

Abstract—Reproductive organs from 393 male and 382 female porbeagles (*Lamna nasus*), caught in the western North Atlantic Ocean, were examined to determine size at maturity and reproductive cycle. Males ranged in size from 86 to 246 cm fork length (FL) and females ranged from 94 to 288 cm FL. Maturity in males was best described by an inflection in the relationship of clasper length to fork length when combined with clasper calcification. Males matured between 162 and 185 cm FL and 50% were mature at 174 cm FL. In females, all reproductive organ measurements related to body length showed a strong inflection around the size of maturity. Females matured between 210 and 230 cm FL and 50% were mature at 218 cm FL. After a protracted fall mating period (September–November), females give birth to an average of 4.0 young in spring (April–June). As in other lamnids, young are nourished through oophagy. Evidence from this study indicated a one-year reproductive cycle and gestation period lasting 8–9 months.

The reproductive biology of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean

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The porbeagle (*Lamna nasus*), a pelagic shark in the family Lamnidae, inhabits the cold temperate waters of the North and South Atlantic, South Pacific, and southern Indian Oceans, as well as the subantarctic region of the Southern Ocean (Svetlov, 1978; Compagno, 1984). In the western North (NW) Atlantic Ocean, the porbeagle ranges from the Flemish Cap and the Grand Banks off southern Newfoundland, Canada, to the Gulf of Maine and (rarely) south to New Jersey (Templeman, 1963; Compagno, 1984). The porbeagle is most commonly encountered from the Gulf of Maine to the Grand Banks, where it has been the subject of a commercial fishery since 1961 (O'Boyle et al.¹; Campana et al.^{2,3}). Seasonal abundance is related to north–south migrations (Aasen, 1963; Campana et al.³; Aasen⁴).

Lamnids sharks are ovoviviparous and nourish their embryos by oophagy (Lohberger, 1910). Early descriptions of porbeagle embryos exhibiting oophagy were documented by Swenander (1907) and Shann (1911, 1923), and more recently by Francis and Stevens (2000). Litter size has been variously reported as one to five pups (Dunlop,

1897; Swenander, 1907; Shann, 1911, 1923; Gauld, 1989; Francis and Stevens, 2000). Birth size has been reported as

¹ O'Boyle, R. N., G. M. Fowler, P. C. F. Hurley, M. A. Showell, W. T. Stobo, and C. Jones. 1996. Observations on porbeagle (*Lamna nasus*) in the north Atlantic. DFO (Department of Fisheries and Oceans) Atl. Fish. Res. Doc. 96/24, 29 p. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

² Campana, S., L. Marks, W. Joyce, P. Hurley, M. Showell, and D. Kulka. 1999. An analytical assessment of the porbeagle shark (*Lamna nasus*) population in the Northwest Atlantic. CSAC (Canadian Stock Assessment Secretariate) Res. Doc. 99/158, 57 p. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

³ Campana, S., W. Joyce, L. Marks, P. Hurley, L. J. Natanson, N. E. Kohler, C. F. Jensen, J. J. Mello, and H. L. Pratt Jr. 2000. The rise and fall (again) of the porbeagle shark population in the Northwest Atlantic. Unpubl. manuscript. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

⁴ Aasen, O. 1961. Some observations on the biology of the porbeagle shark (*Lamna nasus* L.). ICES C.M. Copenhagen 1961, Near Northern Seas Committee 109:1–7.

60–80 cm total length (TL) (54–72 cm fork length [FL]) (Shann, 1923; Compagno 1984, Francis and Stevens, 2000). Bigelow and Schroeder (1948) speculated that females are gravid by 152 cm TL (136 cm FL), whereas Aasen (1963) concluded that females mature between 200 and 250 cm TL (193–240 FL) and males mature between 150 and 200 cm TL (146–193 FL). In a more comprehensive study, Francis and Stevens (2000) found that females mature between 165 and 180 cm FL in the South Pacific.

In this study, we present the results of a comprehensive examination of porbeagle reproduction in the NW Atlantic Ocean. We define the sizes and stages of maturity for both sexes and provide insights into the reproductive cycle, as well as embryo sex ratios and litter sizes. These parameters will be useful for the refinement of fishery management plans for the porbeagle shark in the NW Atlantic Ocean.

Materials and methods

Porbeagles were collected with pelagic longline onboard both U.S. and Canadian commercial fishing vessels and U.S. research vessels fishing in U.S. and Canadian waters from the Gulf of Maine and Georges Bank (northeastern U.S.) to the Grand Banks off southern Newfoundland. Several specimens were obtained at a sport-fishing tournament held on Stellwagen Bank, Massachusetts. Sampling took place between 1979 and 1999, but most of the data were obtained during 1993, 1994, and 1999.

Morphometrics

For each shark, five lengths were measured over the curve of the body to the nearest half centimeter (cm): interdorsal length (posterior dorsal fin base to origin of second dorsal fin; IDL); dorsal length (origin of first dorsal fin to precaudal pit; DL); precaudal length (snout to precaudal pit; PCL); fork length (snout to fork of tail; FL); and total length (snout to a perpendicular line from the tip of the upper caudal fin in a natural position; TL). Total length of embryos were measured along a straight line with the tip of the tail fully extended (TL_s) because of the difficulty in obtaining over-the-body or FL measurements (or both) in embryos less than 6 cm TL. FL and PCL were taken when possible. FL are reported for all sharks in our study; TL values are presented for embryos with calculated or measured FL in parentheses. TL can be converted to FL by using the following regression (Campana et al.³):

$$FL = 0.885(TL) + 0.99 \quad [r^2=0.99, n=361].$$

All other length and weight conversions can be found in Campana et al.² Aasen's (1963) TL values were converted to FL by using the approximate formula:

$$FL = 0.947*(AasenTL) + 3.64 \text{ (Campana}^5\text{)}.$$

TL_s can be converted to FL for embryos by using the regression

$$FL = 0.832(TL_s) - 0.19 \quad [r^2=0.99, n=131].$$

Whole weight in kilograms (kg) was taken when possible. Literature values of TL were converted to FL for comparison and the conversions are presented throughout the text in parentheses. The converted values from the literature should be considered good estimates only because of the variation in measurement techniques between studies.

Maturity indicators

A number of measurements, weights, and conditions were taken on reproductive organs in both sexes to develop indices of maturity following Pratt (1979, 1993, 1996). Most specimens were measured fresh; however, some frozen reproductive tracts were also measured. Reproductive tracts were measured on the right side of the specimen. Organ terminology follows Pratt (1979) (Fig. 1, A and B).

For more detail, uteri were divided visually into anterior and posterior segments. The anterior segment is defined as the portion between the origin of the uterus at the isthmus and the point where both uteri join. The posterior segment is the portion from the junction to the posterior constriction of the uterus (Fig. 1B). A length measurement was taken for the anterior uterus, and width was taken midway along this portion of the uterus.

Active ovulation was defined as occurring if 1) ova were entering the ostium or were present inside the upper oviduct, 2) ova and capsules were present in the oviducal gland, 3) encapsulated ova were present in the isthmus, and 4) encapsulated ova were present in the uterus.

Prior mating activity was assessed according to the presence or absence of a vaginal membrane (hymen), determined by passing a probe through the posterior end of the uterus into the cloaca. The presence of vaginal mating scars was used to determine if recent mating had taken place. Scars were identified as either healed or recent. Maturity status of both sexes was assigned to each shark based on all reproductive organ characteristics (Pratt, 1979). The size at 50% maturity was determined by fitting a logistic regression to a plot of percent maturity versus FL.

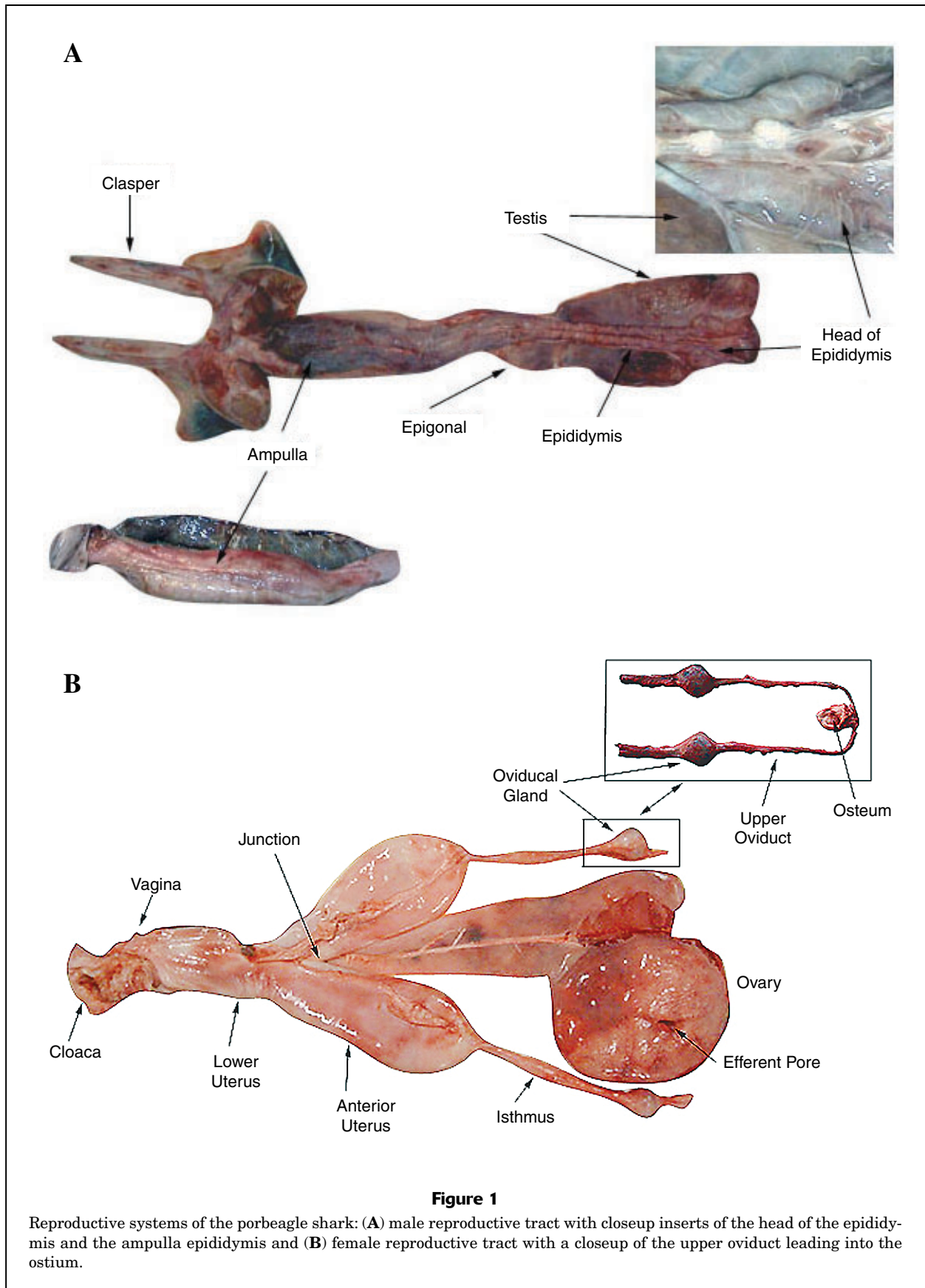
Embryos were either frozen or preserved in 10% buffered formalin. Litter size and embryo sex were determined in the field or in the laboratory under a dissecting microscope. Embryo growth was related to month. Linear regressions were fitted to the relationship between mean embryo length and month for samples from the NW Atlantic and southwest Pacific Oceans and compared with analysis of covariance (ANCOVA).

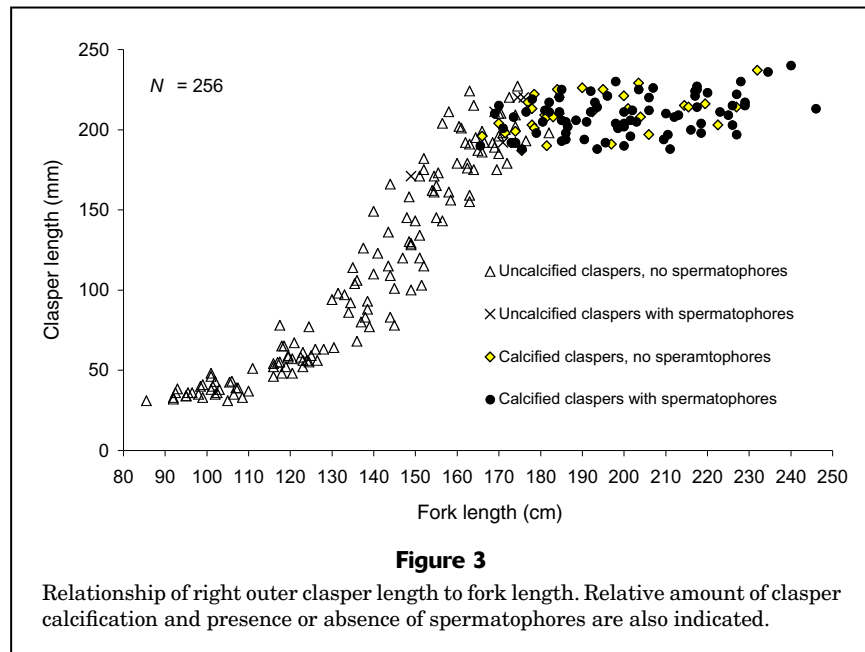
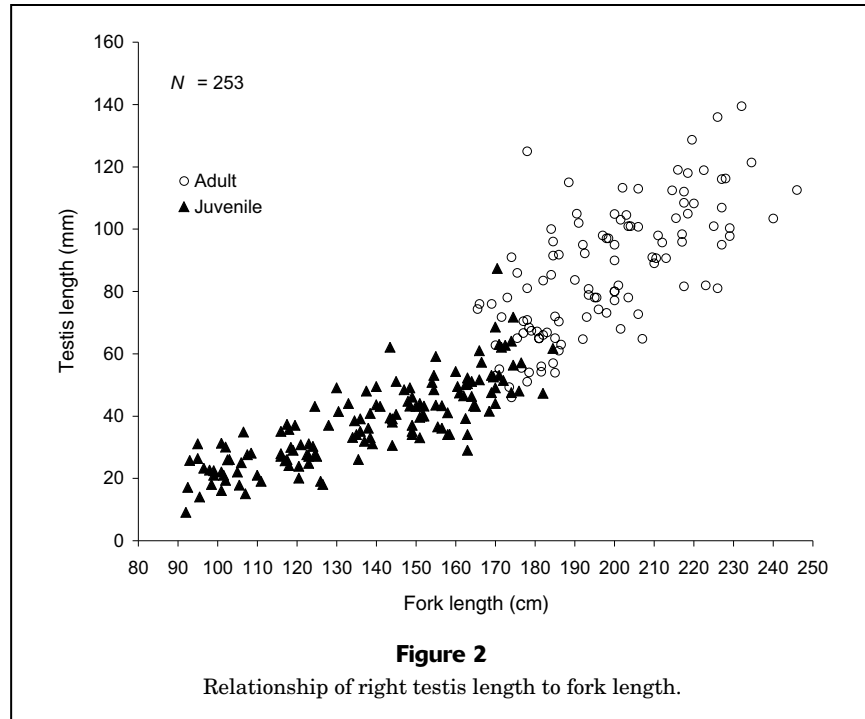
Results

Male length at maturity

Reproductive data were obtained from 393 male porbeagle sharks ranging in size from 86 to 246 cm FL, of which

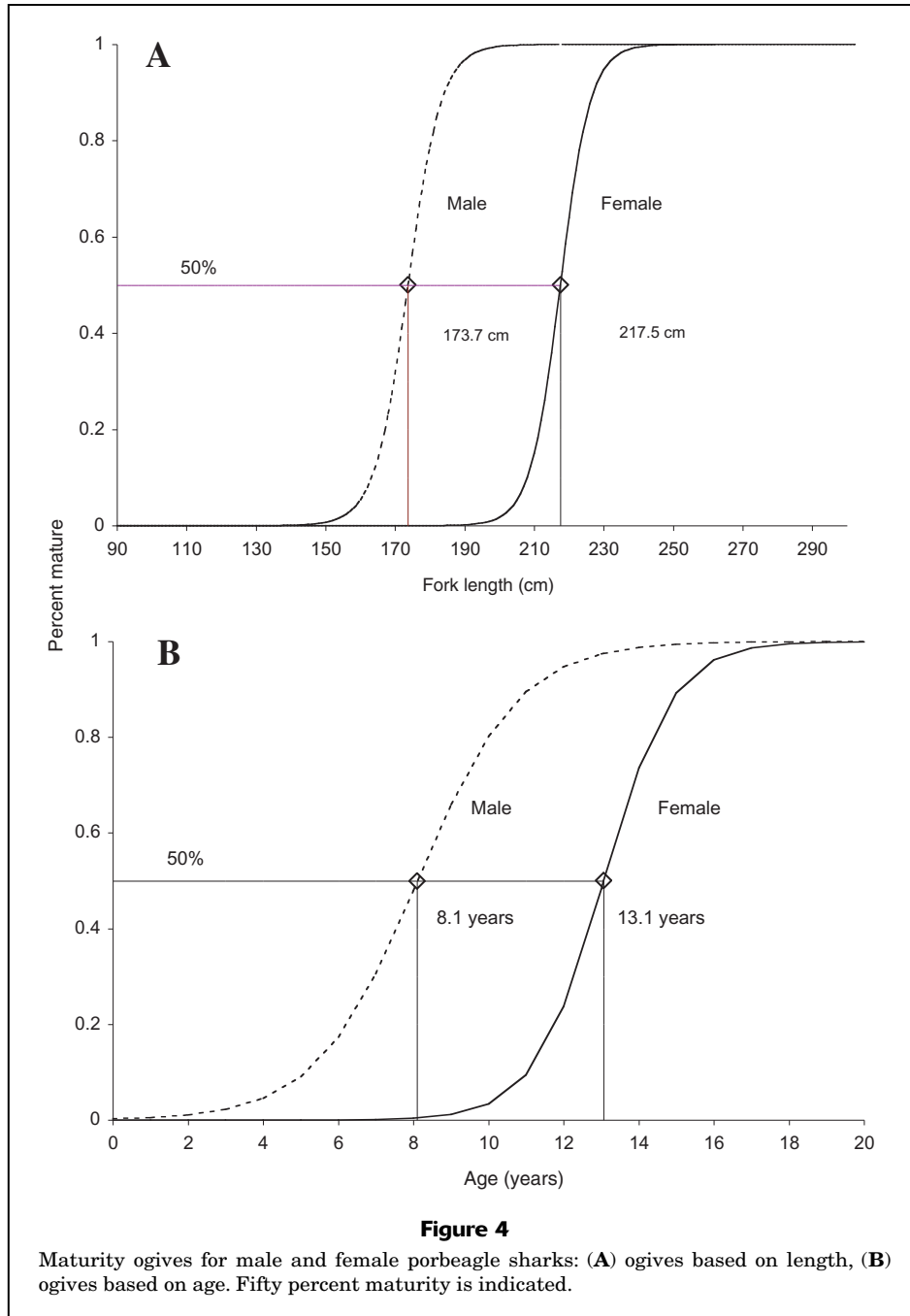
⁵ Campana, S.E. 2000. Unpubl. data. Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada, B2Y 4A2.





reproductive organs were measured for 267. Development of the siphon sacs, as well as internal male reproductive organs—testes (diameter and length), epididymis, and ampulla epididymis—is gradual in relation to FL (Fig. 2). The development of the claspers, however, shows a distinct inflection (Fig. 3). Claspers begin to elongate when the males approach 120 cm FL, and rapid clasper growth begins at 135 cm FL and slows by about 170 cm FL when they have reached their maximum adult size of 19–24 cm.

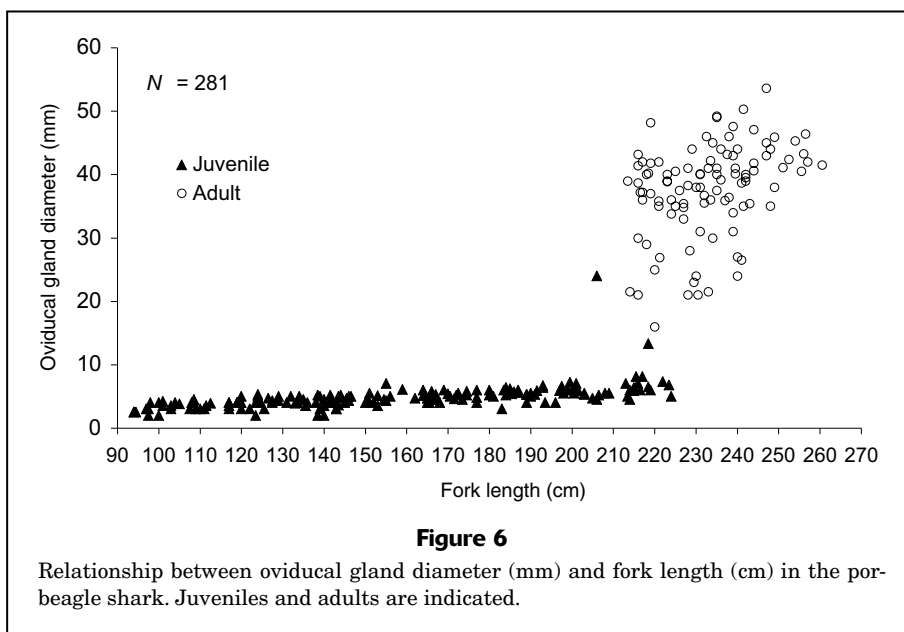
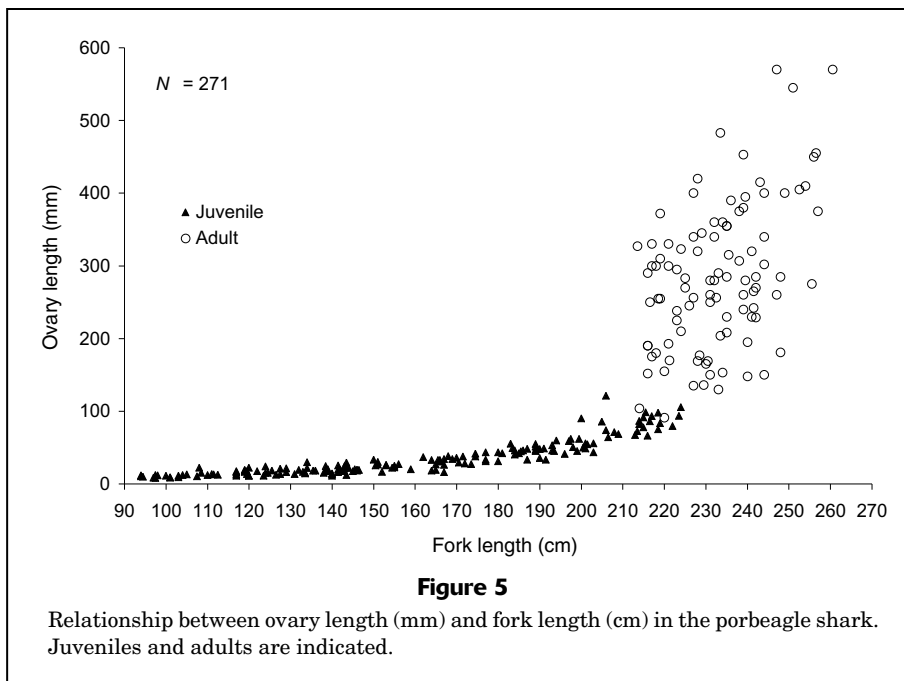
The largest shark with uncalcified claspers but containing spermatophores in the ampulla epididymis was 176 cm FL, and the smallest shark with calcified claspers, but with no spermatophores, was 166 cm FL. Claspers rotate freely at all sizes in the porbeagle; therefore clasper rotation is not a good measure of maturity. Males of 135 to 184.5 cm FL are in a transitional phase leading to maturity. At this stage, claspers are lengthening and the head of the clasper (rhipidion) is beginning to develop, whereas at 149 cm FL



and greater, spermatophores appear in the ampulla epididymis. By 162 cm FL fully calcified claspers were observed. Individual variation exists in body length and the order in which these developments take place. All males observed were mature by 185 cm FL based on clasper calcification and the ability of the rhipidion to open. The presence of spermatophores may be used in addition; however, absence of spermatophores can be attributed to season as well as to maturity. Each clasper bears a sharp, conical, calcified spur near the tip which folds out of the distal surface as the rhipidion opens. In adults, the sharp spur tip was either

covered by an epidermal membranous sheath, or naked. A naked spur is an indicator of mating activity because mating ruptures the sheath. The FL at which 50% of the male population is mature, based primarily on clasper condition, was estimated as 174 cm FL (Fig. 4A).

Both testis size and the amount of spermatophores in the ampulla epididymis showed distinct fluctuations related to the mating season. From November through mid December, the testis lobes were noticeably reduced in diameter, the testes were smaller, and the epigonal organ had infiltrated the space previously occupied by the

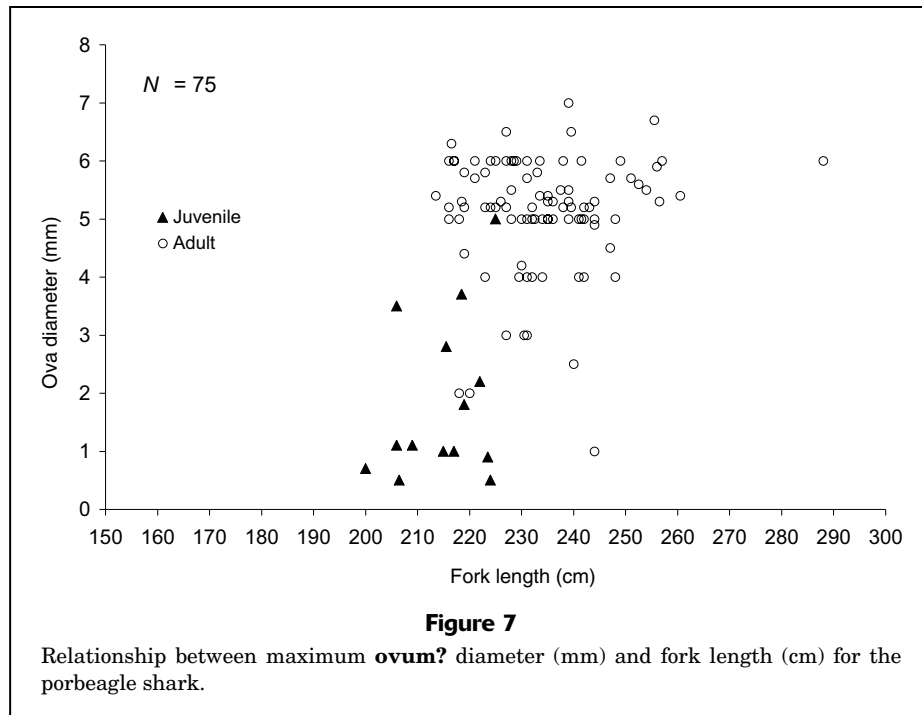


testes. Spermatophores in the ampulla epididymides were at their greatest volume in September–December; in February–May relatively few spermatophores were observed, and by June the concentration started to increase.

Female length at maturity

Reproductive data were obtained from 382 female porbeagle sharks ranging in size from 94 to 288 cm FL, of which reproductive organs were measured for 284. The relationship between the measurements of internal reproductive organs (ovary length and width, anterior uterus length

and width, and shell gland (oviducal gland) width to FL) showed a sharp increase between 210 and 220 cm FL (Figs. 5 and 6). Oocytes are not visible to the naked eye in juveniles less than about 200 cm FL, and in larger, immature females, small, clear, yolkless oocytes range in size from 0.5 to 3.7 mm in diameter. In mature females, vitellogenic oocytes range from 2.2 to 7.0 mm. The increase in oocyte diameter, as well as the development from clear yolkless oocytes to vitellogenic oocytes, occurs between 210 and 225 cm FL (Fig. 7). Criteria for maturity in female porbeagles include the presence of embryos or fertilized ova in the uteri, and indications of past pregnancy, such



as flaccid uteri with trophonemata and reduced ovaries containing few maturing or mature oocytes. Juvenile females have small undeveloped ovaries with white to clear oocytes; the uterus appears narrow and constricted, and the oviducal gland is seen as a barely perceptible widening of the oviduct. The juvenile and mature virgin sharks that we examined had a membrane separating the vagina from the cloaca, whereas mature (reproductively active) sharks had no membrane. In nongravid females, maturity is based on the presence of mature oocytes in a developed ovary, an expanded uterus, a well-developed oviducal gland, internal and external mating scars, and the absence of a vaginal membrane. The smallest mature female in our sample was 210 cm FL based on the absence of a vaginal membrane and the condition of the internal reproductive organs, and the largest immature female was 230 cm FL based on the presence of a vaginal membrane and internal organ condition. Fifty percent of the female porbeagle population was mature at 218 cm FL (Fig. 4A).

Mating injuries

Fresh mating scars, containing at least small areas of unhealed dermal lacerations, were observed from late September through mid-December, during which time most adult females appeared to have recently mated or were in the early stages of pregnancy. Scars and cuts were often observed on either or both pectoral fins as single or multiple jaw outlines, and the trailing edge of the fin was often shredded. Tooth scrape marks, puncture wounds, and gouges, some as open, penetrating subdermal lacerations, were observed mainly along the posterior lateral, dorsal, or ventral body surface. None of the wounds

appeared to have penetrated the abdominal wall nor were they debilitating. No infected or necrotic tissue was seen in these wounds. Most mature female porbeagles had distinct fresh or healed mating scars.

Internal mating scars were observed on the vaginal walls from late September through mid-December. The scars were generally small, round to ovoid, hematose marks on an otherwise white to light yellow vaginal wall. These were probably caused by the spur that holds the clasper in place during copulation.

Gravid females, embryo growth, and nutrition

Data from 80 litters and 309 embryos were obtained from gravid females sampled from mid-September through April. In addition to embryos, these females had several different types of egg capsules in their oviducal gland, isthmus, and uteri. These were empty capsules, capsules containing one large ovum without a visible embryo (single ovum capsules), capsules with one developing embryo and attached yolk sac, capsules with 22–45 blastodisc-stage ova, and capsules containing 8–100 nonblastodisc-stage ova (nutritive capsules), some appearing atretic and in which individual ova were difficult to detect. The number of capsules present in each uterus ranged from none to 63 (Fig. 8).

The proportion of mature nongravid females with recent mating scars, but no obvious fertilized ova, decreased from September through December, whereas the proportion of gravid females increased (Fig. 9). All mature females examined in December were gravid. During October, several mature females contained either parts of, or entire, spermatophores in the uteri, but no ova capsules, indicating

that mating had taken place but that ova were not yet fertilized. On the basis of the occurrence of early-stage gravid females, the ripe condition of the males, and the presence of recent mating scars, we concluded that most mating occurs from late September through November. Mature males with copious amounts of spermatophores and mature females were captured on the same gear numerous times during the fall.

The right uterus of the one gravid female observed during late September had one single ovum capsule with no visible embryos, along with several blastodisc or nutritive capsules, whereas the contents of other uterus appeared to have been aborted. This was the only recently mated female observed in September. Some gravid females in October and November contained capsules with a single ovum, 6–7 mm diameter, in addition to varying numbers of empty, blastodisc, or nutritive capsules. These single ovum blastodisc capsules (usually two per uteri) were considered to be the annual developing embryos, their single ovum larger than those of the aggregate blastodisc or nutritive capsules. Gravid females examined during October had either single ovum capsules or embryos 0.9–6.8 cm TL_s (0.6–5.3 cm FL), and those seen in November had a decrease in occurrence of single-ovum capsules, and embryos ranged from 1.1 to 37.8 cm TL_s (0.7–31.2 FL). No gravid females with single ovum capsules were seen during December, and embryos ranged from 2.3 to 43.1 cm FL (Fig. 10). Only one nearterm, gravid porbeagle, caught in mid-April, was examined in our study. This shark had three embryos ranging in size from 59 to 72 cm TL_s (50–59 cm FL). The considerable variation in embryo length among litters during early gestation indicates a protracted mating season.

Postpartum females were observed from the first week of May to the first week of June. Our data from these females suggested that parturition extends from early April through early June. The presence of postpartum females in May–June after the September–November mating indicates a gestation period of about 8–9 months.

Although numerous gravid females are present from late September through December on the Scotian shelf and Grand Banks region, mature gravid or nongravid female sharks are seldom seen from January through June in the Canadian fishery. Gravid females were caught between Georges Bank and the Grand Banks (Fig. 11).

Fecundity

Embryos were found to be at the same developmental stage in each female, although embryo size varied as much as 14.6 cm in one litter. Runts were encountered in five females and although clearly developing, were considerably smaller than the coexisting embryos. Fecundity was calculated by using all embryos. The average number of embryos per porbeagle was 4.0 (304 embryos from 76 litters) although litters ranged from 3 to 6. In 66 litters there were two embryos per uterus. The sex ratio of 202 embryos (99 male and 103 female) was not significantly different from one ($\chi^2=0.08$, $P>0.1$).

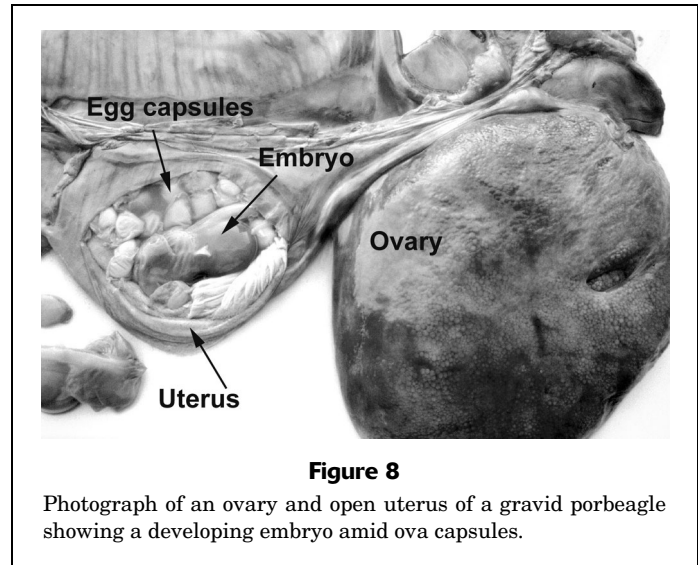


Figure 8

Photograph of an ovary and open uterus of a gravid porbeagle showing a developing embryo amid ova capsules.

In the uteri of six females, fertilized ova were found in the same ova capsule with one to three late developing yolk sac embryos. Some of these fertilized ova appeared to be decomposing. These capsules were in the same uteri as a larger, developing litter, but the size of the embryos associated with the capsules (averaging 4–20% of the average size of the developing litter) were smaller than runts (runts averaged 24–43% of the average size of siblings) or the main litter. Because of their small size in relation to the developing litter, and their appearance of decomposition, it was presumed that they were ova that had been fertilized late by remaining sperm and that had probably not continued to develop. However, this is not to rule out the possibility that some of these embryos could have developed into runts or be consumed when littermates initiated feeding on egg capsules. Further research is being conducted on this subject and will be reported at a later date.

Embryonic development and growth

Newly fertilized ova, without visible embryos, were 6–7 mm in diameter. As the embryo developed, their yolk sacs decreased in size, and by the time the embryos were between 4.2 and 9.2 cm TLs (3.3–4.5 cm FL), the yolk sacs were tiny, white, ovoid structures attached to the embryo by a short stalk. Embryos were found in capsules up to 4–4.2 cm TL_s (3.1–3.3 cm FL). The smallest posthatch embryos were 3.2–4.2 cm TL_s (2.5–3.3 cm FL). The abdomens of posthatch embryos between 4.7 and 5.1 cm TL_s (3.7 and 4.0 cm FL) were slightly swollen. Functional embryonic dentition appeared in embryos at 12 cm TL_s (9.8 cm FL). As the embryo continues to grow, the yolk stomach increases in size as a result of *in utero* consumption of ova capsules by the embryo. The stomach becomes grossly distended by the time the embryo reaches 27–43 cm TL_s (23–36 cm FL). The large amounts of yolk material in the stomachs of these embryos was characteristic of oophagy. Frequently, parts of ova capsules, parts of, or whole, ova, and white flocculent material were observed in the clear intrauterine fluid surround-

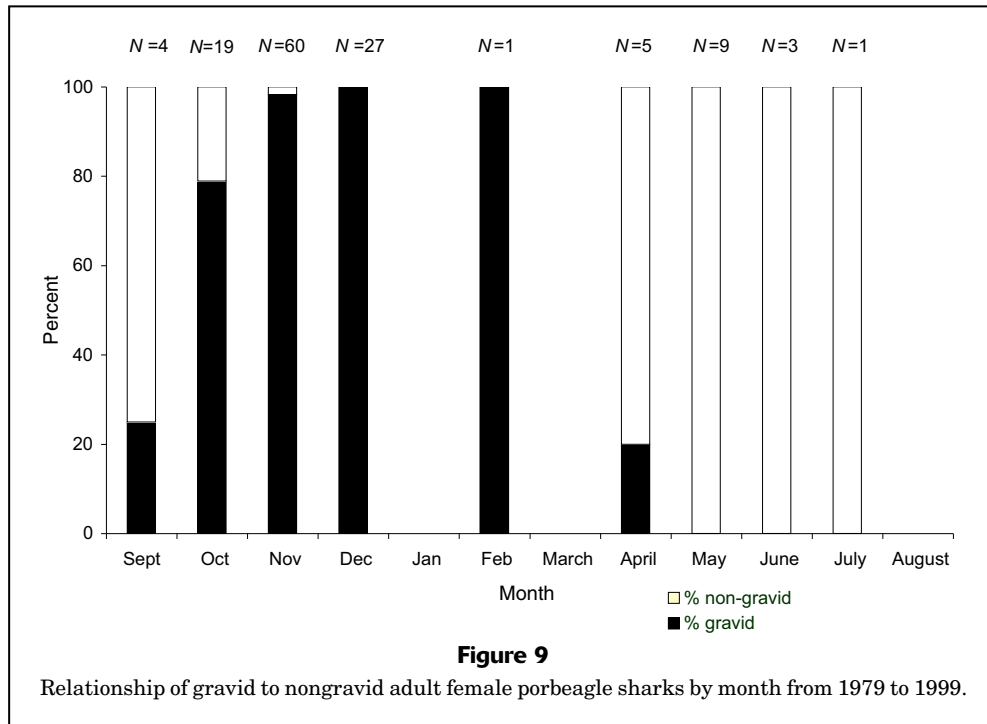


Figure 9
Relationship of gravid to nongravid adult female porbeagle sharks by month from 1979 to 1999.

ing the embryos, suggesting recent embryo feeding. One embryo was seen with a whole, undamaged ova capsule protruding from its mouth. The stomach contents of embryos from several litters did not show parts of other embryos, suggesting that adelphophagy (competitive embryonic cannibalism), found in the sandtiger shark (Gilmore et al., 1983) does not occur in the porbeagle. The existence of developing runts in several litters and consistently two embryos per uterus reinforces these observations. A slight modification to our knowledge of oophagy would be the possible consumption of the late-fertilized ova capsules that had small undeveloped and decomposing embryos along with unfertilized ova, as mentioned previously. Most gravid porbeagles examined during this study were ovulating and, therefore, nourishing their embryos. The times at which ovulation ceases, ovary size decreases, and the large amount of yolk in the stomach is consumed, need further definition.

The mean growth rate of embryos from this study was 11.4 cm per month; however, this is most likely inflated by the lack of larger embryos. Combining data from the present study with previous data from the North Atlantic, which includes later term embryos (Francis and Stevens, 2000), leads to an estimate of 8.15 cm per month. The regression of growth per month for the North Atlantic embryos was significantly different from that of the South Pacific population in intercept (time of year) but not in slope (growth rate) (ANOVA $P > 0.10$ slopes, $P < 0.1$ intercept) (Fig. 10).

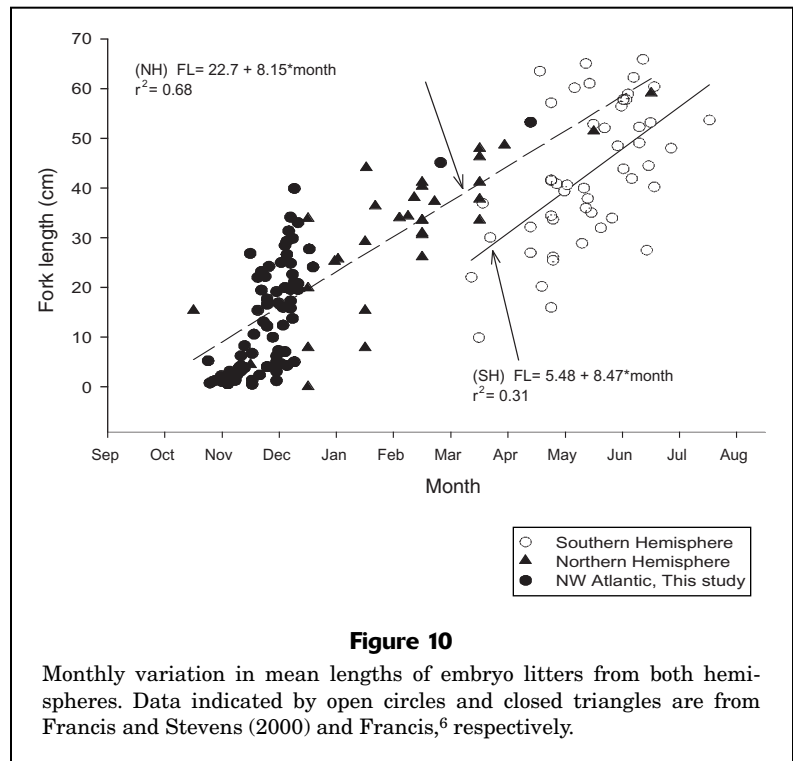


Figure 10
Monthly variation in mean lengths of embryo litters from both hemispheres. Data indicated by open circles and closed triangles are from Francis and Stevens (2000) and Francis,⁶ respectively.

Neonates and young of the year

The smallest free-swimming porbeagle examined during this study was 77.5 cm FL (87 cm TL) on 24 May. Other records of free-swimming individuals measured in April–June, ranged from 55 to 79 cm FL (mean=71 cm FL, $n=9$)

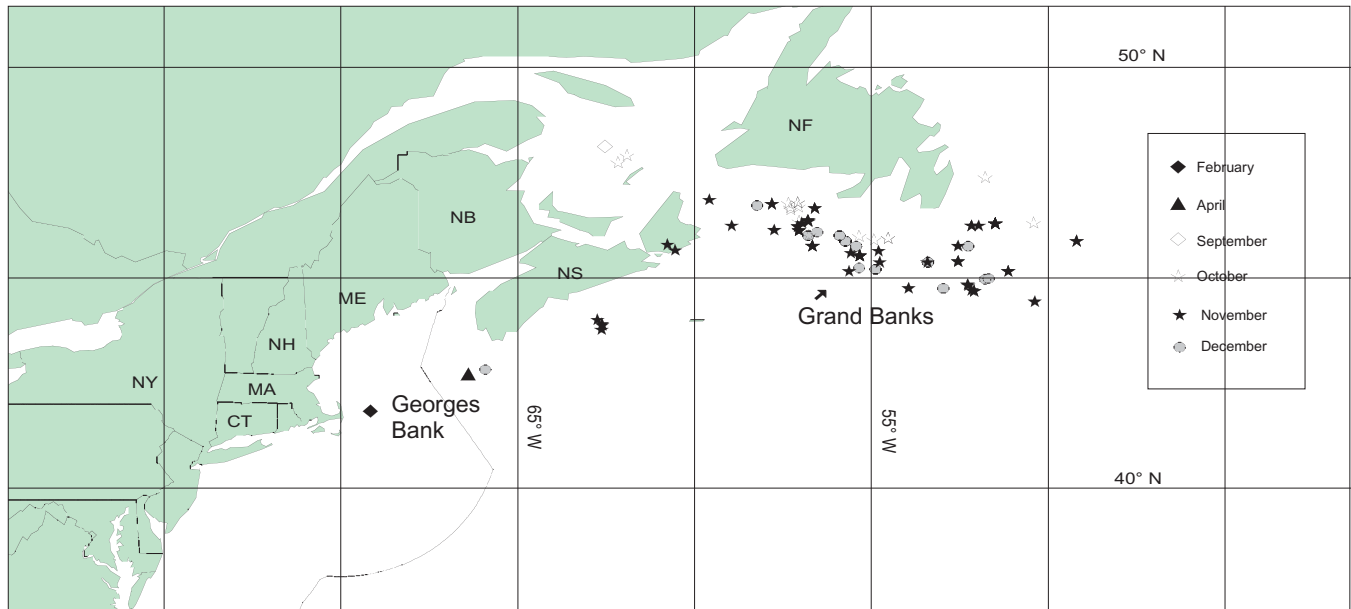


Figure 11

Map of the capture locations of all gravid female porbeagles by month of capture. Approximate locations of Georges Bank and the Grand Banks are indicated.

(Kohler⁶). The largest embryos in our study from one litter in April were 49–60 cm FL (59–72 cm TL).

Discussion

In the NW Atlantic, male porbeagles mature between 166 and 184 cm FL, and 50% maturity was at 174 cm FL, which corresponds to an age of 8 years (Fig. 4B; Natanson et al., 2002). The most accurate means of determining male maturity is clasper length and calcification. Because of the distinct seasonal variability, the presence of seminal products alone, is not a good indicator of maturity. Clasper rotation occurred at all sizes, eliminating it as a maturity indicator. Our estimate of length at maturity substantially refines Aasen's⁴ estimate of 150 to 200 cm TL (146–193 cm FL) for this population. Aasen⁴ based his estimates on clasper length in relation to dorsal length.

Female NW Atlantic porbeagle sharks mature between 210 and 230 cm FL and 50% maturity was at 218 cm FL, at an age of 13 years (Fig. 4B; Natanson et al., 2002). The sizes of all female reproductive organs measured showed a definitive inflection at maturity in relation to body size and are good indicators of maturity. Aasen⁴ estimated female maturity between 2.0 and 2.5 m TL (193–240 cm FL) based on uterus length. Our estimates compare well to the upper part of his range; however our data do not support his lower size at maturity.

The seasonality of spermatophore production, observations of females with fresh mating scars, and observations of males and females on the same longline indicated that

porbeagles mate in the fall, primarily between September and November. In an earlier study, sperm in the shell gland of a female, and the presence of a male caught on the same longline set in October, also suggested a fall mating period (Pratt, 1993). Aasen (1963) proposed a fall mating season (September–October) based on an increase in the amount of sperm present in the males “towards the end of August.” This period agrees with the suggestion of a long mating season in the SW Pacific porbeagle population (Francis and Stevens, 2000). During this time, females have fresh external mating scars, internal vaginal scars, and spermatophores in the uterus. Gauld (1989) suggested that mating occurs during December–January in the northeast Atlantic on the basis of fresh mating scars on the pectoral fins.

Mating injuries have been documented for many species of sharks. Bite marks on females during mating have been documented in the blue (*Prionace glauca*), nurse (*Ginglymostoma cirratum*), sandtiger, (*Carcharias taurus*), blacknose (*Carcharhinus acronotus*) finetooth (*C. isodon*), blacktip (*C. limbatus*), sandbar (*C. plumbeus*), and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks (Stevens, 1974; Gilmore et al., 1983; Schwartz, 1984; Castro, 1993, 1996, 2000). Fresh bite marks may coincide with insemination and ovulation, marking the approximate beginning of the gestation period (Parsons, 1983; Castro, 1996). Matthews (1950) noted lacerations in the vagina of the basking shark (*Cetorhinus maximus*) from the clasper spur. Pratt (1979) also observed abrasions from claspers in the vagina of female blue sharks.

Gravid females typically carry single-ovum capsules from September to November, and developing embryos from October to April. Aasen (1963) reported no gravid porbeagles from July to September 1961, in the NW At-

⁶ Kohler, N. K. 2000. Unpubl. data. NMFS Apex Predators Program, 28 Tarzwell Dr., Narragansett, RI 02882.

lantic. Bigelow and Schroeder (1948) described gravid porbeagles in the Gulf of Maine during November, January, and August, although the latter month conflicts with both the present findings and those of Aasen (1963). Aasen (1963) reported that pregnant females carrying large embryos were observed in late May at the Flemish Cap. Templeman (1963) reported three gravid females from the SW Grand Banks during January and February 1953–56. Gauld (1989) reported the presence of gravid females from December to June in the NE Atlantic ocean, whereas Francis and Stevens (2000) reported gravid females from March to July in the SW Pacific Ocean.

Length variability within and between litters has been found in most porbeagle studies (Fig. 10). We found a difference of up to 14.6 cm in the lengths of individuals in one litter. Gauld (1989) found length differences of up to 11 cm within individual litters, and Shann (1923) found a 12–15 cm difference in embryo length within individual litters. Runts were observed in pregnant porbeagles in our study as well as by Francis and Stevens (2000).

As with other lamnids, female porbeagle sharks nurture their young through oophagy. Upon hatching from the single-ovum capsules and after absorption of the external yolk sac, embryos begin orally feeding on yolk-filled nutritive ova capsules. As a result, the internal yolk stomach of the embryos expands to the large size characteristic of lamnid embryos at this stage in their development. Evidence from this study suggests that adelphophagy does not occur in the porbeagle. The ova capsules observed in our study were similar to those found in the sandtiger and other lamnid sharks described by Gubanov (1972), Fujita (1981), Gruber and Compagno (1981), Gilmore et al. (1983), Francis and Stevens (2000), and Mollet et al. (2000).

Embryonic growth was estimated at 8.15 cm per month in our study (Fig. 10). Francis and Stevens (2000) estimated embryonic growth of approximately 7.48 cm per month for embryos in the South Pacific. New data from the South Pacific (Francis⁷) refined this estimate to 8.47 cm per month. Examination of more late-term embryos will further refine this estimate for the NW Atlantic.

Our results indicated a one year reproductive cycle, with gestation lasting 8–9 months. Mating occurs between September and December. Based on the one late-term female and several postpartum females it appears that parturition occurs from early April through June. Aasen (1963) estimated that parturition occurs from late May to early June in the NW Atlantic and suggested about an 8-month gestation period based on the lack of gravid female porbeagles from June to September. All females we examined in December were gravid. Although a nongravid mature portion of the female population could reside elsewhere, we have no data to support this and thus assume that porbeagle females reproduce annually. Parturition time and location and late embryonic development and growth rates need further investigation.

Mean litter size in the NW Atlantic was found to be 4.0—usually two embryos per uteri. Mean litter size from the SW Pacific Ocean was 3.8 from 138 embryos representing 43 litters (Francis and Stevens, 2000). Mean litter size from the NE Atlantic Ocean was 3.7 based on 12 litters examined by Gauld (1989). The sex ratio of the embryos examined in our study was 1:1, which agrees with the findings of Francis and Stevens (2000) for the SW Pacific Ocean. The smallest free-swimming porbeagles in the NMFS historical tagging database range in size from 55 to 79 cm FL (mean 71 cm FL)⁷ from April to June; this length range, along with that of the one late-term litter (50–59 cm FL), suggests a birth size similar to Aasen's⁴ (1963) prediction of 67 cm FL and to Francis and Stevens' (2000) estimate of 58–67 cm FL for the SW Pacific. However, length at birth needs further analysis because few neonates were observed during the parturition period.

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Literature cited

- Aasen, O.
1963. Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. Fisk. Skrift. Ser. Havund. 13(6):20–37.
- Bigelow, H. B., and W. C. Schroeder.
1948. Fishes of the Western North Atlantic. Part 1. Lancelets, cyclostomes, sharks. Mem. Sears Found. Mar. Res., 576 p.
- Castro, J. I.
1993. The biology of the finetooth shark, *Carcharhinus isodon*. Environ. Biol. Fish. 36:219–232.
1996. The biology of the blacktip shark, *Carcharhinus limbatus*, off the Southeastern United States. Bull. Mar. Sci. 59(3):508–522.
2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. Environ. Biol. Fish. 58:1–28.
- Compagno, L. J. V.
1984. FAO species catalogues. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of the shark species known to date, parts 1 and 2. FAO Fish. Synopsis 125, vol. 4, parts 1 and 2, 655 p. FAO, Rome.
- Dunlop, J.
1897. The habits and anatomical structure of the porbeagle shark (*Lamna cornubica*, L., Cuv.). Proceedings and Trans-

⁷ Francis, M. 2000. Personal commun. National Institute of Water and Atmospheric Research P.O. Box 14-901, Kilbirnie, Wellington, New Zealand.

- actions of the Natural History Society of Glasgow 4:136–137.
- Francis, M. P., and J. D. Stevens.
2000. Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the southwest Pacific Ocean. *Fish Bull.* 98:41–63.
- Fujita, K.
1981. Oviphageous embryos of the pseudocarchariid shark, *Pseudocarcharias kamoharai*, from the central Pacific. *Jap. J. Ichthyol.* 28:37–44.
- Gauld, J. A.
1989. Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploitation of the species. *Scot. Fish. Res. Rep.* 45, 15 p.
- Gilmore, R. G., J. W. Dodrill, and P. A. Linley.
1983. Reproductive and embryonic development of the sandtiger shark, *Odontaspis taurus* (Rafinesque). *Fish. Bull.* 81(2):201–225.
- Gruber, S. H., and L. J. V. Compagno.
1981. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*. *Fish. Bull.* 79(4):617–640.
- Gubanov, Y. P.
1972. On the biology of the thresher shark, *Alopias vulpinus* (Bonnaterre), in the northwest Indian Ocean. *J. Ichthyol.* 12(4):591–600.
- Lohberger, J.
1910. Über zwei riesige Embryonen von *Lamna*. *Abhand. Math.-Phys. Klasse König Bayer. Akad. Wissen. München suppl. Bd. 4 no. 2 Abhandlung*, 45 p.
- Matthews, L. H.
1950. Reproduction of the basking shark, *Cetorhinus maximus* (Gunnerus). *Phil. Trans. R. Soc. Lond., Ser. B., Biol. Sci.* 234:247–316.
- Mollet, H. F., G. Cliff, H. L. Pratt Jr., and J. D. Stevens.
2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus*, Rafinesque, 1810 with comments on the embryonic development of lamnoids. *Fish. Bull.* 98:299–318.
- Natanson, L. J., J. J. Mello, and S. E. Campana.
2002. Validated age and growth of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. *Fish. Bull.* 100:266–278.
- Parsons, G. R.
1983. The reproductive biology of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Richardson). *Fish. Bull.* 81:61–73.
- Pratt, H. L., Jr.
1979. Reproduction in the blue shark, *Prionace glauca*. *Fish. Bull.* 77:445–470.
1993. The storage of spermatozoa in the oviducal glands of western North Atlantic sharks. *Environ. Biol. Fish.* 38:139–149.
1996. Reproduction in the male white shark. *In* Great white sharks, the biology of *Carcharodon carcharias*. Proceedings of the symposium on the biology of the white shark, Bodega Marine Lab., Bodega, CA, 4 March, 1993 (A. P. Klimley and D. G. Ainley, eds.), p. 131–138. Acad. Press, San Diego, CA.
- Schwartz, F. J.
1984. Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus* in North Carolina. *NE Gulf Sci.* 7(1):29–47.
- Shann, E. W.
1911. A description of the advanced embryonic stage of *Lamna cornubica*. *Ann. Rep. Fish. Board Scotland* 28(3):73–79.
1923. The embryonic development of the porbeagle shark, *Lamna cornubica*. *Proc. Zool. Soc. Lond.* 11:161–171.
- Stevens, J. D.
1974. The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.) from British waters. *J. Mar. Biol. Assoc. U.K.* 54:373–378.
- Svetlov, M. F.
1978. The porbeagle, *Lamna nasus*, in Antarctic waters. *J. Ichthyol.* 18(5):850–851.
- Swenander, G.
1907. Über die Ernährung des Embryos der *Lamna cornubica*. *Zool. Stud. Tullberg, Uppsala* 1907:283–288.
- Templeman, W.
1963. Distribution of sharks in the Canadian Atlantic (with special reference to Newfoundland waters). *Bull. Fish. Res. Board Can.* 140, 77 p.