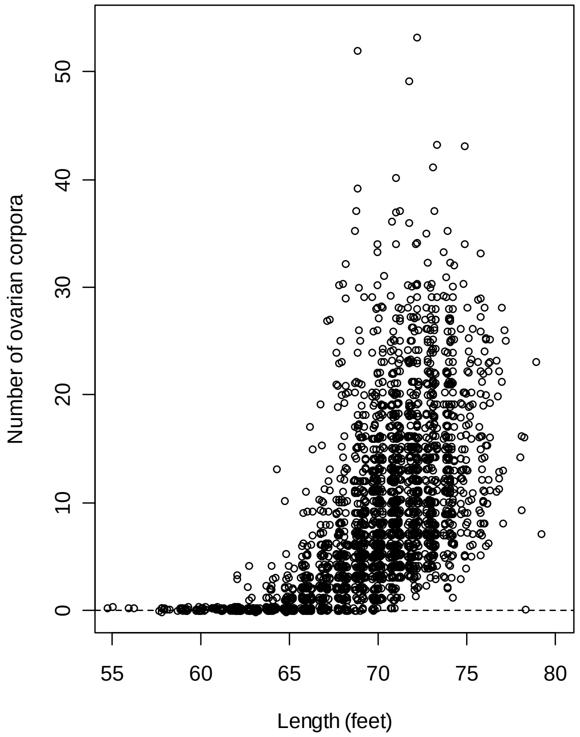

Figure 2. Distribution of ovarian corpora count against length for fin whales, showing a similar relationship to that seen for pygmy and Antarctic blue whales. Lengths have been jittered by adding a random number between -0.33 and 0.33, and ovarian corpora counts have been jittered by adding a random number between -0.2 and 0.2.

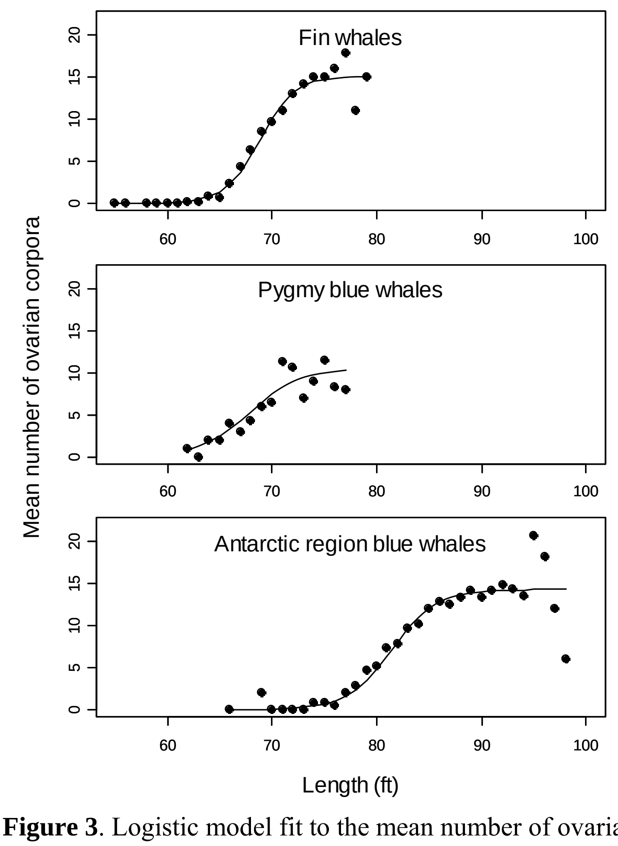

Figure 3. Logistic model fit to the mean number of ovarian corpora at each length for fin whales, pygmy blue whales and for blue whales in the Antarctic region. For this plot, Antarctic region blue whales are treated as a single distribution, not as a mixture of Antarctic blue and pygmy blue distributions.

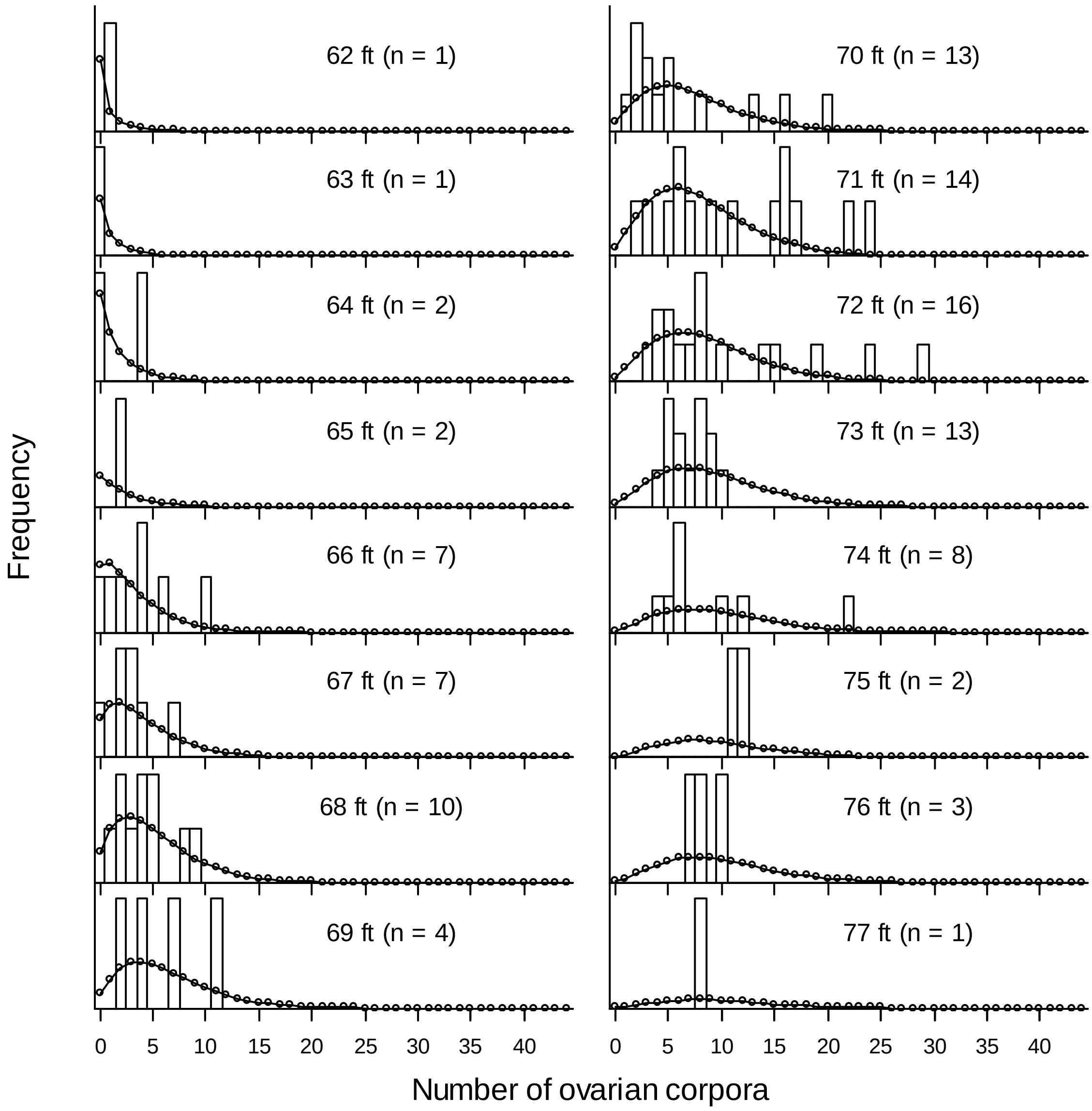

Figure 4. Fit of the model to pygmy blue whale ovarian corpora data.

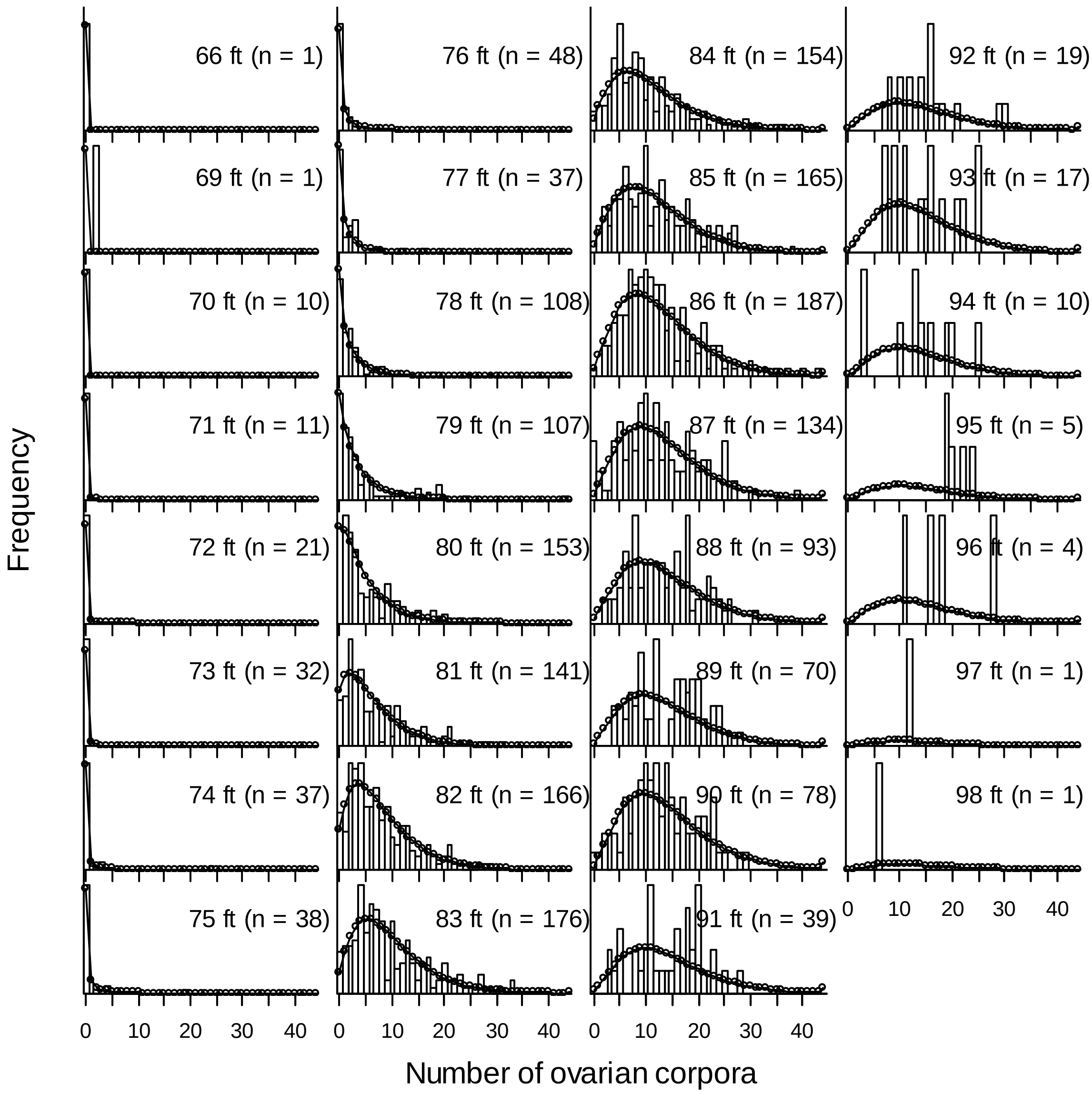

Figure 5. Fit of the model to ovarian corpora data from the Antarctic region. The fit is a mixture model of the pygmy and Antarctic distributions (≤ 79 ft), but the probability associated with the pygmy distribution is so small that the increase in the fit is almost undetectable.

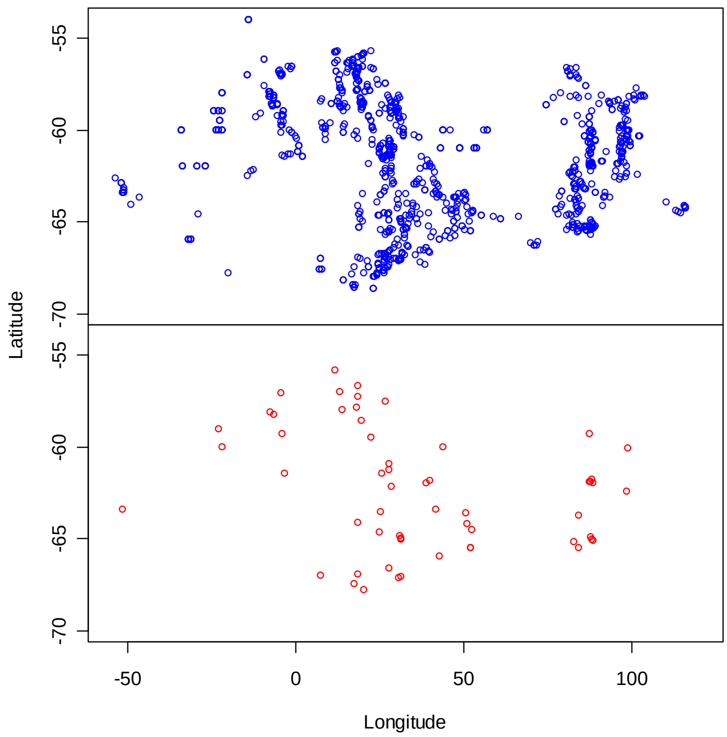

Figure 6. Geographical distribution of data in Laurie (1937). Top panel: catch distribution of all data, bottom panel: catch distribution for blue whales with "problematic" corpora data according to Laurie (1937).