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Synopsis

Shark populations tend to be highly vulnerable to overexploitation due to low fecundity and slow growth rates. Recent fishing pressure on the smooth dogfish in the northwest Atlantic has created a necessity for more information about their basic biology. Length and age at maturity, fecundity, and reproductive season were estimated. Total length at 50% maturity was 102 cm for females, and 86 cm for males. The majority of females were mature at age 4 or 5, and all males were mature at 2 or 3 years of age. Females had an 11–12 month gestation with parturition occurring in May, ovulation occurring between May and July likely in late May and early June, and mating occurring between May and September. Fecundity ranged between 3 and 18 pups per litter, and was positively related to length and age, with a mean of 9.53 pups per litter. Sperm was found in the terminal zone of the oviducal gland of females throughout the year.

Introduction

Smooth dogfish, *Mustelus canis*, are primarily demersal sharks that inhabit continental and insular shelves and upper slopes and are typically found in inshore waters down to 200 m depth (Compagno 1984). The North Atlantic population of smooth dogfish migrates seasonally likely in response to changing water temperatures. In winter, they are found between the Carolinas and the outlet of Chesapeake Bay and in summer they range from the mid Atlantic to southern New England (Bigelow & Schroeder 1948).

In the early 1990's commercial landings of smooth dogfish on the east coast of the United States began to increase. In order to understand how the population will respond to this increased mortality, it is necessary to know the lengths and ages at maturity, and estimate fecundity of the population. It is also important to know the timing of the reproductive cycle and the location of the mating and pupping grounds. Another question relevant to the management of the population is whether or not these animals store sperm. If smooth dogfish are able to store sperm and can use this sperm for repeated insemination this may increase the proportion of males in the population that could be harvested.

While the smooth dogfish is an abundant animal on the east coast much of their basic reproductive biology is not well known or needs further clarification. The purpose of this study is to determine accurate lengths and ages at maturity, obtain estimates of fecundity, reexamine and perhaps clarify the timing of the reproductive cycle, and to determine if female smooth dogfish store sperm throughout the year.

Methods

Males

Reproductive samples were collected from National Marine Fisheries Service (NMFS) groundfish and longline surveys, Virginia Institute of Marine Science (VIMS) longline surveys, Grice Marine Laboratory longline surveys, from the Massachusetts state trawl survey, and from the Massachusetts Division of Marine Fisheries (MDMF). A section of the testis was removed from at least five male smooth dogfish during each sampling period and preserved in 10% formalin or Bouin's solution. Maturity in males was determined by clasper size and calcification. Clasper length was plotted against total length to determine size at maturity because, in most elasmobranch species, there is a rapid increase in clasper size as males reach sexual maturity. Males were initially classified as mature if their claspers were calcified. Vertebral samples were taken from smooth dogfish at the same time as the reproductive samples and were used to age these fish (Conrath 2000). The proportion of animals that were mature at each length and age was plotted to determine a length and age at 50% maturity.

The timing of the male reproductive cycle was determined by staging the testes. A cross section of the testis was removed from the middle of the preserved testis section. This section was then rinsed in a series of water washes, placed in a tissue cassette, and the Bouin's fixed tissues were rinsed with a solution of 50% ethanol (ETOH) saturated with lithium carbonate to remove soluble picrates, then rinsed in 70% ETOH. The cassettes were then placed in a tissue processor to dehydrate them and infiltrate them with paraffin. A rotary microtome was used to cut 5 μm thick sections of the tissue, which were then stained with hematoxylin and eosin and cover slipped with a synthetic mounting media. The testis section was then viewed under a compound microscope and the proportion of the testis occupied by the following stages, defined by Maruska et al. (1996), was measured along a straight-line distance across the cross section of the testis, starting from the germinal zone (Figure 3). The mean proportion of the testis occupied by each stage throughout different months of the year was compared to determine if there was a recognizable seasonal pattern in testis development.

Females

The entire female reproductive tract was examined at the time of capture and at least five female reproductive tracts from each sampling period were preserved in 10% formalin or Bouin's solution for later analysis. The diameter of the largest ova was measured, any pups present in the uteri were sexed and measured, eggs in the uteri were counted, and one oviducal gland was preserved in 10% formalin or Bouin's solution. Female maturity was assessed at this time and females were considered mature if they had fully developed ova in their ovary, eggs or embryos present in the uteri, or expanded uteri indicating the previous presence of eggs or pups. Vertebral samples were also taken from

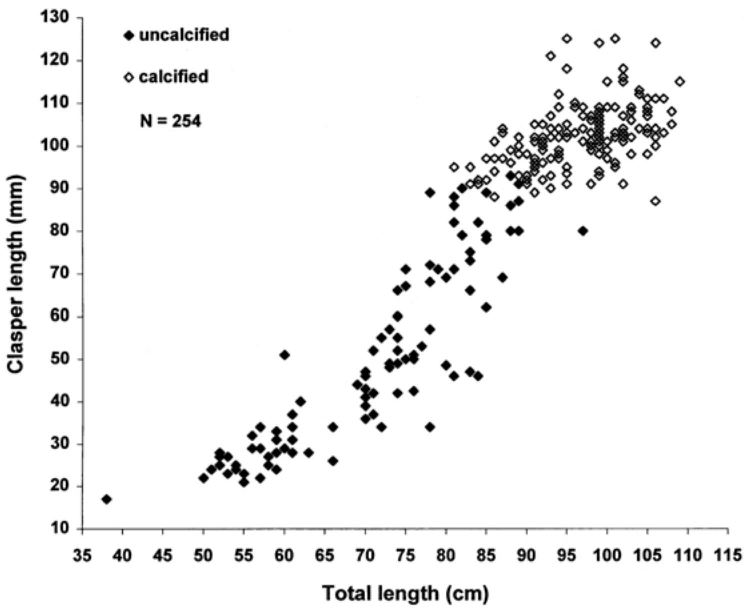


Figure 1. The relationship between clasper length (CL) and total length (TL) of *M. canis*.

females and percent maturity curves based on age and length created.

Fecundity was determined by observing the number and size of embryos found in pregnant females from September through May. The number and size of embryos present in different size and age females was compared to determine if fecundity increases with length or age. The size at birth was determined by comparing the size of embryos close to the time of parturition with the smallest caught free-living animals.

The largest ovum in the ovary was measured (maximum ova diameter) and the mean maximum ova diameter (MOD) for each month was compared to determine the timing of the female reproductive cycle. The presence and size of eggs and pups found in uteri of females collected throughout the year were compared to further define the female reproductive cycle.

To determine if female smooth dogfish store sperm, the posterior third of the preserved oviducal gland was sectioned following Pratt (1993). This section was embedded in paraffin, sectioned, and stained with hematoxylin and eosin (following the same standard histological procedures as used in preparing the testis histological sections). The sections were then viewed with a compound microscope to determine if sperm was present in the oviducal gland. At least five oviducal glands from each of the following months: May, September, November, December, February, and March, were examined.

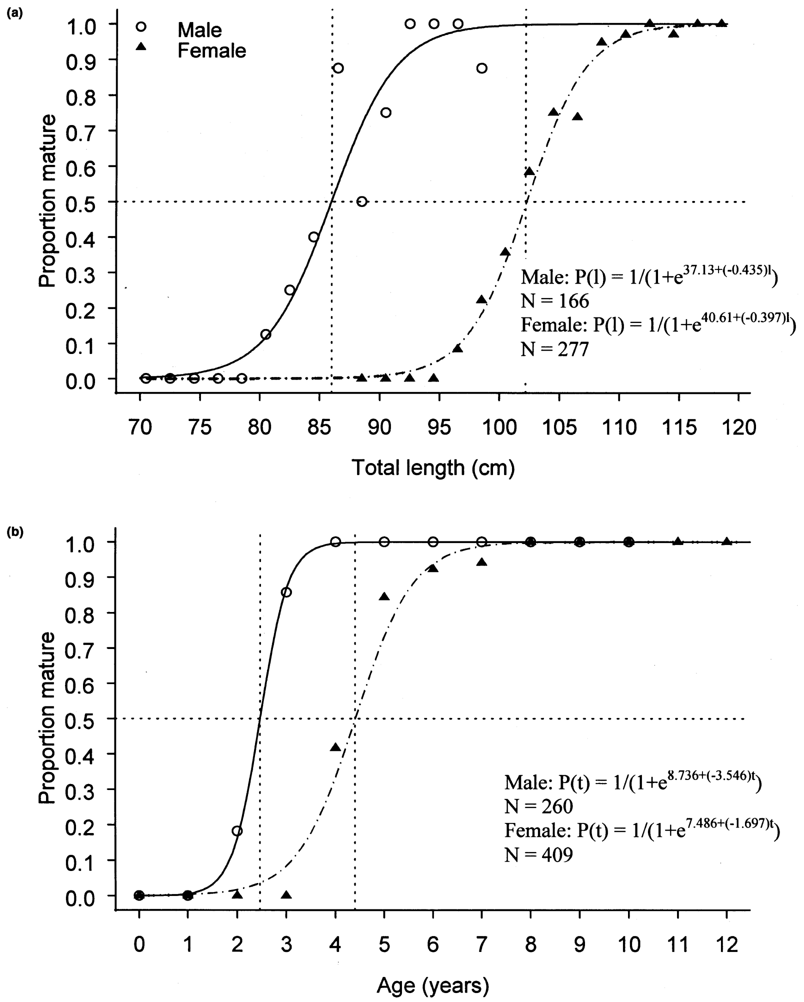


Figure 2. a – Maturity ogives for total length (TL) of male and female *M. canis*, b – maturity ogives for age of male and female *M. canis*.

Results

Males

A plot of clasper length versus total length showed an increase in clasper growth rates around 70 cm TL and a plateau in clasper growth rates around 80 cm TL, indicating male smooth dogfish begin to mature around 80 cm TL (Figure 1). Based on clasper calcification the smallest mature male was 81 cm TL and the largest immature male was 97 cm TL. A logistic plot of the proportion of mature males at 2 cm TL intervals resulted in the following equation:

$$P(l) = 1/(1 + e^{37.13+(-0.435)l}),$$

where l equals age, and P(l) equals the proportion mature at length l. This equation was solved to determine that 50% of males were mature at 86 cm TL (Figure 2a). A logistic plot of the proportion of mature males at each age resulted in the following equation:

$$P(t) = 1/(1 + e^{8.736+(-3.546)t}),$$

where t equals age, and P(t) equals the proportion of males mature at age t (Figure 2b). The youngest mature male was 2 years and the oldest immature male was 3 years of age.

A cross section of the testis is shown in Figure 3, and the stages of the testis, modeled after Maruska et al. (1996), are shown in Figure 4. Stage one consists of spermatogonia and loosely organized germ cells not yet bound by a basement membrane into a spermatocyst. During stage two spermatogonia and Sertoli cells divide and are bound by a basement membrane forming the spermatocyst which is a 'genetic clone plus associated Sertoli cells' (Callard 1991). A layer of spermatogonia and associated Sertoli cells surround a central lumen during this stage and are bounded by a basement membrane. In stage three the spermatogonia undergo mitosis to become primary spermatocytes, which will then undergo the first meiotic division to become secondary spermatocytes. In stage four the secondary spermatocytes have undergone the second meiotic division to become spermatids. Stage 5 consists of immature sperm which are spermatids that have undergone spermiogenesis and possess a head and tail region, but individual sperm have not organized into bundles yet. During stage six these spermatozoa organize into tightly shaped packets arranged spirally along the outside of the spermatocysts. Unlike Maruska et al. (1996) the seventh 'degenerate' stage was classified as the area of the testis posterior to

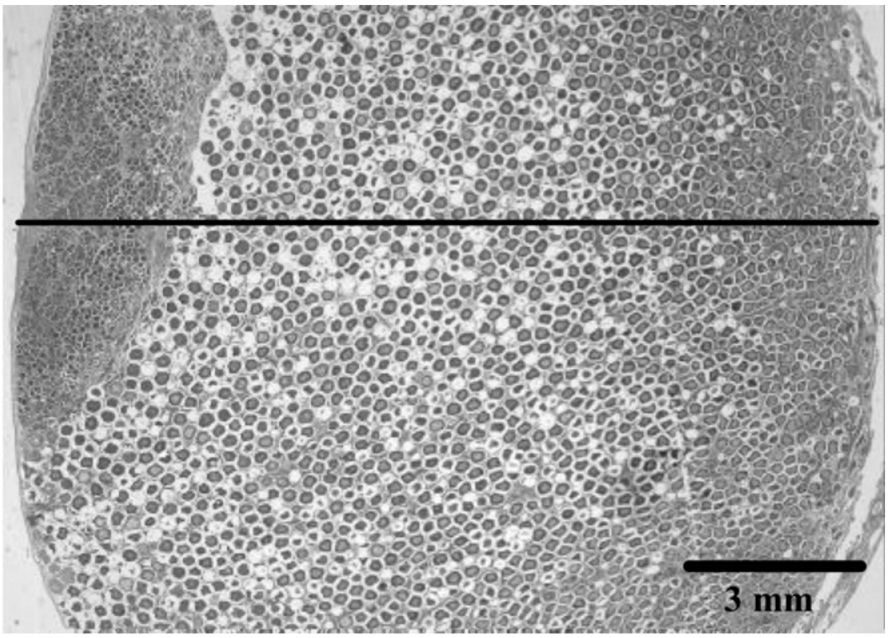


Figure 3. Cross section of a *M. canis* testis, stained with hematoxylin and eosin.

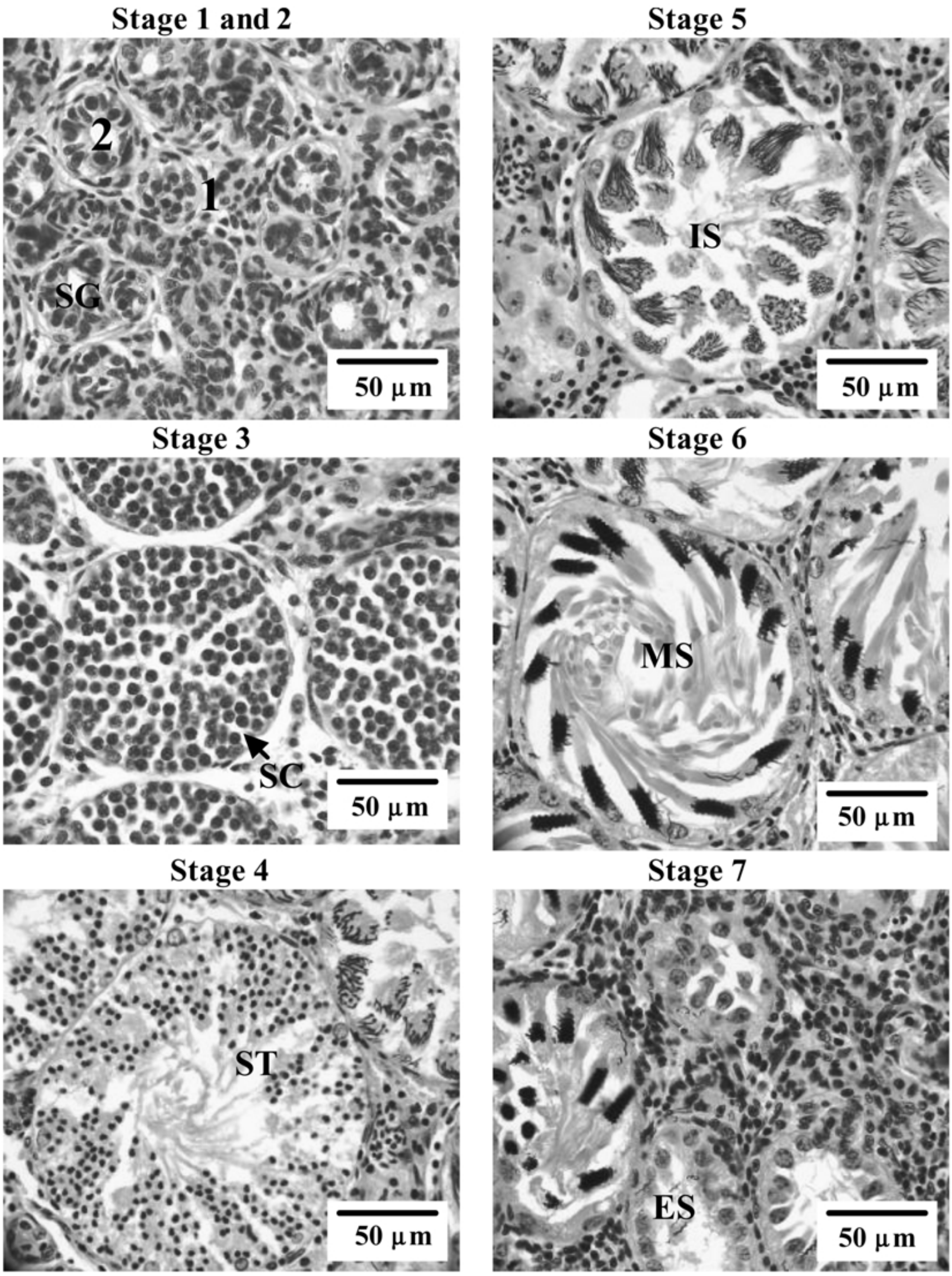


Figure 4. Sperm stages of the testis: stages 1–7, SG = spermatogonia, SC = spermatocytes, ST = spermatids, IS = immature sperm, MS = mature spermatozoa, ES = empty spermatocyst, SG = spermatogonia.

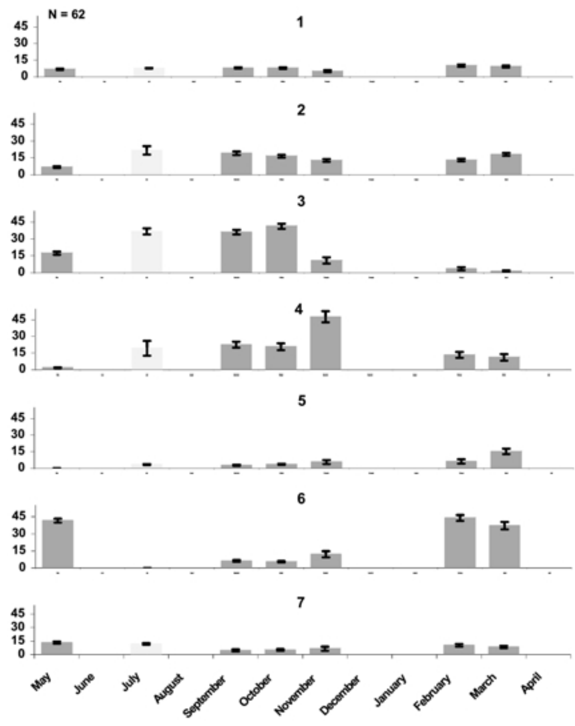


Figure 5. The mean proportion of the testis occupied by each stage for May through April (July N = 1, error bars are standard error).

stage six, which consists of empty spermatocysts, free spermatagonia, and free spermatozoa, rather than the area of the primary zone margin (between stages two and three). A plot of the proportion of the stages of the testes indicated that during September through October the majority of the testes were primarily occupied by stage 3: the spermatocyte stage (Figure 5). This was also true of one animal sectioned from July, but due to the small sample size this was not conclusive. During November the majority of the testes were occupied primarily by stage 4, the spermatid stage. By March and continuing through May the majority of the testes were occupied by spermatocysts in stage 6, the mature sperm stage. Thus mating most likely occurs between the months of May and September.

Females

Female smooth dogfish began to mature around 95 cm TL. The smallest mature female was 97 cm TL and the largest immature female was 114 cm TL. A logistic plot of the proportion of mature females against total length resulted in the following equation:

$$P(l) = 1/(1 + e^{40.61+(-0.397)l}),$$

where P(l) equals the proportion mature at length l, and l equals length. At a length 102 cm 50% of females were mature (Figure 2a). A logistic plot of the proportion of mature females at each age resulted in the following equation:

$$P(t) = 1/(1 + e^{7.486+(-1.697)t}),$$

where t is age and P(t) is the proportion mature at age t. The youngest mature female was 4 years old and the oldest immature female was 7 years old (Figure 2b).

The fecundity of female smooth dogfish ranged from 3 to 18 pups with an average of 9.53 pups per litter. There was a positive linear relationship between the total length of the female and the number of pups (Figure 6a):

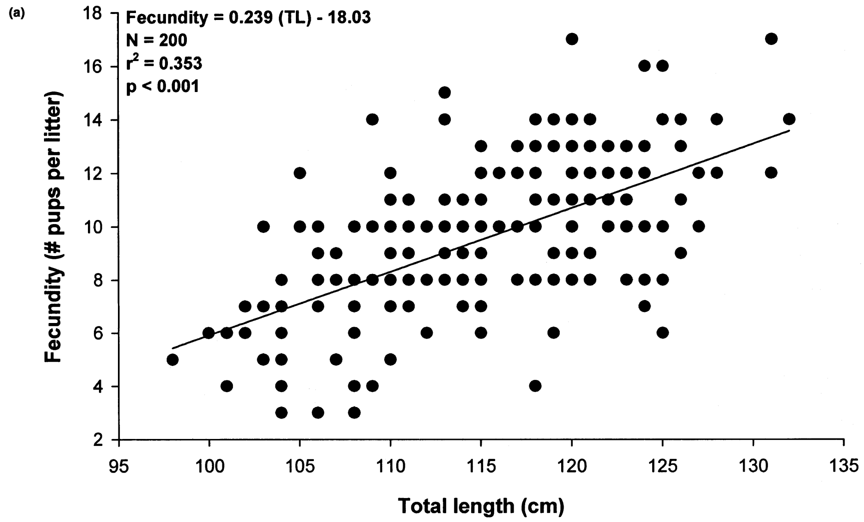
$$\text{fecundity} = 0.2394(\text{TL}) - 18.031$$

($p < 0.001$ and $r^2 = 0.353$). A regression of fecundity versus age indicated the following significant positive exponential relationship between age and fecundity (Figure 6b):

$$\text{fecundity} = 42.47(1 - e^{-0.496(\text{age})}) - 31.31$$

($p < 0.001$ and $r^2 = 0.283$).

Mature female smooth dogfish caught in May were either pregnant with near term pups, were post partum, or were pregnant with small eggs present in the uteri. Therefore the time between parturition and mating is likely of short duration, with all of these events occurring by the end of May or the beginning of June, perhaps with only hours to a few weeks, between parturition and mating. Ova increase in size until May and then become dramatically smaller by July (Figure 7a). The eggs do not start to take up considerable yolk until November or December. The presence of large yolked eggs in the ovary of females with near term pups indicates a yearly reproductive cycle. Every mature female caught between the months of June and April was pregnant further indicating a yearly reproductive cycle with an 11–12 month gestation. Pregnant females caught at the same time all had similar sized pups



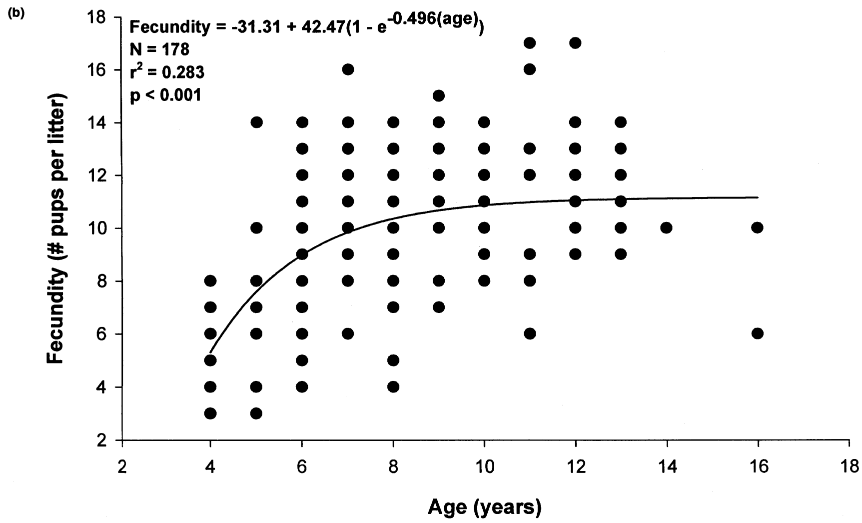


Figure 6. a – The relationship between fecundity (number of pups per litter) and total length (TL), b – the relationship between fecundity (number of pups per litter) and age for female *M. canis*.

further indicating a short mating and ovulation period (Figure 7b).

The embryos from near term animals in this study ranged in length from 30 to 39 cm TL and the smallest free living animals were 33–35 cm TL. Size at birth therefore likely ranges from 30 to 40 cm TL. There is a noticeable plateau in pup growth during the winter months (Figure 7b).

A minimum of five oviducal glands were examined histologically for sperm storage from each of the following months: May, September, October, November, December, and March. Figure 8a shows a cross section of the posterior third of an oviducal gland from a smooth dogfish. Zones of the oviducal gland were identified according to the terminology of Hamlett et al. (1999). They describe four fundamental zones of the elasmobranch oviducal gland based on the morphology of the epithelium: the proximal club zone, the papillary zone, the baffle zone, and the terminal zone. The jelly coats that surround the egg are produced within the proximal club and papillary zones and various types of egg investments are produced within the

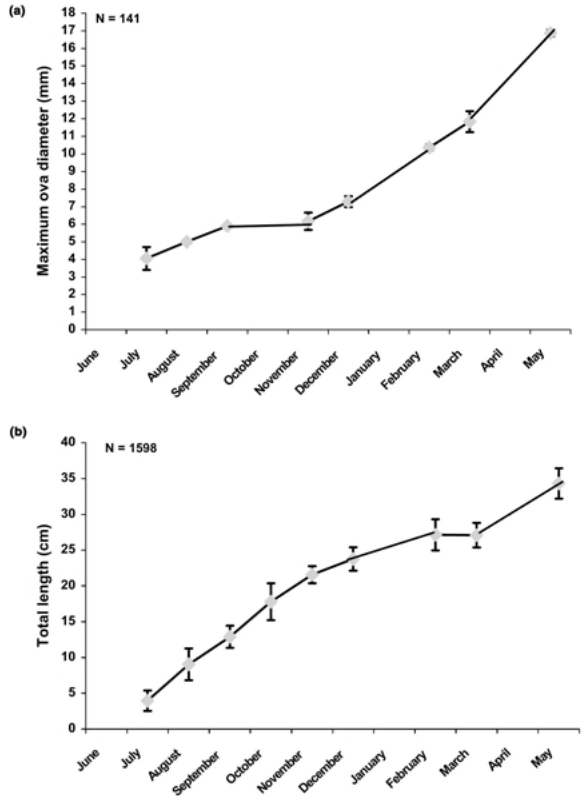


Figure 7. a – Mean maximum ova diameter (MOD), June through May, b – mean *M. canis* pup length for May through April (error bars are standard deviation).

baffle zone (Hamlett & Koob 1999). In this study sperm was found within the terminal zone of all sectioned *M. canis* oviducal glands from each month. Figure 8b shows a typical sperm bundle found within an oviducal gland.

Discussion

This study estimated older ages at maturity than previous studies, for both male and female smooth dogfish. Moss (1972) hypothesized an age at maturity of 1 year based on an aging study using tooth replacement rates. Francis (1981) used Holden's (1974) method and estimated male age at maturity was 1.1–2.1 years and female age at maturity of 2.0–2.7 years. This method has subsequently been discredited by Pratt & Casey (1990) who determined that this method does not work well for sharks. The present study found the majority of males were not mature until 3 years old and the majority of females were not mature until 5 years old.

Reproductive biology has been studied for several species in the genus *Mustelus* (Table 1). Female lengths at maturity ranged from 70 to 130 cm TL (Francis & Mace 1980, Massey & Francis 1989, Lenanton et al. 1990, Teshima 1981, Taniuchi et al. 1983, Yamaguchi et al. 1997). Male lengths at maturity range from 68 to 93 cm TL. The size at maturity of *M. canis* seems to resemble rig, *M. lenticulatus*, from Pegasus Bay, New Zealand (Lenanton et al. 1990) most closely, with rig lengths at maturity being only a few centimeters larger than *M. canis*. Reported age at maturity for *Mustelus* species range from 1 to 9 years for males and 1 to 15 years for females.

The change in maximum ova diameter, the change in sperm stage proportions, and gross observation of female reproductive tracts throughout the year support the conclusion that this population of smooth dogfish has an annual reproductive cycle. Ovulation occurs between May and June based on maximum ova diameter changes throughout the year. Animals were sampled in May that had eggs in the uteri and large ova still in the ovary. These animals were likely still ovulating, and thus, even though there were pregnant animals in May with eggs in the uteri, the MOD still remained high. This would indicate the ovulation period probably begins in mid-late May and may continue into early June. This suggests an 11–12 month gestation, slightly longer than 10 month gestation suggested by other authors (Bigelow & Schroeder 1948).

Tewinkle (1950) found in early June mature female smooth dogfish were post partum, and ovulation occurred between mid June and mid July. This difference in the timing of mating is perhaps due to differences in the timing of the reproductive cycle geographically. The animals we sampled in May were from the Chesapeake Bight (coastal Virginia), which is on the southern end of their summer distribution whereas the animals she studied came from the Woods Hole area (Massachusetts), which is on the northern end of their distribution. She estimated ovulation occurred at a rate of two ova ovulated followed by 30–40 h between ovulations with one egg going into each uterus. All the other *Mustelus* species reported here had an annual cycle with a 9–12 month gestation (Table 1).

Fecundity and size at birth estimates for this species closely agree with those found in the literature. We found litters ranging in size from 3 to 18 animals. Our estimates of size at birth from 30 to 40 cm TL are in close agreement with those published in the species accounts, 34–39 cm TL (Bigelow & Schroeder 1948)

a
b

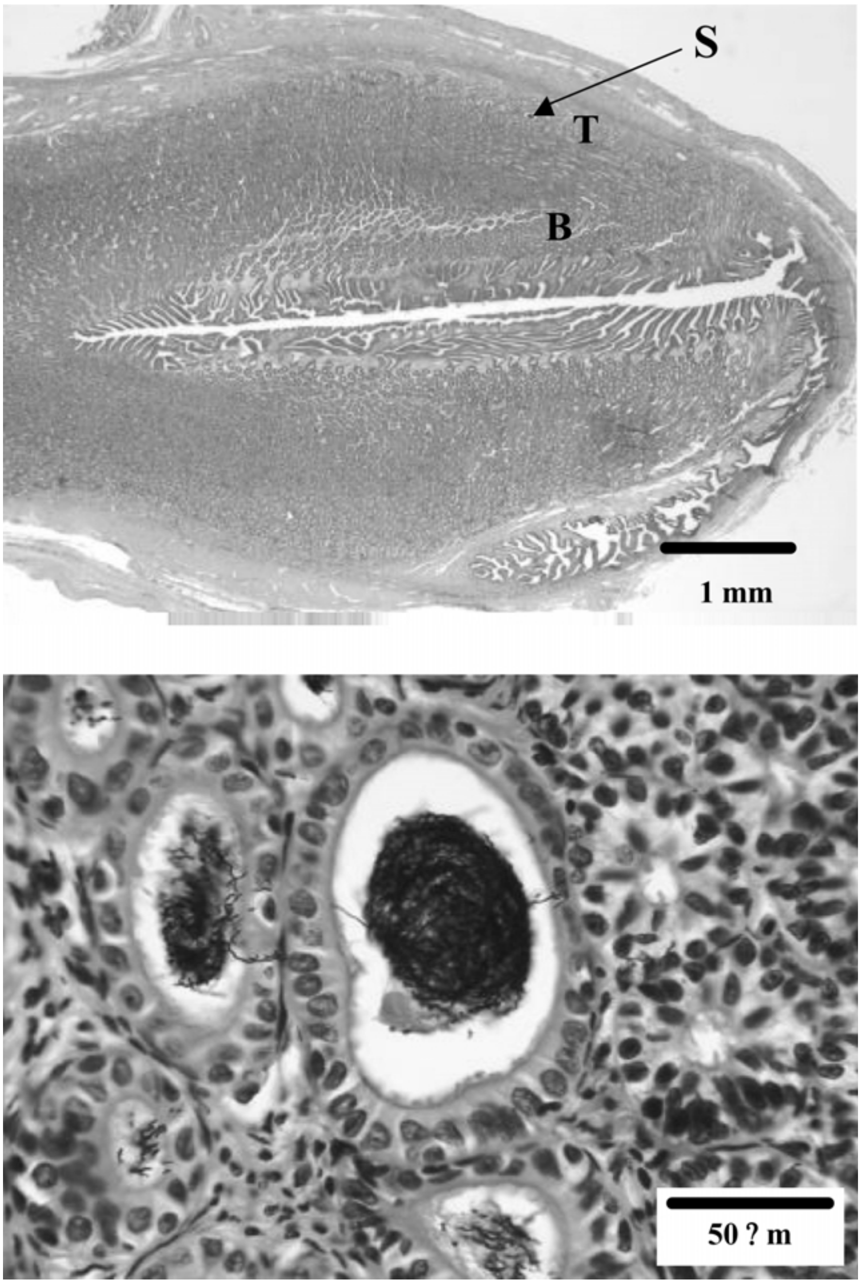


Figure 8. a – Cross section of the posterior third of a *M. canis* oviducal gland (S = sperm bundle, T = terminal zone, B = baffle zone), b – sperm bundles found within the terminal zone of the oviducal gland.

and a paper on first year growth of smooth dogfish, 28–39 cm TL (Rountree & Abel 1996).

Fecundity has a significant positive relationship with both age and length. As the females become larger this increase in total length and girth results in a larger space in the body cavity to accommodate pups. Fecundity is more closely related to length than to age likely due to the variability in ages of larger animals. Both relationships have a low r^2 value indicating the data do not fit the relationship closely and that neither age nor

Table 1. Reproductive parameters of various *Mustelus* species (RCP = reproductive cycle periodicity, FSR = fecundity size relationship).

Species	Length at maturity (cm)	Gestation (months)	Litter size	Length at birth (cm)	RCP	FSR	Reference
M. lenticulatus	M 82–85 F 85–95	11	up to 24 mean = 10.73	30–32	Annual	Yes	Francis & Mace (1980)
M. lenticulatus	M 89 F 106	9–12	6–24		Annual	Yes	Massey & Francis (1989)
M. antarcticus	M 93 F 120–130	11–12	1–31	30–36	Annual	Yes	Lenanton et al. (1990)
M. griseus	M 70–75 F 68–76	10	5–16	30 (estimated)	Annual	Yes	Teshima (1981)
M. manazo	M 60–65 F 63–70	10	1–8	30 (estimated)	Annual	Yes	Teshima (1981)
M. manazo	M&F 62–70	10	1–22 mean = 4.9		Annual	Yes	Taniuchi et al. (1983)
M. manazo	M 68.7 F 70.1	11–12	2–13	20–30	Annual	Yes	Yamaguchi et al. (1997)
M. canis	M 85 F 102	11	3–17	30–40	Annual	Yes	Present study

length are very accurate predictors of fecundity. Several *Mustelus* studies have shown a positive relationship between fecundity and total length, a linear relationship in all of those cases except for rig, *M. lenticulatus*, which have an exponential relationship between fecundity and total length (Francis & Mace 1980) (Table 1). The number of pups for *Mustelus* species ranges from 1 to 31. The smooth dogfish falls within this range with 3–20 pups per litter.

Mustelus pups generally range in size from 20 to 36 cm TL. *M. canis* has pups on the larger end of this size range with pups similar in size to those of *M. antarcticus* (Lenanton et al. 1990) and *M. lenticulatus* (Massey & Francis 1989). Pup growth seems to plateau in the winter months from December through March, this corresponds to when they are the furthest south in their wintering grounds.

The present study found that mating likely occurs between May and September based on the change in proportional area occupied by different sperm stages within the testes of male smooth dogfish. During May stage 5, the mature spermatozoa stage occupies the largest area of the testis and by September stage 3, the spermatocyte stage occupies the largest area of the testis. This occurs presumably because the mature spermatoza are used in mating during the period between May and September. Teshima (1981) staged testes of *M. manazo* and *M. griseus* comparing proportions of spermatocysts in the following stages: spermatogonia, spermatocytes, spermatids, and spermatozoa. He found the largest fluxes were in spermatocytes and spermatozoa, with the spermatocytes dominating the testes from July to October, followed by a period from November to January where spermatid proportions increased, and a later period between February and May where spermatozoa dominated the testes. Based on these findings Teshima (1981) hypothesized both species were mating between June and August.

Female smooth dogfish store sperm in the lower one third of their oviducal gland throughout the year. Since mating likely does not occur during or after September sperm is stored for a minimum of 8 months. The present study confirms Hamlett et al.'s (1998) statement that year round sperm storage occurs exclusively in the terminal zone of *M. canis*. Pratt (1993) examined 11 species of sharks and found some sperm storage in nine of these species. Both Hamlett et al. (1998) and Pratt (1993) determined that stored sperm is located in the posterior, terminal zone of the oviducal gland, not in the more anterior baffle zone. Teshima (1981) observed that a specimen of *M. manazo* also had spermatozoa present in the oviducal gland 8 months after their proposed mating season.

This study found that mating, fertilization, and ovulation all occur between May and September and that sperm is stored year round in the terminal zone of the oviducal gland for a period of at least 8 months. This leads to the question of whether female smooth dogfish have the ability to fertilize eggs using stored sperm from a mating that occurred during a previous summer. Since fertilization is thought to occur anterior to the terminal zone, in the baffle zone, to use stored sperm for fertilization, sperm would have to move up the oviducal gland from the terminal zone to the baffle zone in order to inseminate the ova. Hamlett et al. (1998) suggest that it is possible the sperm bundles are released under the stimulation of hormones. Further studies are on going to better define sperm storage in *M. canis* and other elasmobranch species (Hamlett et al. 1999).

This population appears to have a high reproductive output for a shark species with a yearly reproductive cycle and a mean fecundity of 9.53 pups per litter. In addition every mature female caught between June and April was pregnant. This indicates the population at the time of this study had a comparatively high productivity for a shark species.

Acknowledgements

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