Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the southwest Pacific Ocean

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Abstract.–Porbeagle sharks, *Lamna nasus,* are caught in large numbers as bycatch in tuna longline fisheries in the southwest Pacific Ocean. Information on reproduction, embryonic development, and size and sex composition was collected by scientific observers from New Zealand and Australian waters, and supplemented with data from other sources. Most sharks were juveniles less than 150 cm fork length (FL), and length-frequency distributions showed 3–5 modal peaks that we interpret as age classes. Juveniles grow linearly and rapidly (16–20 cm per year), reaching 110–125 cm FL in three years. Females mature at around 165–180 cm. Litter size is usually four embryos and parturition probably peaks in June–July (winter). This finding contrasts with data for North Atlantic porbeagles which give birth in spring–summer. Embryos grow about 7 cm per month, and are born at 58–67 cm FL. The gestation period appears to be about 8–9 months, but there is considerable variability in embryo length at any one time, suggesting an extended mating period. Embryos are nourished by oophagy, and develop a grossly distended abdomen as their "yolk stomach" fills with ova. Small embryos have fang-like functional teeth that tear open egg capsules to release the contained ova. The fangs are shed at 34–38 cm FL. The weight of yolk in the stomach peaks at 30–42 cm FL, and accounts for up to 81% of total body weight. Waste products of yolk digestion accumulate steadily in the spiral valve throughout gestation, and the liver reaches its maximum size in near-term embryos as excess energy from yolk digestion is stored for postnatal use.

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The porbeagle, *Lamna nasus* (Bonnaterre, 1788) is a pelagic mackerel shark (family Lamnidae) that inhabits cool, temperate oceans. It occurs in the North Atlantic Ocean and in a circumglobal band in the southern Pacific, Atlantic and Indian Oceans (Compagno, 1984; Last and Stevens, 1994; Yatsu, 1995). It is absent from the North Pacific, where it is replaced by its closest relative, the salmon shark (*Lamna ditropis*).

Lamnid sharks produce a small number of large, live young that are nourished by oophagy (Gilmore, 1993). In this unusual form of embryonic development, the pregnant female ovulates an enormous number of ova which are consumed by the embryos in the uteri. The embryos develop grossly swollen abdomens as they store large quantities of yolk for later growth. Oophagy was first described in porbeagles (Swenander, 1906, 1907; Shann, 1911, 1923) and salmon sharks (Lohberger, 1910), but has only recently been confirmed in shortfin and longfin makos (*Isurus oxyrinchus* and *I. paucus*) and white sharks (*Carcharodon carcharias*) (Gilmore, 1983; Stevens, 1983; Francis, 1996; Uchida et al., 1996).

The unusual bloated appearance of porbeagle embryos has led to a number of reports in the literature (Bigelow and Schroeder, 1948; Graham, 1956; Templeman, 1963), but the absence of a series of embryos at different stages of gestation has hampered attempts to understand their development. Litters usually consist of four embryos (Templeman, 1963; Gauld, 1989), which are thought to be born at about 60–80 cm total length (TL) (Shann, 1923; Compagno, 1984; Last and Stevens, 1994). Female size at maturity is often cited as 152 cm TL (Bigelow and Schroeder, 1948; Compagno, 1984; Last and Stevens, 1994), apparently based on two pregnant females reported to have been "about five feet long" (Shann, 1911). However, no other mature females under 2 m TL have been reported, leading some authors to regard the length at maturity as 2–2.5 m TL (Aasen, 1963; Pratt and Casey, 1990). The length of the gestation period is unknown; estimates, however, range from eight months to two years (Shann, 1923; Aasen, 1963; Gauld, 1989). The timing of parturition is variously stated as spring, summer, or autumn in the North Atlantic (Bigelow and Schroeder, 1948; Aasen, 1963; Gauld, 1989). Thus, despite the early discovery of oophagy in porbeagles, little is known about their reproduction. Most parameter estimates are imprecise, and several are speculative or conflicting.

Few pregnant females have been reported from the Southern Hemisphere, and few details have been provided for any of them. Graham (1939, 1956) reported one caught at Otago Heads, New Zealand, in 1933. It had three embryos that were approaching full term and weighed 3.4–4.3 kg each. Graham (1956) also examined several other pregnant females but he reported few details. Duhamel and Ozouf-Costaz (1982) found four small embryos in a female caught in 1981 near Kerguelen Island in the southern Indian Ocean (51°S, 70°E).

Growth curves are available for northwest Atlantic porbeagles, based on modal analysis of length-frequency distributions, and back-calculation of length-at-age from bands on a vertebra (Aasen, 1963). They suggest that growth is relatively fast, at least in the first few years, and that longevity is 20–30 years. No growth information is available for the Southern Hemisphere.

Porbeagles have been exploited for their flesh for many decades, and have proven to be vulnerable to overfishing. A target longline fishery in the northwest Atlantic in the 1960s lasted only six years before collapsing (Anderson, 1990; Pratt and Casey, 1990). In the Southern Hemisphere, porbeagles have not been targeted, but they are frequently taken as bycatch in tuna fisheries, especially the pelagic driftnet fishery for albacore (*Thunnus alalunga*) during 1982–91 in the South Pacific (Murray, 1994; Yatsu, 1995), and the longline fishery for southern bluefin tuna (*Thunnus maccoyii*) and bigeye tuna (*Thunnus obesus*) in the southern Indian and Pacific Oceans (Stevens et al., 1983; Francis et al., 1999). In the New Zealand longline fishery, porbeagles are the second most commonly caught shark after the blue shark (*Prionace glauca*) (Francis et al., 1999).

The collapse of the northwest Atlantic fishery in the 1960s provides ample justification for a cautious approach to managing porbeagles. In view of recent increased landings in the North Atlantic (O'Boyle et al., 1996), and the size and scope of the tuna longline fishery in the southern oceans, there is an urgent need for improved information on reproduction, growth, and stock productivity as a basis for effective management. Much of the Southern Hemisphere longline fishery occurs in international waters, making monitoring and management difficult. Recently, the New Zealand and Australian governments implemented scientific observer programs to monitor catches of foreign and domestic longline vessels in their respective Exclusive Economic Zones (EEZs). These programs provided an opportunity to collect information on the reproduction and growth of porbeagles. In this paper, we describe the geographical distribution and length composition of sharks taken by longline vessels in the southwest Pacific, estimate the growth rate of embryos and juveniles, and describe embryonic development and oophagy. We also estimate the length of the gestation period, the timing of parturition, and the size at birth, and compare these with estimates for North Atlantic porbeagles.

Materials and methods

Data sources

Most of our data and specimens were collected by scientific observers aboard Japanese and domestic tuna longline vessels operating in the New Zealand and Australian EEZs. In New Zealand, fishing and observer effort was concentrated in two regions: 1) northeast New Zealand (north and east coasts of North Island and the Kermadec Islands), and 2) southwest New Zealand (east and west coasts of South Island) (Fig. 1). In Australia, most effort was around Tasmania (Fig. 2). New Zealand observers began recording the quantity of bycatch in 1987, measuring and sexing porbeagles in 1990, and examining females for embryos in 1992. In Australia, the respective years were 1988, 1990 and 1991. The primary task of observers was to monitor the target tuna species (mainly southern bluefin and bigeye tuna). Porbeagles were counted on most longline sets but were not always measured or examined for embryos. Therefore our data represent a subsample of the catch taken by observed longliners. The opportunistic nature of this collection process, and the low catch rate of pregnant females, necessitated the accumulation of specimens and data over a lengthy period.

Embryos collected by observers were supplemented by specimens and data from other sources, and the literature, including three litters from Heard and Kerguelen Islands in the southern Indian Ocean (Table 1). The four embryos from the Kerguelen female were deposited in the Museum National d'Histoire Naturelle (MNHN 1981-1432–1981-1435) (Duhamel and Ozouf-Costaz, 1982), and were photographed and remeasured for us by Duhamel.[1] A 185-cm-fork length (FL) female from Macquarie Island (Fig. 1) was the only intact pregnant female we examined.

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[1] Duhamel, G. 1997. Museum National d'Histoire Naturelle (MNHN), 75231 Paris cedex 05, France. Personal commun.

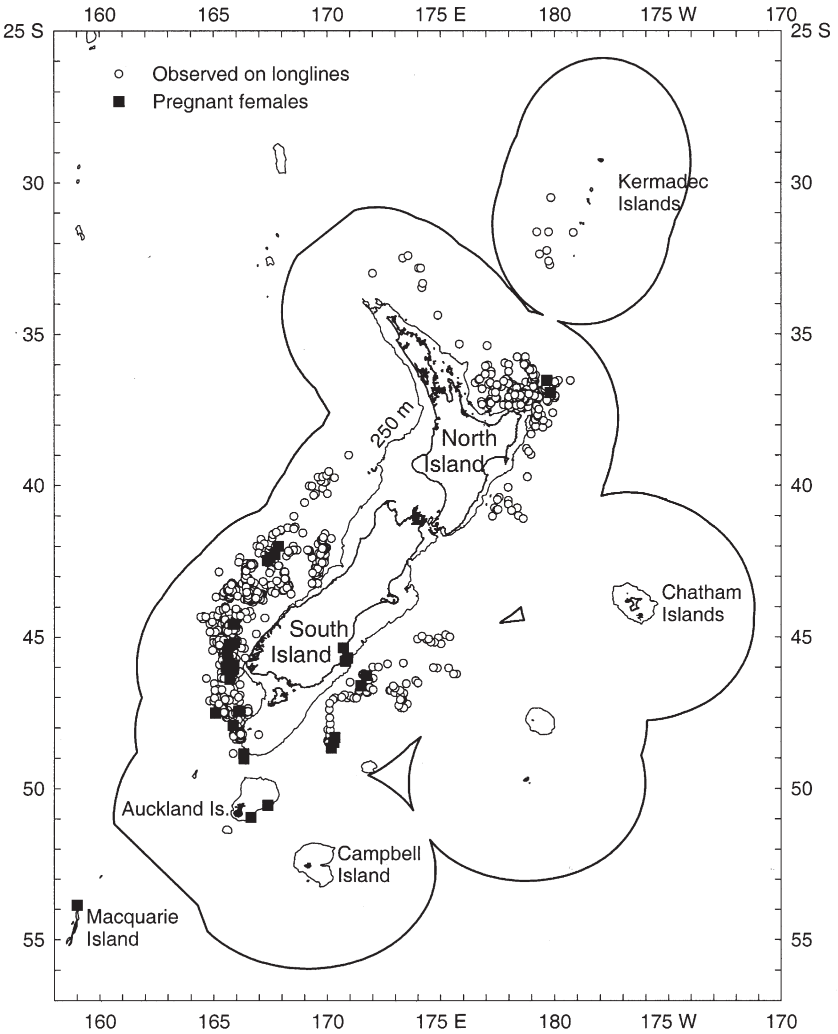

Figure 1

Map of the New Zealand region showing start positions of tuna longline sets from which porbeagles were recorded, and capture locations of pregnant females (n=35). The 250-m isobath and Exclusive Economic Zone are also shown.

Size and growth

Porbeagles were measured in one or more of three ways: precaudal length (PL; snout to the precaudal pit), FL (snout to the fork in the tail), and TL (snout to the tip of the tail). TL can be measured in two different ways—with the tail in the natural position (TL_{nat}) (Bigelow and Schroeder, 1948), or with the tail flexed down so that the upper caudal lobe lies parallel to the long axis of the body (TL_{flex}) (Compagno, 1984). Observers probably measured TL_{nat} on postnatal porbeagles because TL_{flex} is difficult to measure in species with a relatively rigid caudal fin. TL_{nat} measurements in embryos are not strictly comparable with TL_{nat} measurements in postnatal porbeagles because of the curved and folded nature of the caudal fin in embryos.

Most observers measured FL; therefore we adopted that as our standard. Regression equations relating FL to TL and PL are given in the "Results" section. Literature reports of TL were converted to FL before comparison with our data. Hereafter, FL is reported unless otherwise stated. Porbeagles were also sexed, weighed whole, and sometimes weighed after processing. Data were inspected for outliers on bivariate plots of PL, FL, TL, whole weight, and processed weight. Obvious errors were corrected if possible, and deleted if not. Before 1993, some New Zealand observers confused porbeagles and shortfin makos. We therefore restricted our New Zealand analyses of length, weight and location to data collected from 1993 onwards.

Initial inspection of the length-frequency data revealed modes that might correspond with juvenile age

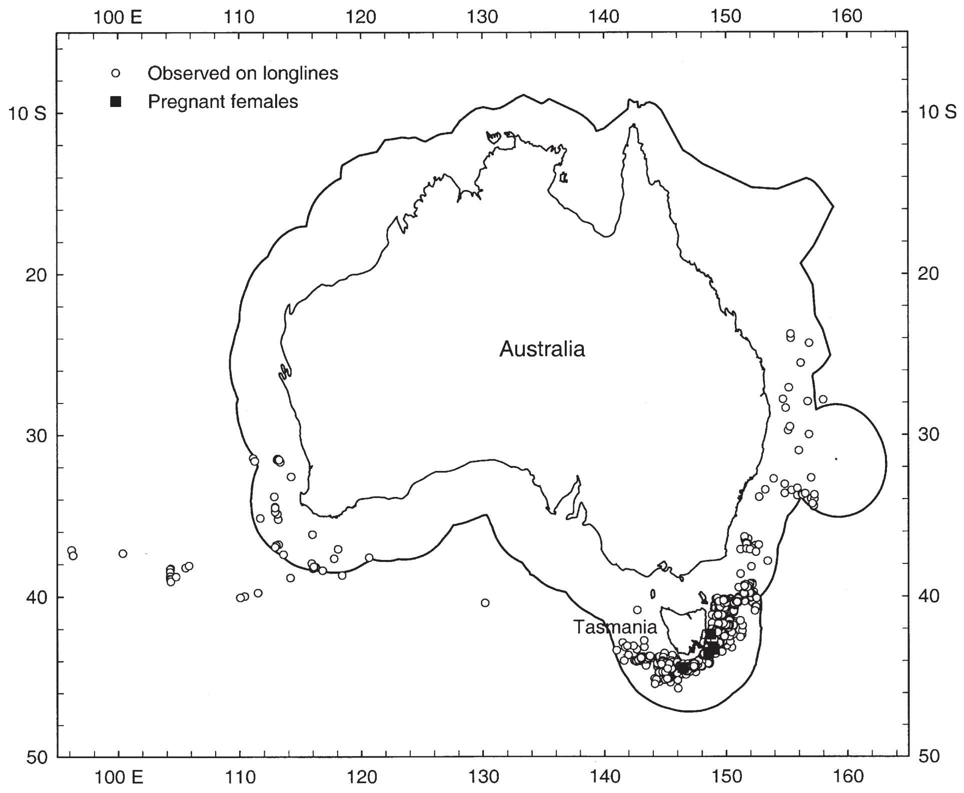

Figure 2

Map of the Australian region showing start positions of tuna longline sets from which porbeagles were recorded, and capture locations of pregnant females (n=5). The Exclusive Economic Zone is also shown.

classes. To assist modal discrimination, we limited our length-frequency analyses to the period April–July, during which 87% of New Zealand and 86% of Australian length measurements were taken. The MIX computer program (MacDonald and Pitcher, 1979; MacDonald, 1987; MacDonald and Green, 1988) was applied separately to the New Zealand and Australian length-frequency data for combined sexes to decompose the distributions into their component age classes. The program estimates the mean length, and the standard deviation of the lengths, for each age class, and the proportion of the sample in each age class. Length-frequency data were grouped into 3-cm class intervals, and truncated at 162 cm (New Zealand) and 150 cm (Australia) before analysis because large sharks were poorly represented in the samples. For each data set, we fitted a MIX model with three age classes and then progressively added extra age classes until there was no significant improvement in the χ^2 goodness of fit (MacDonald and Green, 1988). Occasionally, partially constrained fits (alternately fixing the standard deviations and proportions of one or two of the older age classes) were necessary for successful convergence (MacDonald and Green, 1988). This had no effect on the estimates of mean length, which were never constrained.

Embryos and ova

Embryos were placed in plastic bags and frozen; sometimes only partial litters were retained. Rarely, the uteri were removed intact and frozen with the embryos still inside. In the laboratory, embryos were thawed, sexed, and their jaws were examined for functional teeth. The embryos were then weighed, and measured (usually PL, FL, TL_{nat}, and TL_{flex}). FL was estimated from TL for three embryos without FL measurements (see "Results" section for regression equations). The liver and the contents of the stomach and intestine were weighed separately. Stomach contents were expressed as a percentage of total weight. Liver weight, and the weight of the intestinal contents were expressed as percentages of yolk-free embryonic weight to avoid distortions caused by the large variation in the stomach contents.

The uteri and right ovary[2] of the Macquarie Island female were examined. The diameters of a subsample of ovarian ova were measured using an image analysis system attached to a binocular microscope, and an

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[2] The left ovary of lamnid sharks is vestigial (Pratt, 1988).

estimate was made of the total number present by counting ova in six weighed subsamples.

The four MNHN embryos from Kerguelen Island were measured for TL, FL, and weight in December 1997. Because there was a mean shrinkage of 4.4% from the original TL measurements (Duhamel and Ozouf-Costaz, 1982), we applied an equivalent shrinkage correction to the 1997 FL measurements. Fresh embryo weights were not reported by Duhamel and Ozouf-Costaz (1982), and we have not used the 1997 weights because they probably underestimate the original weights due to dissolution and leaching of lipids from the yolk in the stomach. Similarly, measurements from the Museum of New Zealand (NMNZ) embryos are not included here because of likely shrinkage and weight loss following preservation.

North Atlantic embryo lengths and dates of capture were obtained from the literature for comparison with Southern Hemisphere data (Swenander, 1906, 1907; Shann, 1911, 1923; Nordgård, 1926; Bigelow and Schroeder, 1948; Templeman, 1963; Gauld, 1989; Moss[3]; Newton[4]). For some litters, only one or two embryos were measured. Data were used only if they specified the month of capture, and some measurements that were known or thought to have been made on preserved specimens were corrected for shrinkage.

Results

Geographical distribution

Porbeagles have a wide latitudinal distribution. In the New Zealand region, they range from the Kermadec Islands (30°30'S) to Macquarie Island (53°52'S) (Fig. 1). In the Australian EEZ, they range from near the Tropic of Capricorn in southern Queensland (23°44'S) to south of Tasmania (45°44'S) (Fig. 2). The large number of capture records from northeast and southwest New Zealand, and around Tasmania, reflect concentration of fishing effort, and not necessarily high shark densities. Porbeagles also occur near Heard Island (51–52°S), and Kerguelen Island (51°S) in the southern Indian Ocean (Duhamel and Ozouf-Costaz, 1982).

Porbeagles were caught off southern Queensland (Fig. 2, north of 31°S) only in winter (June–September), when water temperatures were lowest. Sea surface temperature (SST) at the time of capture of six sharks off Queensland in July–August 1997 was 21.3–21.6°C, about 4°C lower than normal.

Sea surface temperature was recorded at about hourly intervals during hauling of each longline in New Zealand. The number of sharks caught per 1000 hooks (CPUE) was determined for each set and plotted against the mean of the hourly SSTs. There was no apparent trend in CPUE between 9.85°C (the minimum set temperature) and 19.5°C (mean CPUE=1.82, maximum=44.8, n=1292 sets). Between 19.5 and 23.0°C, mean CPUE was lower (mean=0.54, maximum = 5.0, n=105), and above 23.0°C no porbeagles were caught (n=23).

Most pregnant females were caught in the cooler southern waters of New Zealand and Australia (Figs. 1 and 2), and some were taken from the subantarctic Auckland, Macquarie, Heard, and Kerguelen Islands (50–54°S). However, two were also caught in northeast New Zealand. For longline-caught females, SST was 10.2–17.2°C (mean 12.9°C, n=32), and bottom depth at the capture locality was 600–4300 m (mean=2104 m, n=11). The two Heard Island pregnant females were taken by bottom trawl at depths of 248 and 259 m and bottom temperatures of 2.9 and 2.5°C, respectively. The Auckland Islands female was caught by midwater trawl at 160–164 m and a temperature of 11.9°C. Porbeagles have also been caught by bottom trawl near Macquarie Island at temperatures of 1°C (Williams[5]).

Length, weight, and growth

The relationships between PL and FL (both in cm) for New Zealand porbeagles were as follows:

$$PL = -1.366 + 0.907\,FL \qquad (n=866,\ r^2=0.995,$$
$$FL = 1.990 + 1.098\,PL \qquad \text{range 61–223 cm FL, 54–208 cm PL}$$

The relationships between TL and FL (both in cm) for Australian porbeagles were as follows:

$$TL = 4.165 + 1.098\,FL \qquad (n=173,\ r^2=0.967,$$
$$FL = -0.567 + 0.881\,TL \qquad \text{range 63–180 cm FL, 71–202 cm TL)}$$

Length-weight data were available for 641 New Zealand porbeagles (330 males, 309 females, and 2 unsexed) over the range 61–228 cm FL and 3–153 kg weight. However 96.7% of the sample was less than 150 cm FL; therefore the results represent only juveniles. There was no evidence from the raw data, or the residuals from a log-log regression, of a difference between the sexes. The regression equation for combined sexes was as follows:

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[3] Moss, S. A. 1995. University of Massachusetts, North Dartmouth, MA 02747, USA. Personal commun.

[4] Newton, A. 1996. The Marine Laboratory, P.O. Box 101, Aberdeen, Scotland. Personal commun.

[5] Williams, R. 1997. Australian Antarctic Division, Tasmania, Australia. Personal commun.

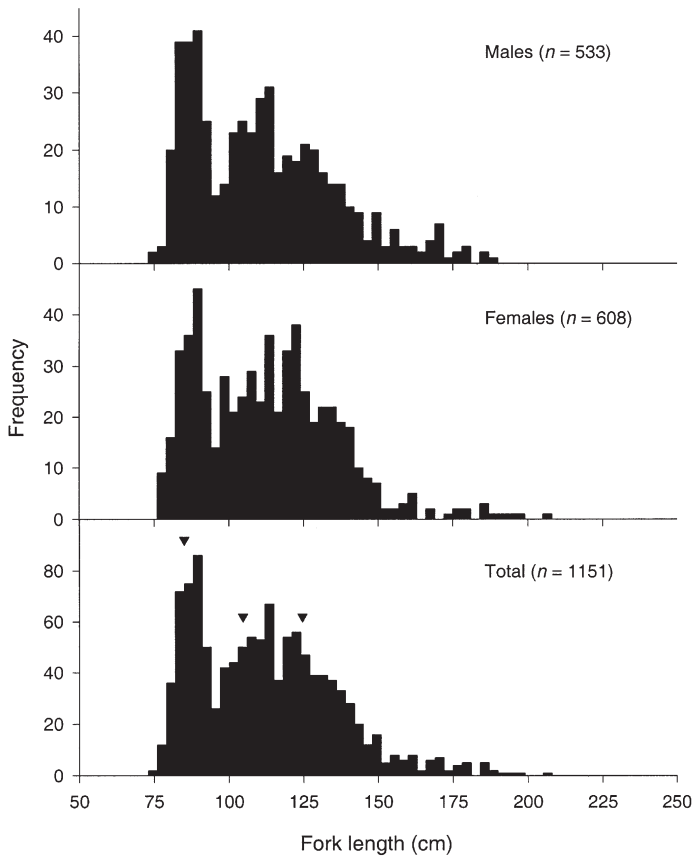

Figure 3A

Porbeagle length-frequency distributions by sex for April–July: (**A**) southwest New Zealand; (**B**) northeast New Zealand; (**C**) Australia. The bottom panel in each series includes some unsexed sharks. n = sample size. Triangles indicate mean lengths of the age classes identified by MIX modal decomposition.

$$\text{Log}_{10}(weight) = -5.050 + 3.128\ \text{Log}_{10}(FL), \quad (n = 641,\ r^2 = 0.956)$$

where weight is expressed in kg and FL in cm.

In New Zealand, length ranges were 64–228 cm for males and 61–206 cm for females (Fig. 3, A and B). Most were shorter than 150 cm. The size distributions were similar for males and females up to 150 cm, and the sex ratio (both subregions combined) was not significantly different from one (M:F=0.93:1; χ^2=1.99, P>0.1). However, males outnumbered females above 150 cm by 3.18:1 (χ^2=16.28, P<0.01).

In southwest New Zealand, there was a strong modal peak at 79–93 cm for both sexes, and for males there were also clear peaks at 100–115 cm and 118–133 cm (Fig. 3A). The best MIX fit to the combined sexes data consisted of three age classes whose mean lengths are shown in Fig. 3A. Sample sizes were small in northeast New Zealand; therefore no MIX model was applied. A strong mode was present at 67–88 cm (Fig. 3B), and indistinct modes were present for both sexes at about the same position as the second and third modes in southwest New Zealand.

In Australia, length ranges were 61–204 cm for males and 58–208 cm for females (Fig. 3C). Most were shorter than 150 cm, with a strong mode at 76–94 cm. The size distributions of males and females were similar. The sex ratio of sharks smaller than 150 cm did not differ significantly from one (1.07:1; χ^2=1.47, P>0.1), but males outnumbered females above 150 cm by 2.71:1 (χ^2=11.08, P<0.01). The best MIX fit to the combined sexes data consisted of five age classes whose mean lengths are shown in Figure 3C.

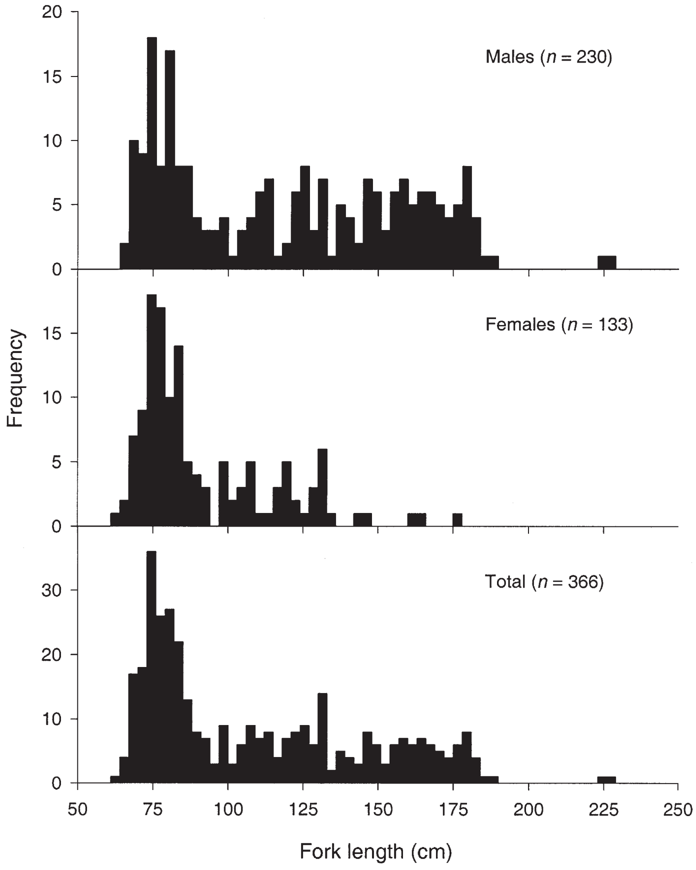

Figure 3B

The mean lengths of the modes for southwest New Zealand and Australia were plotted against age, which was calculated from a theoretical birth date of 1 June (see below) and mean sampling dates of 5 May and 16 June, respectively (Fig. 4). Thus the ages classes were sampled near their respective birth dates. We interpret the five Australian modes as representing sharks that were recently born, and 1–4 years old, and the three southwest New Zealand modes as those representing sharks that were 1–3 years old. The first length mode in the northeast New Zealand distribution was substantially shorter than the first southwest New Zealand mode and the second Australian mode, and we are uncertain about assigning an age to it. At age 1 year, southwest New Zealand and Australian porbeagles were similar in length, but for older ages New Zealand sharks were slightly larger. Growth in both regions was linear over the range of the data (Fig. 4):

southwest
New Zealand: $FL = 66.5 + 19.8\ (Age)$ $(r^2{=}1.000)$

Australia: $FL = 65.4 + 16.1\ (Age)$ $(r^2{=}0.997)$

Female length at maturity and reproductive development

Maturity status was not recorded; therefore we cannot estimated length at maturity. However, 37 pregnant females ranged from 167[6]–199 cm (mean=185 cm), suggesting that female maturity is reached around 165–180 cm.

The Macquarie Island female had four embryos 21.5–23.2 cm long. The right ovary was of the "internal" type, which is typical of lamnid sharks (Pratt, 1988). It weighed 2.75 kg (2.35% of total weight) and was undergoing active oogenesis. The entire ovary was packed with ova; other than a thin external envelope it had no macroscopically visible ovarian tissue. There was a single large efferent pore in the ovary, from which ova are shed (Stevens, 1983; Gilmore, 1993).

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[6] FL of 167 cm was calculated from a PL of 151 cm.

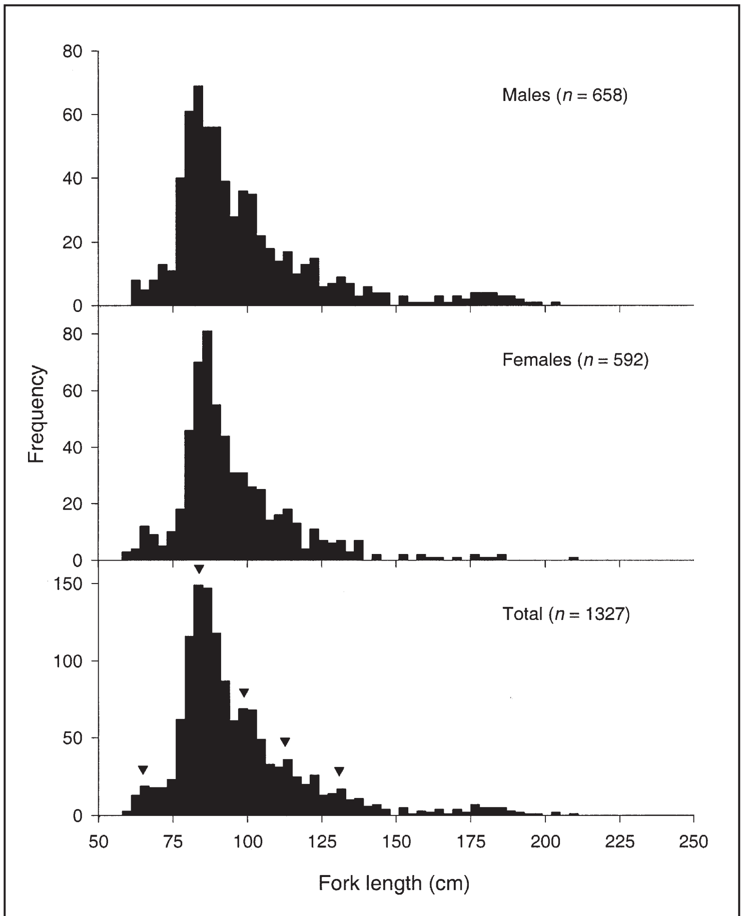

Figure 3C

The mean ovum count from six weighed subsamples was 72.2 ova per gram (SE=2.6), producing an estimated total number of 198,000 ova. Ova diameters were mostly 1.5–3.3 mm; a group of larger ova had diameters of 3.4–4.7 mm (Fig. 5). In addition to the embryos, the right uterus contained three egg capsules, and in the left uterus a 22.0-cm embryo had an egg capsule lodged in its mouth. Three of the capsules were empty and the fourth contained four ova (Fig. 6). Uterus width, estimated from a photograph containing a ruler, was about 10 cm. In other females with near-term embryos, uterus width was about 20 cm. The anterior quarter of the uterus had many longitudinal folds or pleats, and the rest was covered with small papillae and had a velvety texture.

Litter size, embryonic growth, and gestation

Data were obtained from 43 litters and 138 embryos (Table 1). All but four of the 40 litters for which litter size was known contained four embryos, two in each uterus. The exceptions were two litters reported by Graham (1939, 1956) with two and three embryos respectively, one reported by Hanchet[7] with three embryos, and a New Zealand longline-caught litter with two midterm embryos. Mean litter size was 3.85. Of 132 embryos that were sexed, 73 were males and 59 were females, producing a sex ratio not significantly different from one (χ^2=1.48, P>0.1).

Regression equations relating different embryo length measurements (in cm) were:

$$PL = -0.125 + 0.885\,FL \qquad (n=97,\ r^2=0.999)$$
$$TL_{\text{nat}} = 0.180 + 1.162\,FL \qquad (n=96,\ r^2=0.998)$$
$$FL = -0.085 + 0.859\,TL_{\text{nat}} \qquad (n=96,\ \mathrm{r}^2=0.998)$$
$$TL_{\text{flex}} = 0.836 + 1.170\,FL \qquad (n=87,\ r^2=0.998)$$
$$FL = -0.644 + 0.853\,TL_{\text{flex}} \qquad (n=87,\ r^2=0.998)$$

A log-log regression of yolk-free embryo weight (kg) against FL (cm) gave

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[7] Hanchet, S. 1996. National Institute of Water and Atmospheric Research (NIWA), P. O. Box 893, Nelson, New Zealand. Personal commun.

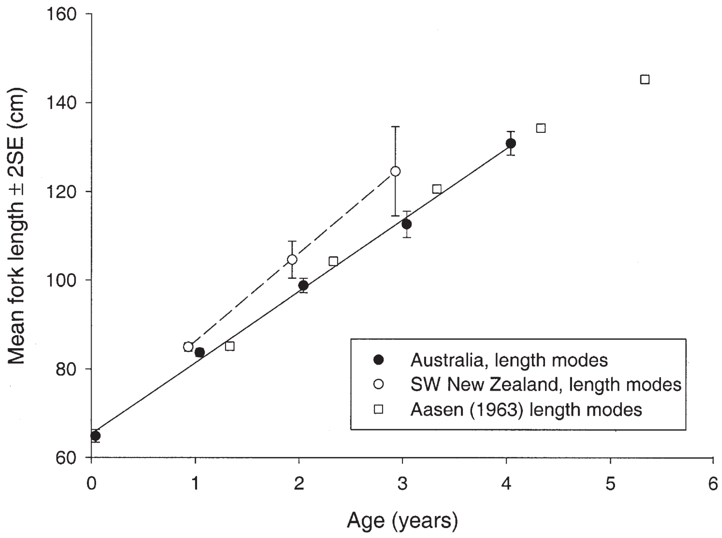

Figure 4

Porbeagle mean lengths-at-age determined by MIX analysis of the southwest New Zealand and Australian data in Figure 3, A and C, with fitted linear regressions. Also shown are Aasen's (1963) northwest Atlantic length-frequency modes, which were plotted assuming a 9 April theoretical birth date (1.7 months earlier than the Southern Hemisphere) and a mean sampling date of 9 August.

Table 1

Sources, numbers, collection periods and collection localities of Southern Hemisphere porbeagle embryos. NZ = New Zealand; NMNZ = Museum of New Zealand. Additional pregnant females reported by Graham (1956) were not included because of lack of data.

Source	Number of litters	Number of embryos	Collection period	Collection locality
Tuna longline	27	87	1992–98	New Zealand
Tuna longline	5	17	1991–95	Tasmania, Australia
Bottom trawl	2	8	1997	Heard Island
Bottom trawl	1	4	1995	Macquarie Island
Midwater trawl	1	4	1996	Auckland Island, NZ
NMNZ P22122	1	3	1987	Auckland Island, NZ
Hanchet[1]	2	2	1982–83	Otago, NZ
Berquist[2]	1	4	1998	Otago, NZ
Graham (1939, 1956)	2	5	1933	Otago, NZ
Duhamel and Ozouf-Costaz (1982)	1	4	1981	Kerguelen Island
Total	43	138		

[1] See Footnote 7 in the main text.

[2] Berquist, R. 1997. Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand. Personal commun.

$$\mathrm{Log}_{10}\,(weight) = -4.719 + 2.916\ \mathrm{Log}_{10}\,(FL) \quad (n=100,\ r^2=0.974)$$

The Kerguelen Island embryos reported by Duhamel and Ozouf-Costaz (1982) were the smallest in our sample, with estimated FLs of 9.6–10.4 cm. Our largest embryos were in litters of 62.0–67.0 cm, 64.2–65.6 cm, and 64.3–66.6 cm. Typically, all embryos in a litter were similar in length, but two litters each contained one unusually small embryo (runt) (Table 2). Variation in length within a litter increased with mean length, but the percentage range in length was relatively constant.

Table 2

Fork lengths and weights of stomach contents, intestinal contents, and livers of embryos from two litters that contained one unusually small embryo.

	Litter 1	Litter 2
Embryo fork lengths (cm)	22.5, 27.7, 29.0, 30.8	51.4, 55.3, 55.3, 63.8
Length range (cm)	8.3	12.4
Length range as percentage of mean length (%)	30.2	22.0
Smallest embryo		
Stomach contents (kg)	0.015	0.077
Intestine contents (kg)	0.007	0.069
Liver (kg)	0.003	0.056
Other three embryos		
Stomach contents (kg)	0.117–0.440	0.183–0.340
Intestine contents (kg)	0.114–0.296	0.092–0.130
Liver (kg)	0.006–0.017	0.151–0.364

All embryos were collected between 11 March and 16 July, reflecting the seasonality of the longline fisheries. The mean length of Southern Hemisphere embryos in a litter increased significantly ($P<0.01$) with sampling date (Fig. 7):

$$Mean\ FL\ (\text{cm}) = 9.36 + 7.48\ month, \quad (n=39,\ r^2=0.27)$$

where "month" is defined as the number of months elapsed since 1 January. There was considerable unexplained variability. For example, in April, mean embryo length varied between 20.3 and 63.5 cm. Inspection of the data by year of collection and sampling location showed that the variability was not caused by interannual or spatial differences. A regression equation fitted to North Atlantic embryo data (Fig. 7) was

$$Mean\ FL\ (\text{cm}) = 23.51 + 6.78\ month \quad (n=29,\ r^2=0.70)$$

The North Atlantic regression explained a much higher proportion of the variation but displayed considerable length variability in early gestation. A homogeneity of slopes test showed that the regression slopes for the two hemispheres were not significantly different ($P=0.76$). The pooled data had a regression slope (=embryonic growth rate) of 7.1 cm per month, and the regression intercepts differed significantly (analysis of covariance, $P=0.004$) by 12.0 cm, which is equivalent to a temporal displacement of about 1.7 months.

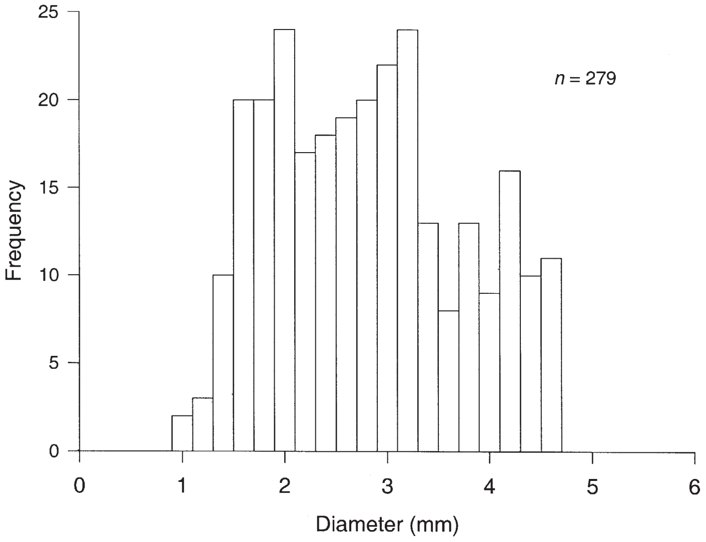

Figure 5

Frequency distribution of ovarian ova diameters from a pregnant porbeagle from Macquarie Island. n = sample size.

Small, postnatal juveniles 58–68 cm long ($n=53$), were observed on Australian longlines between 22 May and 9 September, with a mean capture date of 15 July. Large embryos (up to 67 cm) were observed between mid-April and mid-June (Fig. 7). In the Southern Hemisphere, the large variation in embryo length at any one time, and the long period over which small juveniles, assumed to be newborn, were collected, indicate that the parturition period is lengthy. Parturition probably peaks in June–July (winter) but may

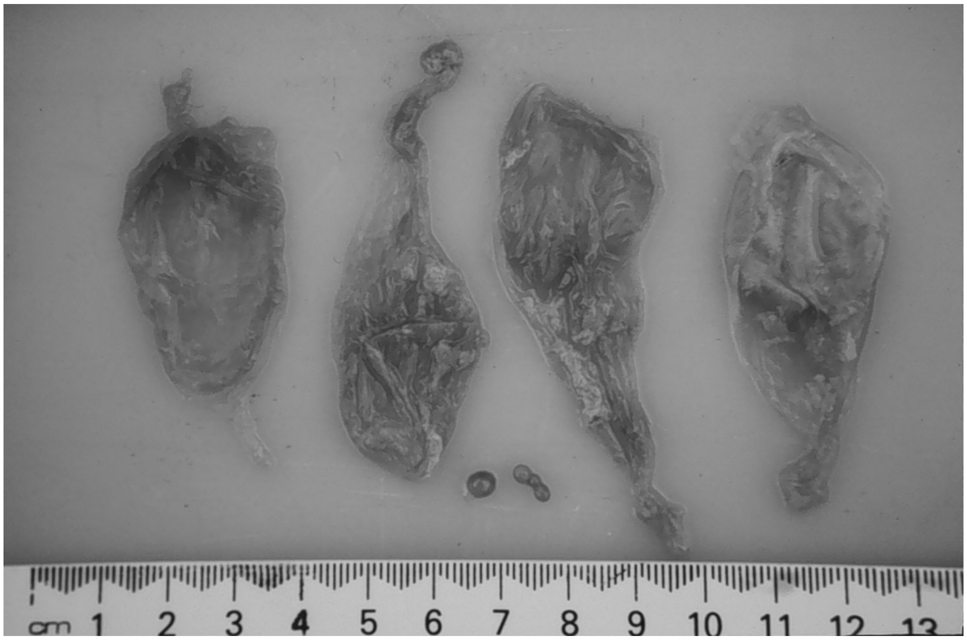

Figure 6

Four empty egg capsules found in the uteri and in the mouth of an embryo, from a pregnant porbeagle from Macquarie Island. Also shown are several loose ova found in one of the egg capsules. The largest egg case was 75 mm long.

extend from April to September. For aging purposes, we defined the theoretical birth date as 1 June. Based on the lengths of the smallest juvenile and the largest embryo, the length at birth is 58–67 cm. If a growth rate of 7.48 cm per month is maintained by Southern Hemisphere porbeagles throughout gestation, the gestation period is about 8–9 months. However, the unexplained variability in Fig. 7 compromises our ability to accurately estimate the gestation period.

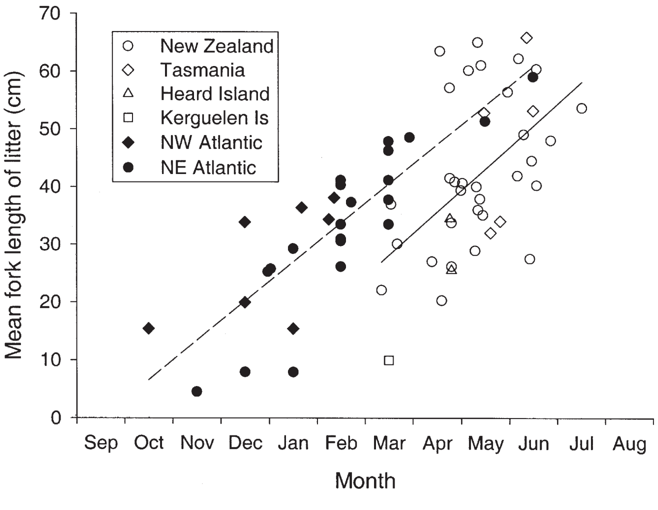

Figure 7

Monthly variation in the mean lengths of porbeagle embryos from four Southern Hemisphere locations (white symbols, n=39, r^2=0.27), and the northwest and northeast Atlantic (black symbols, n=29, r^2=0.70).

Embryonic development

Porbeagle embryos develop the distended yolk stomach that is characteristic of all oophagous lamnid sharks (Fig. 8). In the Kerguelen embryos (9.6–10.4 cm), such distension was already apparent. The caudal fin was notably curved, with the upper lobe much longer than the lower lobe, and there were no external gill filaments. At 19.8–20.7 cm, the bulging yolk stomach was the most noticeable feature, along with a marked lateral expansion of the head and branchial region (Fig. 8A). The body lacked pigmentation (except for the eyes), and appeared pink because of the presence of blood vessels under the skin. At 34.2 cm, the yolk stomach had become enormously distended, and measured 22.6 cm long by 15.9 cm high; the branchial and throat regions remained

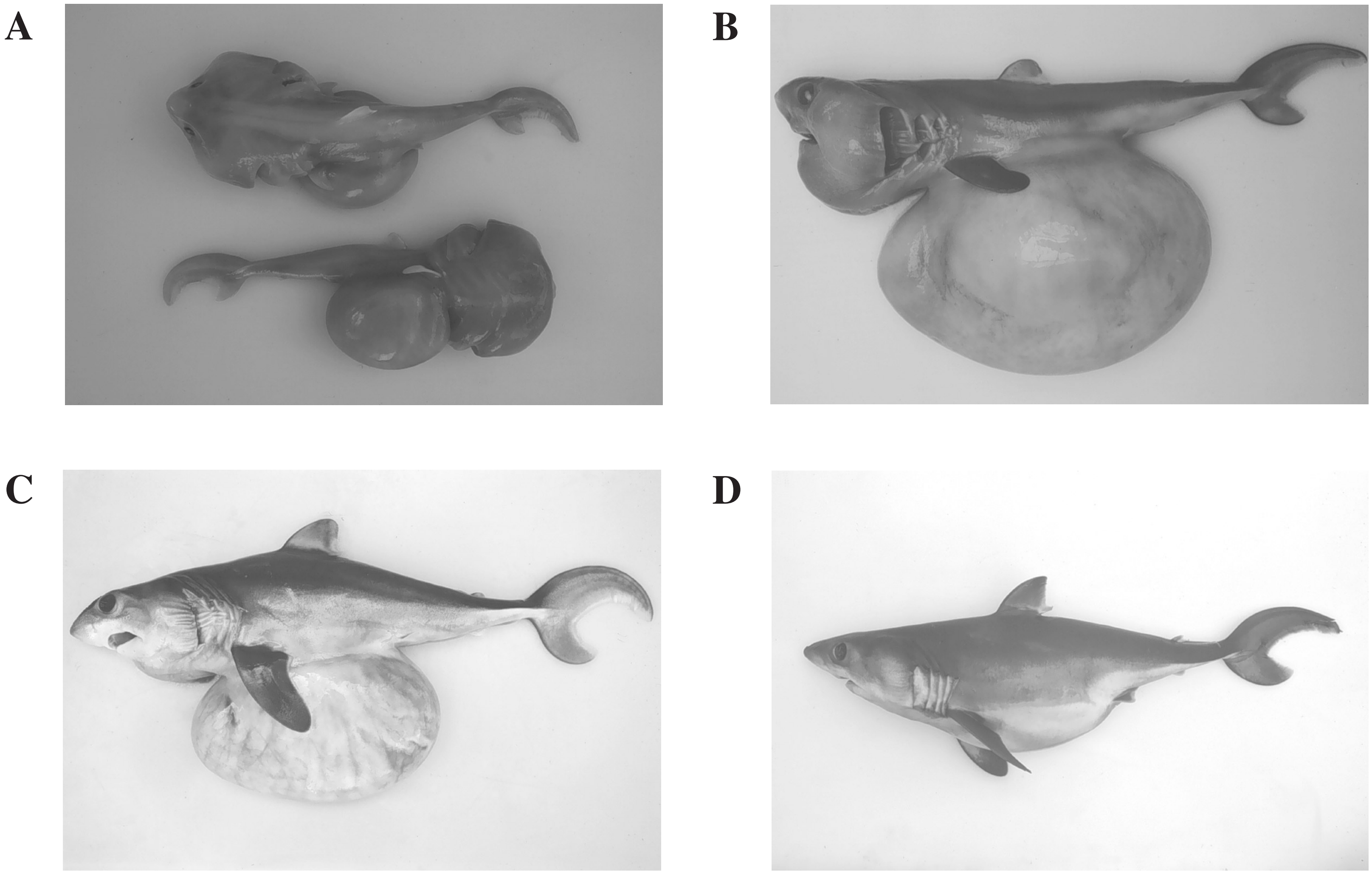

Figure 8

Changes in porbeagle embryo external shape with increasing size (not to same scale). (**A**) 20.7-cm female (top) and 19.8-cm male (bottom). (**B**) 34.2-cm female. (**C**) 40.3-cm female. (**D**) 58.0-cm female.

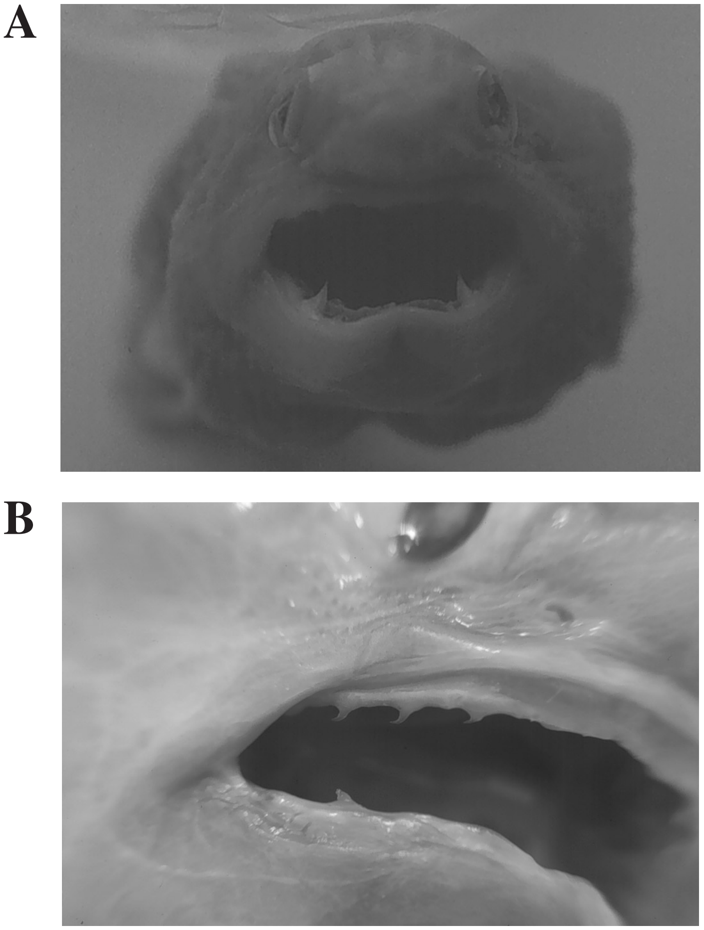

Figure 9

Anterior view of the heads of (**A**) 9.6-cm embryo, and (**B**) 26.4 cm female embryo showing the functional fangs. (Photo A. by G. Duhamel.)

swollen, and the upper body and pectoral fins had become pigmented (Fig. 8B). At 40.3 cm, pigmentation was essentially the same as in postnatal porbeagles, the swelling of the head had disappeared, and the yolk stomach had begun to shrink (Fig. 8C). At 58.0 cm the juvenile body form had been attained, apart from an enlarged abdomen (Fig. 8D). Other embryos around this size and larger had a more streamlined shape, with little noticeable abdominal distension.

Distension of the abdomen during early development causes the subdermal muscle layers to split along the ventral midline, extending anteriorly as far as the fifth gill slits. The expanding stomach protrudes between the muscle layers and stretches the abdominal skin. Later, the stomach shrinks back inside the muscle layers, and the stretched skin returns to its original shape. A distinct "scar" remains in the ventral midline in the area between the origins of the pectoral fins and the fifth gill slits, marking the anteriormost point of the split muscle layers.

Small embryos had large, erect, tubular, recurved "fangs" in both jaws (Fig. 9, A and B). These teeth, which were quite unlike those found in postnatal porbeagles, were clearly functional. In the Kerguelen embryos (9.6–10.4 cm), the tooth formula was (1+1/1+1), and the lower teeth were massive in relation to mouth size (Fig. 9A). Larger embryos (19.8–38.3 cm) had more functional upper teeth (3+3/1+1) (Fig. 9B). Additional minute teeth were visible under a light microscope, but they appeared vestigial and nonfunctional and were not included in the tooth formula. Replacement fangs were present behind the functional series, but they were irregularly spaced and usually located between the functional teeth. Oval scars on the gum of both jaws external to functional fangs indicated that fangs are progressively shed and replaced. The largest embryo with fangs was 38.3 cm, and the smallest embryo without fangs was 33.9 cm. In the range of overlap, there were 12 embryos with fangs and 8 without fangs. Therefore, the fangs are shed between 34 and 38 cm.

Most of the larger embryos without fangs possessed several series of developing, nonerect, nonfunctional teeth shaped like those found in postnatal porbeagles, except that they lacked lateral cusps. One near-term litter had three embryos with nonfunctional upper teeth but partially erect lower teeth, whereas the fourth had nonfunctional teeth in both jaws.

The stomach contents consisted wholly or mostly of viscous, amorphous, light yellow yolk. In many embryos there were also discrete masses of clear, white or greyish gelatinous material, probably the remains of empty egg capsules, embedded in the yolk. This gelatinous material usually represented less than 10% of the stomach contents and has been included in the yolk weights reported below. Occasionally we found shed fangs in the stomachs, but the thick glutinous nature of the yolk made them difficult to find, and it was impossible to assess their frequency or abundance.

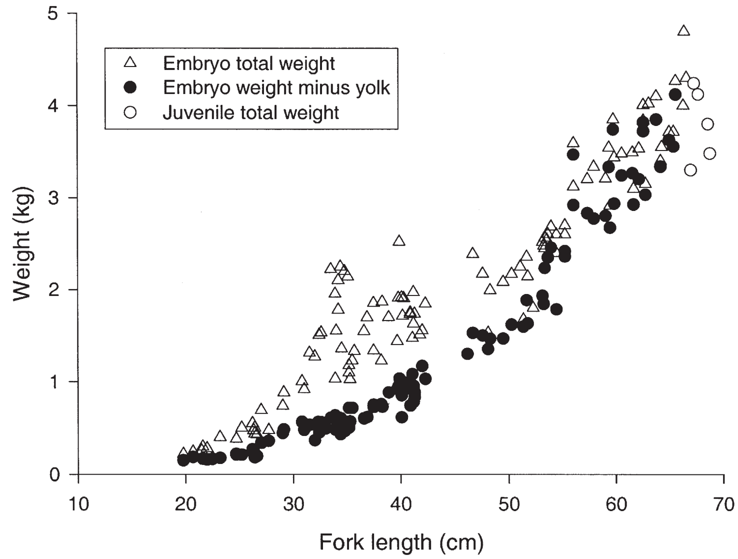

Figure 10

Variation in total weight and yolkfree weight with length for porbeagle embryos. Also shown are total weights of five small juveniles.

Embryonic total weight increased rapidly between 20 and 35 cm, changed little between 35 and 50 cm, then increased again during the rest of the gestation period (Fig. 10). Embryonic weight minus yolk weight increased steadily throughout gestation. The weights of five free-living juveniles shorter than 70 cm were similar to the yolk-free weights of the largest embryos.

The weight of yolk in the stomach increased steadily between 20 and 30 cm, before increasing rapidly to peak at 30–42 cm (Fig. 11). Yolk weight at 30–42 cm varied from 0.39 kg to 1.82 kg, representing 26.7–80.8% of total body weight. Absolute and percentage yolk weight both generally declined at lengths greater than 42 cm. Three embryos longer than 60 cm still had around 1 kg of yolk in their stomachs, but it represented a low proportion of their total weight (ca. 17–22%[8]). All embryos longer than 50 cm had yolk or gelatinous material in their stomachs, suggesting that the yolk may not be completely digested before birth.

The spiral valve of the intestine contained a thick, gritty, greenish-brown sludge that is the waste product of yolk digestion. The smallest embryos dissected (19.8–20.7 cm) contained small amounts of waste, and the quantity of waste increased steadily throughout gestation (Fig. 11). Intestinal contents composed the greatest percentage of yolk-free weight at 30–50 cm. Newborn porbeagles had smaller quantities of intestinal waste than large embryos, suggesting that the waste is retained until after birth.

Liver weight increased exponentially with FL, showing the most rapid increase above 55 cm (Fig. 11). Relative liver weight also increased to a maximum in the longest embryos. Postnatal porbeagles usually had smaller livers, both in absolute and relative terms, than those of the largest embryos, indicating that energy reserves stored in the liver are consumed by the young after birth.

The runts in two litters had low stomach and intestine contents, and liver weights (Table 2). The 22.5-cm runt in litter 1 had numerous short (1–3 mm) lacerations on its distended abdomen, and a few elsewhere on its body, presumably inflicted by the teeth of its larger sibling. However none of the gashes had penetrated the body cavity, and they did not appear to be life-threatening.

Five pairs of uteri containing embryos were obtained. The orientation of the embryos could be determined for only five of the 10 uteri; these five uteri contained embryos 38.2–62.6 cm long. In all cases, the two embryos were facing in opposite directions.

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[8] Not shown in the percent yolk weight panel of Fig. 11 because embryo total weights were not measured accurately.

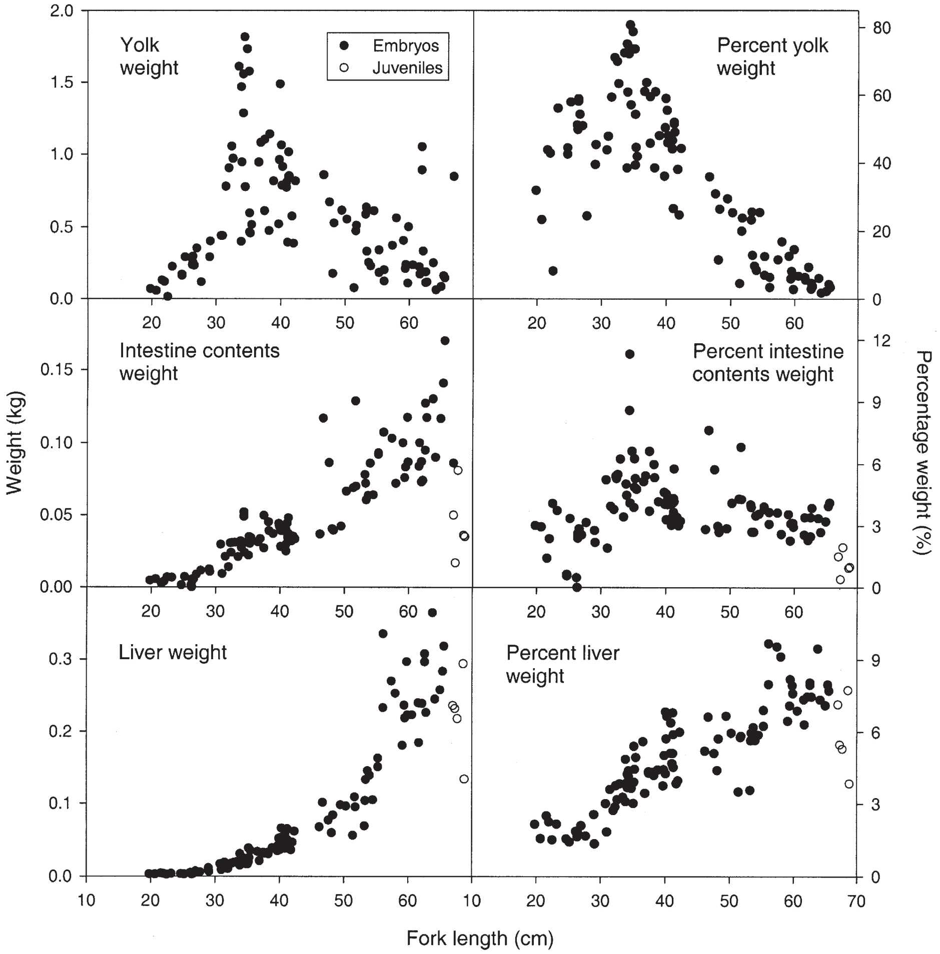

Figure 11

Variation in the weight of yolk, intestine contents, and liver with length (left panels), and the percentage of the total weight contributed by yolk, and percentages of yolkfree weight contributed by intestinal contents and liver (right panels) for porbeagle embryos. Comparable data for five small juveniles are also shown.

Discussion

Geographical distribution

Porbeagles occur throughout the New Zealand EEZ and the southern half of the Australian EEZ. On the east coast of Australia, they reach subtropical waters (to 23°44'S), but only during winter. At the other extreme, porbeagles are found in subantarctic waters in the Indian and southwest Pacific Oceans, reaching almost 54°S. Our results are consistent with observations of porbeagles between about 28 and 58°S across the entire South Pacific between New Zealand and Chile (Yatsu, 1995). Porbeagles are caught only north of 30°S in winter–spring (August–November), and they penetrate farther south during summer and autumn (Yatsu, 1995).

Sea surface temperature at locations where porbeagles were caught was 9.9–22.6°C, but catch rates were low above 19.5°C. This is similar to SSTs reported previously for porbeagles in the South Pacific by Stevens et al. (1983) (7.6–22.8°C, with most captures less than 16.7°C) and Yatsu (1995) (5–20°C with most captures less than 15 °C). Temperatures at the actual depth of capture would be similar to these because most longlines fished at 50–100 m depth, which is shallower than the depth of the mixed ocean layer in autumn–winter. Bottom temperatures for trawl-caught porbeagles were as low as 1–3°C, which is consistent with temperatures of 1.7°C (Svetlov, 1978) and 3.1–4.1°C (Templeman, 1963) reported elsewhere. Thus the temperature range inhabited by porbeagles in the Southern Hemisphere is probably about 1–23°C, with abundance declining above about 19°C. The preferred temperature in the North Atlantic is less than 18°C (Aasen, 1963).

Porbeagles can maintain their body temperature up to 11°C above that of the surrounding water (Carey et al., 1985). Among the small group of endothermic sharks, they are exceeded in this capacity only by salmon sharks (Carey et al., 1985). The apparent preference for higher latitudes by large (Yatsu, 1995) and pregnant porbeagles may indicate an increased ability to thermoregulate in larger sharks. High body temperature is probably necessary for lamnid sharks to function as active predators of fast-moving prey in cold water (Goldman, 1997).

In the North Atlantic, porbeagle abundance varies seasonally and spatially (Aasen, 1961, 1963; Templeman, 1963; Mejuto and Garcés, 1984; Mejuto, 1985; Gauld, 1989), and there are indications of seasonal variability in their vertical distribution (Bigelow and Schroeder, 1948; Aasen, 1961, 1963). Limited tagging results show that they are capable of movements up to 2370 km (Aasen, 1962; Stevens, 1976, 1990). In combination with evidence of seasonal latitudinal migration in the South Pacific (Yatsu, 1995), this range of movement suggests that Southern Hemisphere porbeagles may exhibit complex seasonal, spatial, and length-related distribution patterns. Our data were collected mainly during April–July, and therefore provide little information on seasonality.

Length, weight, and growth

Several length-weight relationships have been published for the North Atlantic (Aasen, 1961; Mejuto and Garcés, 1984; Gauld, 1989; Stevens, 1990; Ellis and Shackley, 1995; Kohler et al., 1995). All were based on small samples, except those of Gauld (1989), who found a significant difference between males and females above 180 cm. Our New Zealand sample comprised mainly sharks less than 150 cm, and compared with the length-weight relationships of Mejuto and Garcés (1984), Gauld (1989) and Kohler et al. (1995), our length-weight relationship rises too steeply beyond 150 cm. Our relationship should therefore not be extrapolated beyond 150 cm.

The largest porbeagles in our samples were 228 cm (male) and 208 cm (female). The maximum length reached in the North Atlantic is not clear. Maxima of 253 cm (288 cm TL) and 278 cm (317 cm TL) for Scottish males and females, respectively, appear to be the largest reliable measurements (Gauld, 1989). Lengths of 294–325 cm (“estimated … 11 feet”, “ca 11–12 feet”, or “340–370” cm TL) reported by McKenzie (1959) and Templeman (1963) were obviously not measured accurately and may have been overestimated. A TL of 12 feet equals 365.8 cm TL, which likely forms the basis for the maximum length of 365 cm TL reported by Pratt and Casey (1990). If Southern Hemisphere porbeagles grow as large as those in the North Atlantic, our samples do not include the larger size classes. Tuna longlines catch shortfin makos that exceed 300 cm FL (senior author, pers. obs.); therefore, they should be capable of retaining large porbeagles. The latter evidently inhabit latitudinal or depth ranges outside our sampling area, which is inhabited mainly by juveniles.

Males and females were equally represented at lengths up to 150 cm. At greater lengths, males significantly outnumbered females by about 3:1 in both New Zealand and Australia. Skewed sex ratios have been reported frequently in the North Atlantic, in favor of males (Mejuto and Garcés, 1984; Mejuto, 1985; Ellis and Shackley, 1995), females (Gauld, 1989), or either sex depending on the length range or sample (Aasen, 1963; O’Boyle et al., 1996). Aasen (1963) found that the overall sex ratio in large samples was close to 1:1. These results indicate that juveniles do not segregate by sex, but that larger sharks do.

MIX analysis discriminated 3 and 5 length modes respectively in southwest New Zealand and Australia, which we interpret as age classes. In northeast New Zealand, the mean sampling date was 25 June, over seven weeks after the mean sampling date for southwest New Zealand; therefore the first mode in the former could represent new-born sharks. Alternatively, it may represent slow-growing one-year-olds. The latter interpretation is supported by the similarity of the positions of modes 2 and 3 in both northeast and southwest New Zealand.

Juveniles grow linearly and rapidly, reaching 110–125 cm FL in three years. They may grow slightly faster in southwest New Zealand (20 cm/year) than in Australia (16 cm/year), but the standard errors were large for New Zealand 2- and 3-year-olds, and the comparison could be biased by incorrect determination of the number of modes in the length-frequency data. The modal lengths for Australian juveniles agree well with the first four modes for northwest Atlantic porbeagles presented by Aasen (1963) (Fig. 4), providing that our modes represent age classes. Aasen (1963) presented two growth curves—one based on length-frequency modes, and the other on back-calculated lengths-at-age from a single vertebra from a 226-cm female. [9] His two growth curves were practically identical.

Our growth estimates also agree with length-increment data for five tagged northeast Atlantic porbea-

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[9] In a preliminary report, Aasen (1961) presented vertebral age data for 50 porbeagles. However the mean lengths-at-age differed substantially from those presented later, and Aasen (1963) stated that his earlier results “were not very accurate.”

gles (Stevens, 1976, 1990). Their lengths at tagging and recapture were only estimated; therefore growth increments were approximate. The sharks were relatively small when released (84–105 cm), and were at liberty for 0.75–13 years. Annual growth increments were about 9–32 cm, with a mean of 20.4 cm. Despite good agreement among all sources of porbeagle growth data, a vertebral-based growth curve from adequate sample sizes and covering the full size range is still required for both hemispheres.

Longevity is unknown, but Aasen (1963) aged his 226 cm female as 19+ years and suggested that they may live around 30 years. This conclusion needs confirmation because longevity is often used to estimate the natural mortality rate, which is an important parameter in population models.

Length at maturity and reproductive development

The lengths of pregnant females (167–199 cm, mean 185 cm) suggest that females mature at about 165–180 cm. This estimate is consistent with reports of a 191-cm mature female from the South Atlantic (Svetlov, 1978), and immature females of 138, 139, and 150 cm from around New Zealand (Stevens et al., 1983; Duffy[10]). The length at maturity of North Atlantic females is controversial. Shann (1911) reported two pregnant females of "about five feet long" (152 cm TL, or 133 cm FL). In both cases, the length estimate was probably third-hand, and it is unlikely that the females were measured. That estimate of length at maturity, which we believe to be unreliable and too low, has permeated the literature (Bigelow and Schroeder, 1948; Compagno, 1984; Last and Stevens, 1994). Other authors have reported a wide maturity range of 175–220 cm FL (Aasen, 1961, 1963; Pratt and Casey, 1990). Templeman (1963) and Moss[3] reported females of 191 and 203 cm to be immature. The smallest mature females reported by Templeman (1963) and Gauld (1989) were 203 and 196 cm respectively, and Pratt (1993) examined one of 227 cm. Aasen (1961) showed that uterine width increased rapidly in females longer than 197 cm. These results suggest that North Atlantic females mature at about 195–205 cm (218–229 cm TL), which is higher than the range determined for the Southern Hemisphere. A similar between-hemisphere difference in length at maturity has been found for shortfin makos (Mollet et al.[11]).

There was no information on length at maturity in males in our data. On the basis of changes in clasper length and calcification, North Atlantic males apparently mature at a smaller size than do females, in the range 131–175 cm (150–200 cm TL) (Aasen, 1961; Ellis and Shackley, 1995).

The "internal" type ovary from our Macquarie Island pregnant female conformed with the morphology found in all lamnid and alopiid sharks examined so far (Pratt, 1988). It weighed 2.75 kg (2.35% of total weight). The ovary of Swenander's (1906, 1907) 246-cm North Atlantic pregnant female measured 41 by 28 cm, and weighed 6.3 kg, or 3.6% of estimated total weight. Mean embryo lengths in the two females were 22.1 cm and about 25 cm respectively. The embryo stomach contents peak at 30–42 cm, suggesting that ovarian size and ovulation may peak when embryos are about 25–30 cm long. In the shortfin mako, the ovary of an actively ovulating female with early-term embryos weighed about 5% of her total weight, whereas the ovaries of females carrying near-term embryos were spent and weighed as little as 0.2–0.3% of total weight (Mollet et al.[11]). In sandtiger sharks (*Carcharias taurus*), relative ovarian weight peaks at 6–7% of body weight, and then declines during the second half of gestation (Gilmore et al., 1983; Gilmore, 1993; Mollet et al.[11]). A low relative ovary weight was also reported in a longfin mako with near-term embryos (Gilmore, 1983).

The size-frequency distribution of ova from the Macquarie Island female indicated that they are ovulated at around 4–5 mm. Ova diameters measured in two pregnant North Atlantic females after preservation in 10% formalin were mainly in the range 2.3–4.3 mm, with the largest measuring 6.0 mm (Moss[3]). Swenander (1906, 1907) reported ova diameters between 1 and 5–6 mm in a North Atlantic pregnant female, and encapsulated 4–5 mm ova in the uteri of another female. Maximum ova diameters in other oophagous sharks range between 4 and 10 mm (Springer, 1948; Bass et al., 1975; Otake and Mizue, 1981; Gilmore, 1983; Gilmore et al., 1983; Stevens, 1983; Uchida et al., 1996; Chen et al., 1997).

Empty and near-empty egg capsules were found in the uteri of the Macquarie Island female, and in the mouth of one of its embryos. Moss[3] also found empty egg capsules in the mouths and gill slits of embryos measuring 33.8 and 36.2 cm. Apparently, embryos are capable of rupturing egg capsules and swallowing the contents, although the occasional presence of gelatinous material resembling egg capsules in embryo stomachs (Swenander, 1907; this study) suggests that whole or empty capsules are sometimes swallowed. Swenander (1906, 1907) found over 40 egg capsules, each measuring about 80 by 15 mm and containing

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[10] Duffy, C. 1998. Department of Conservation, Private Bag 3072, Hamilton, New Zealand. Personal commun.

[11] Mollet, H. F., G. Cliff, H. L. Pratt, and J. D. Stevens. 1998. Reproductive biology of female shortfin mako *Isurus oxyrinchus* Rafinesque 1809. H. F. Mollet, Monterey Bay Aquarium, Monterey, California 93940, Unpubl. manuscript.

21–28 individual ova, in the uteri of a female that contained four embryos about 4.3–4.7 cm long. Duhamel and Ozouf-Costaz (1982) found 102 nonfertile eggs in the uteri of their Kerguelen Island female, which carried embryos of 9.6–10.4 mm. No photographs were taken of the eggs, and it is unclear whether they were egg capsules or individual ova (Duhamel[1]).

The emerging picture for oophagous sharks is that large numbers of nutritive egg capsules accumulate in the uteri during the early stages of gestation, and they are rapidly consumed as the embryos grow large enough to puncture and eventually swallow them (Gruber and Compagno, 1981; Otake and Mizue, 1981; Gilmore, 1983; Gilmore et al., 1983; Mollet et al.[11]). Ovulation peaks during midgestation, but full egg capsules are rarely found in the uteri, probably because they are eaten soon after entering the uteri. During later gestation, ovulation ceases and embryos metabolise their accumulated stomach contents for energy, growth, and storage in the liver.

Litter size, embryonic growth, and gestation

In 36 out of 40 of our pregnant females, litter size was four, with a mean of 3.85 embryos. Litters of two or three were occasionally recorded. In the North Atlantic, Shann (1911, 1923) stated that litters commonly consisted of two embryos (range 1–4), but his data almost certainly included several partial litters (see Table I in Shann, 1923). Templeman (1963) found three, four and four embryos in his three litters, and Gauld (1989) found four to be the most common number of embryos in a litter, with a mean of 3.7 (n=12).[12] One litter of five has also been reported (Bigelow and Schroeder, 1948). Our sample of Southern Hemisphere litters is the largest yet assembled, and Gauld's (1989) is the largest from the North Atlantic. Both samples had very similar mean numbers of embryos. We conclude that litter size is usually four, but smaller litters are occasionally found; litters larger than four are extremely rare. Some litters with fewer than four embryos were probably incomplete. Abortion of embryos during capture is common among nonlamnid sharks, but it is difficult to imagine midterm embryos with grossly distended abdomens being aborted, even when the mother is compressed in a trawl net. One of our New Zealand longline litters containing two midterm embryos, 37.5 and 38.3 cm long, was presumably complete. Abortion of near-term embryos is quite possible.

Linear regressions fitted to the length-month data for both hemispheres suggest that embryos have a rapid growth rate of about 7 cm per month, but there was much unexplained variability (Fig. 7). The estimated growth rate is almost twice that of shortfin mako embryos (3.7 cm per month) (Mollet et al.[11]). The length of the gestation period appears to be about 8–9 months in both hemispheres. During July–September, Aasen (1963) found no embryos in the northwest Atlantic despite examining hundreds of mature females. He argued that the gestation period was 8 months, and that the females he examined were undergoing a short rest period between pregnancies. Our interpretation agrees with that of Aasen (1963).

A contrary hypothesis involving a gestation period of 1–2 years has been advanced by Shann (1923) and Gauld (1989). They argued that the high variability in embryo length and the apparent presence of two cohorts of embryos were inconsistent with a gestation period of less than one year. We cannot rule out their hypothesis, and we are conscious that our Southern Hemisphere data are limited in seasonal scope and that pooling data across locations and years is not desirable. However, we believe the data from both hemispheres are most consistent with a gestation period of less than one year. The implied rapid embryonic growth rate is not unreasonable given the abundant embryonic food supply and the relatively high growth rates of postnatal juveniles discussed above.

The high variability in the embryo length data might be explained by an extended mating period. In the northwest Atlantic, Aasen (1963) found males with seminal vesicles that were filling at the end of August, indicating that mating would begin in September. Pratt (1993) reported a mature female caught in October with moderate amounts of spermatozoa in the oviducal gland and with fresh vaginal abrasions. A mature male with haematose claspers was caught on the same longline, providing strong evidence of mating in October. Gauld (1989) found females with fresh bite marks, thought to be inflicted during mating, on females near the Shetland Islands in December–January. These observations suggest that mating lasts from September to January in the North Atlantic.

If our hypothesis of rapid embryonic growth and high intracohort variability is correct, parturition probably peaks in June–July (winter) in the Southern Hemisphere and possibly extends from April to September. Parturition in the Northern Hemisphere may peak around two months earlier (spring–summer). The presence of distinct length modes in juvenile length-frequency distributions from New Zealand, Australia, and the northwest Atlantic (Aasen, 1963) confirms that parturition is restricted to part of the year, rather than occurring year-round. Svetlov (1978) reported the capture

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[12] Gilmore's Table 1 contains a number of errors. The reference to Aasen (1966) in the *Lamna nasus* section should presumably be Aasen (1963); the two Swenander (1907) litters contained four embryos each rather than 2; and the 219-cm TL shark with four embryos attributed to Nakaya (1971) was actually a male, and no embryos were mentioned by Nakaya.

of a female in the South Atlantic in March and stated: "The shark had recently spawned, to judge by external characters (an inflamed area of the body around the anus) and the state of the ovaries." He did not elaborate further on the ovaries, so it is difficult to assess his report. If the female was postpartum, the timing is one month earlier than our suggested parturition period for Southern Hemisphere porbeagles. Another possibility is that the inflammation around the cloaca may have been the result of recent mating.

If the gestation and rest periods combined last one year, and females reproduce every year, annual fecundity is 3.85 young per female. If there is a resting period of just over one year between pregnancies, annual fecundity would be half that amount. It is therefore important to determine whether Aasen's (1963) suggestion of a one-year cycle is valid for both hemispheres. The gestation period in shortfin makos is thought to be 18 months, with a reproductive cycle of three years (Mollet et al.[11]). Interestingly, the greater average fecundity of makos would result in an annual fecundity of about four per female (Mollet et al.[11]), which is similar to the reproductive output of porbeagles assuming a one-year cycle.

For Southern Hemisphere porbeagles, the length at birth was estimated to be 58–67 cm (68–79 cm TL), based on the lengths of the largest embryos and the shortest postnatal juveniles. In the North Atlantic, the largest reported embryos were 60–64 cm (Pennant, in Shann, 1911) and 65 cm (Gauld, 1989). Bigelow and Schroeder (1948) reported a 55.7-cm specimen (66.0 cm TL; USNM 47528), but it was an embryo rather than a postnatal juvenile (Williams[13]). The embryo would have been about 58 cm before preservation. Postnatal porbeagles of 66 and 70 cm were reported by Imms and Day respectively (in Shann, 1911). These observations indicate that porbeagles are born at about the same length in both hemispheres.

Embryonic development

We assembled a comprehensive series of porbeagle embryos ranging from early gestation (9.6 cm long) to full-term, enabling us to describe the main morphological changes that occur during gestation. Previous studies that described and illustrated embryos were based on only a few embryos, most of which were midterm (Swenander, 1906, 1907; Shann, 1911; Nordgård, 1926; Bigelow and Schroeder, 1948; Templeman, 1963).The following review of embryonic development is derived from our observations, supplemented by literature reports.

Embryos 4.3–4.7 cm long have external gills and well-developed branchial regions (Swenander, 1907). They have nearly absorbed their yolk sacs and have a large spiral valve, but there is no yolk in the digestive system. Swenander (1907) stated that "these embryos are too small to be able to swallow entire egg capsules and their teeth are not sufficiently developed to tear open the egg capsules." They have not begun to feed at this stage, despite the large number of egg capsules present in the uteri, but precocial teeth have already formed. At 10 cm, the lower jaw contains two relatively massive fangs (Fig. 9A) that appear capable of tearing open egg capsules. The upper teeth are much less developed and there is only one functional tooth on each side of each jaw. Lower jaw teeth also develop earlier than upper jaw teeth in sandtiger sharks (Hamlett, 1983). The abdomen is swollen and the embryos have presumably begun feeding (the stomachs were not dissected). Large numbers of egg capsules are present in the uteri. The external gills have been resorbed. By 15 cm, the abdomen is distended, and the head and branchial region are gelatinous and grossly enlarged (Bigelow and Schroeder, 1948).

Between 20 and 42 cm, development is dominated by the consumption of large numbers of egg capsules, leading to a great increase in the relative size and distension of the yolk stomach (Swenander, 1907; Shann, 1911, 1923; Bigelow and Schroeder, 1948; Templeman, 1963; Moss[3]; Fig. 8). Large fangs are present in both jaws (Swenander, 1907; Templeman, 1963; Moss[3]; Fig. 9) and are used to open the egg capsules before removal of the contents; how this is accomplished is unknown. At 30–42 cm, yolk accounts for up to 81% of total weight (Fig. 11; Templeman, 1963). The stomach yolk in midterm embryos of shortfin makos peaks at about 60–70% of total weight (Mollet et al.[11]). Relative and absolute amounts of yolk in porbeagles and other oophagous sharks decline during the rest of gestation (Fig. 11; Mollet et al.[11]).

Porbeagle embryos shed their fangs at about 34–38 cm. Embryonic fangs (the "emb" teeth of Gilmore, 1993) have also been reported in salmon sharks, common and bigeye thresher sharks (*Alopias vulpinus* and *A. superciliosus*), shortfin makos and sandtiger sharks (Lohberger, 1910; Bass et al., 1975; Gruber and Compagno, 1981; Gilmore et al., 1983; Hamlett, 1983; Gilmore, 1993; Chen et al., 1997). They probably occur in all oophagous species, and in at least some species, they are shed part-way through gestation. In bigeye thresher sharks, fangs appear at about 11 cm TL and disappear at about 60 cm TL (Chen et al., 1997). In sandtiger sharks, they appear at 4–5 cm TL, and are lost some time before birth (Gilmore et al., 1983; Hamlett, 1983).

We suspect that female porbeagles cease ovulation at about the time the embryonic fangs are lost, as

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[13] Williams, J. T. 1997. National Museum of Natural History, Washington DC 20560–0159. Personal commun.

has been reported for shortfin makos and sandtigers (Gilmore et al., 1983; Mollet et al.[11]). The embryos then rely on the yolk stored in their stomachs to provide the energy needed for growth and respiration during the rest of the gestation period. However it is also possible that females continue ovulating, and that the toothless embryos feed by swallowing whole egg capsules or by squashing them in their mouths. Whole egg capsules have been reported from the stomachs of near-term embryos of the bigeye thresher shark (Gilmore, 1983; Moreno and Morón, 1992), but not from near-term lamnid sharks. Clarification of this point requires examination of the ovaries of near-term females to assess their ovulatory state.

Above 35 cm, the waste products of yolk digestion continue to accumulate in the intestine. The greenish coloured waste is characteristic of oophagous sharks (Swenander, 1907; Lohberger, 1910; Shann, 1923; Springer, 1948; Uchida et al., 1996). The gritty nature of the intestinal contents was also mentioned by Swenander (1907) and has been reported to consist of "crystal-like pieces" in white shark embryos (Uchida et al., 1996). The composition of this material is unknown. The liver grows most rapidly in the second half of gestation as energy reserves are transferred to it for storage. An increase in the relative weight of the liver in larger embryos has also been observed in shortfin makos (Mollet et al.[11]).

During the second half of gestation, several series of "post-natal" teeth develop, but they are folded back in the jaws and are nonfunctional. In white sharks, some of these teeth are shed and swallowed by the embryos (Francis, 1996; Uchida et al., 1996). The teeth probably become erect near or soon after birth, as has been found in near-term white shark embryos (Francis, 1996; Uchida et al., 1996).

Typically, embryos in a porbeagle litter are of similar size, but occasionally a large size range is encountered. Gauld (1989) found one litter with embryos ranging from 55.6 to 65.0 cm, and Shann (1923) reported a litter with a range of 38.1–50.9 cm. The runts in our two litters had small quantities of stomach and intestinal contents, and small livers, but were otherwise developing normally. This suggests that sibling competition may occur when a dominant embryo with its snout nuzzled into the anterior end of the uterus consumes most of the egg capsules as they pass into the uterus, leaving few for its sibling. However, all four embryos are usually adequately nourished, and the two embryos in each uterus are usually oriented in opposite directions. This suggests that the direction of orientation within the uterus may be a problem only if the mother is unable to produce enough egg capsules to satisfy both embryos.

At birth, embryos may still have yolk in their stomachs. Near-term white shark embryos have been reported with either empty (apart from some ingested teeth and denticles) or yolk-filled stomachs (Francis, 1996; Uchida et al., 1996). Near-term shortfin mako embryos and new-born sandtiger sharks may also have small amounts of yolk in their stomachs (Cadenat, 1956; Bass et al., 1975; Gilmore et al., 1983; Mollet et al.[11]). Along with the energy stored in the liver, this yolk supplies the nutritional needs of the embryos until they learn to feed. However, the livers of porbeagle embryos never exceeded 10% of the yolk-free embryo weight, compared with 13.5–18.6% in near-term white shark embryos (Francis, 1996; Uchida et al., 1996).

Hubbs (1923) reported a 9.1 kg (20 lb) embryo collected in late August in Maine, USA. The weight is clearly too large to be a porbeagle embryo because they are not known to exceed 5 kg (Fig. 10). Moss[3] suggests that the embryo may have been from a sandtiger shark.

The presence of an "umbilical scar" or "yolk sac scar" in postnatal oophagous sharks has puzzled many scientists who were aware that the embryos have no placental connection to their mothers (Gilmore, 1983; Stevens, 1983; Klimley, 1985; Cliff et al., 1990, 1996; Pratt and Casey, 1990; Moreno and Morón, 1992; Francis, 1996; Uchida et al., 1996). Our observations show that distension of the stomach stretches the abdominal skin and separates subdermal muscle layers as far forward as the fifth gill slits. As yolk is consumed the stomach shrinks and the muscle layers return to their original position, leaving a scar in the pectoral-gill region. The scar is sometimes faint or absent.

In all lamnid sharks, embryos are nourished by oophagy. Contrary to earlier suggestions, there is no evidence that lamnid embryos indulge in uterine cannibalism (adelphophagy), an extreme extension of oophagy that has been confirmed only in the sandtiger shark (Gilmore, 1993). All lamnids, and most oophagous sharks, produce litters larger than two (one per uterus) (Francis, 1996), providing strong circumstantial evidence that adelphophagy does not occur in those species (Gilmore, 1993). One porbeagle embryo had nonlethal abdominal lacerations, probably resulting from incidental damage inflicted by its larger sibling while searching for egg capsules, which are about the same size as the smaller embryo's abdomen. This searching behavior could provide a mechanism for the development of adelphophagy from oophagy.

Unresolved questions

Two puzzling features of the reproduction of porbeagles demand further investigation. The first concerns the gross abdominal distension during midgestation, a phenomenon that must create problems for the mother in accommodating them. It would seem energetically and hydrodynamically more efficient for a pregnant female to match her ovulation rate to the immediate growth and energy needs of the embryo, rather than to provide an over-supply of food during a short time period. We speculate that the answer lies in the availability of food resources. Porbeagles feed mainly on small to medium pelagic fishes and cephalopods, but also eat larger demersal teleosts and elasmobranchs (Bigelow and Schroeder, 1948; Graham, 1956; Aasen, 1961; Templeman, 1963; Stevens et al., 1983; Gauld, 1989; Yatsu, 1995). Oophagy may be an adaptation that allows pregnant porbeagles (and other oophagous species) to maximize their use of food resources that are abundant only during a short season.

The lack of a six-month phase shift between the reproductive cycles of Northern and Southern Hemisphere porbeagles is surprising, and suggests that water temperature and day length have little influence on reproduction. This may be due to porbeagles having a highly developed endothermic ability (Carey et al., 1985) which buffers body temperature against seasonal fluctuations in temperature. But why should the timing of reproduction be so similar in the two hemispheres? The shortfin mako is also endothermic, although not to such a high degree as porbeagles (Carey et al., 1985), and its reproductive cycles are six months out of phase in the two hemispheres (Mollet et al.[11]). In the northwest Atlantic, porbeagle parturition coincides with the arrival of migratory stocks of Atlantic mackerel, capelin and 0+ Atlantic herring (Moss[3]). Linking parturition with the period of peak abundance of the common prey species in each hemisphere would provide new-born young with their best chance of rapid growth and survival. Unfortunately, neither of these hypotheses can be tested, because there is no information on the existence or timing of abundance cycles of porbeagle prey in the Southern Hemisphere.

This study has clarified several important aspects of the reproductive biology of porbeagles, including the length of the gestation period, mean fecundity, length at birth, and the timing of parturition. Growth rates have been estimated for embryos and juveniles and are consistent with other studies. However considerable imprecision and uncertainty remain in all of these estimates, especially the lengths of the gestation period and reproductive cycle, and therefore the annual fecundity. Such information is crucial to the determination of stock productivity in porbeagles; therefore better estimates are required before effective stock assessment and management can be achieved.

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