Female length at sexual maturity for pygmy and Antarctic blue whales based on Soviet ovarian corpora, 1961–72

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ABSTRACT

Female blue whale ovarian corpora data were translated and encoded from the USSR's *Slava* (1961/62–1965/66) and *Sovietskaya Ukraina* (1961/62–1971/72) expeditions. Complete ovarian data were available for 1,425 blue whales (1,272 pygmy, 153 Antarctic). Catches north of 52°S were assumed to be pygmy blue whales (*Balaenoptera musculus brevicauda*), while those south of 56°S were assumed to be Antarctic (true) blue whales (*B. m. intermedia*), although there was some evidence for a small proportion (<1%) of both Antarctic blue whales north of 52°S and pygmy blue whales south of 56°S. A small proportion of lengths were rounded to the nearest metre, and many whales shorter than 18.0 were recorded as 18.0 m or greater (whale stretching). A Bayesian logistic model fitted to the data provided estimates of L_{50} and L_{95} (the lengths at which 50% and 95% of females are sexually mature). For pygmy blue whales L_{50} was 19.2 m (95% interval 19.1–19.3 m) and L_{95} was 20.5 m (95% interval 20.4–20.7 m). These estimates are more precise than those from Japanese data because the Soviet vessels recorded 32 times more pygmy blue whales shorter than the legal minimum length (21.3 m). Among small areas, L_{50} varied from 18.4 to 19.9 m for pygmy blue whales; all estimates were much shorter than the 23.4 m from the Antarctic. The status of northern Indian Ocean pygmy blue whales is unclear: L_{50} for these blue whales was statistically significantly shorter than L_{50} for both the southern Indian Ocean and around Australia, but the magnitude of the differences was small: 0.5–0.6 m.

INTRODUCTION

Blue whale (*Balaenoptera musculus*) ovaries contain marks called corpora lutea and corpora albicantia (Laurie, 1937; Mackintosh, 1942), as do the ovaries of many other mammals. In brief, during each ovulation, a soft body called a corpus luteum forms in one of the ovaries, which regresses over time to form a permanent scar called a corpus albicantium. A more detailed explanation of female cetacean reproductive morphology is given in Anon (1984). Previous authors have referred to the sum of the corpora lutea and corpora albicantia as "corpora lutea" (Laurie, 1937; Ichihara, 1966), but we prefer the more inclusive term "ovarian corpora".

It is generally assumed that permanent corpora albicantia are formed following every ovulation, irrespective of whether pregnancy results (Mackintosh and Wheeler, 1929; Laurie, 1937). There is a linear relationship between ear plug laminae and ovarian corpora counts in pygmy blue whales (Ichihara, 1966), a positive relationship between length and number of ovarian corpora (e.g. Laurie, 1937; Brinkmann, 1948; Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951), and the division between physical immature and physically mature blue whales is at about 11–12 ovarian corpora (Laurie, 1937; Brinkmann, 1948; Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951). A recent long-term ultrasound study (Brook *et al.*, 2002) on a single bottlenose dolphin revealed that permanent corpora albicantia are not formed after every ovulation, but only after pregnancy. While these results are probably not applicable to blue whales, which form much larger corpora lutea, it is notable that pygmy blue whales seldom ovulate, and when they do, pregnancy invariably follows.

Ovarian corpora have been used to estimate biological parameters and to separate subspecies of blue whales. Early ageing analyses relied on ovarian corpora counts, but were incorrectly calibrated because it was assumed that the age at sexual maturity was 2 yr (Mackintosh and Wheeler, 1929) and that one or more ovarian corpora are added every year (e.g. Laurie, 1937). Better age calibration of ovarian corpora counts could come from comparing counts to ear plug laminae, which are thought to provide reliable estimates of age (Purves, 1955; Laws and Purves, 1956). Laminae are laid down once a year for fin whales (Roe, 1967) and sei whales (Lockyer, 1974); and likely also for humpback whales (e.g. Best, 2006), although many papers in the 1950s and 1960s assumed that two laminae were formed every year (e.g. Ichihara, 1966). Few ear plug counts are available for blue whales because this method was developed after the severe depletion of blue whales and only shortly before the ban on their catches in the mid-1960s. For this reason, there are only 32 published records for pygmy blue whales (*B. m. brevicauda*) (Ichihara, 1966). Additional ear plug records (171 females and 229 males) from Sazhinov (1970) and a doctoral dissertation by the same author in 1980 are little known outside the USSR. A regression of the pygmy blue whale records against the corresponding corpora data suggests that they accumulated corpora at 0.4 yr^{-1}, and attain sexual maturity at 11 yr (T.A.B., unpublished analysis). For Antarctic blue whales, limited unpublished ear plug data (whereabouts unknown) from the 1956/57–1958/59 seasons were used to estimate the rate of corpora accumulation (0.4 yr^{-1}) and sexual maturity (10 yr) (Ohsumi, 1979).

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The length at maturity for female pygmy blue whales is imprecisely known. Available estimates from Japanese catches were based on few (n = 6) ovarian corpora counts from the critical 60–65 ft (18.3–19.8 m) length range (Ichihara, 1966) because Japanese whalers generally adhered to the legal minimum length of 70 ft (21.3 m). Estimated length at sexual maturity was 19.0 m from Soviet data in the northern Indian Ocean (Mikhalev, 2000), but this estimate was not based on a formal statistical model.

The subspecific status of blue whales is unclear at present. Three subspecies are widely recognised: *B. m. musculus* (northern blue whales) in the North Pacific and North Atlantic, *B. m. intermedia* (Burmeister, 1871) (Antarctic or true blue whales) in the Antarctic in the austral summer, and *B. m. brevicauda* (Ichihara, 1966) (pygmy blue whales) in the Indian Ocean. A fourth subspecies, *B. m. indica* (Blyth, 1859) from the northern Indian Ocean is currently accepted as a valid name, which would have priority over *B. m. intermedia* and *B. m. brevicauda*, but its distinguishing features are poorly known (Rice, 1998), and we consider northern Indian Ocean blue whales to be synonymous with pygmy blue whales. Our reasoning is that Soviet whalers considered their extensive catches in the northern Indian Ocean to be pygmy blue whales in the southern Indian Ocean (Zemsky and Sazhinov, 1982; Mikhalev, 2000). An additional undescribed subspecies may be present in the south-east Pacific (Branch *et al*., accepted), although insufficient data exist at present for a formal description.

Ovarian corpora data have been used to estimate that only 0.4% (95% CI 0.0–1.1%) of blue whales in the Antarctic are pygmy blue whales (Branch, 2006), of interest because estimates of Antarctic blue whales come from surveys in the Antarctic. This analysis was limited by the small number (n = 103) of pygmy blue whale corpora data (Ichihara, 1961, 1966), in contrast to >2,000 published ovarian corpora counts for Antarctic blue whales.

In the 1990s a new source of ovarian corpora data was revealed when the USSR admitted to extensive illegal whaling in the 1960s and 1970s throughout the Southern Hemisphere and northern Indian Ocean (Yablokov, 1994; Zemsky *et al.*, 1995; Mikhalev, 1997; Yablokov *et al.*, 1998; Mikhalev, 2000). During these expeditions nearly 10,000 blue whales were caught, despite an IWC-mandated ban on blue whale catches. The 70 ft (21.3 m) minimum length regulation was ignored, as were catch seasons imposed on whaling operations. Since then, most of the original Soviet logbook records of length, sex and catch location have been encoded into a database held by International Whaling Commission (IWC), but additional biological data including ovarian corpora counts were not encoded during the first phase of data entry.

To add to this database, we translated and encoded all ovarian corpora data from the available logbooks for both Antarctic and pygmy blue whales. The encoded data greatly increase the available corpora data for pygmy blue whales, especially for lengths under the legal minimum of 70 ft (21.3 m). Based on these data we estimated the lengths at which 50% and 95% of female pygmy blue whales become sexually mature, and examine how these vary among regions.

METHODS

Data sources

Extracted copies of the logbook pages were provided to T.A.B. by the IWC Secretariat for the *Sovietskaya Ukraina* (1961/62–1971/72) and *Slava* (1961/62–1964/65) expeditions, while Y.M. had access to the original logbooks. About two-thirds of the data were translated by T.A.B. using the notes provided by the IWC, and validated by Y.M. The remainder were encoded by Y.M. and checked by T.A.B.

Corpora data

Ovarian data typically consisted of three or four pieces of numerical information for each ovary. Where three numbers were recorded, the first was the number of functioning corpora lutea, the second the "traces of pregnancy", and the third the "traces of ovulation". The distinction between cetacean corpora from pregnancy and ovulation, although proposed by some USSR scientists (Ivashin, 1984), is problematic, because there are no reliable criteria for this distinction in pygmy blue whales (Mikhalev, 2000). Therefore, for our analysis total corpora counts were obtained by summing over the number of corpora lutea, traces of pregnancy and traces of ovulation. Where four numbers were recorded, the first is the number of foetuses and is excluded from the total corpora count.

Ovarian data were excluded from the analyses if a datum was missing (n=1), if data were recorded for only one ovary (n=141), or if corpora counts were non-zero but the whale was "immature" (n=2). Of those with complete data, one outlier was also excluded: a 15.6 m female with one corpus (Table 1) previously noted by Mikhalev (2000). All other blue whales shorter than 18.0 m had zero ovarian corpora.

In many cases (n=312), females were recorded as "immature" (presumably based on ovarian examination), but no corpora counts were given. Some expeditions did not record zero corpora counts for immature blue whales, while other expedition recorded a series of zeros. To avoid under-representing immature females from those expeditions, zero corpora counts were assumed for all females denoted as immature.

Regions

Data from the Antarctic (south of 56°S) were separated from those north of 52°S. The northern data were nearly all in the Indian Ocean, and were further subdivided into broad regions (Figure 1) and local areas (Figure 2). Broad regions were loosely based on the divisions listed by Zemsky and Sazhinov (1982): northern Indian Ocean, southern Indian Ocean, and Australia. Local areas were defined to include small areas containing dense catches of blue whales, with no large gaps

between catches and at least 50 samples in each area. There were three blue whales longer than the maximum pygmy blue whale length of 24.1 m (Ichihara, 1966) north of 52°S. More details of these whales are provided in Table 1 and in the Results; they were excluded from the analyses.

Assumed subspecies

The two subspecies were seldom distinguished in the catch records. Based on previous studies, it can be assumed that nearly all catches south of 56°S were Antarctic blue whales. For example, ovarian corpora suggest that 0.4% (95% CI 0.0–1.1%) of the Antarctic catches were pygmy blue whales (Branch, 2006); while an examination of the lengths of sexually mature females south of 52°S estimated that 0.8% (95% interval 0.7–1.1%) of Antarctic catches were pygmy blue whales (Branch *et al.*, accepted). Catches north of 52°S in the Indian Ocean are nearly all pygmy blue whales, based on USSR and Japanese reports (Ichihara, 1966; Zemsky and Sazhinov, 1982), and a Bayesian mixture model of the length distributions of sexually mature females (99.9% pygmy; 95% interval 99.4–100%, Branch *et al.*, accepted).

Mean length at sexual maturity

The estimated probability of being sexually mature at a given length ($\hat{p}_L$) was assumed to conform to a logistic equation with two parameters: the lengths at which 50% (L_{50}) and 95% (L_{95}) of the females are sexually mature. For each 0.1-m length interval, variability around $\hat{p}_L$ was assumed to be binomial. Thus the likelihood ℓ of observing m_L sexually mature females and $n_L - m_L$ sexually immature females at each of the L lengths, is given by:

$$\hat{p}_L = \left[1 + \exp\left(-\ln 19 \cdot \frac{L - L_{50}}{L_{95} - L_{50}}\right)\right]^{-1}$$

$$\ell = \prod_L (\hat{p}_L)^{m_L} (1 - \hat{p}_L)^{n_L - m_L}$$

This model was fitted to the data using Bayesian methods, implemented in AD Model Builder. This method involves assigning a prior distribution to each of the parameters, and then combining the priors and the likelihood to obtain posterior distributions for the parameters of interest (e.g. Punt and Hilborn, 1997). The posterior distributions characterize the probabilities associated with different values of the parameters. Prior distributions for L_{50} and L_{95} were assumed to be uniform with bounds of 13 m and 30 m. Posteriors were obtained using Markov Chain Monte Carlo (MCMC) methods. MCMC chains of 1 million draws were evenly subsampled to produce 1,000 posterior draws. Posteriors were considered converged when the autocorrelation between successive sampled draws was between -0.06 and 0.06. Separate Bayesian models were run for each local area, each broad region and for each subspecies. Posterior probability intervals are sometimes called Bayesian intervals, credibility intervals or probability intervals; for brevity we refer to them as 95% intervals throughout.

The hypothesis that L_{50} was the same in each broad region was tested by finding the percentage of posterior draws in which L_{50} from one region was greater than L_{50} from another.

Possible problems with the data

A prominent feature of the pygmy blue whale data is that some catches that were actually shorter than 18.0 m were "stretched" so that the recorded measurement was 18.0 m or slightly more (Figure 3). This feature has been noted previously, both for these data (Mikhalev, 2000), blue whale catches in general (Donovan, 2000; Branch *et al.*, accepted), and for other species (Best, 1989). There was, however, no evidence of whale stretching to the legal minimum length of 70 ft (21.3 m), because this legal minimum was ignored by the Soviet whalers. Whale stretching could result in a slight bias to the estimated length at sexual maturity, because immature blue whales shorter than 18.0 m may have been recorded as 18.0 m or longer. As a sensitivity test, all records between 17.5 m and 18.5 m were excluded and the mean length at maturity for pygmy blue whales re-estimated.

One additional point to note is that a small percentage of records were rounded to the nearest metre, as can be seen by peaks at 16.0, 17.0, and 19.0 m. Soviet whalers recorded measurements in metres; in other blue whale records that were measured in feet, rounding to 5 ft intervals is a common feature (Donovan, 2000; Branch *et al.*, accepted).

Whale ovaries may have been examined in two main ways: either by a surface count of visible ovarian corpora, or by slicing thin sections to better detect ovarian corpora. The latter method is more time consuming but yields more accurate (and higher) ovarian corpora counts. For example, Ichihara (1961) reported 27 measurements made by on-board Japanese inspectors of 68–77 ft female pygmy blue whales, with corpora counts of 1–12 (mean 5.4), but noted that a single pair of ovaries from a 70 ft individual examined carefully with a bacon slicer yielded 13 ovarian corpora. It is not known which method was used to obtain the Soviet data, but surface counts were probably used for most of the data, probably resulting in under-counting when the true number of ovarian corpora was high.

RESULTS

Ovarian data and information about maturity were extracted for 1,577 female blue whale catches in the Southern Hemisphere and northern Indian Ocean. Of these, complete corpora records for both ovaries were available for 1,431 blue whales, divided as follows: 153 were south of 56°S (Antarctic region), and 1,272 were north of 52°S and shorter than 24.1 m (presumed pygmy blue whales). Seven records with complete data were excluded from further analyses (Table 1); one was an outlier, three were caught between 52°S and 56°S, and three were north of 52°S but longer than 24.1 m. Further data for the three excluded whales north of 52°S, outlined briefly below, led us to conclude that these were Antarctic blue whales.

Whale #775. Logbook annotation identifies as an Antarctic blue whale. Other catches north of 52°S with 4 ovarian corpora (n = 98; mean = 20.6 m; SD = 0.94 m; range = 18.0–23.0 m) averaged 3.7 m shorter. The probability that whale #775 comes from the same population as these other whales is 4×10^{-5}, assuming they are distributed ~N(20.6, 0.94^2). This blue whale catch was isolated from other blue whale catches on the same expedition: the previous record with corpora data was at 8°38'N 70°31'E, and the following record was at 57°36'S 88°40'E.

Whale #1735. Logbook identifies this as "Бл.а", i.e. an Antarctic blue whale. Other catches north of 52°S with 3 ovarian corpora (n = 94; mean = 20.5 m; SD = 0.93 m; range = 18.8–22.5 m) were on average 4.0 m shorter. The probability that whale #1735 comes from the same distribution as these other whales is 1×10^{-5}, assuming they are ~N(20.5, 0.93^2). Although other pygmy blue whales were caught in the same region before and after this catch, there were 128 intervening catches of other species before this catch, and 81 afterwards, thus this whale was separate from any pygmy blue whale aggregations.

Whale #2381. Summary on bottom of page appears to indicate Antarctic blue whale. This individual was 2.6 m longer than the maximum pygmy blue whale length. It was isolated from other blue whale catches on the same expedition: the previous record was at 35°S 50°E and the next record was at 47°13'S 41°15'E.

Ovarian corpora counts for pygmy blue whales are given in Table 2 and plotted in Figure 4. The shortest sexually mature pygmy blue whale was 18.0 m, and the longest sexually immature pygmy blue whale female was 20.9 m. The highest ovarian corpora count was 32 (*Sovietskaya Ukraina*, 1971/72, #2990, at 48°15´S 43°00´E). If it is assumed that the age at sexual maturity is 10 years and 0.4 ovarian corpora are added each year (see Introduction), then this individual was about 90 years old.

Ovarian corpora counts for the Antarctic region are given in Table 2 and plotted in Figure 5. The shortest sexually mature female was 21.4 m, and the longest immature female was 25.6 m. The highest count for an Antarctic blue whale was 24 (*Sovietskaya Ukraina*, 1965/66, #2830, at 70°50´S 173°50´W). At least two of the blue whales in the Antarctic region had a combination of length and corpora count typical of pygmy blue whales (Figures 4–5). These two were individuals of length 21.4 m and 6 corpora (*Sovietskaya Ukraina*, 1962/63, #1264, at 60°05´S 49°12´E), and length 22.0 m and 8 corpora (*Sovietskaya Ukraina*, 1965/66, #1076, at 66°00´S 161°45´E).

Estimated L_{50} in the local areas ranged from 18.4 m off Oman to 19.9 m in the south-east Indian Ocean (Table 4, Figure 6). For the broad regions (Table 4, Figure 7), blue whales in the northern Indian Ocean reached L_{50} at 18.8 m, about 0.5 m smaller than those in the southern Indian Ocean (19.3 m) or around Australia (19.4 m). The northern Indian Ocean population was significantly smaller (probability < 0.001) than in other two broad regions, but the southern Indian Ocean and Australia were not significantly different from each other (probability 0.157). The greatest contrast in the L_{50} estimates was between the Antarctic region (assumed the same as the Antarctic subspecies) and the data from any of the other regions (Figure 7): the Antarctic region had a mean L_{50} of 23.4 m which was significantly greater (probability < 0.001) than for any of the small areas, broad regions, or for pygmy blue whales as a whole.

We estimated that L_{50} for pygmy blue whales was 19.2 m (95% interval 19.1–19.3 m) and L_{95} was 20.5 m (95% interval 20.4–20.7 m); the model fit is shown in Figure 8. When records in the 17.5–18.5 m range were omitted as a sensitivity to test the effect of whale stretching, these estimates change only slightly to L_{50} = 19.1 m (95% interval 19.0–19.2 m) and L_{95} = 20.6 m (95% interval 20.4–20.8 m).

DISCUSSION

Pygmy blue whales

The pooled data for pygmy blue whales (north of 52°S, excluding three probable Antarctic blue whales) from the *Sovietskaya Ukraina* and *Slava* included 1,272 records, greatly expanding the available ovarian corpora data for this subspecies. The only published pygmy blue whale ovarian corpora data are 28 individuals (Ichihara, 1961) and 76 individuals (Ichihara, 1966), although additional unpublished data exist (H. Kato, pers. comm.). The Soviet records included 1,021 pygmy blue whales shorter than the legal minimum length (70 ft, 21.3 m), whereas few published Japanese records (n = 32) were shorter than the legal minimum (Ichihara, 1966). Soviet whalers also circumvented the regulations in a number of other ways as widely reported elsewhere (Yablokov, 1994; Zemsky *et al.*, 1995; Mikhalev, 1997; Yablokov *et al.*, 1998): catches of both Antarctic and pygmy blue whales continued well after their catches were banned by the IWC (this decision was made in 1963 for

Antarctic blue whales and in 1965 for pygmy blue whales) and many blue whales were caught far north of the legal northern boundary for pelagic whaling of 40°S.

We estimated that L_{50} for pygmy blue whales was 19.2 m (95% interval 19.1–19.3 m), and L_{95} was 20.5 m (95% interval 20.4–20.7 m). These estimates are more precise and accurate than previous estimates of mean length at sexual maturity based on the Japanese data: 20.7 m (Ichihara, 1961), <19.8 m (Ichihara, 1963), and "about" 19.2 m (Ichihara, 1966), because of the greater number of records shorter than 21.3 m (1,021 vs. 32).

When data were grouped into local areas, length at 50% sexual maturity varied by up to 1.2 m among the different pygmy blue whale areas, but all were substantially shorter than estimates from the Antarctic.

Among the broad regions, females blue whales from the northern Indian Ocean had a significantly shorter L_{50} (18.8 m; 95% interval 18.6–19.0 m) than those from the south Indian Ocean (19.3 m; 19.2–19.5 m) and around Australia (19.4 m; 19.2–19.6). While significantly different, the magnitude of the difference is small (0.5–0.6 m). The estimate for the northern Indian Ocean is slightly smaller than the 19.0 m estimated by Mikhalev (2000).

Antarctic blue whales

Soviet data from the Antarctic region (assumed to be for Antarctic blue whales) were limited in number (n = 153), which is not surprising given their rarity by the 1960s (Branch *et al.*, 2004). Estimated L_{50} was 23.4 m (95% Bayesian interval 22.9–23.9). The median is slightly shorter than point estimates published previously: 23.7 m (Mackintosh and Wheeler, 1929) updated to 23.5 m (Mackintosh, 1942); 23.5–23.8 m (Brinkmann, 1948); about 23.8 m (Nishiwaki and Hayashi, 1950), and 23.7 m (Ichihara, 1966). Laurie's (1937) estimate of 24.1–24.4 m is invalid since he only examined whales of 23.8 m or longer. The most authoritative of these previous estimates is the 23.5 m obtained by Mackintosh (1942). Although our estimate is slightly shorter than 23.5 m, it has wide associated 95% intervals, and there is only a 70% probability that our estimate is smaller than 23.5 m. These Russian data therefore provide no statistical evidence for a decline in length at sexual maturity despite depletion by more than 99% (Branch *et al.*, 2004), although the sample sizes are probably too small to detect any such decline.

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Table 1. Blue whale records excluded from the analysis and the reasons for exclusion.

Fleet	Season	Code	Position		Length	Corpora	Reason excluded	Comments
Slava	1962/63	795	54°01'S	70°45'E	19.3	2	Between 52°S and 56°S	Possibly pygmy subspecies
Sovietskaya Ukraina	1962/63	1368	55°31'S	53°20'E	19.8	0	Between 52°S and 56°S	Subspecies unknown
Sovietskaya Ukraina	1964/65	867	01°20'S	53°20'E	15.6	1	Length outlier for non-zero ovarian corpora	No other non-zero corpus count shorter than 18.0 m.
Sovietskaya Ukraina	1968/69	2817	52°10'S	14°20'E	20.5	8	Between 52°S and 56°S	Probably pygmy subspecies
Sovietskaya Ukraina	1966/67	775	34°50'S	74°40'E	24.3	4	North of 52°S but >24.1 m	Antarctic subspecies, see text
Sovietskaya Ukraina	1967/68	1735	34°40'S	53°20'E	24.5	3	North of 52°S but >24.1 m	Antarctic subspecies, see text
Sovietskaya Ukraina	1971/72	2381	39°30'S	30°12'E	26.7	12	North of 52°S but >24.1 m	Antarctic subspecies, see text

Table 2. Frequency of ovarian corpora counts for **pygmy** blue whales (north of 52°S and shorter than 24.1 m) at each length (m).

Length	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19	21	32	Total
13.2	2																					2
13.3	1																					1
13.6	1																					1
13.7	1																					1
13.8	2																					2
13.9	1																					1
14.0	4																					4
14.1	1																					1
14.2	2																					2
14.3	2																					2
14.4	2																					2
14.5	1																					1
14.6	6																					6
14.7	3																					3
14.8	1																					1
14.9	2																					2
15.0	5																					5
15.2	4																					4
15.3	2																					2
15.4	3																					3
15.5	9																					9
15.6	4																					4
15.7	4																					4
15.8	1																					1
15.9	2																					2
16.0	14																					14
16.1	12																					12
16.2	4																					4
16.3	6																					6
16.4	4																					4
16.5	5																					5
16.6	3																					3
16.7	4																					4
16.8	7																					7
16.9	4																					4
17.0	18																					18
17.1	2																					2
17.2	8																					8
17.3	3																					3
17.4	8																					8
17.5	8																					8
17.6	7																					7
17.7	1																					1
17.8	5																					5
17.9	3																					3
18.0	55				1	1																57
18.1	51	1																				52
18.2	29	1						1														31
18.3	21	1			1			1														24
18.4	18																					18
18.5	17	3																				20
18.6	16	1	1																			18

18.7	12		4					1															17
18.8	7	2		3																			12
18.9	3	1	3																				7
19.0	11	5	3	1	1			2															23
19.1	5		4	1		1	1					1											13
19.2	7	3	2	2	2	1	1																18
19.3	6	3	1	1	3																		14
19.4	6	4	1	4	7																		22
19.5	6	3	3	3	2	2	1	1	1				1										23
19.6	6	1	2	1	1								1										12
19.7	7	2	4	4		2			1														20
19.8	4	3	4	5	3			1			1												21
19.9	4	4	2	6	3							1											20
20.0	3	4	8	4	6		1	1	1	3													31
20.1	3	3	1	2	6	3	4		2		1												25
20.2	4	5	7	4	3	2	4	1	1	3	1		1										36
20.3	1	2	5	5	4		3	1	1	2	1	1											26
20.4	1	1	5	4	2	3	3	2	1		1	1											24
20.5	3	1	6		5	5	1	4	2		1	2			1								31
20.6	3	2	6	3	1	5	4		4	1						1							30
20.7	3	5	7	4	3	1	3	2	4	2	2	1		1									38
20.8	2	2	4	4	3	3	1	4	3	1	2	1			1								31
20.9	4	1	8	3	7	4	1	1		1	1		1										32
21.0		2	4	1	3	3	4	6	3	4	2	2	1	1	1								37
21.1		1		1	3	3	2	4	6	1	2		1				1						25
21.2		1	1	2	1	2	4	2	6		1			1									21
21.3					2	4	2	3	2	4	1		1		1			1					21
21.4		2	1	6	6	4	1	2	5	3				1									31
21.5		1	3	4	3	2	1	5	1				1	1	1								23
21.6			1	2	6	7	1	3	2		2	1											25
21.7		2	3	3	2	3	1	2	3	1	2	1							2				25
21.8		1	2	3	1	3	6	2		3		1							1				23
21.9				3	2		1				2						1						9
22.0				1	2	2	2	2	1	2		2		1	1	1					1		18
22.1			1			3	3	2		1		1		1		1							13
22.2							1	3	1		3	1		2									11
22.3				1		2	2	3			2												10
22.4				2			1				1	1								1			6
22.5				1				1			3	1											6
22.6					1			1	1				1		1								5
22.7							1	1					1	1			1						5
22.8			1		1	1					1												4
22.9								3		1													4
23.0					1		1				2	1											5
23.1						1					1												2
23.3						1																	1
23.4											1												1
23.6													1										1
23.7							1																1
24.0			1																				1
Total	510	74	109	94	98	74	63	68	52	33	37	20	11	10	7	3	3	1	3	1	1	1272	

Table 3. Frequency of ovarian counts for blue whales in the **Antarctic** region (south of 56°S) at each length (m).

Length	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	17	19	20	22	24	Total
17.7	1																					1
18.2	1																					1
18.3	1																					1
18.4	2																					2
18.5	1																					1
18.8	1																					1
19.0	1																					1
19.1	1																					1
19.5	1																					1
19.7	3																					3
19.8	1																					1
20.0	3																					3
20.1	3																					3
20.3	2																					2
20.4	1																					1
20.7	1																					1
21.0	1																					1
21.1	1																					1
21.2	1																					1
21.3	3																					3
21.4	5						1															6
21.5	2		1																			3
21.7		1																				1
21.8	5																					5
21.9	1																					1
22.0			1						1													2
22.1	3																					3
22.2	1																					1
22.3	2																					2
22.4	2																					2
22.6	1					1																2
22.7	2							1														3
22.8					1																	1
22.9	1																					1
23.0	2																					2
23.1	1																					1
23.3	2																					2
23.4			1																			1
23.5				1																		1
23.8	1																					1
23.9	1																					1
24.0	1			1																		2
24.1						1																1
24.5	1	1				1																3
24.7									1								1					2
24.8		1	1		1			1														4
24.9					1																	1
25.0													1									1
25.2						1																1
25.3				1					2													3
25.4	1		1	1	1																	4
25.5		1		1					1		1				1							5

25.6	1								1		1													3
25.7									1			1												2
26.0			1			1	1				1					1								5
26.1			1											1				1			1			4
26.2										1	1													2
26.3			1				1	1		1														4
26.4						1																		1
26.5									1				1											2
26.6							1			1														2
26.7				1				1			1					1								4
26.8								1												1				2
26.9						1																		1
27.0		1				1								1										3
27.1									1															1
27.3										1			1											2
27.4										1														1
27.5											1													1
27.6						1	1		1					1			1							5
27.7													1											1
27.8						1				1			1											3
28.0										1														1
28.1									1															1
28.3														1										1
28.5										1														1
28.8														1										1
Total	66	5	8	6	4	10	5	5	11	8	6	1	5	1	6	1	1	1	1	1	1			153

Table 4. Posterior medians and 95% credible intervals for the length at 50% maturity (L_{50}) and the length at 95% maturity (L_{95}), for local areas and broad regions, and for the entire geographic range of pygmy and Antarctic blue whales. See Figures 1 and 2 and the text for definitions of the areas and categories used.

			L_{50} (m)		L_{95} (m)	
		n	Median	95% interval	Median	95% interval
Local areas	Oman	93	18.4	(17.4; 19.0)	20.5	(19.8; 21.6)
	India	91	18.5	(17.9; 18.8)	19.4	(19.0; 20.0)
	Somalia	126	19.1	(18.8; 19.4)	20.3	(19.8; 20.9)
	S Madagascar	144	18.9	(18.6; 19.2)	20.0	(19.6; 20.6)
	SW Indian Ocean	363	19.5	(19.3; 19.6)	20.8	(20.5; 21.1)
	SE Indian Ocean	50	19.9	(19.2; 20.5)	21.7	(20.9; 23.2)
	W Australia	206	19.3	(19.1; 19.6)	20.4	(20.1; 20.8)
	Australian Bight	75	19.3	(18.9; 19.7)	21.1	(20.4; 22.1)
	Tasmania	53	19.6	(19.2; 20.1)	21.1	(20.4; 22.4)
Broad regions	N Indian Ocean	327	18.8	(18.6; 19.0)	20.1	(19.8; 20.4)
	S Indian Ocean	584	19.3	(19.2; 19.5)	20.7	(20.5; 21.0)
	Australia	361	19.4	(19.2; 19.6)	20.6	(20.3; 20.9)
	Antarctic	153	23.4	(22.9; 23.9)	25.9	(25.1; 26.9)
Subspecies	Pygmy	1272	19.2	(19.1; 19.3)	20.5	(20.4; 20.7)
	Antarctic	153	23.4	(22.9; 23.9)	25.9	(25.1; 26.9)

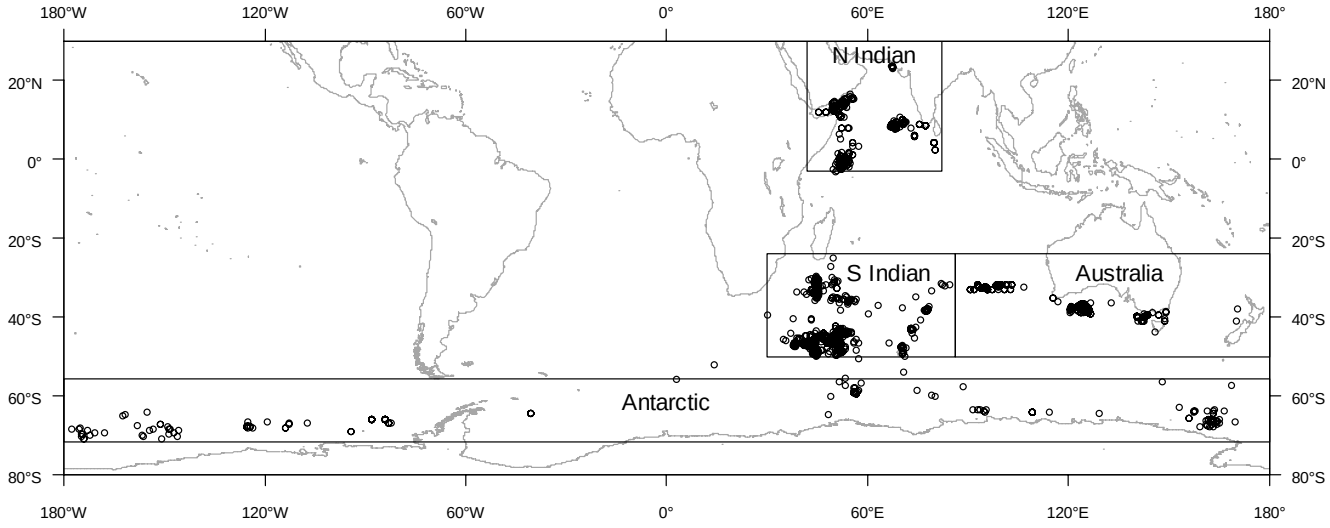

Figure 1. Positions of blue whales in the Southern Hemisphere and northern Indian Ocean from which corpora lutea were obtained, showing the four **broad regions**.

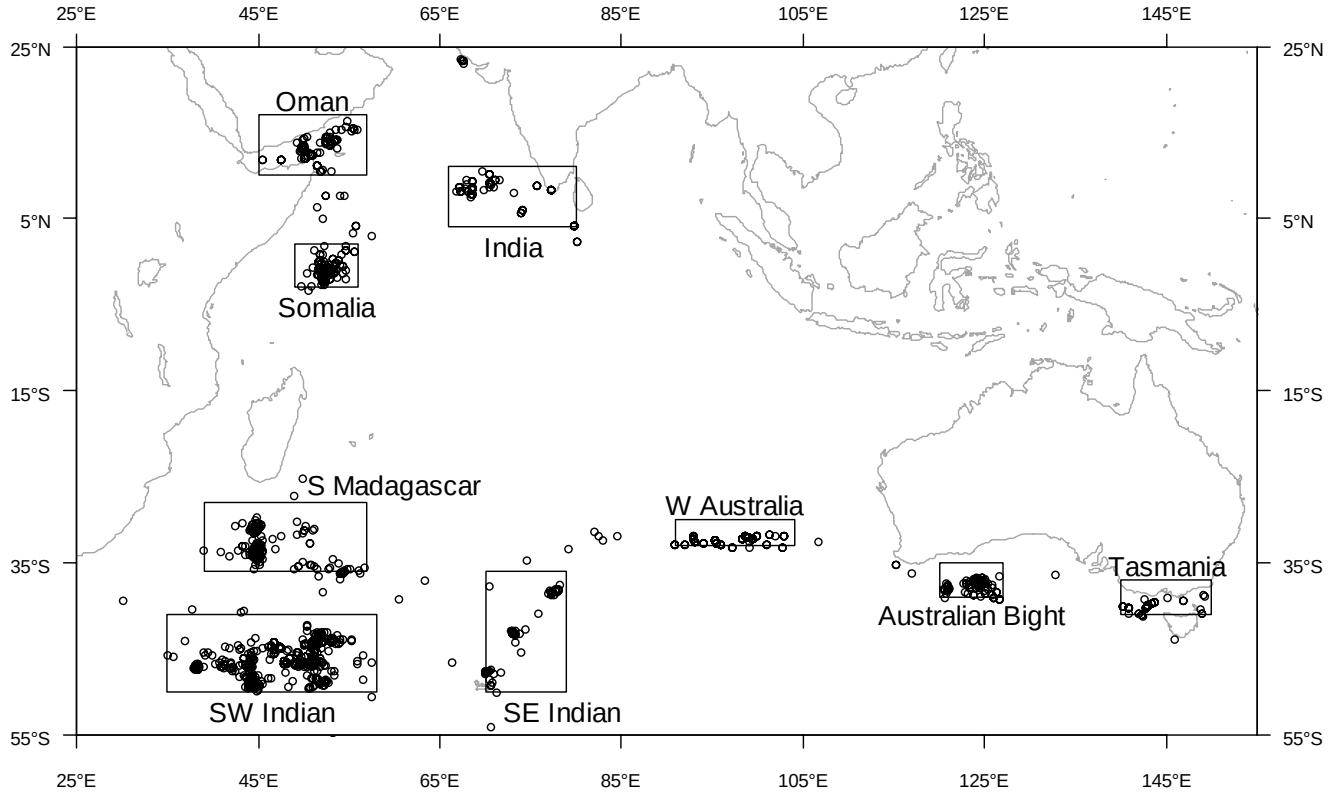

Figure 2. Positions of blue whale catches in the Indian Ocean and around Australia from which corpora data were obtained, showing the boundaries of the **local areas** for pygmy blue whales. At least 50 sets of ovaries were examined in each local area.

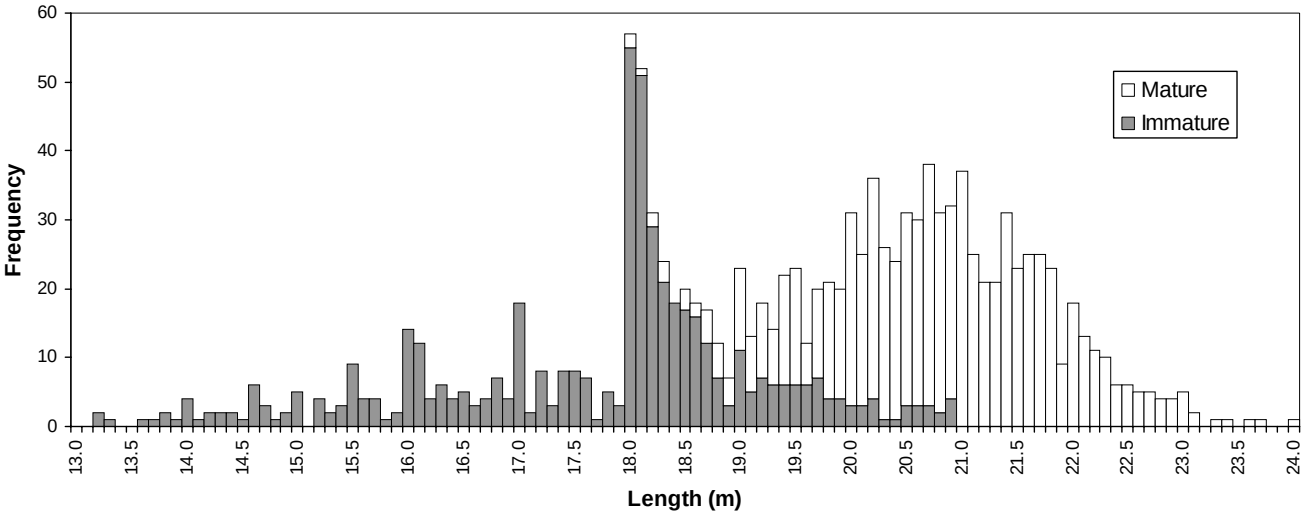

Figure 3. Number of pygmy blue whale records of each length that were immature and mature. These records were all from north of 52°S and excluded three probable Antarctic blue whales that were longer than 24.1 m. Whale "stretching" is evident from the high peak of records at 18.0 m; while there is also some suggestion of rounding to 1 m intervals in the data.

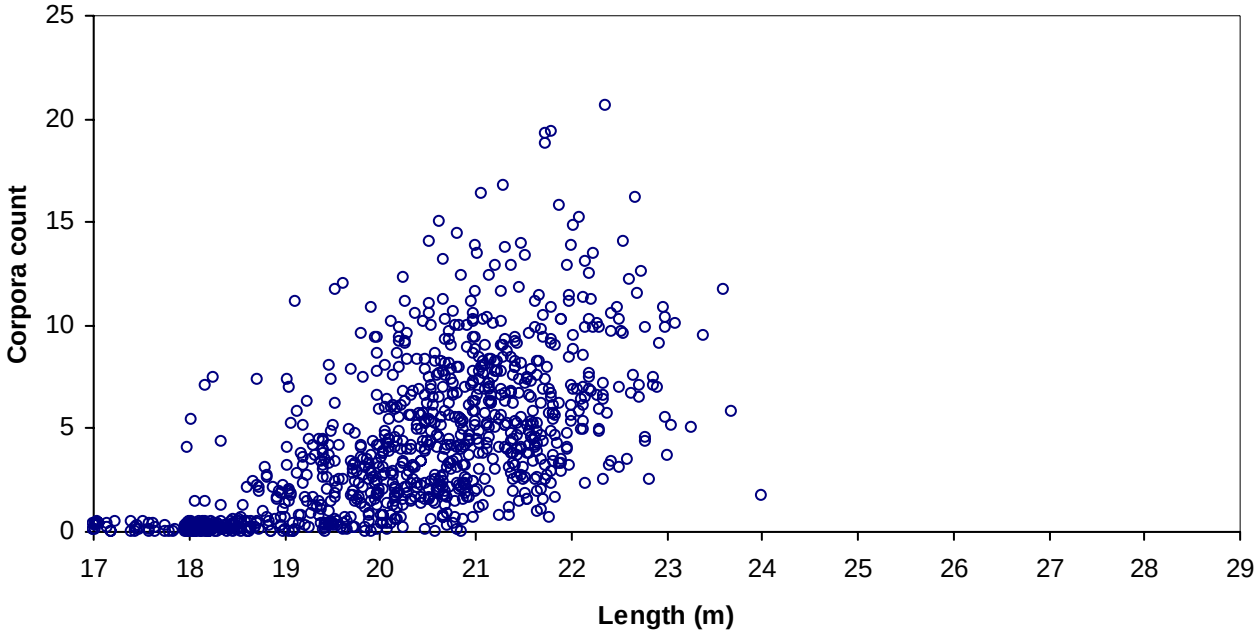

Figure 4. Relationship between length and ovarian corpora for 1,272 **pygmy** blue whales throughout the Indian Ocean and around the southern coast of Australia (north of 52°S). Pygmy blue whales were defined as catches north of 52°S and ≤ 24.1 m. Three catches longer than 24.1 m were omitted from the figure, see text for details. Data have been jittered by adding a random number between -0.005 and 0.005 to the length and between -0.5 and 0.5 to the corpora count. One whale with 32 corpora (length 22.0 m) and 129 whales shorter than 17 m (with zero corpora) are outside the bounds of the figure.

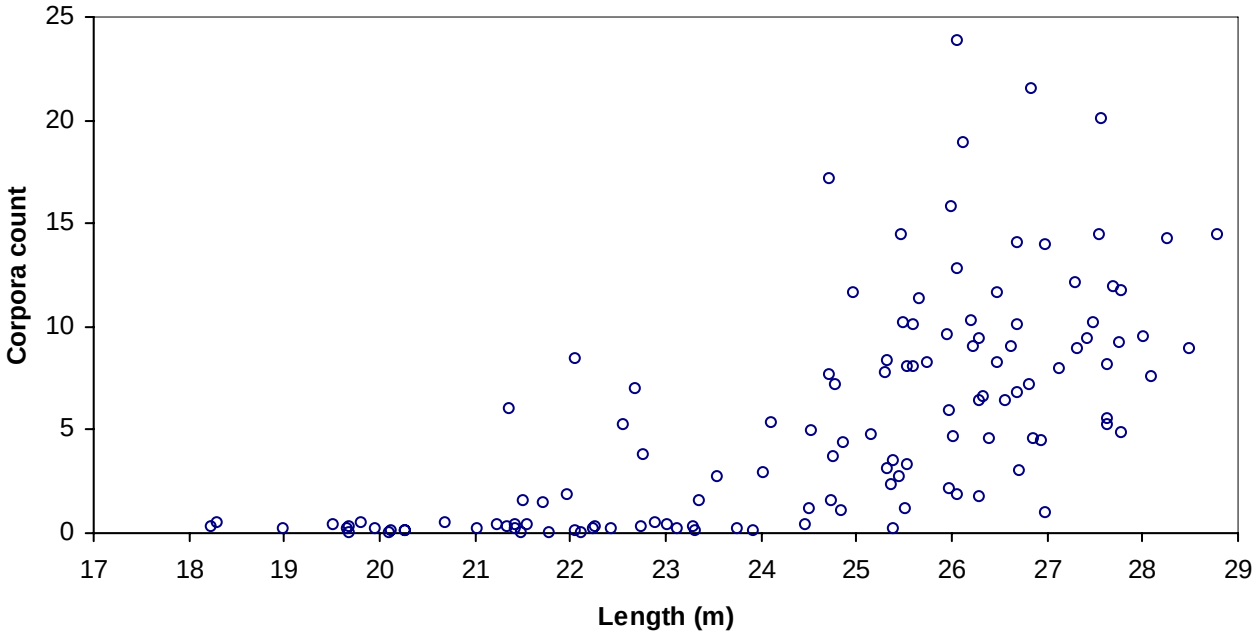

Figure 5. Relationship between length and ovarian corpora for 154 blue whales in the **Antarctic region** (south of 56°S). Data have been jittered by adding a random number between -0.005 and 0.005 to the length and between -0.25 and 0.25 to the corpora count.

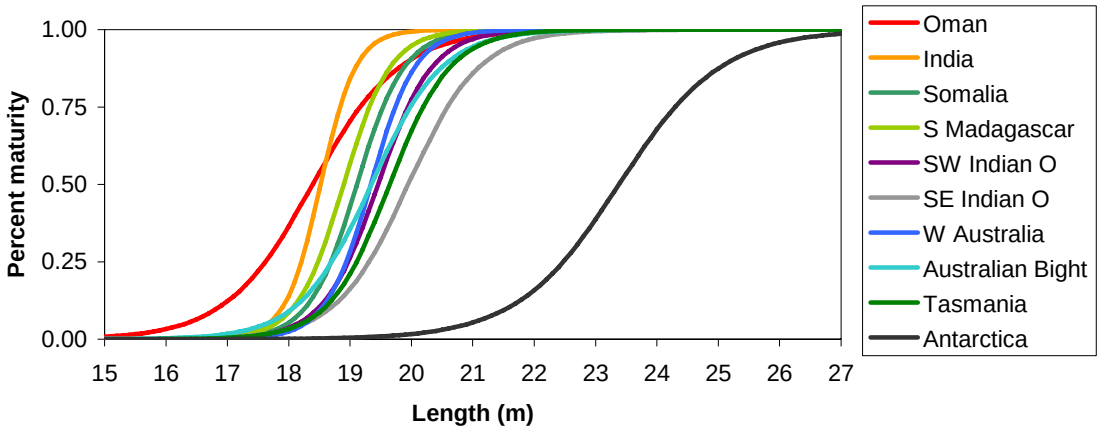

Figure 6. Logistic curves for percentage sexual maturity of female blue whales in different **local areas**. The median of the posterior distribution is plotted.

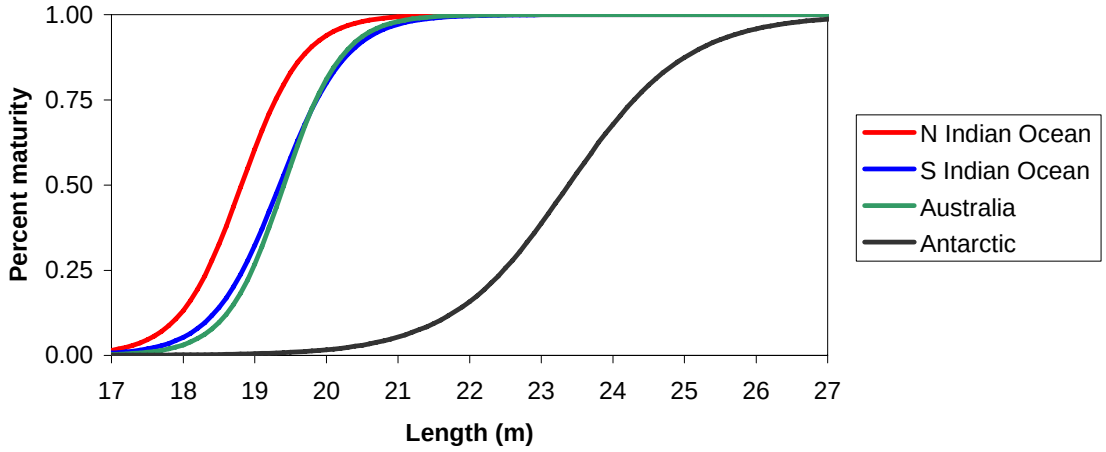

Figure 7. Logistic curves for percentage sexual maturity of female blue whales in different **large regions**. The median of the posterior distribution is plotted.

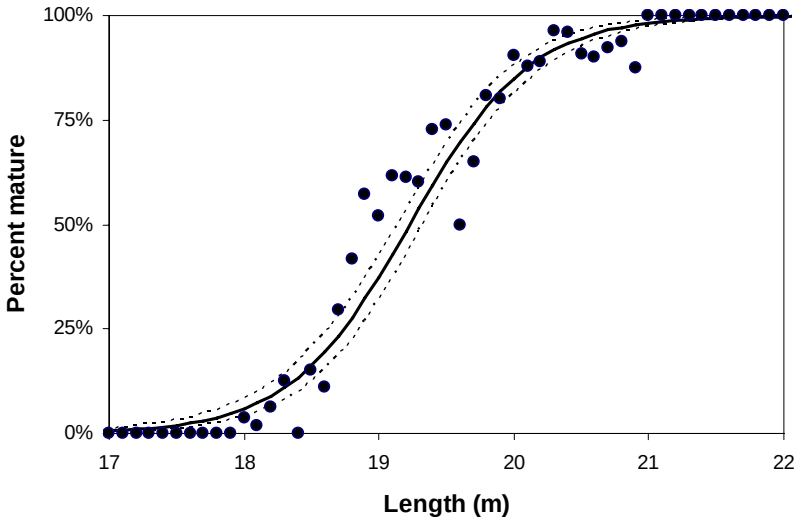

Figure 8. Median and 95% credibility intervals for logistic curve fit to sexual maturity data for pygmy blue whales. All whales smaller than 17 m were sexually immature and all whales larger than 22 m were sexually mature.