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Population Dynamics of the Smooth Dogfish, *Mustelus canis*, in the Northwest Atlantic

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POPULATION DYNAMICS OF THE SMOOTH DOGFISH, *Mustelus canis*, IN THE
NORTHWEST ATLANTIC

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

by

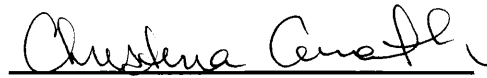
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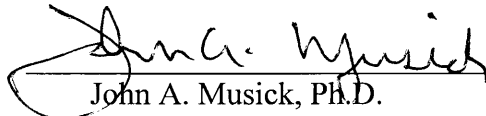
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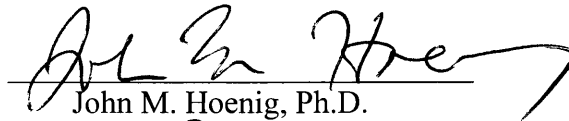


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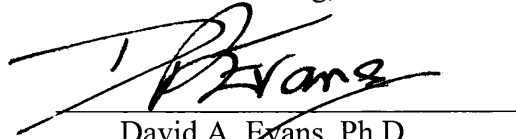
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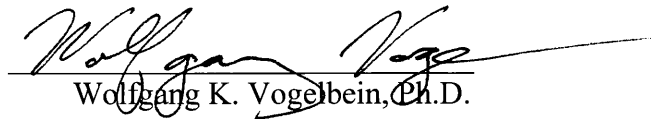
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Dedicated to the Conrath “clan”: Mom, Dad, Ed, Teresa, Kaylin, Misty, Don, and Kaitlyn

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ABSTRACT

Shark populations tend to be highly vulnerable to overexploitation due to low fecundity and slow growth rates. In the early 1990's a gillnet fishery targeting the North Atlantic population of smooth dogfish started on the East Coast of the United States. Smooth dogfish are small coastal sharks that appear to grow quickly and have a high fecundity, possibly making this population more resilient to fishing mortality than many other shark populations. However, no demographic modeling has been done to predict how increased mortality from fishing will affect this population. Although this is a seasonally abundant animal on the East Coast of the United States very little has been published about its growth and reproduction, parameters necessary for a demographic analysis.

Growth bands in vertebral samples were used to estimate ages for 894 smooth dogfish. Age-length data were used to determine von Bertalanffy growth parameters for the population. von Bertalanffy growth parameters were $K = 0.292 \text{ y}^{-1}$, $L_{\infty} = 123.57 \text{ cm}$, and $t_0 = -1.94 \text{ years}$ for females, and $K = 0.440 \text{ y}^{-1}$, $L_{\infty} = 105.17 \text{ cm}$, and $t_0 = -1.52 \text{ years}$ for males.

Length and age at maturity, fecundity, and reproductive season were estimated for the population. Total length at 50% maturity was estimated at 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 of this population had an 11 – 12 month gestation with parturition occurring in May, ovulation occurring between May and July most 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 is stored in the oviducal gland of females throughout the year.

Natural mortality of the population was estimated using four life history methods and catch curve analysis. The growth, reproduction, and mortality estimates were used to construct three life tables, which were then modified to include compensation and fishing mortality. Estimated mortality rates ranged from 0.15 to 0.53. While the population appears to be highly productive for an elasmobranch species with high fecundity and growth rates, the life table analysis indicates this population may not be able to withstand a high fishing mortality especially if fishing is started before the age of maturity. If exploitation of this population continues it will be important to monitor the population to ensure that it remains stable.

POPULATION DYNAMICS OF THE SMOOTH DOGFISH, *Mustelus canis*, IN THE
NORTHWEST ATLANTIC

GENERAL INTRODUCTION

EXPERIMENTAL SPECIES

The smooth dogfish, *Mustelus canis*, is a small shark found throughout the western Atlantic from Massachusetts to Florida, in the northern Gulf of Mexico, including Cuba, Jamaica, Barbados, Bermuda, Bahamas, and from southern Brazil to northern Argentina (Compagno 1984). Heemstra (1997) divided the species *M. canis* into two subspecies: a continental form (*M. canis canis*) found from the Bay of Fundy to Florida and the Gulf of Mexico, Venezuela, Surinam, French Guinea, Brazil, Uruguay, and Mar de Plata, Argentina; and an insular form (*M. canis insularis*) found in deeper waters of the Caribbean islands, the Bahamas, and Bermuda. The two subspecies are distinguishable by vertebral counts, as well as differences in dorsal and caudal fin size and shape. Several discrete populations of smooth dogfish likely exist and are separated by large geographic areas with little intermigration between different populations (Bigelow and Schroeder 1948).

Smooth dogfish are primarily demersal sharks that inhabit continental and insular shelves and upper slopes and are typically found in inshore waters down to 200m 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, with bottom water temperatures ranging from 6-7°C up to 10-15°C. They begin to migrate northward when temperatures in the

middle Atlantic and southern New England reach at least 6-7°C. By May, smooth dogfish appear in the mid Atlantic and southern New England where they undergo parturition and mating. When water temperatures drop below 10-12° C in late October and November, they return south in large numbers to their wintering grounds (Bigelow and Schroeder 1948).

Smooth dogfish possess low flattened teeth specialized for crushing crustacean prey. Their diet consists primarily of large crustaceans especially crabs as well as lobsters, but also includes squid, small bony fish (menhaden, stickleback, wrasses, porgies, sculpins, and puffers), gastropods, bivalves, marine annelid worms, and occasionally garbage (chicken heads, *etc.*)(Bigelow and Schroeder 1948; Gelsleichter et al., 1999).

Smooth dogfish are viviparous sharks that form a yolk-sac placenta, and have litters ranging in size from 4-20 pups. Bigelow and Schroeder (1948) reported an annual reproductive cycle, with mating occurring from mid to late summer, beginning in July. Tewinkle (1950), however, suggested that ovulation occurs from mid June to mid July, in which case mating would likely occur by mid June. Gestation is reported to last about 10 months, with females giving birth from early May to mid July (Bigelow and Schroeder 1948). Females are reported to reach maturity at about 90 cm total length (TL) and males are reported to reach maturity around 82 cm TL (Compagno 1984). Reported size at birth ranges from 28-39 cm TL and Mid-Atlantic Bight estuaries may serve as critical nursery grounds for this species (Rountree and Able 1996).

IMPORTANCE OF THE STUDY

Historically, elasmobranch fisheries tend to drastically decline after a short period of time and overfished populations may take decades or longer to recover. Documented examples of collapsed fisheries include the California soupfin shark, Australian school shark, basking shark, and the Scottish-Norwegian spiny dogfish fisheries (Holden 1974). Musick (1999) stated long lived marine animals tend to be highly vulnerable to over-exploitation due to variable and infrequent recruitment, low fecundity, slow growth and late maturity. Holden (1974) questioned the sustainability of elasmobranch fisheries. Walker (1998) stated that the concern should not be whether or not elasmobranch fisheries are sustainable, but focus should be placed on “the relative exploitability of shark species.” Due to differences in life history parameters some elasmobranch populations appear to be more productive and therefore more resilient to exploitation.

In order to support a directed fishery, a stock would have to be naturally abundant, have a relatively high fecundity, and a relatively fast growth rate (Pratt and Casey 1990). Hoff and Musick (1990) discussed the fact that management is hampered by a lack of information and they pointed out critical informational needs, including information on: pupping and nursing grounds, validated age and growth, age and sex relative distributions, and migrations, statistically valid sampling to describe catch by species, fishery sampling data, tagging studies, and independent fishery indices.

Anderson (1990) stated that lack of data is the major problem with elasmobranch stock assessment and discussed the use of biomass dynamic models and age structured models for elasmobranch stock assessment. Biomass dynamic models incorporate little information about the biological structure of the stock and therefore can not be used to make detailed descriptions of the status of the stock. Age structured models can be used to make more detailed and realistic predictions based on the dynamics of the stock.

While several demographic analyses of elasmobranch populations using age structure models have been published (Cailliet 1992; Cailliet et al., 1992; Sminkey and Musick 1996; Cortes and Parsons 1996), Walker (1998) stated many of these studies will lead to overly pessimistic prognoses for the populations under study because they do not account for any compensatory responses to increased exploitation. Compensatory responses to exploitation include changes in natural mortality, growth, and fecundity. Wood et al. (1979) created an age structured model for spiny dogfish, *Squalus acanthias*, in British Columbia waters. They modeled compensatory changes in natural mortality and growth to see which would be more effective and which fit the data more closely. They concluded that changes in natural mortality were the most likely compensatory mechanism for spiny dogfish. Walker (1992) derived a dynamic pool simulation model for gummy sharks, *Mustelus antarcticus*, in Southern Australian waters. He found that historical evidence suggested that the rates of growth and reproduction had not increased, suggesting that any compensatory response to fishing in this population was due to changes in natural mortality of pre-recruit animals.

Smooth dogfish have not historically been targeted in a commercial fishery. They have, however been collected for classroom dissections (Bigelow and Schroeder 1948).

Smooth dogfish commercial landings began to increase on the East Coast of the United States in the early 1990s (Figure 1) (National Marine Fisheries Service (NMFS) 2000). Smooth dogfish have been landed in significant numbers (i.e., over 50 metric tons) from Massachusetts, New Jersey, Maryland, Virginia, and North Carolina (Figure 2). A gill net fishery for smooth dogfish recently began on the Eastern Shore of Virginia and North Carolina. Total landings of smooth dogfish in Virginia waters remained fairly low until 1993, when landings exceeded 220,000 pounds; total landings increased to around 300,000 pounds in 1994 and 1995, and then further increased to over 650,000 pounds in 1996. Smooth dogfish landings in Virginia then decreased to less than 150,000 pounds in 1997, and further decreased to less than 50,000 pounds in 1998 (NMFS 2000). In North Carolina, smooth dogfish landings have only been reported separately from spiny dogfish landings since 1995. In 1995, total landings reached over two million pounds, but dropped in 1996 and 1997 to around 500,000 pounds. Landings in North Carolina further decreased to 370,000 pounds in 1998 (NMFS 2000). However, one problem with smooth dogfish catch statistics is the large number of reported dogfish landings that are not classified as smooth or spiny. These landings of unclassified dogfish often exceed the total reported smooth dogfish landings (Figure 3); therefore the total value of actual smooth dogfish caught may be significantly higher than what is reported (NMFS 2000). While time of the year and location can be used to clarify some of these landings, the determination of accurate landings remains difficult.

Mustelus species tend to have high growth rates and fecundities (Tanaka and Mizue 1979; Yudin and Cailliet 1990; Francis and Francis 1992; Yamaguchi et al., 1996; Francis and Mace 1980; Teshima 1981; Taniuchi et al., 1983; Massey and Francis 1989;

Lenanton et al., 1990; Yamaguchi et al., 1997) which may make them more productive and more resilient to exploitation. The objective of this study was to determine the age, growth, and reproductive parameters necessary for a demographic analysis. Life tables were then used to examine how recent increases in fishing mortality will affect the North Atlantic population of smooth dogfish.

Figure 1: Reported smooth dogfish landings from NMFS commercial catch statistics for the Atlantic and Gulf states, from 1981-1998.

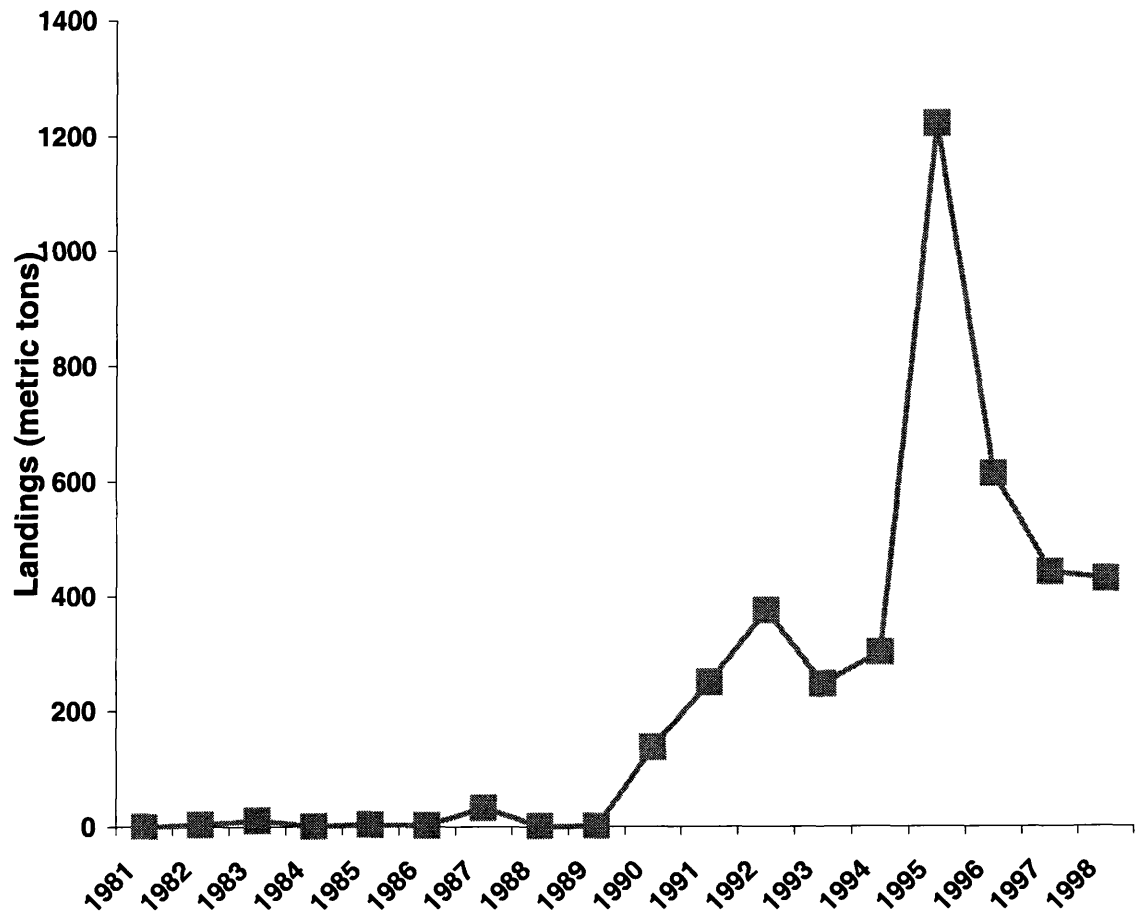


Figure 2: Reported smooth dogfish landings by state from NMFS commercial catch statistics, from 1990-1998.

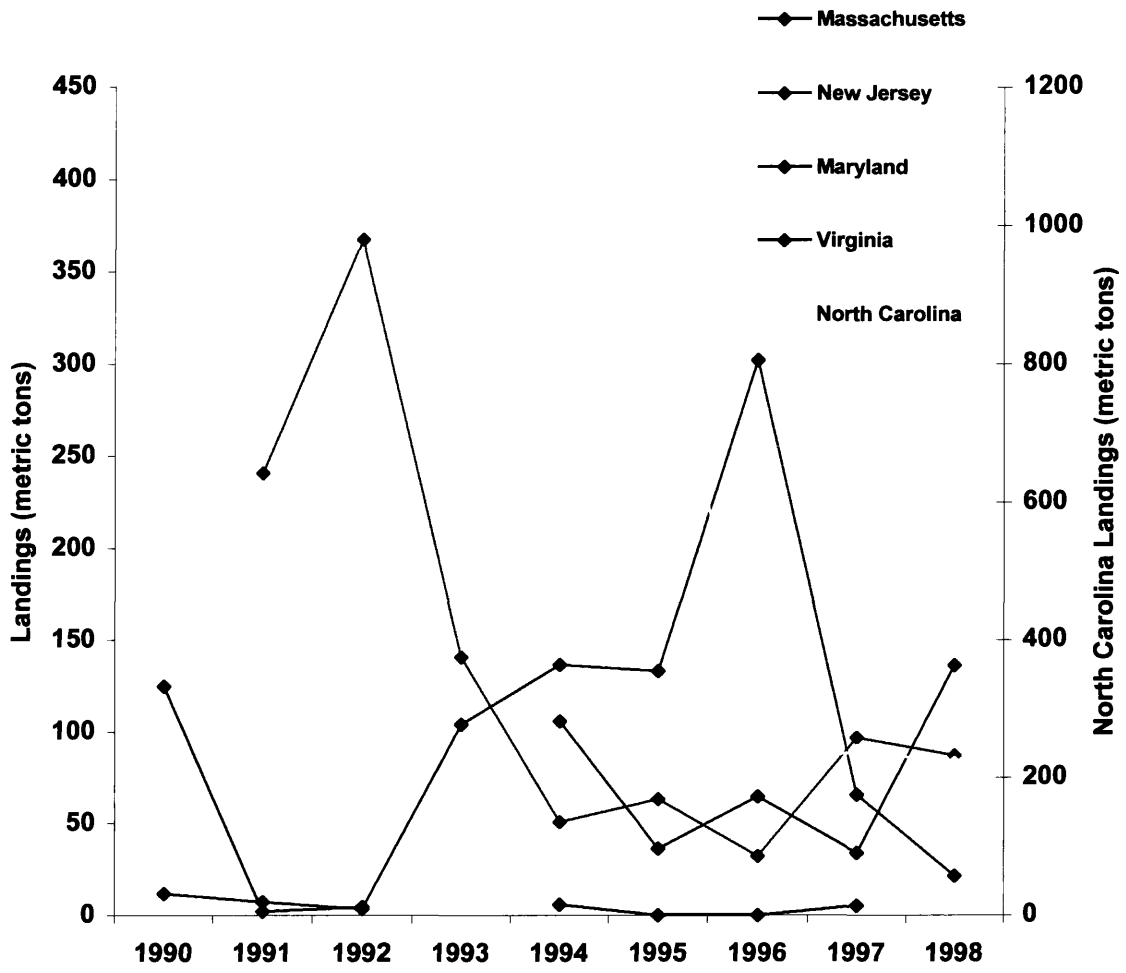
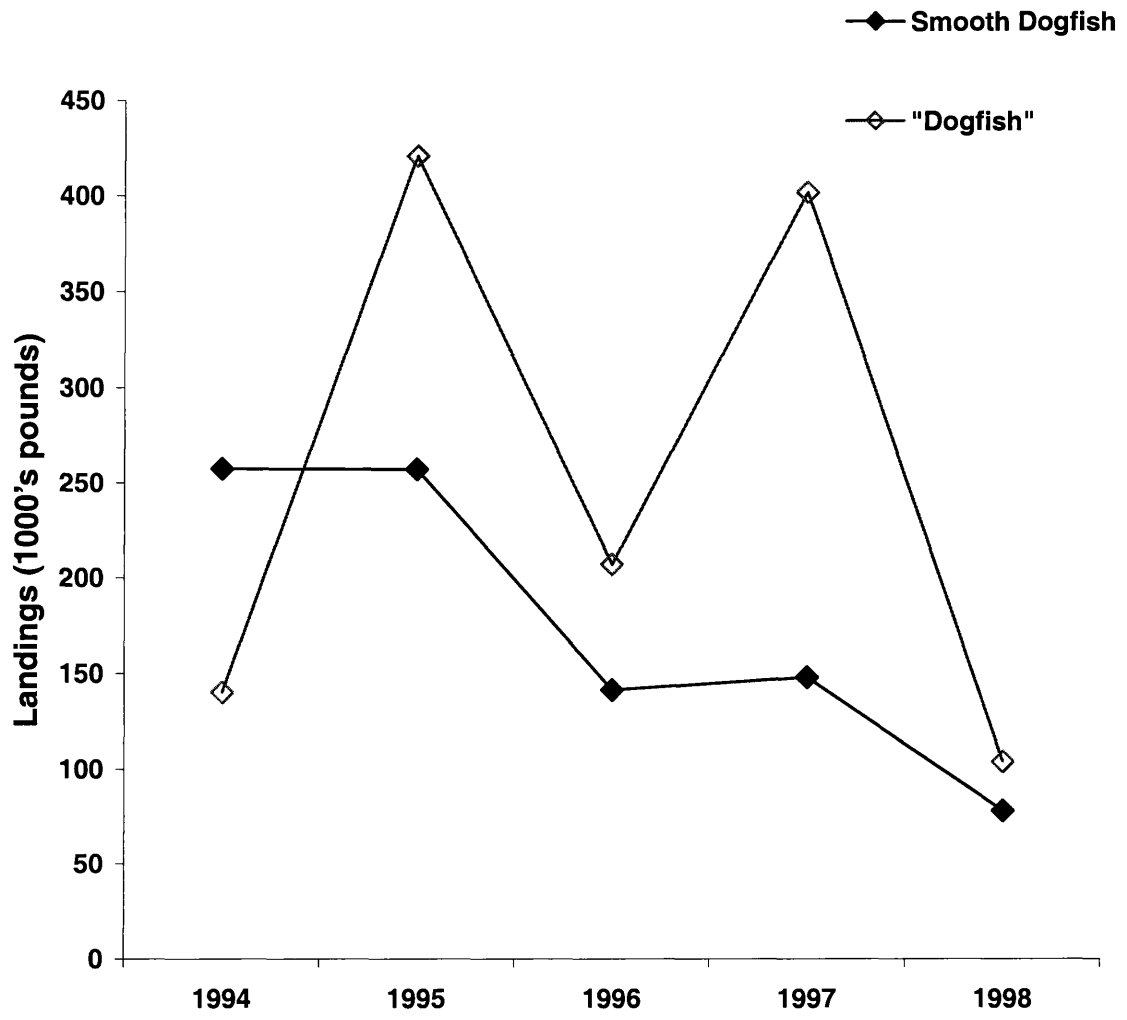


Figure 3: Reported smooth dogfish and dogfish landings from NMFS commercial catch statistics for the Atlantic coast, from 1990-1998.



Chapter 1

Age and Growth of *Mustelus canis*

INTRODUCTION

Age and growth data are a necessary component of an age structured demographic analysis. Age and growth parameters are most commonly determined by direct observation, length frequency analysis, or by the use of annular patterns on calcified structures. Everhart and Young (1981) defined three criteria for using such structures to determine age: the structure has to remain constant in number and identity, growth of the structure must be proportional to growth of the fish, and the annulus must form yearly.

It is necessary in age and growth studies based on hard part structures to justify the assumption that growth bands found within the hard part are formed yearly and this is done through the process of verification or validation. Cailliet (1990) defined verification as, “ the process of confirming an age estimate by comparison with other indeterminate methods,” and stated that validation, “requires proving the accuracy of an age estimate by comparison with a determinate method.” Beamish and McFarlane (1990) stated that validation must prove that the mark considered an annulus forms once a year and that the fish is the age estimated. Ideally growth bands would be validated for each age class of the population and this is primarily accomplished by using known age fish or by mark and recapture studies. As validation is very difficult for many elasmobranch species, various methods of verification are often used including size frequency analysis and centrum edge analysis (Branstetter and Stiles 1987; Davenport and Stevens 1988; Killam and Parsons 1989; Natanson and Cailliet 1990; Ferreira and Vooren

1991). Centrum edge or marginal increment analysis involves measuring changes in the distance between the last band and the edge of the hard part, from hard parts sampled throughout the year and comparing these distances to determine if there is an annual pattern.

In most age and growth studies it is not possible to know if the estimate of age is true or accurate but two reader's estimates of age can be compared to see if they are similar or precise. Precision of age estimates has traditionally been determined by using percent agreement. Beamish and Fournier (1981) criticized this method because it does not take into account the age of the species and stated it is therefore not comparable between species. They proposed using the average percent error (APE) following the equation:

$$APE = 100 \times 1/N \sum (1/R \sum (|X_{ij} - X_j|)),$$

where N is the number of fished age, R is the number of times each fish is aged, X_{ij} is the i th age of the j th fish and X_j is the average age of the j th fish. Chang (1982) suggested using the same equation except replacing the absolute deviation with the standard deviation:

$$\text{Coefficient of Variation (CV)} = 100 \times 1/N \sum (((X_{ij}-X_j)^2/R-1))/X_j.$$

He stated this is more appropriate because variance is an unbiased and consistent estimator. Kimura and Lyons (1991) suggested using the coefficient of variation across age ranges for estimating precision. Campana et al. (1995) stated that separate measures of bias and precision are necessary. They stated it was first necessary to check for systematic differences before using any kind of precision test. They supported the use of

an age bias plot to test for systematic differences and the use of Chang's CV to test for precision stating it is more statistically rigorous than percent agreement or APE. Hoenig et al. (1995) criticized the use of indices of precision because they do not test for systematic differences, do not take into account differences in precision with ages, and they do not distinguish between several sources of variability. They stress the importance of testing for systematic differences between readers, and suggested using Bowker's test to test the hypothesis that values in a contingency table are symmetric about the main diagonal.

The most commonly used model for elasmobranch growth is the von Bertalanffy growth function (von Bertalanffy, 1938). The model is:

$$L_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where t is age, L_t is length at age t , L_∞ is the mean asymptotic length, K is the von Bertalanffy growth coefficient, and t_0 is the theoretical time at which the length is zero. The purpose of this study is to age North Atlantic (NA) smooth dogfish using their vertebrae, to determine maximum age and age at maturity for males and females of the NA population, and to calculate a von Bertalanffy growth curve for this population. The estimated growth parameters will ultimately be used in demographic modeling of this population to determine its resilience to harvesting.

MATERIALS AND METHODS

Smooth dogfish vertebral 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). Total length (TL), precaudal length (PCL), and clasper length (CL) were measured and sex recorded at the time of collection. Total length was measured along a straight line from the tip of the snout to the end of the tail, which was stretched down to take the measurement. Precaudal length was measured along a straight line from the tip of the snout to the precaudal notch. Clasper length was measured from the posterior margin of the cloaca to the tip of the clasper. A section of the vertebral column containing eight to twelve vertebrae was removed from directly under the first dorsal fin. Vertebrae were either stored frozen or were cleaned, soaked in 70% ETOH for twenty-four hours, air dried for twenty-four hours, and placed in coin envelopes. Dried vertebrae were sagittally sectioned through the focus using an isomet saw. One cut was made on small vertebrae; on larger vertebrae a second sagittal cut was made a short distance from the first cut to obtain a thinner section of the vertebrae. Then the section/half was affixed to a slide using a mounting medium and sanded using wet fine grit sand paper to a thickness of about 0.5mm. The vertebrae were then viewed with a binocular dissecting microscope using transmitted light.

The pattern on the vertebrae consists of wide translucent bands separated by narrow opaque bands that extend from the intermedialia on to the corpus calcareum (Figure 1-1). An angle change is present around 2mm from the focus of each vertebra and was considered to be a birthmark, likely formed when the animal is born due to a change in growth rates at this time. The growth band was considered to be the narrow opaque zone, which is presumed to form due to a slowing, or stopping of growth during

the winter months. This study followed the criteria found in Casey et al. (1985) who defined an “annulus” as a mark that appears as an opaque band in the intermedialia and continues as an opaque band into the corpus calcareum.

Vertebral radius was measured from the focus of the vertebra along the axis of the corpus calcarium to the edge of the vertebra (Figure 1-1). Total length (TL) was plotted against vertebral radius (VR) to determine if the growth of the vertebra is proportional to somatic growth of the animal.

The formation of annual marks was verified using marginal increment analysis. The distance from the last band to the edge of the margin was measured and divided by the width of the last growth band on the vertebra to determine the marginal increment ratio (MIR) (Figure 1-2). The margin width was divided by the distance to the angle change for Age-1 animals. For Age-0 animals the distance from the angle change to the edge of the vertebrae was measured and divided by the distance from the focus to the angle change. The mean MIR for each month was plotted for juvenile size animals to determine if there was a yearly pattern.

In order to determine if there was a seasonal pattern of growth, the mean total length of sampled Age-0 and Age-1 smooth dogfish was plotted for each month. This utilized several years data and assumes that every year class follows the same general growth pattern during their first two years. The mean monthly length of Age-0 animals taken from the 1997 and 1998 cohorts was also plotted, assuming a starting length at birth in May of 40 cm.

Figure 1-1: An age 3+ *Mustelus canis* vertebra, VR = vertebral radius, AC = angle change, 1,2,3 = age 1, 2, and 3 growth bands, CC = corpus calcareum, and I = intermedialia.

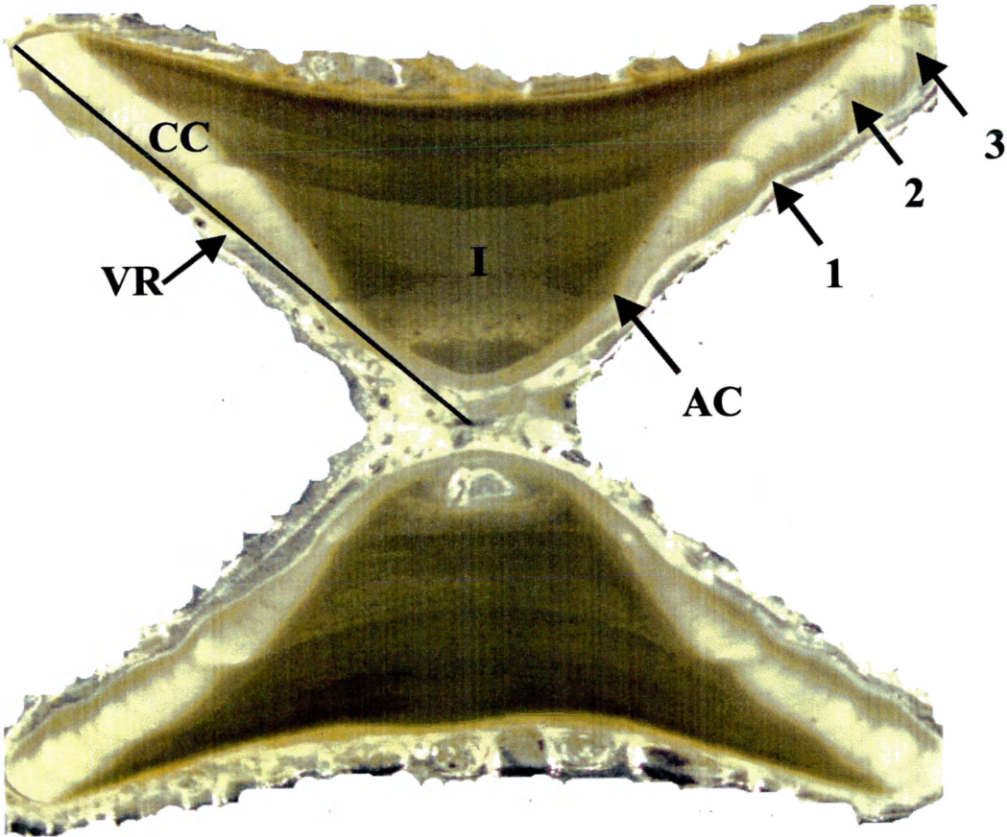
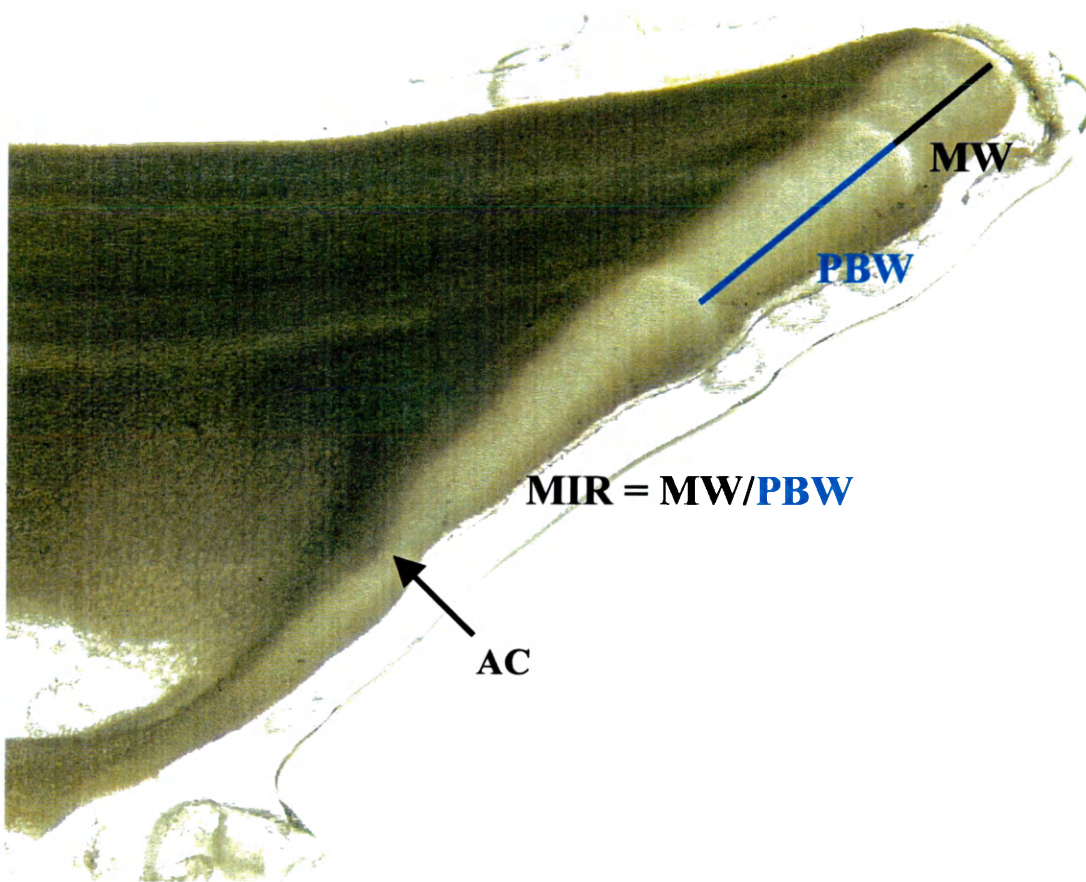


Figure 1-2: An age 2+ *Mustelus canis* vertebra showing the calculation of the marginal increment ratio, MW = margin width, PBW = previous band width, MIR = marginal increment ratio, AC = angle change.



A random sample of twenty vertebrae from each 10 cm size class (33-132cm TL), was read by two readers and a chi-square test was used to test for systematic differences between the two readers' ages. The number of observations above the main diagonal of a contingency table of reader one and reader two's ages was compared with the number of observations below the main diagonal to determine if this ratio was significantly different than a one to one ratio. Percent agreement was used to test for precision between the two readers for each length group.

The number of growth bands and the time of capture were used to assign an age to each animal. The length at age data were used to generate a von Bertalanffy growth curve for males and females using the computer program SigmaPlot (SPSS Inc.), which uses the Marquardt-Levenberg algorithm to estimate curve-fitting parameters (Press et al., 1986; Marquardt 1963; Nash 1979; Shrager 1970; Shrager 1972).

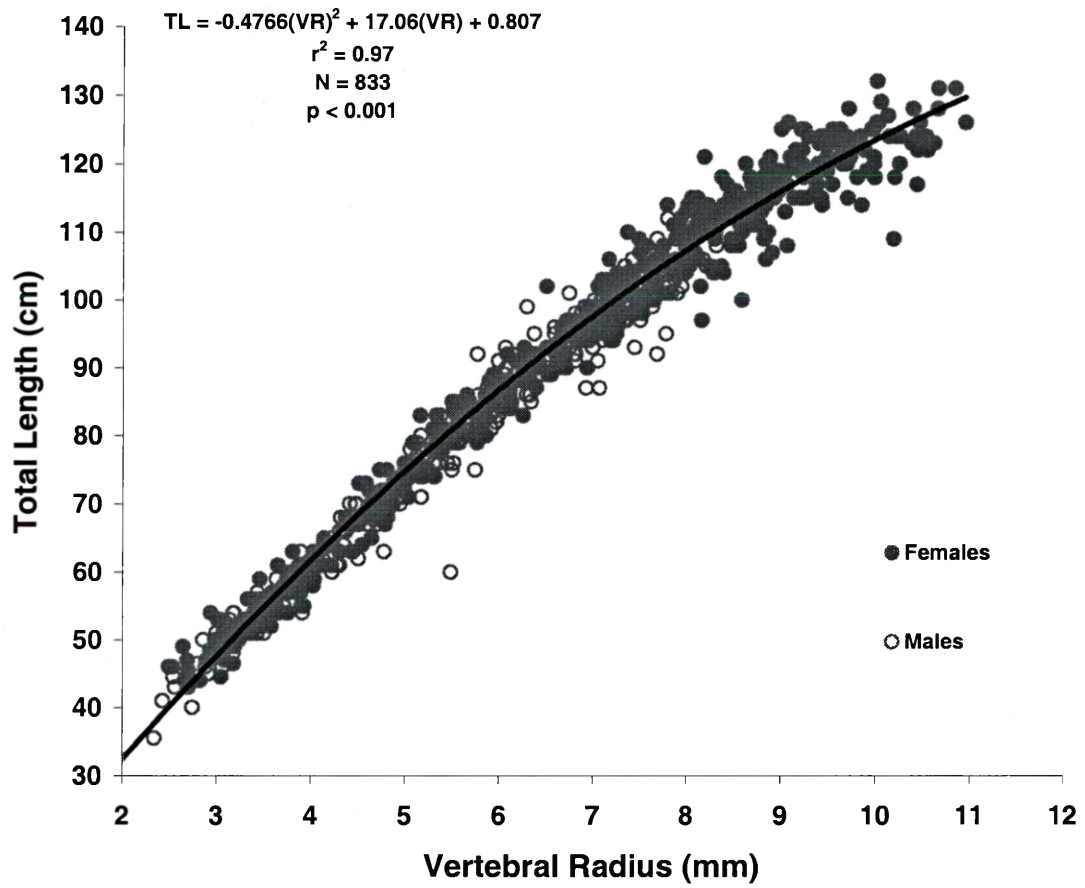
RESULTS

We collected vertebrae from 918 smooth dogfish and aged 894 animals (vertebrae from 24 animals were unreadable) ranging in size from 33 to 132 cm TL. Plots of male and female TL vs. VR were not significantly different (ANCOVA, $p < 0.05$) therefore the data were combined. A plot of TL versus VR resulted in the following positive curvilinear relationship, indicating there is a significant relationship between growth of the vertebrae and growth of the animal (Figure 1-3):

$$TL = -0.477(VR)^2 + 17.06 (VR) + 0.807$$

($N = 833$, $r^2 = 0.97$, $p < 0.001$).

Figure 1-3: Relationship between vertebral radius (VR) and total length (TL) for *Mustelus canis*.



The largest marginal increments were observed in vertebrae from animals collected in March (Figure 1-4). A large drop in marginal width appears to occur in May indicating that band formation occurs between these time periods, most likely during April. The marginal analysis was only conclusive for juvenile size animals (males less than 86 cm TL, females less than 102 cm TL). By the time these animals become mature their growth has slowed down dramatically and the difference between margin widths becomes very small, making it difficult to elucidate monthly changes in margin width.

The plot of seasonal growth of Age-0 and Age-1 smooth dogfish indicates there is a plateau in growth between the months of October and February or March, suggesting slow growth during this period (Figure 1-5). There is also a plateau in growth between October and February for both the 1997 and the 1998 cohorts further indicating a significant decrease in growth rates during this time period (Figure 1-6).

To test for precision, a second reader read a total of 185 animals, twenty from each ten cm size group except for the 33-42 cm size group (n=9) and four vertebrae that were subsequently thrown out as being unreadable. A contingency table of reader one versus reader two's ages was made and a chi-square test resulted in a $X^2 = 3.19$ which was less than the critical value of $X^2_{0.05,1} = 3.84$ thus the hypothesis of symmetry was not rejected (Table 1-1). The overall percent agreement between the two readers was over 84%, the percent agreement within one year was over 96% (Table 1-2). Agreement within one year was high (over 90%) for all size groups except the largest, where it dropped to 79%.

Figure 1-4: Monthly mean marginal increment ratio for male (TL<86 cm) and female (TL <102 cm) smooth dogfish. 1-12 = month (i.e., 1 = January)(error bars are standard error).

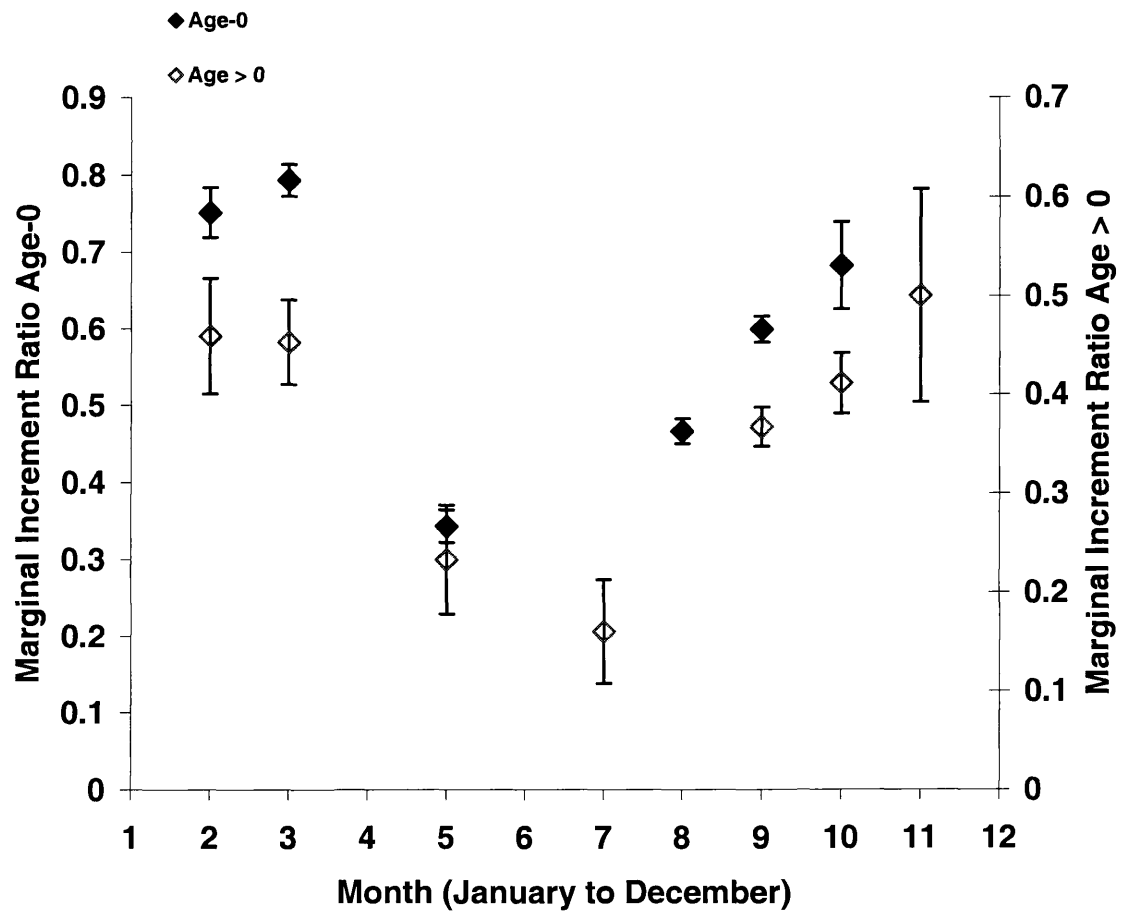


Figure 1-5: *M. canis* seasonal growth: mean size by month of Age-0 and Age-1 animals (error bars are standard error).

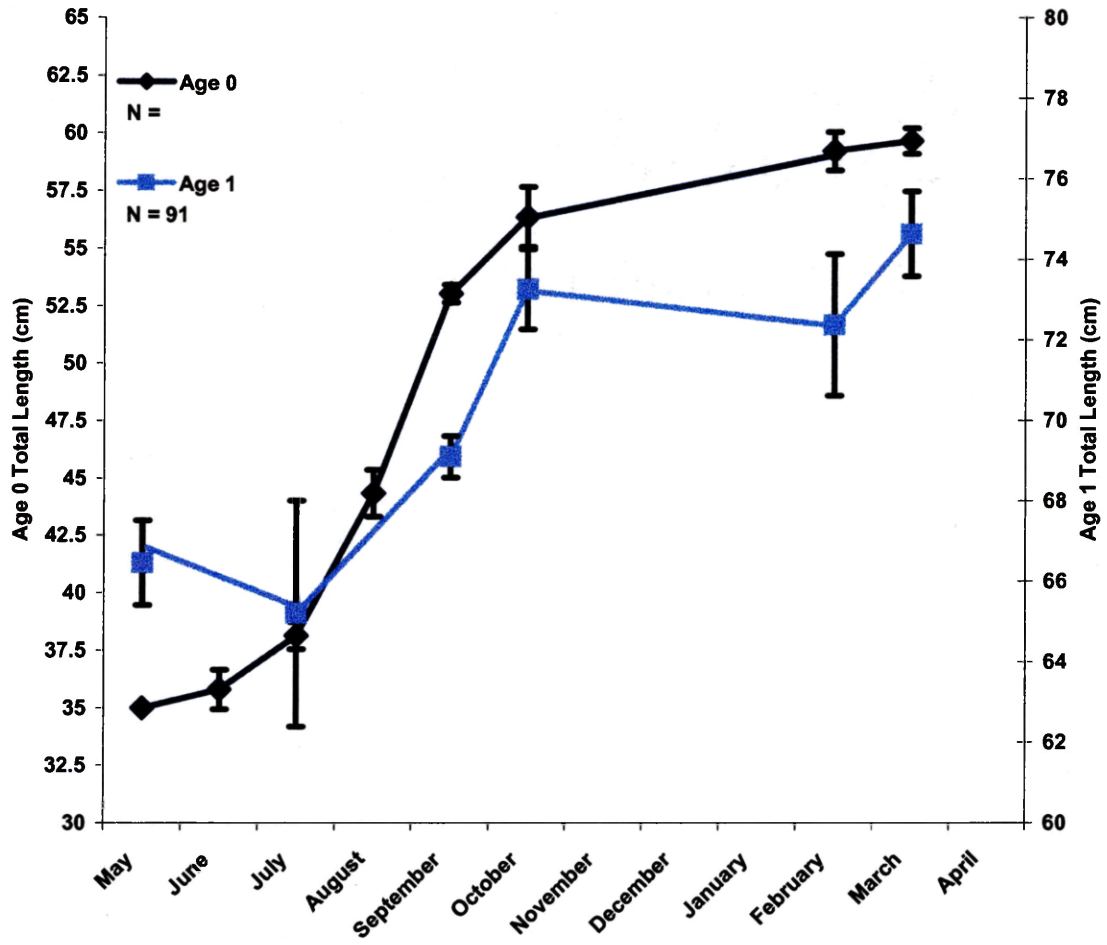


Figure 1-6: *M. canis* seasonal growth: monthly mean size of Age-0 animals in the 1997 and 1998 cohorts (error bars are standard error).

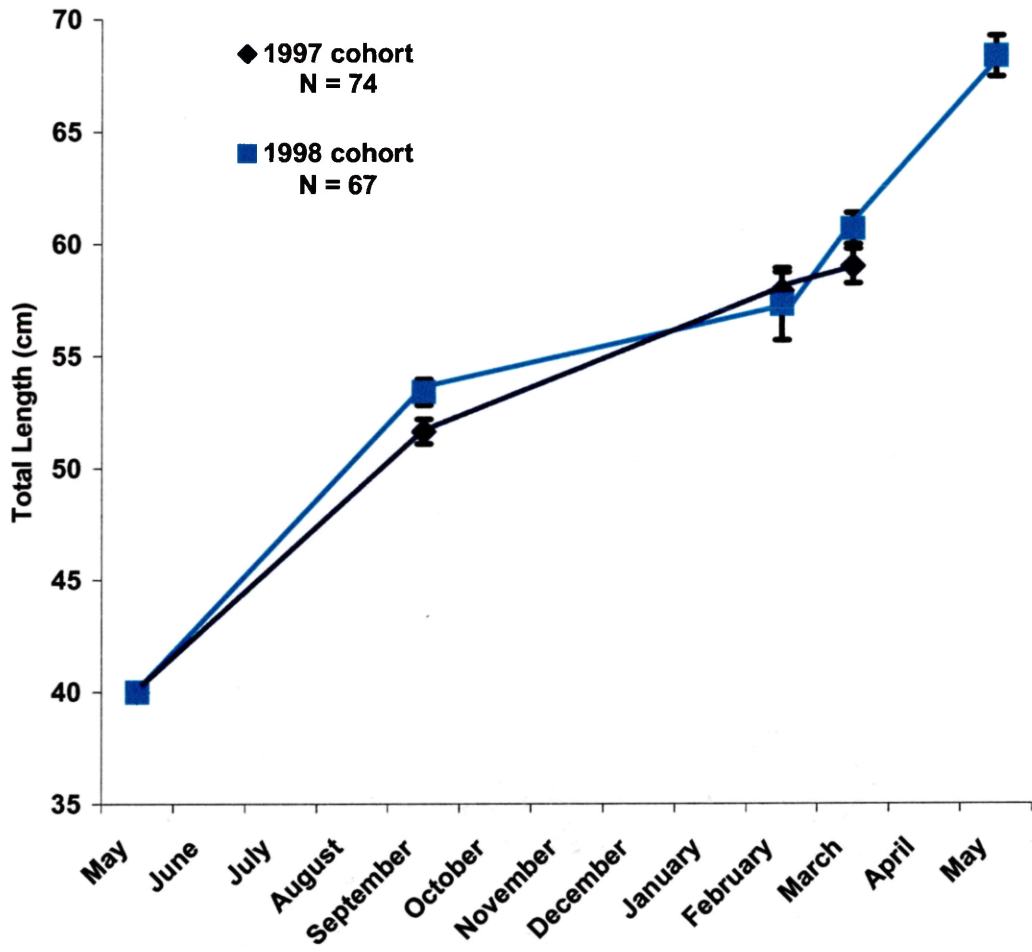


Table 1-2: Percent agreement between reader one's ages and reader two's ages for each ten cm size group, PA = percent agreement.

Size Group	Total read	# Agree	# Agree +/- 1	PA	PA +/- 1 year
33-42 cm	9	9	9	100	100
43-52 cm	20	20	20	100	100
53-62 cm	20	20	20	100	100
63-72 cm	20	20	20	100	100
73-82 cm	19	16	19	84.21	100
83-92 cm	20	18	20	90	100
93-102 cm	20	15	20	75	100
103-112 cm	19	15	18	78.95	94.74
113-122 cm	19	13	18	68.42	94.74
123-132 cm	19	11	15	57.89	78.95
TOTAL	185	157	179	84.86	96.76

Ages were estimated for 531 female and 363 male smooth dogfish (Table 1-3 and Table 1-4). von Bertalanffy growth parameters were calculated separately for males and females due to the approximately 20 cm size difference in both maximum length and length at maturity (Chapter 2) for males and females. Female growth parameters (Figure 1-7) were $L_{\infty} = 123.57$ cm, $K = 0.2919$ y^{-1} , and $t_0 = -1.9432$ years (Table 1-5). The largest female was 132 cm TL and females were found (see Ch 2) to mature at 102 cm TL and 4 to 5 years of age. Male growth parameters (Figure 1-7) were $L_{\infty} = 105.17$ cm, $K = 0.4399$ y^{-1} , and $t_0 = -1.5235$ years (Table 1-5). The largest male in the study was 112 cm TL and males were found to mature at 85 cm TL and 2 to 3 years of age.

DISCUSSION

Marginal increment analysis, precision estimates, and seasonal growth patterns justify the use of vertebrae as an aging tool for the North Atlantic population of smooth dogfish. The marginal increment analysis only included animals of length less than or equal to the length of 50% maturity, therefore the annular nature of the growth bands was only verified for these length groups. Although the marginal widths of the largest animals in the population become too small to discern seasonal differences in these widths, this study assumes that these animals follow the same patterns of growth throughout their lifespan. The vertebrae of the older animals of this population were very difficult to read. The agreement within one year between two readers was high for all size groups (over 90%) with the exception of the largest (123-132 cm) size class. At this length it becomes very difficult to interpret the margin of the vertebrae and to distinguish between real growth bands and growth checks. Therefore the maximum age may be slightly older or

Table 1-3: Female age-length key, LG = size class (TL in cm), columns are ages 0 – 16.

LG	#	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
35-40	5	5																
41-45	4	4																
46-50	16	16																
51-55	26	26																
56-60	21	21																
61-65	18	13	5															
66-70	16	1	15															
71-75	15		12	3														
76-80	12		3	9														
81-85	24		3	19	2													
86-90	26			19	7													
91-95	25			5	16	4												
96-100	38				15	17	2	2	2									
101-105	36				2	18	11	3	1	1								
106-110	47				1	6	14	10	13	3	1	1						1
111-115	73						9	19	21	11	7	3	1		1	1		
116-120	61						3	9	16	7	9	5	4	3	3	0	0	2
121-125	47							4	5	7	4	8	10	5	2	1	1	
126-130	12								1	1	1	2		2	3	1	1	
131-135	3											1		2				

Table 1-4: Male age-length key, LG = size class (TL in cm), columns are age 0 – 10.

LG	#	0	1	2	3	4	5	6	7	8	9	10
31-35	3	3										
36-40	8	3										
41-45	8	8										
46-50	10	10										
51-55	30	30										
56-60	20	19	1									
61-65	13	7	6									
66-70	22	1	21									
71-75	20		18	2								
76-80	18		7	11								
81-85	28		2	20	5	1						
86-90	31			6	19	4	1	1				
91-95	49			4	25	11	5	3	1			
96-100	46				5	17	13	9	2			
101-105	41				1	5	15	10	7	1	2	
106-110	12						1	4	3	2	1	1
111-115	1							1				

Figure 1-7: von Bertalanffy growth curves for male and female *M. canis*.

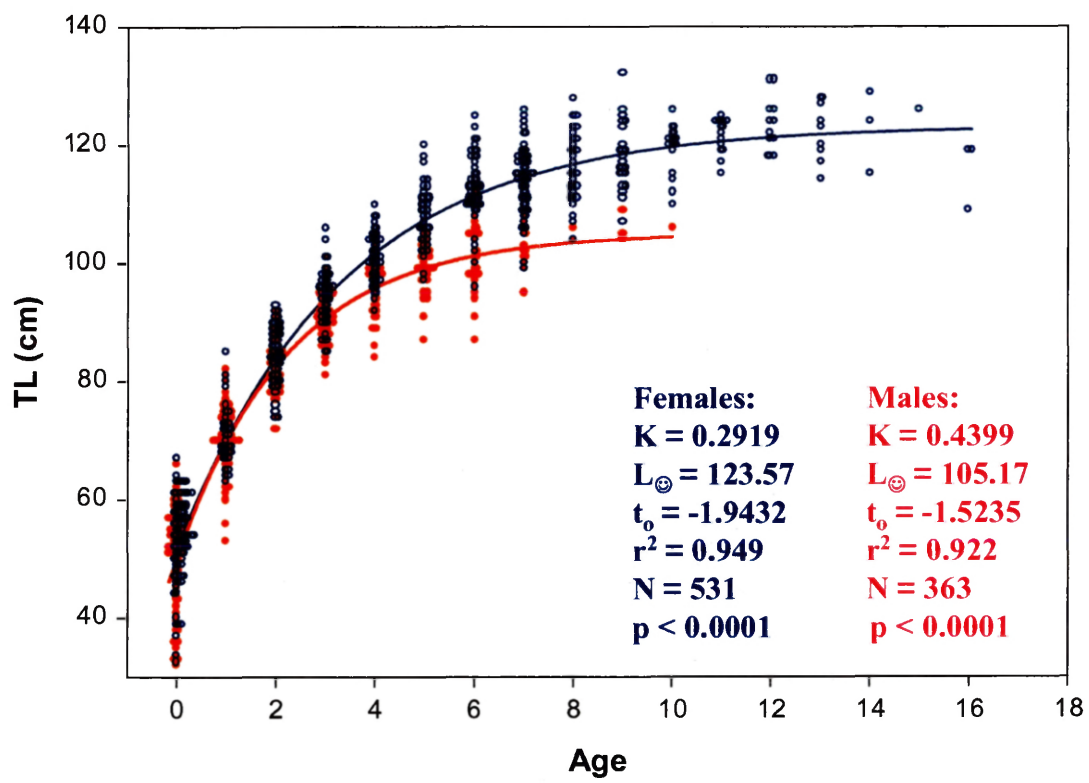


Table 1-5: von Bertalanffy growth parameters for *M. canis*, SE = standard error.

Parameter	Male	Female
L_{∞}	105.17	123.56
L_{∞} SE	1.0402	0.7353
K	0.4399	0.2919
K SE	0.0226	.0089
t_0	-1.5235	-1.9432
t_0 SE	0.0740	.0641
r^2	0.922	0.949
N	363	531
p	<0.0001	<0.0001

younger than the reported maximum of 16 years for females and 10 years for males.

Estimates of seasonal growth indicate that animals in this population experience a plateau in growth during the winter months, at least for the first two years of life. This would indicate that their major period of growth is during the summer between March and October, with a period of slow growth during the winter between October and February or March. This supports a yearly band deposition due to a cessation or slowing of growth. If these animals start to resume a faster growth rate after February or March, this would support the conclusion that a growth band becomes visible in the months of April or May after growth has resumed enough for it to be visible beyond the edge of the band.

Although smooth dogfish have been reported as large as 150 cm TL, the largest animal captured for this study was 132 cm TL, and 135 cm is probably a more reasonable maximum length for this population (Bigelow and Schroeder 1948). Bigelow and Schroeder's (1948) estimate seems to have come from a rough estimate that these animals reach a maximum of "about five feet." Records from over thirty years of the National Marine Fisheries Service, North East Fisheries Science Center biyearly groundfish surveys indicate they have caught only six smooth dogfish over 135 cm. The oldest male and female aged using vertebrae in this study were 10 and 16 years old, respectively. von Bertalanffy growth parameters are considerably different for males and females as are size and ages at maturity.

Moss (1972) constructed von Bertalanffy growth curves for smooth dogfish by relating tooth width to body length. He estimated that smooth dogfish mature after about one year, and reach their maximum size in 7-8 years. He acknowledged that his

estimated growth curve did not account for variation in tooth replacement rate and seasonal differences in body growth rate. Francis (1981) estimated von Bertalanffy growth rates by extrapolation from embryonic growth rates using Holden's (1974) method. This method has subsequently been discredited by Pratt and Casey (1990) who determined that this method does not work well for sharks. Rountree and Able (1996) used length-frequency analysis to determine growth rates in young of the year (YOY) smooth dogfish. They suggested that YOY animals are born in May at 29-38 cm TL and reach 55-70cm TL by October of the same year. Our study indicates NA smooth dogfish are not growing that quickly, with animals growing to an mean of 66.5 cm TL in their entire first year of growth (mean size of estimated Age-1 May captures, $N = 13$, $SE = 0.924$).

Values of K reported from various *Mustelus* species (Table 1-6) range from 0.1 for male *Mustelus lenticulatus* from Pegasus Bay, New Zealand to 0.695 for male *Mustelus manazo*, and from 0.049 for female *Mustelus antarcticus* to 0.42 for female *Mustelus lenticulatus* from Hauraki Gulf, New Zealand (Yudin and Cailliet 1990; Tanaka and Mizue 1979; Yamaguchi et al., 1996; Francis and Francis 1992; Moulton et al., 1992; Goosen and Smale 1997). Smooth dogfish growth coefficients are at the high end of this range with $K = 0.4399$ for males and $K = 0.2919$ for females. Mean asymptotic length (L_{∞}) of *M. canis* is in the middle of the range of L_{∞} values for *Mustelus* species, with L_{∞} values ranging from $L_{\infty} = 71.4$, and 88.6 cm for male and female *M. manazo* (Tanaka and Mizue 1979) to $L_{\infty} = 155.9$ and 233.6 cm for male and female *M. antarcticus* (Moulton et al., 1992). *M. canis* grows very quickly to its maximum length in comparison to other

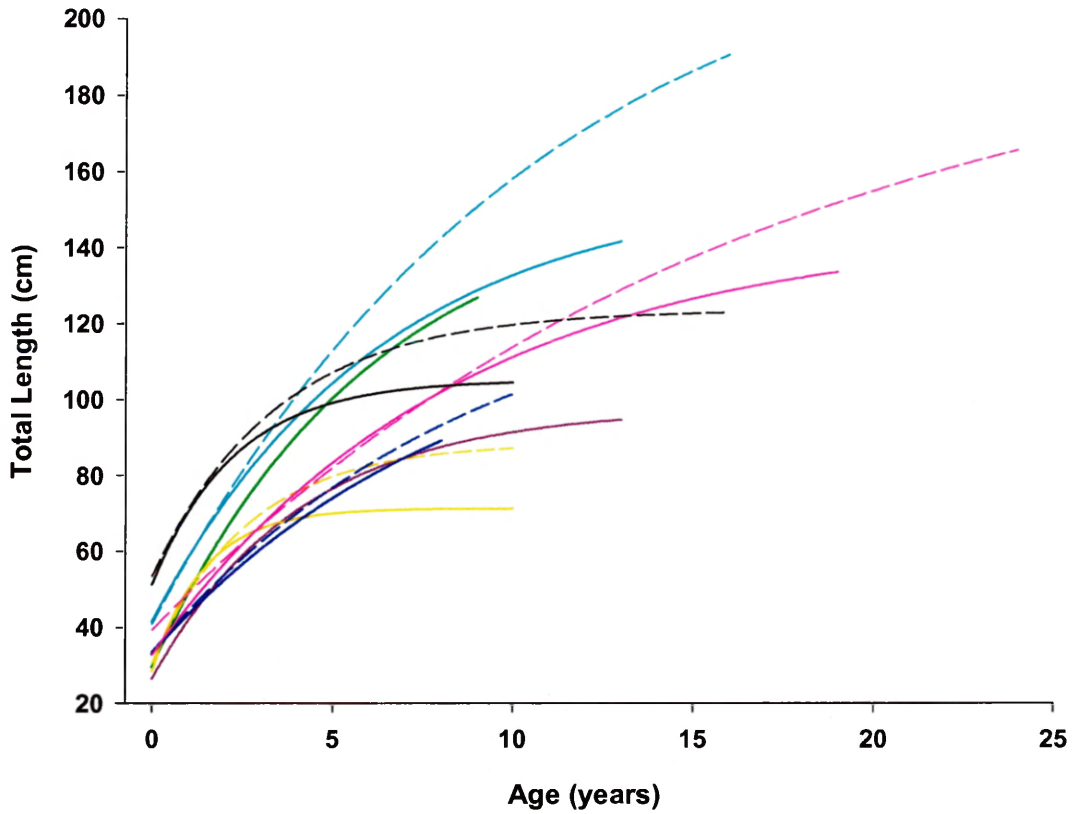
Table 1-6: Age and growth parameters for *Mustelus* species.

Species	Sex	K	L_{∞}	t_0	Age at maturity	Reference
<i>M. californicus</i>	M+F	0.168	154.4	-1.271	1-4 years	Yudin and Cailliet (1990)
<i>M. henlei</i>	M+F	0.244	97.7	-1.296	1-4 years	Yudin and Cailliet (1990)
<i>M. manazo</i>	M	0.695	71.4	-0.734	2-3 years	Tanaka and Mizue (1979)
	F	0.379	88.6	-1.113	2-3 years	Tanaka and Mizue (1979)
<i>M. manazo</i>	M	0.120	124.1	-2.59		Yamaguchi et al. (1996)
	F	0.113	134.1	-2.55		Yamaguchi et al. (1996)
<i>M. lenticulatus</i> PB	M	0.10			5 years	Francis and Francis (1992)
	F	0.40				
<i>M. lenticulatus</i> HG	M	0.16			3.7 years	Francis and Francis (1992)
	F	0.42			4.7 years	
<i>M. antarcticus</i>	M	0.160	155.9	-1.94		Moulton et al. (1992)
	F	0.094	233.6	-2.05		
<i>M. mustelus</i>	M	0.12	1451	-2.14	6-9 years	Goosen and Smale (1997)
	F	0.06	2049	-3.55	12-15 years	
<i>M. canis</i>	M	0.440	105.17	-1.524	3 years	Present study
	F	0.292	123.57	-1.943	4-5 years	

Mustelus species (Figure 1-8). As in almost all other reported *Mustelus* species age and growth accounts, we found male and female growth is virtually identical for their first few years, with males having a faster growth rate due to a plateau in growth at a much smaller size than females (Figure 1-8). However, Francis and Francis (1992) found that female rig (*M. lenticulatus*) grow faster than males but still reach a larger maximum length. Their estimates were based on length-frequency data and they state the lack of large females in their study may have affected their estimates of von Bertalanffy growth coefficients.

The growth coefficients for both male and female smooth dogfish are comparably high for a shark population with previously reported K values ranging from 0.038 for dusky sharks, *Carcharhinus obscurus* (Natanson et al., 1993) to 1.337 for male Australian sharpnose sharks, *Rhizoprionodon taylori* (Simpfendorfer 1993). Smooth dogfish grow very quickly for a shark species and they mature at a relatively young age. These characteristics may make this population more productive and possibly more resilient to exploitation than many other shark populations.

Figure 1-8: von Bertalanffy growth curves of *Mustelus* species.



- *M. californicus* - both sexes (Yudin and Cailliet)
- *M. henlei* - both sexes (Yudin and Cailliet 1990)
- *M. manazo* - male (Tanaka and Mizue 1979)
- - - *M. manazo* - female (Tanaka and Mizue 1979)
- *M. manazo* - male (Yamaguchi et al. 1996)
- - - *M. manazo* - female (Yamaguchi et al. 1996)
- *M. mustelus* - male (Goosen and Smale 1997)
- - - *M. mustelus* - female (Goosen and Smale 1997)
- *M. antarcticus* - male (Moulton et al. 1992)
- - - *M. antarcticus* - female (Moulton et al. 1992)
- *M. canis* - male, present study
- - - *M. canis* - female, present study

Chapter 2

Reproductive Biology of *Mustelus canis*

INTRODUCTION

Increased fishing pressure on the smooth dogfish since 1990 has increased the need for more information about their reproductive biology. It is necessary to know the lengths and ages at maturity, and estimate fecundity of the population to understand how the population will respond to this increased mortality. 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 the population that could be harvested.

Many techniques have been developed for determining the reproductive parameters of elasmobranchs. Size at maturity for both males and females has been determined by comparing the growth of secondary sex characters with body growth, as there is often an increase in the development of these characters as the animals become mature. Waas (1973) estimated size at maturity in male sandbar sharks, *Carcharhinus milberti*, by plotting clasper length and calcification versus precaudal length. He also used the width of the uterus to determine sexual maturity in females. For males, direct observation of sperm in the reproductive tract is also useful in determining the size at

maturity. Pratt (1979) determined size at maturity in blue sharks by cutting open the kidney, and noting the presence or absence of sperm in the ampulla ductus deferens. For females, maturity is often determined by assessing the condition of the reproductive tract. Jones and Geen (1977) defined maturity in female spiny dogfish, *Squalus acanthias*, using the size of ovarian eggs, the size and condition of the uterus, as well as the presence of candles or embryos in the uterus. They graphed the percent of mature females at each length and defined the length at maturity to be the length when 50% of the animals were mature.

The timing of the reproductive cycle in male elasmobranchs is commonly determined by using a gonadosomatic index (GSI), noting the presence of sperm products in the reproductive tract, or through histological examination of the testes. Parsons (1983) took sperm smears from male Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, and used those in combination with a GSI to define mating season. Simpfendorfer (1992) estimated the timing of the mating period by noting the presence of large quantities of spermatozoa in the ductus epididymis of Australian sharpnose sharks, *Rhizoprionodon taylori*. Jones and Geen (1977) histologically examined the testes of male spiny dogfish, *Squalus acanthias*, and determined the percent of ampullae containing each spermatogenic stage, and used this to define maturity and to determine the reproductive cycle.

In female elasmobranchs the timing of reproductive events is usually determined by direct observations of the reproductive tract, and or the development of ovarian eggs. The timing of ovulation and the periodicity of the reproductive cycle can be studied by

comparing ova diameters and the growth of pups within the uterus throughout the year. Capape et al. (1990) studied two angel shark species and plotted the diameter of oocytes and uterine ova against time to determine the timing of reproductive events.

The storage of sperm in the oviduct has been shown by Pratt (1993) to occur in at least nine species of elasmobranchs. He histologically examined stained oviducal glands to see if sperm was present. In a previous paper, Pratt (1979) also proposed that sperm storage could be checked by taking a smear of the posterior one third of the oviducal gland.

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.

MATERIALS AND METHODS

Males:

Reproductive samples were collected at the same time that vertebrae were collected. 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.

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 μ m 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 2-4). Stage one consisted 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 five 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 just after stage six, which consisted of empty spermatocysts, free spermatogonia, and free spermatozoa, rather than the area of the primary zone margin (between stages two and three). 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, or eggs or embryos present in the uteri, or expanded uteri indicating the previous presence of eggs or pups.

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 haematoxylin 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.

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 2-1). Based on clasper calcification the smallest mature male was 81 cm TL and the largest immature male was 97 cm TL. Clasper calcification was determined to be a good predictor of maturity as every histological section taken from males classified to be mature contained mature

sperm. A logistic plot of the proportion of mature males at two cm total length 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 can be solved to determine that 50% of males are mature at 86 cm TL (Figure 2-2). 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 2-3). The youngest mature male was two years and the oldest immature male was three years of age.

A cross section of the testis is shown in Figure 2-4, and the stages of the testis are shown in Figure 2-5 and Figure 2-6. A plot of the proportion of the stages of the testes indicate that during September through October the majority of the testes are primarily occupied by stage 3: the spermatocyte stage (Figure 2-7). This is also true of one animal sectioned from July, but due to the small sample size this is not conclusive. During November the majority of the testes are occupied primarily by stage 4, the spermatid stage. By March and continuing through May the majority of the testes are occupied by spermatocysts in stage 6, the mature sperm stage. Thus mating is most likely occurring between the months of May and September.

Figure 2-1: The relationship between clasper length (CL) and total length (TL) of *M. canis*.

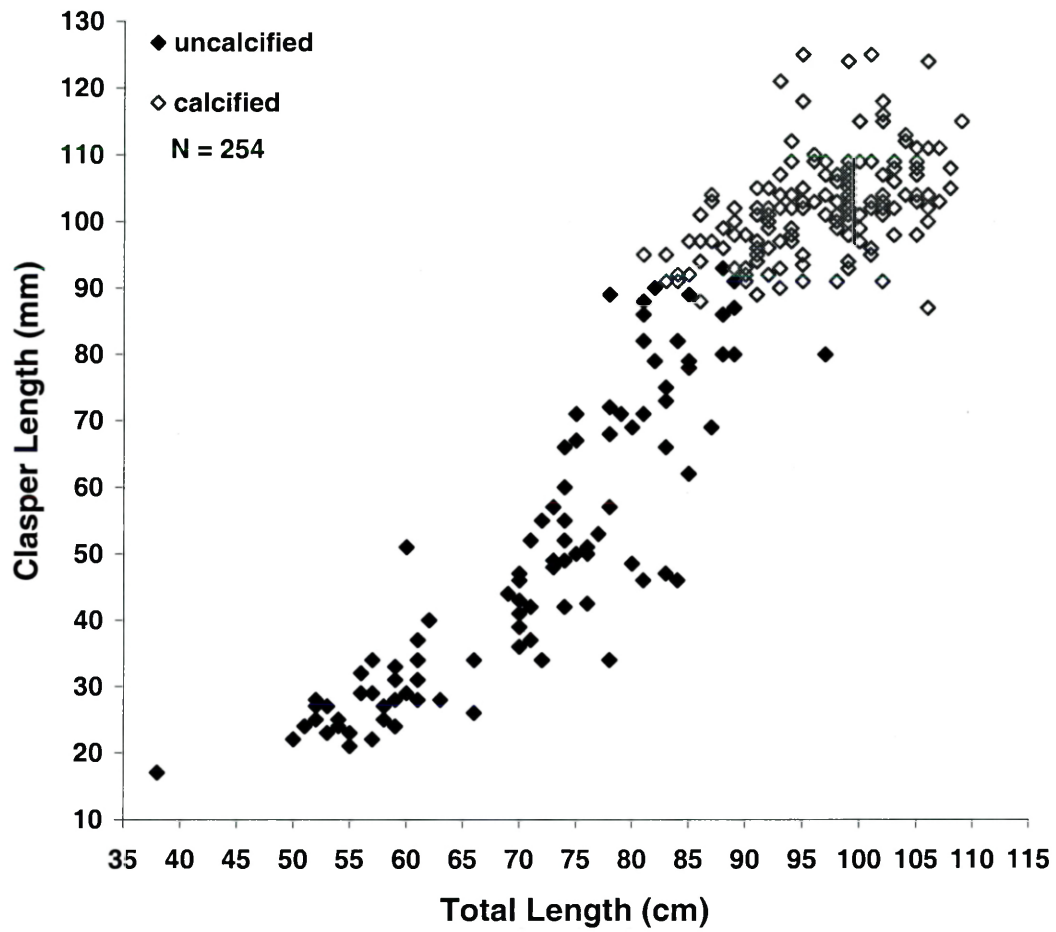


Figure 2-2: Maturity ogives for total length (TL) of male and female *M. canis*.

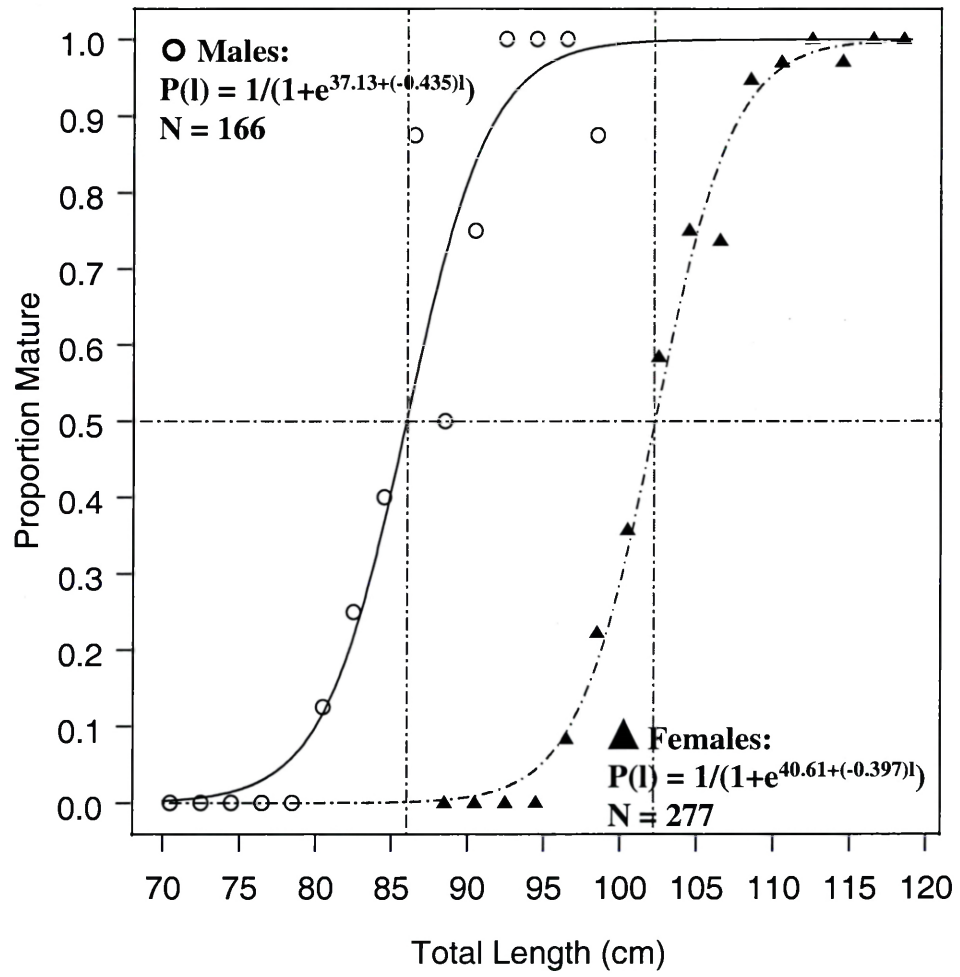


Figure 2-3: Maturity ogives for age of male and female *M. canis*.

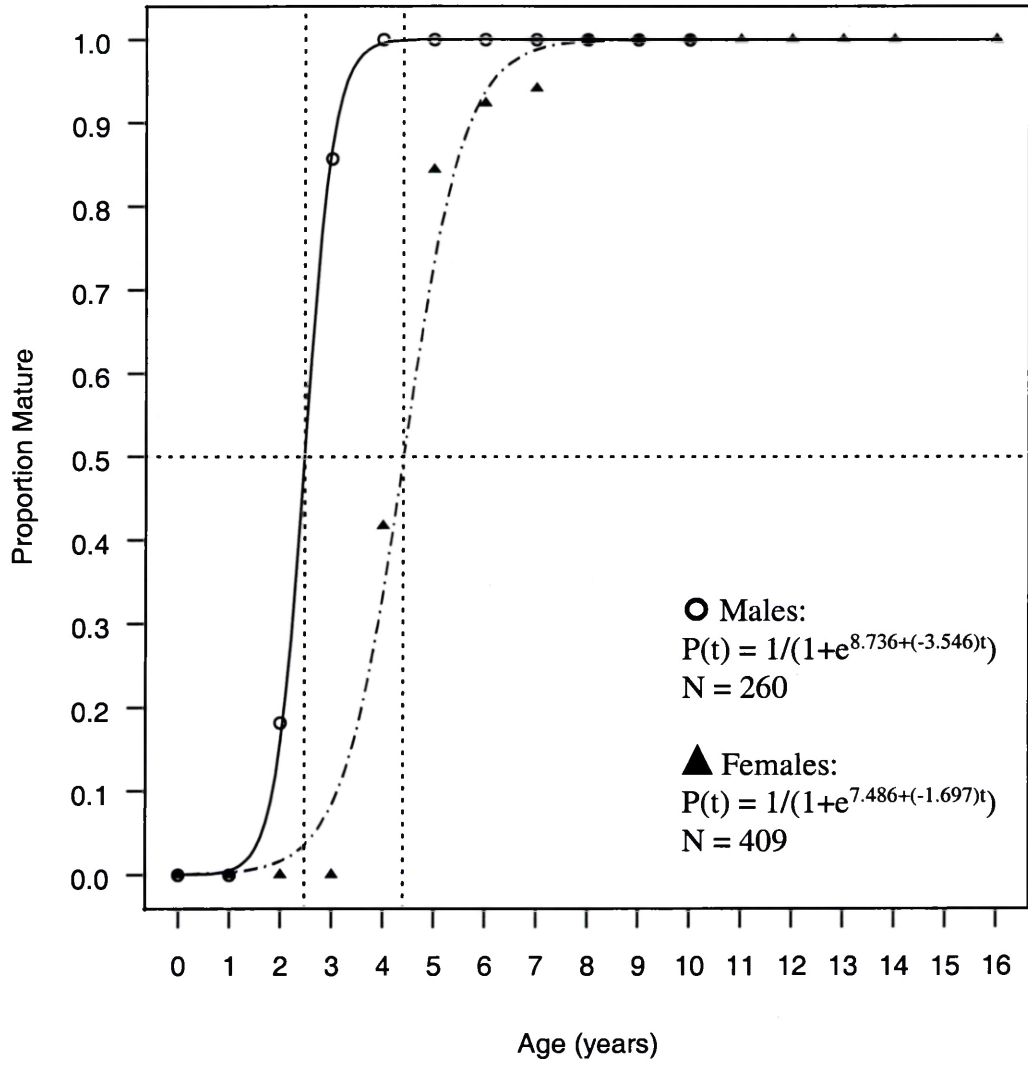


Figure 2-4: Cross section of a *M. canis* testis, stained with hematoxylin and eosin.

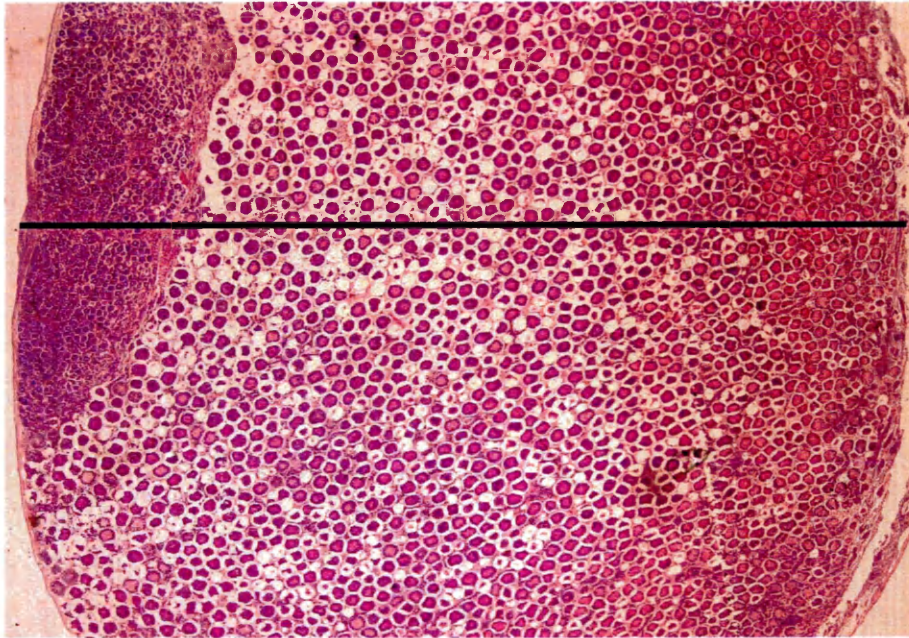
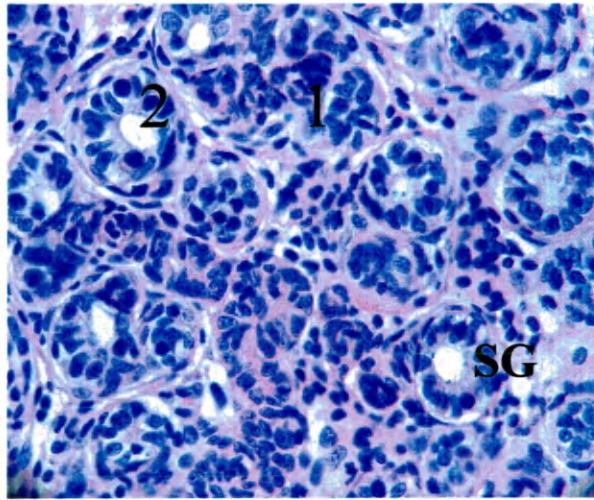
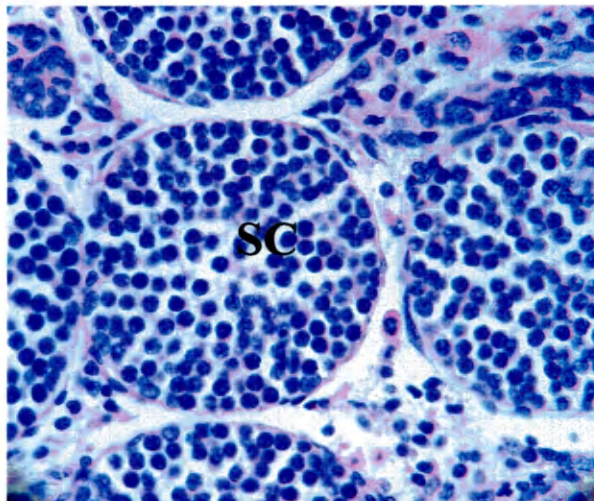


Figure 2-5: Sperm stages of the testis: Stages 1 – 4, SG = spermatogonia, SC = spermatocytes, ST = spermatids.

Stage 1 and 2



Stage 3



Stage 4

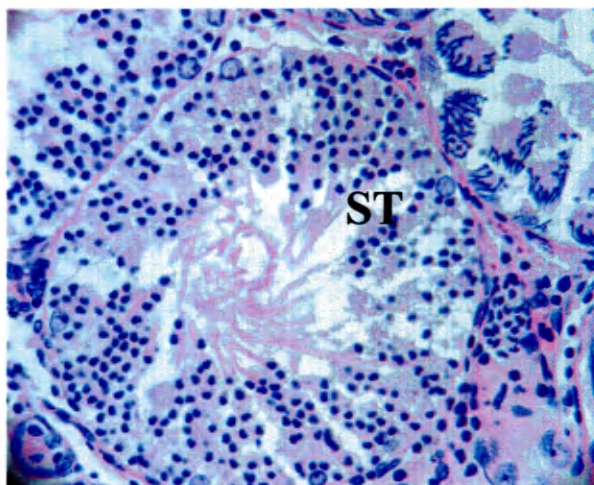
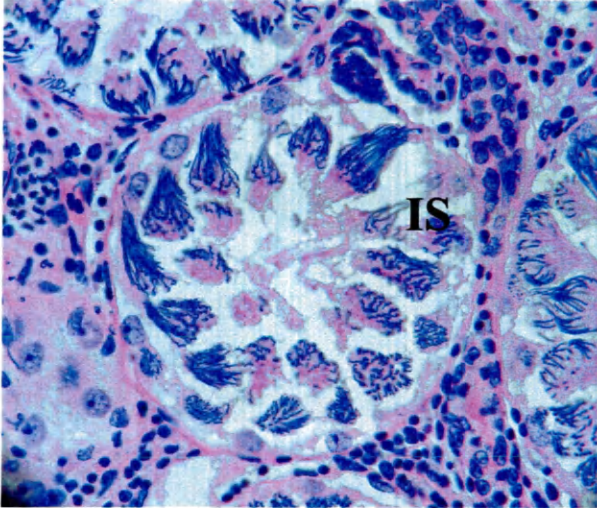
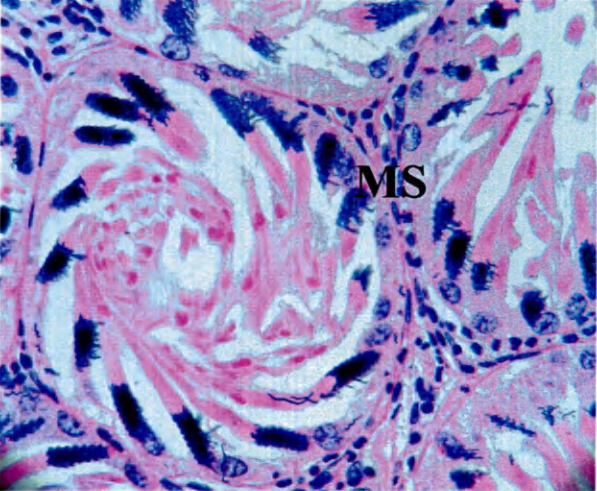


Figure 2-6: Sperm stages of the testis: Stages 5-7, IS = immature sperm, MS = mature spermatozoa, ES = empty spermatocyst, SG = spermatogonia.

Stage 5



Stage 6



Stage 7

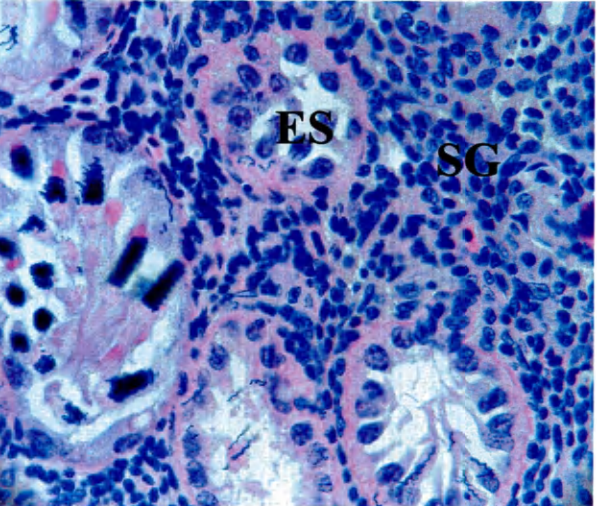
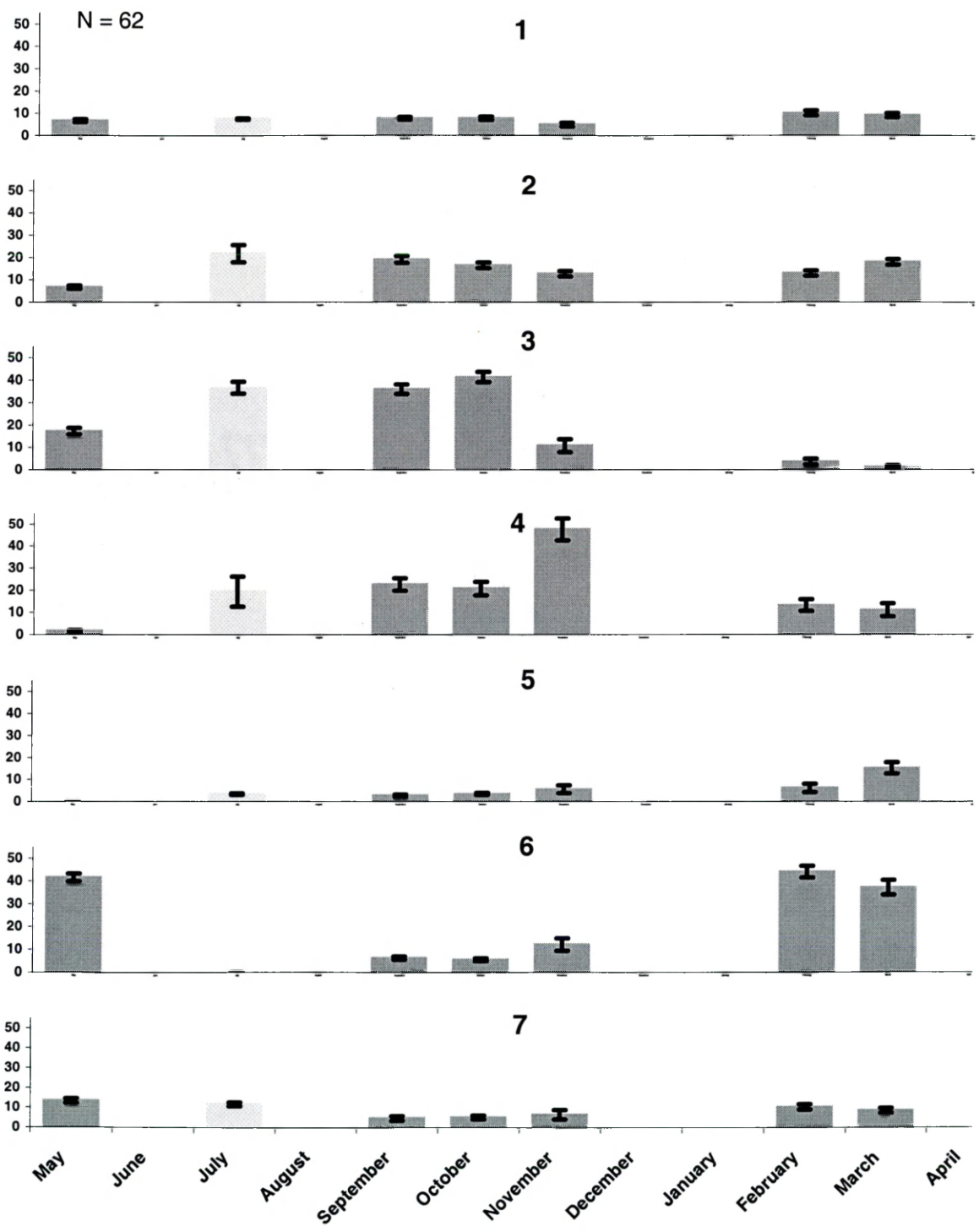


Figure 2-7: The mean proportion of the testis occupied by each stage for May through April (error bars are standard error).



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:

$$P(l) = 1/(1 + e^{40.61+(-.397)l})$$

where P(l) equals the proportion mature at length l, and l equals length. At a length 102 cm fifty percent of females were mature (Figure 2-2). 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 four years old and the oldest immature female was seven years old.

The fecundity of female smooth dogfish ranged from 3 to 18 pups with an average of 9.53 pups per litter. There is a positive linear relationship between the total length of the female and the number of pups (Figure 2-8):

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

($p < 0.001$ and $r^2 = 0.353$). A regression of fecundity versus age indicated the following significant positive exponential relationship between age and fecundity (Figure 2-9):

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

($p < 0.001$ 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

Figure 2-8: The relationship between fecundity (number of pups per litter) and total length (TL) of female *M. canis*.

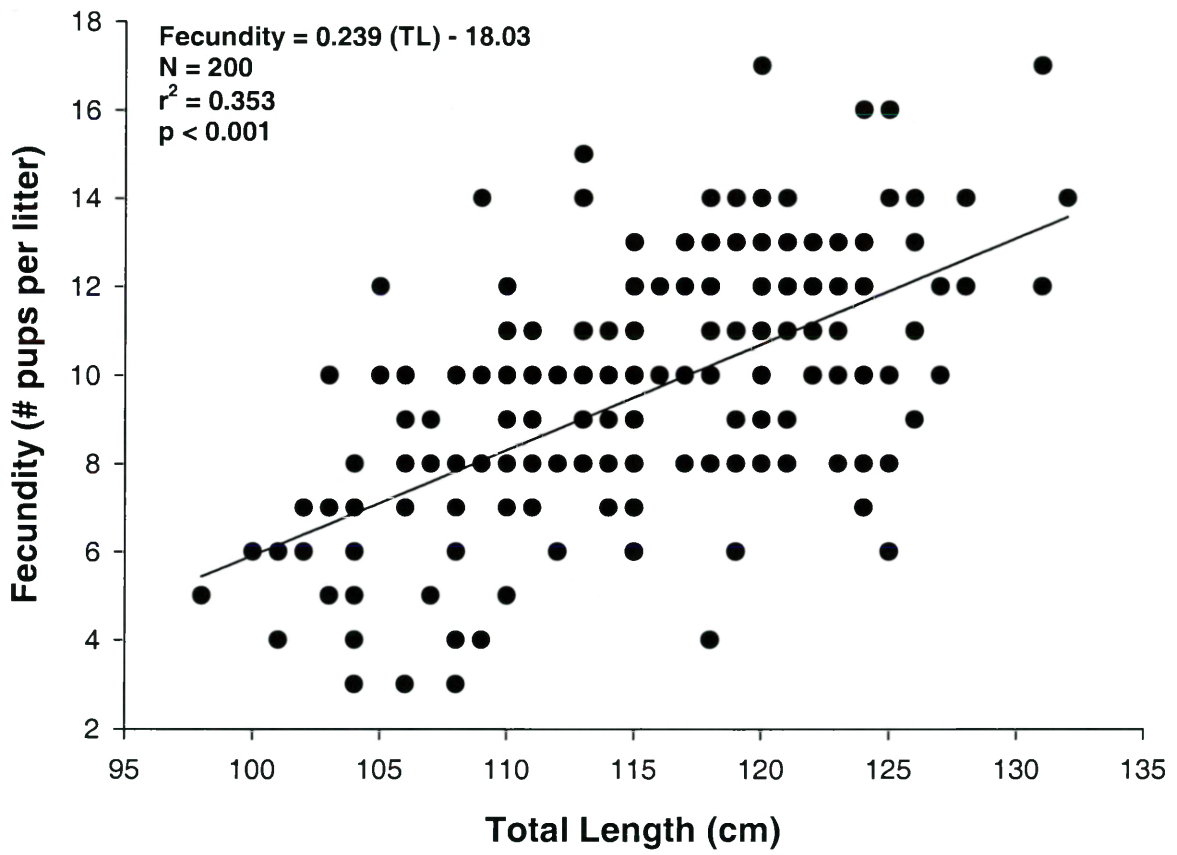
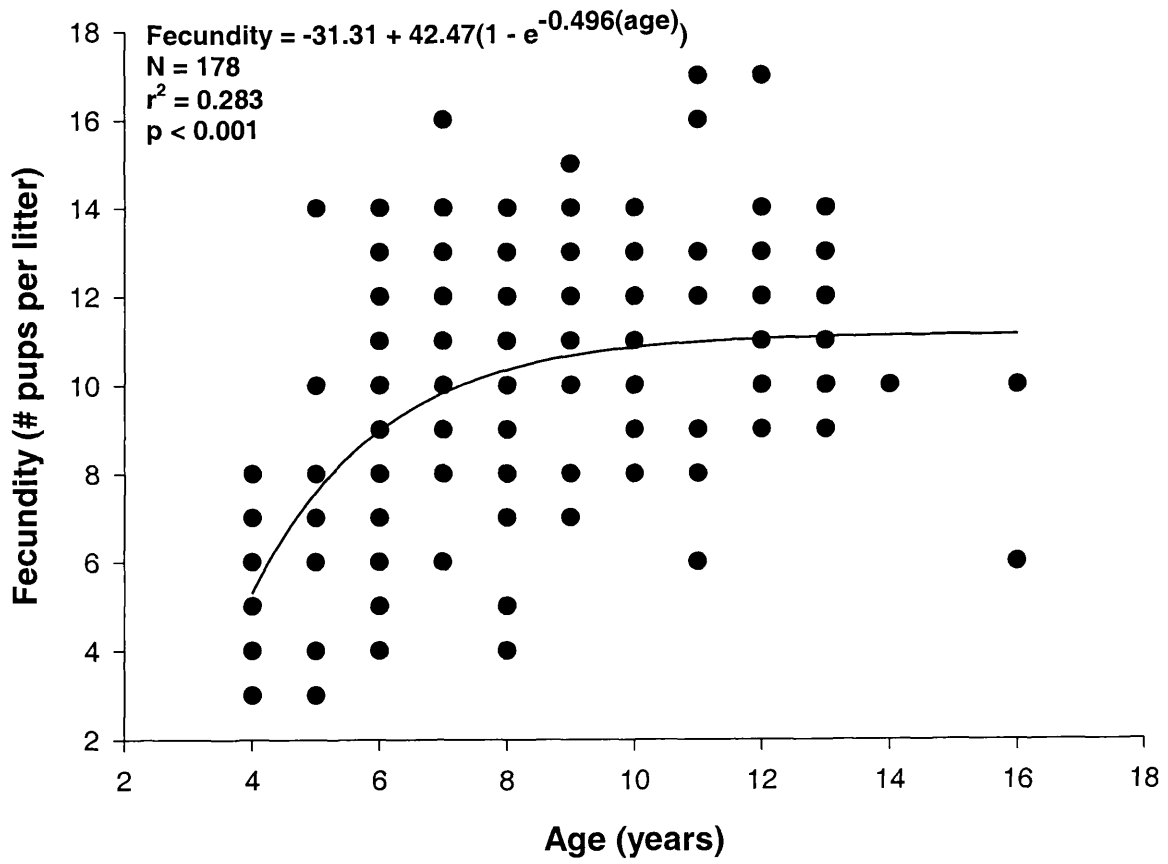


Figure 2-9: The relationship between fecundity (number of pups per litter) and age for female *M. canis*.



events occurring by the end of May or the beginning of June, perhaps with only a few weeks between parturition and mating. Ova increase in size until May and then become dramatically smaller by July (Figure 2-10). 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 to 12 month gestation. Pregnant females caught at the same time all had similar sized pups further indicating a short mating and ovulation period (Figure 2-11).

The embryos from near term animals in this study ranged in length from 30 - 39 cm TL and the smallest free living animals were 33 and 35 cm TL. Size at birth therefore likely ranges from 30 – 40 cm TL. There is a noticeable plateau in pup growth during the winter months (Figure 2-11).

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 2-12 shows a cross section of the posterior third of an oviducal gland from a smooth dogfish. Sperm was found within the terminal zone of all sectioned oviducal glands from each month (Figure 2-13).

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 one year based on an aging study using tooth replacement rates. Francis (1981) used Holden's

Figure 2-10: Mean maximum ova diameter (MOD), June through May (error bars are standard deviation).

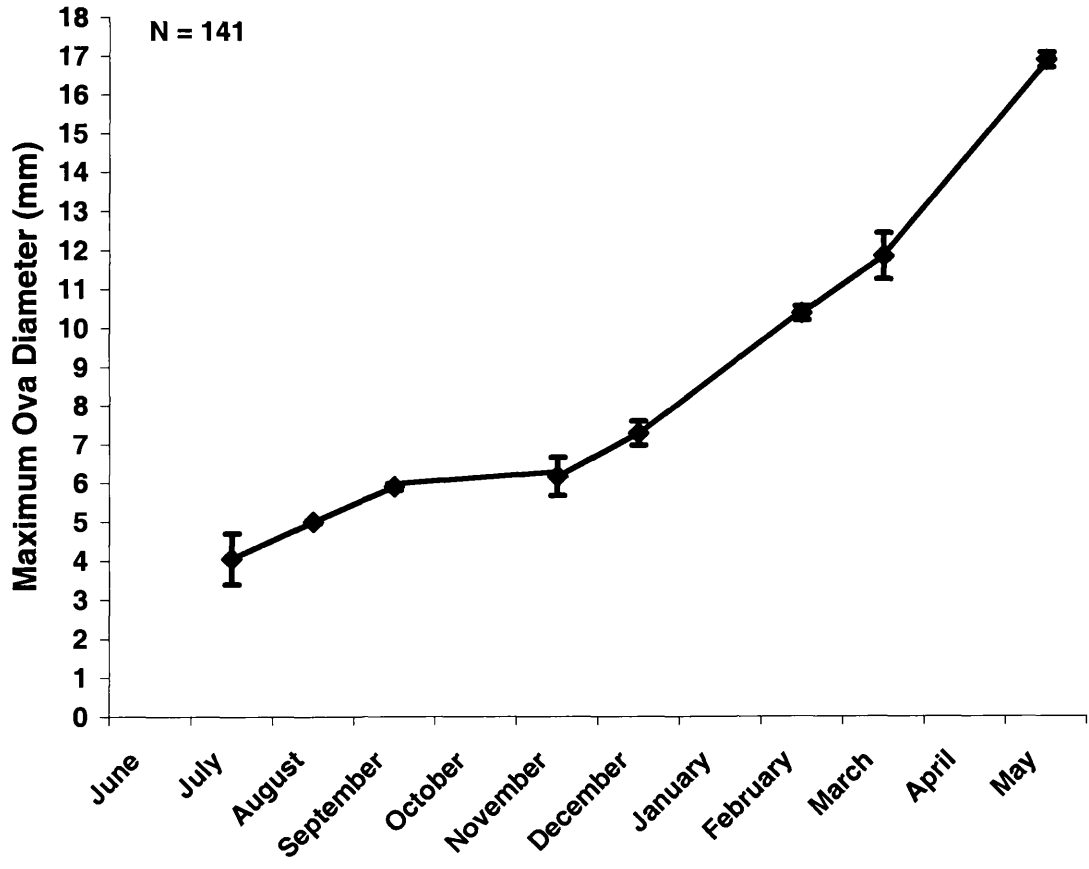


Figure 2-11: Mean *M. canis* pup length for May through April (error bars are standard deviation).

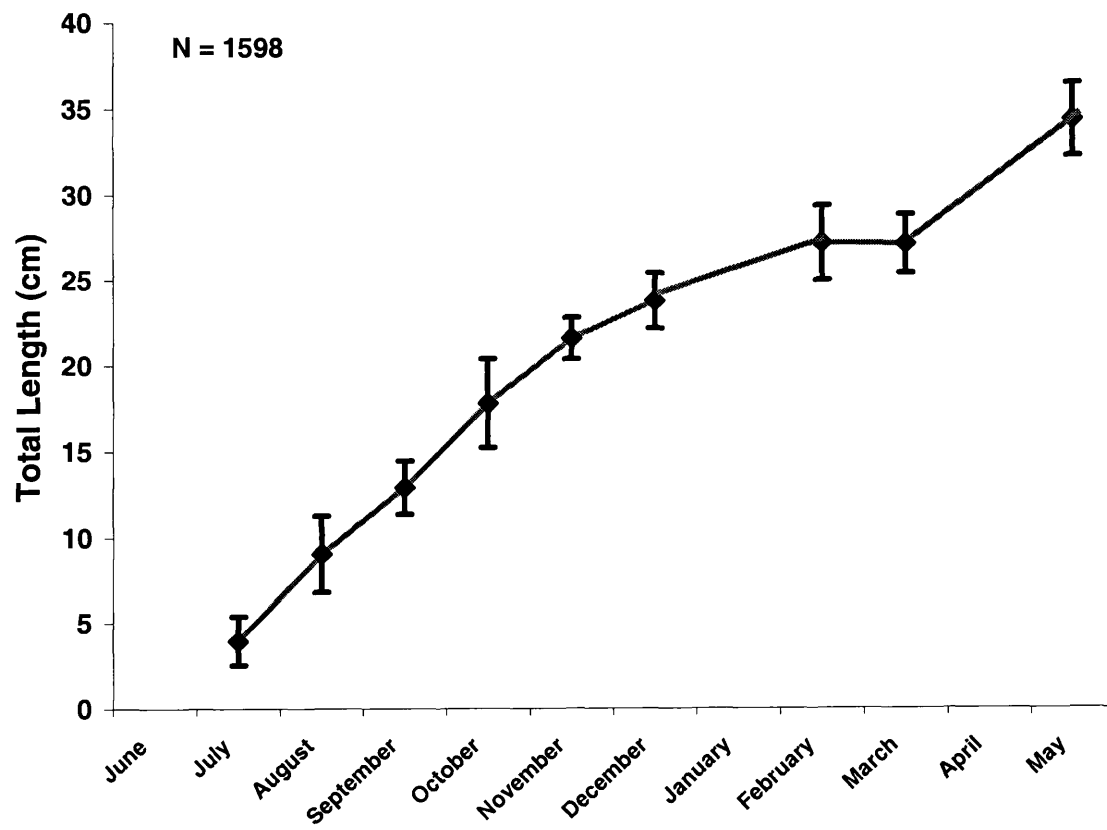


Figure 2-12: Cross section of the posterior third of a *M. canis* oviducal gland, S = sperm bundle.

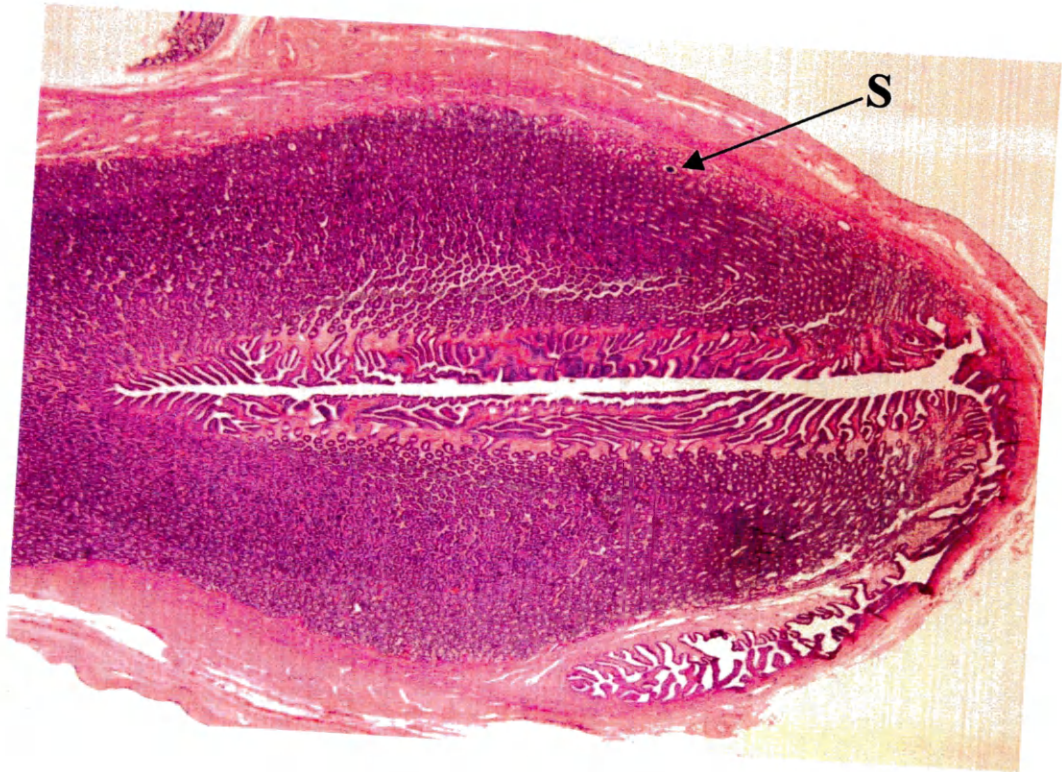
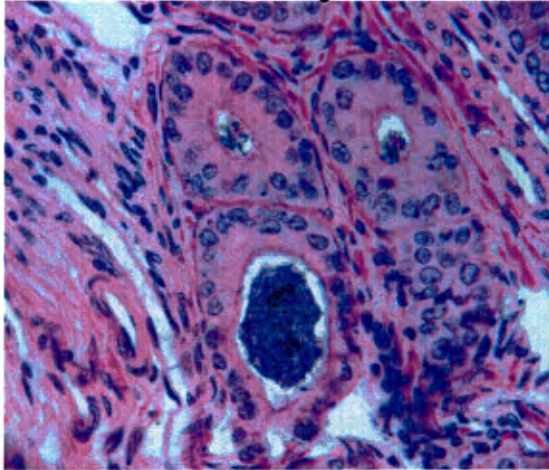
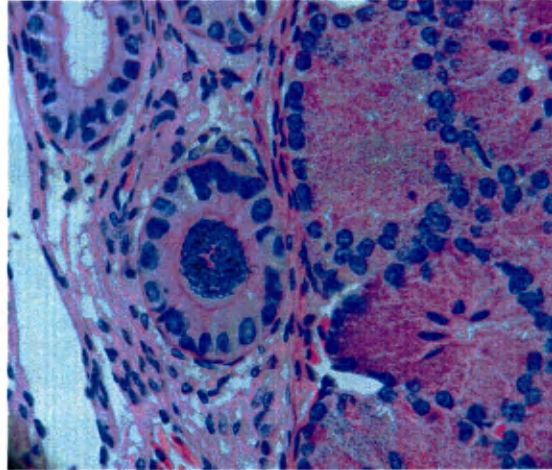


Figure 2-13: Sperm bundles found within the terminal zone of the oviducal gland from May, June, September, November, December, and March.

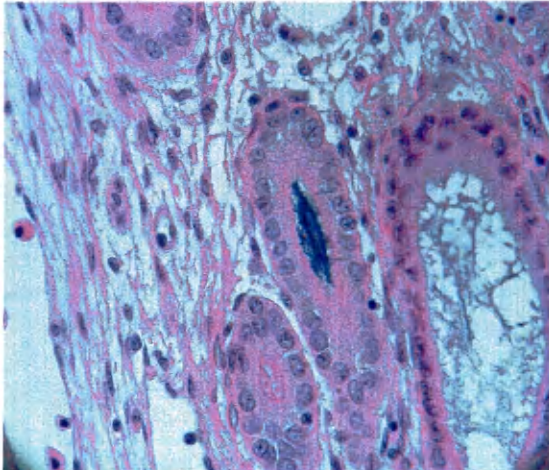
May



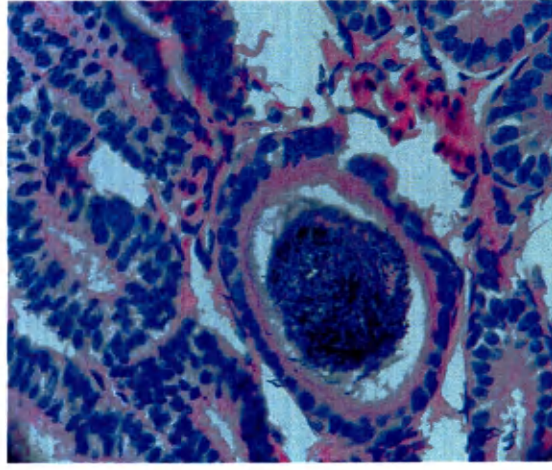
November



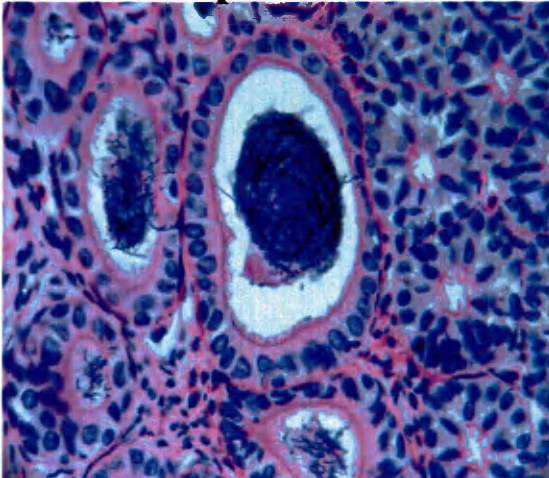
June



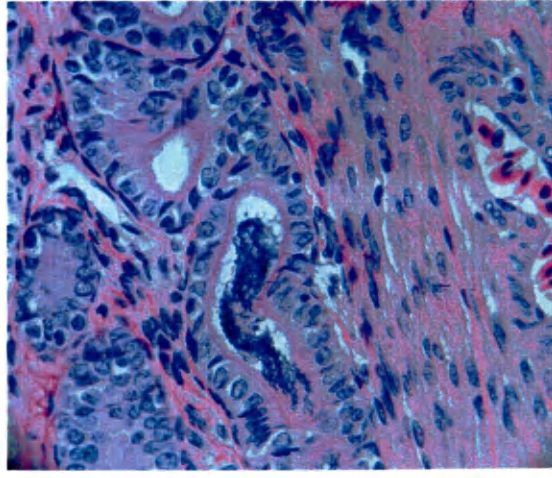
December



September



March



(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. As stated in chapter 1 this method has been discredited. The present study found the majority of males were not mature until three years old and the majority of females were not mature until five years old.

Reproductive biology has been studied for several species in the genus *Mustelus* (Table 2-1). Female lengths at maturity range from 70 to 130 cm TL (Francis and Mace 1980; Massey and Francis 1989; Lenanton et al., 1990; Teshima 1981; Taniuchi et al., 1983; and Yamaguchi et al., 1997). Male lengths at maturity range from 68 to 93 cm TL. The size at maturity of *Mustelus 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 cm 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 eleven to twelve month gestation, slightly

Table 2-1: Reproductive parameters of various *Mustelus* species, RCP = reproductive cycle periodicity, F/S R = fecundity size relationship.

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

longer than 10-month gestation suggested by other authors (Bigelow and 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 occurs at a rate of two ova ovulated followed by 30 – 40 hours 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 2-1).

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 – 18 animals. Compagno (1984) reported litter size between 4 – 20 animals with an average of 10 pups per litter. Our estimates of size at birth from 30 – 40 cm TL are in close agreement with those published in the species accounts, 34 – 39 cm TL (Bigelow and Schroeder 1948) and a paper on first year growth of smooth dogfish, 28 – 39 cm TL (Rountree and 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 curve line closely and indicating that neither age nor 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 showed an exponential relationship between fecundity and total length (Table 2-1). The number of pups for *Mustelus* species ranges from 1- 31. The smooth dogfish falls within this range with 3 – 20 pups per litter.

Mustelus pups generally range in size from 20 – 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 and 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.

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.

Smooth dogfish apparently store sperm in the lower one third of their oviducal gland throughout the year. Teshima (1981) observed that a specimen of *M. manazo* had spermatozoa present in the oviducal gland eight months after their proposed mating season. Hamlett (1998) found sperm bundles in the posterior portion of the smooth

dogfish oviducal gland. Pratt (1993) examined eleven species of sharks and found some sperm storage in nine of these species. He proposed there were three types of sperm storage: one that was not storage at all; short-term storage, where fertilization is delayed; and long-term storage for possibly repeated insemination. Hamlett (1998) noted that both his and Pratt's (1993) studies of sperm storage indicate that sperm is found in the posterior, terminal zone of the oviducal gland. This is problematic because fertilization is thought to occur anterior to this, in the baffle zone, so the sperm would have to move up the gland in order to inseminate the ova. He suggested 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* (Hamlett, personal communication).

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 has a comparatively high productivity and may be more able to support a directed commercial fishery than many other shark species.

Chapter 3

Demographic Analysis of the North Atlantic population of *Mustelus canis*

INTRODUCTION

A life table is a summation of mortality and fecundity estimates to determine if a population will increase or decrease. Krebs (1985) presented a method for constructing a life table using the following columns, x (age), l_x (age specific survivorship), b_x (age specific fecundity), $l_x b_x$ (age specific survivorship multiplied by age specific fecundity), and $x l_x b_x$ (age multiplied by the $l_x b_x$ column). The net reproductive rate (R_0) represents the number of daughters born in a generation divided by the number of daughters born in the previous generation, and is calculated by summing the values in the $l_x b_x$ column. The mean generation length (G) is the mean period elapsing between the birth of the parents and the birth of the offspring, and is calculated by summing the $x l_x b_x$ column and dividing by R_0 . The instantaneous rate of increase in numbers (r) is calculated from the equation:

$$r = \ln(R_0)/G.$$

The population doubling (t_2) or halving time ($t_{1/2}$) is calculated from the instantaneous rate of increase using the equations:

$$t_2 = \ln 2/r \text{ or } t_{1/2} = \ln 0.5/r.$$

This form of life table has been used in several elasmobranch demography papers (Cortes 1995; Cailliet 1992; Sminkey and Musick 1996; Cailliet et al., 1992)

In order to determine the age specific survival (l_x) it is necessary to estimate natural mortality at each age. Several methods for estimating natural mortality have been published, including several methods of estimation based on life history parameters and a method using catch curve analysis. Hoenig (1983) calculated a relationship between maximum age and total mortality (Z) which is equal to M in an unexploited or lightly exploited population, according to the following equation:

$$\ln(Z) = 1.44 - 0.982 \ln(\text{maximum age})$$

Pauly (1979) determined a relationship relating M to environmental temperature and growth parameters following the equation:

$$M = -0.0066 - 0.279 \log L_{\infty} + 0.6543 \log K + 0.4634 \log T$$

where K and L_{∞} are growth parameters from the von Bertalanffy growth function and T is the mean environmental temperature. Chen and Watanabe (1989) estimate M using the relationship between mortality and growth during the stable phase of growth following the relationship:

$$M(t, t+\Delta) = 1/\Delta (e^{K(t+\Delta)} - e^{Kt_0}) / (e^{Kt} - e^{Kt_0})$$

where $t+\Delta$ is a unit of time, K, and t_0 are from the Von Bertalanffy growth function.

Peterson and Wroblewski (1984) derived an equation for determining mortality based a biomass density function, a growth function, and a mortality function. . The relationship they published was:

$$M = 1.92W^{-0.25}$$

where W = biomass of the animal in grams. Their method was published for use with pelagic animals, but McGurk (1986) found that this relationship works for 16 orders of magnitude of size of fish. Myers and Doyle (1983) used the evolutionary constraints on

fish life histories to estimate natural mortality. Their calculation requires growth rates over the life span, fecundity estimated over the life span, an estimate of the energy contents of eggs, and an estimate of age and size at sexual maturity as well as surplus energy estimates. Catch curves are also used to estimate natural mortality according to the equation:

$$\log(\text{catch}) = b - Z(\text{age})$$

where Z = mortality, and b is a constant (Hilborn and Walters 1992). The log of the catch can be plotted against age and a simple linear regression performed to determine the slope of the equation which estimates total mortality.

The survivorship can be calculated from the total mortality rate using the equation:

$$S = e^{-Z},$$

where S = survivorship and Z = total natural mortality. The total mortality Z is calculated by adding the natural mortality (M) and the fishing mortality (F).

The above estimators of M assume that natural mortality is constant over the life of the animal, except for the Peterson and Wroblewski (1984) method estimate which varies with the weight of the animal. First year survivorship however is likely to be higher as the animals are smaller and more vulnerable to predation and can be estimated by assuming an initially stable population and solving for first year survivorship using the mortality estimates calculated above. The first year survivorship (S_0) can be calculated according to the following relationship:

$$S_0 = 1 / \left(b_1 + \sum_{x=1}^{I-1} \left[b_{x+1} \prod_{j=1}^x S_j \right] \right)$$

where b_x is the fecundity at age x , S_j is the survival at age j , and I is the maximum age.

No population modeling has been done to predict how the North Atlantic population of smooth dogfish will respond to recent increases in fishing pressure, and what level of fishing mortality can be sustained to maintain a stable population of smooth dogfish. The objective of this study was to estimate natural mortality parameters and construct a life table using the previously determined age, growth, and reproductive parameters (Krebbs 1985). This life table will then be used to examine how different levels of fishing mortality and ages of entry into the fishery affect the population, including compensatory changes in juvenile natural mortality.

MATERIALS AND METHODS

A life table following Krebs (1985) was constructed to determine the net reproductive rate (R_0), the mean generation length (G), and the population's instantaneous rate of change (r). Natural mortality was estimated using four published relationships: 1. Hoenig (1983), 2. Pauly (1979), 3. Chen and Watanabe (1989), and 4. Peterson and Wroblewski (1984), and by creating catch curves from catch records of female smooth dogfish from the NMFS North East Fisheries Service Center fall groundfish surveys. Survivorship for ages 1-16 was calculated using these natural mortality estimates and assuming initial fishing mortality is negligible. First year survivorship was calculated from these survivorship estimates, the age specific fecundities (discussed below), and by assuming the population is initially stable ($r=0$).

The l_x column of the life table is the age specific survivorship and was calculated by multiplying the proportion surviving in the previous year by the survivorship of the present year. The b_x column is the expected number of female offspring per female living to year x . Fecundity was calculated from the relationship of fecundity to age from chapter 2 and then dividing the number of pups by two to determine the number of female pups per female. This number was then divided by the proportion mature in the previous year (from Chapter 2 ogive) to determine the age specific fecundity.

The survivorship function in the life table was altered by adding fishing mortality to the total mortality at different ages of entry into the population to determine how the parameters R_0 , G , and r change. Trials were run by adding $F = 0.1, 0.2, 0.3,$ and 0.5 starting at age 0 and at age 5 for each of the following scenarios. Since we are beginning with a stable population where $r = 0$ it is necessary to assume some level of compensation will occur in response to this additional mortality. Three different compensatory scenarios were examined: 1) a “best case scenario” where juvenile M was set equal to the estimate M of the adult population, 2) a “worst case scenario” where first year M decreased by 25 % , and 3) an “intermediate case scenario” where first year M decreased by 50% .

Another set of analysis was run to determine how sensitive the out put parameters (R_0 , G , and r) of the life table were to estimates of first year survivorship (S_0), natural mortality (M), and maximum age (t_{max}). Sensitivity were run by halving and doubling estimated S_0 , using the lowest and highest estimates of M , and by adding and subtracting five years from the maximum age ($t_{max} = 11,$ and 21 years). In order to examine how differing methods of compensation would affect the output parameters, we ran a set of

trials lowering the age at maturity by one and two years, and increasing fecundity by $\frac{1}{2}$ female pup per year and by 1 female pup per year.

RESULTS

Natural mortality estimates from the five methods ranged from 0.15 to 0.53 (Table 3-1). In order to obtain a temperature estimate for the Pauly calculation, a range of bottom temperatures were obtained from the North East Fisheries Service Center (NEFSC) NMFS groundfish survey smooth dogfish catch locations from March (winter grounds) and September (summer grounds). The bottom temperatures of catch locations ranged from 5 – 27 ° C. Smooth dogfish occupy a large range of temperatures and this results in a large range of mortality values using the Pauly equation. The catch curve mortality values were very small and may have been confounded by sexual and size segregation of these animals, as well as their progress on their migration south into their winter grounds. Since it was difficult to determine the average temperature of the population and due to the problems with the catch curves the remaining three estimators of M were used in our demographic analysis. Mortality estimates calculated using the Hoenig (1983) estimate, the Peterson and Wroblewski (1984) estimates, and the Chen and Watanabe estimate (1989) were used to determine first year survivorship.

First year survivorship (S_0) was calculated assuming a stable population $r = 0$, and a constant M of 0.28, 0.31, and the range of mortalities from age 1-16 determined using the Peterson and Wroblewski (1984) method. First year survival was determined to be 0.196, and 0.245 when M is 0.28 and 0.31 and 0.163, for the Peterson and Wroblewski (1984) method estimates. The input parameters for the following life table analysis are found in Table 3-2.

Table 3-1: Estimated natural mortality (M) rates for *M. canis*:

(Reference/Author)	Relationship	M
Hoening (1983)	$\ln(Z) = 1.44 - 0.982 \ln(t_{\max})$ Z=total mortality, tmax = maximum age = 16	0.28
Pauly (1979)	$\ln M = -0.0066 - 0.279 \ln(L_{\infty}) + 0.6543 \ln(K) + 0.4634 \ln(T)$ L _∞ , K from von Bertalanffy growth function T = average temperature = 5 – 27C	0.24 – 0.529
Chen and Watanabe (1989)	$M(t, t+\Delta) = 1/\Delta (e^{K(t+\Delta)} - e^{Kt}) / (e^{Kt} - e^{Kt_0})$ K, t ₀ – from von Bertalanffy growth function, t+Δ = time interval	0.31
Peterson and Wroblewski (1984)	$M = 1.92W^{-0.25}$ W = weight (grams)	0.41 Age-0 0.33 Age-1 0.29 Age-2 0.26 Age-3 0.25 Age-4 0.24 Age-5 0.23 Age-6 0.23 Age-7 0.22 Age-8 0.22 Age-9 0.22 Age-10 0.22 Age-11 0.22 Age-12 0.22 Age-13 0.22 Age-14 0.22 Age-15 0.21 Age-16
Present study	Catch curve analysis: Mean M from 1989 –1998 yearly catch curves.	0.1529

Table 3-2: Input parameters for *M. canis* demographic analysis, t_{\max} = maximum age, t_{mat} = age at maturity, Fec = fecundity, M = natural mortality for ages 1-16, $I S_0$ = initial first year survivorship, $C S_0$ = compensation first year survivorship.

Parameter	Best case estimate	Worst case estimate	Intermediate case estimate
t_{\max}	16	16	16
t_{mat}	5	5	5
Fec	$(-31.31 + 42.47(1 - e^{-0.496(\text{age})})$	$(-31.31 + 42.47(1 - e^{-0.496(\text{age})})$	$(-31.31 + 42.47(1 - e^{-0.496(\text{age})})$
M	PW (Table 3-1)	0.31	0.28
$I S_0$	0.163	0.245	0.196
$C S_0$	0.807	0.349	0.443

We created three stable life tables (Table 3-3 - 3-5) using these combinations of mortality. Table 1 incorporated the Peterson and Wroblewski (1984) method M estimates for age 1 – 16 which plateau at the lowest rate of our mortality estimates and result in the lowest calculated S_0 . Table 2 incorporated the highest estimate of $M = 0.31$ and therefore the highest estimate of $S_0 = 0.245$. Table 3 incorporated the intermediate mortality values with $M = 0.28$ and $S_0 = 0.196$.

The population is initially assumed to be stable $r = 0$, therefore it is necessary to include compensation when fishing mortality is added to the life table analysis. As a “best case” scenario table 1 with the lowest M estimates was used and S was increased for each age class (including Age-0) to 0.807, the value of S for the oldest animals in the population. As a “worst case” scenario we used table 2 with the highest M level and decreased M of first year animals by 25 %, which increased S_0 to 0.349 As an “intermediate case” scenario we took the intermediate value of $M = 0.28$ and decreased the mortality of first year animals by 50% resulting in a S_0 of 0.443.

The ‘best case’ scenario resulted in positive r values at all F values if fishing was not started until the age of maturity. However if fishing was started at age zero, the result was a negative r value for F equal to 0.3 and 0.5 (Table 3-6). The worse case scenario resulted in negative r values for all F values except for $F = 0.1$ and starting at five years of age. The intermediate scenario resulted in negative r values for all scenarios where F was added to age 0 animals. When F was added to age 5 animals in the intermediate scenario, this resulted in positive r values for $F = 0.1 - 0.3$, but a negative value when $F = 0.5$.

Table 3-3: Stable life table 1, F = fishing mortality, M = natural mortality, S = survivorship, x = age, l_x = age specific survivorship, b_x = age specific fecundity, R_0 = net reproductive rate, G = mean generation time, r = rate of population increase.

F	M	S	x	l_x	b_x	$l_x b_x$	$x l_x b_x$	R_0	G	r
0	1.81	0.163	0	1.00				1.00	8.96	0
0	0.33	0.721	1	0.16						
0	0.29	0.751	2	0.12						
0	0.26	0.768	3	0.09						
0	0.25	0.780	4	0.07						
0	0.24	0.788	5	0.05	1.521	0.08	0.40			
0	0.23	0.793	6	0.04	3.795	0.16	0.95			
0	0.23	0.797	7	0.03	4.542	0.15	1.05			
0	0.22	0.800	8	0.02	4.847	0.13	1.02			
0	0.22	0.802	9	0.02	5.335	0.11	1.01			
0	0.22	0.803	10	0.01	5.431	0.09	0.92			
0	0.22	0.804	11	0.01	5.489	0.07	0.82			
0	0.22	0.804	12	0.01	5.524	0.06	0.72			
0	0.22	0.805	13	0.01	5.546	0.05	0.63			
0	0.22	0.806	14	0.01	5.559	0.04	0.55			
0	0.22	0.806	15	0.01	5.568	0.03	0.47			
0	0.21	0.806	16	0.00	5.572	0.03	0.41			

Table 3-4: Stable life table 2, F = fishing mortality, M = natural mortality, S = survivorship, x = age, l_x = age specific survivorship, b_x = age specific fecundity, R_0 = net reproductive rate, G = mean generation time, r = rate of population increase.

F	M	S	x	l_x	b_x	$l_x b_x$	$x l_x b_x$	R_0	G	r
0	1.40	0.245	0	1.00				1.00	8.28	0
0	0.31	0.733	1	0.25						
0	0.31	0.733	2	0.18						
0	0.31	0.733	3	0.13						
0	0.31	0.733	4	0.10						
0	0.31	0.733	5	0.07	1.521	0.11	0.54			
0	0.31	0.733	6	0.05	3.795	0.20	1.19			
0	0.31	0.733	7	0.04	4.542	0.17	1.22			
0	0.31	0.733	8	0.03	4.847	0.14	1.09			
0	0.31	0.733	9	0.02	5.335	0.01	0.99			
0	0.31	0.733	10	0.02	5.431	0.08	0.82			
0	0.31	0.733	11	0.01	5.489	0.06	0.67			
0	0.31	0.733	12	0.01	5.524	0.04	0.54			
0	0.31	0.733	13	0.01	5.546	0.03	0.43			
0	0.31	0.733	14	0.00	5.559	0.02	0.34			
0	0.31	0.733	15	0.00	5.568	0.02	0.27			
0	0.31	0.733	16	0.00	5.572	0.01	0.21			

Table 3-5: Stable life table 3, F = fishing mortality, M = natural mortality, S = survivorship, x = age, l_x = age specific survivorship, b_x = age specific fecundity, R_0 = net reproductive rate, G = mean generation time, r = rate of population increase.

F	M	S	x	l_x	b_x	$l_x b_x$	$x l_x b_x$	R_0	G	R
0	1.63	0.196	0	1.00				1.00	8.50	0
0	0.28	0.756	1	0.20						
0	0.28	0.756	2	0.15						
0	0.28	0.756	3	0.11						
0	0.28	0.756	4	0.08						
0	0.28	0.756	5	0.06	1.521	0.10	0.49			
0	0.28	0.756	6	0.05	3.795	0.18	1.10			
0	0.28	0.756	7	0.04	4.542	0.17	1.16			
0	0.28	0.756	8	0.03	4.847	0.13	1.07			
0	0.28	0.756	9	0.02	5.335	0.11	1.00			
0	0.28	0.756	10	0.02	5.431	0.09	0.86			
0	0.28	0.756	11	0.01	5.489	0.07	0.72			
0	0.28	0.756	12	0.01	5.524	0.05	0.60			
0	0.28	0.756	13	0.01	5.546	0.04	0.49			
0	0.28	0.756	14	0.01	5.559	0.03	0.40			
0	0.28	0.756	15	0.00	5.568	0.02	0.32			
0	0.28	0.756	16	0.00	5.572	0.02	0.26			

Table 3-6: Life table analysis: best case scenario, $M = 0.215$, $S_0 = 0.807$, worst cast scenario, $M = 0.31$, $S_0 = 0.349$, intermediate case scenario, $M = 0.28$, $S_0 = 0.443$.

Age	F	Ro	G	R	t_2
BEST					
0	0.1	2.87	8.247	0.128	5.43
0	0.2	1.30	7.640	0.0341	20.32
0	0.3	0.62	7.175	-0.0668	-10.38
0	0.5	0.16	6.547	-0.282	-2.458
5	0.1	4.73	8.247	0.188	3.68
5	0.2	3.53	7.640	0.165	4.20
5	0.3	2.78	7.175	0.142	4.87
5	0.5	1.92	6.547	0.0999	6.94
WORST					
0	0.1	0.64	7.666	-0.0578	-12.00
0	0.2	0.31	7.196	-0.165	-4.21
0	0.3	0.15	6.837	-0.276	-2.51
0	0.5	0.04	6.341	-0.505	-1.37
5	0.1	1.06	7.666	0.00745	93.08
5	0.2	0.83	7.196	-0.0257	-26.97
5	0.3	0.68	6.837	-0.0564	-12.28
5	0.5	0.50	6.341	-0.110	-6.28
INTERMEDIATE					
0	0.1	1.00	7.835	-0.00044	-1566.40
0	0.2	0.47	7.324	-0.104	-6.68
0	0.3	0.23	6.935	-0.212	-3.26
0	0.5	0.06	6.402	-0.438	-1.58
5	0.1	1.64	7.835	.0634	10.94
5	0.2	1.27	7.324	0.0327	21.17
5	0.3	1.03	6.935	0.00400	173.34
5	0.5	0.74	6.402	-0.0471	-14.72

To test the sensitivity of our analysis, trials were run using table 3, and altering the input parameters in the following ways: $\frac{1}{2} S_0$, $2S_0$, $M = 0.15$, $M = 0.53$, maximum age = 11, maximum age = 21, age at maturity -1 , age at maturity -2 , fecundity $+\frac{1}{2}$, fecundity $+1$ (Table 3-7). Halving and doubling S_0 resulted in doubling or halving R_0 , had no effect on G , and resulted in r values of 0.080 and -0.081 , respectively. Changing the value of M had the largest effect on R_0 and r , with R_0 ranging from 0.18 to 2.9 and r ranging from -2.381 to $.1086$, G also changed from 7.10 to 9.80. Altering t_{max} had a large effect on generation time, but less of an effect on G and r , increasing t_{max} had very little effect but this is likely due to the fact that mortality was based on a 16 year lifespan. Adding fecundity had little effect on G but did increase r and R_0 , whereas decreasing the age at maturity decreased G as well as increasing r and R_0 .

DISCUSSION

The result of changing fishing and natural mortality rates in the life table emphasized the importance of ensuring the fishery does not target juvenile smooth dogfish. Even under the best possible conditions, only a low level of F would maintain the population at a stable level if the fishery takes the entire size range of animals. Several other demographic analyses of elasmobranch populations emphasize the need to target mature size or larger animals (Liu and Chen 1999; Sminkey and Musick 1996; Cailliet et al., 1992).

Furthermore, these results indicated smooth dogfish may not be able to withstand high levels of fishing mortality. In the worst case scenario any fishing mortality over 0.2 caused the population to decline. However in the intermediate scenario as long as fishing

Table 3-7: Sensitivity analysis applied to Table 3-5, $M = 0.28$, $S_0 = 0.196$.

Trial	Revised parameter	R_0	G	r	t_2
Stable		1.00	8.603	0	
1	$0.5(S_0)$	0.50	8.498	-0.0819	-8.46
2	$2(S_0)$	1.99	8.498	0.0812	8.54
3	$M = 0.15$	2.83	9.606	0.108	6.40
4	$M = 0.53$	0.19	7.116	-0.237	-2.93
5	Max age = 11	0.84	7.589	-0.0225	-30.77
6	Max age =21	1.04	8.866	0.00390	177.53
7	Fecundity + $\frac{1}{2}$	1.12	8.404	0.0138	50.07
8	Fecundity + 1	1.25	8.329	0.0268	25.90
9	Mat. Age + 1	1.34	7.602	0.0381	18.21
10	Mat. Age + 2	1.78	6.688	0.0865	8.01

is not started until the animals are at the age of maturity, the animals could be fished at higher levels. The best case scenario indicated these animals could be fished at a high level as long as fishing began after the age of maturity.

The life table model assumed that the population is initially stable, $r = 0$, however as discussed in the general introduction, the population is being targeted and is likely caught as bycatch in other fisheries. If the level of fishing mortality is significant, then our assumption that $Z = M$ is violated as well as the assumption that $r = 0$. This affects our estimates of natural mortality. Fishing may remove the largest, oldest individuals in the population, which would make our estimate of maximum age too low and our estimate of M calculated using Hoenig's (1983) relationship with maximum age too high. Fishing may result in the population growing faster to compensate for this additional mortality which will result in an overestimation of M when calculated using the Chen and Watanabe (1989) method estimate which uses this value in its calculation. However this will result in an underestimation of M using the Peterson and Wroblewski (1984) method estimates because weight at each age would then be larger resulting in a smaller M value at each size. This over or under estimation of M is then carried over into our estimation of first year survivorship which will be estimated to high using the Hoenig(1983) method and the Chen and Watanabe (1989) method and too low using the Peterson and Wroblewski (1984) method.

If the population is already being fished at a level that affects it significantly then compensation is already occurring and mortality and population growth rates likely are already altered. If fishing mortality were then removed the population would likely be growing and natural mortality rates would likely be lower as a compensatory response.

Other methods of compensation have been proposed for populations responding to fishing pressure, including changes in growth resulting in earlier ages at maturity, and changes in fecundity. This population grows and matures very quickly and it seems unlikely they could increase growth rates drastically enough to significantly change the age at maturity. There is a positive relationship between length of the female and fecundity, indicating females have more pups as they grow and get older. Due to the lack of body space in the female it seems unlikely they would be able to increase fecundity without a decrease in pup size. The sensitivity analysis indicated that an increase in fecundity would increase the R_0 and r estimates but has little effect on the generation time. Decreasing the age at maturity has a greater effect on R_0 and r and decreases generation time. The other possibility of compensation is a decrease in the mortality of older animals.

Natural mortality is very difficult to determine accurately and the sensitivity analysis of the life table indicated that this parameter has a large effect on the output parameters (R_0 , G , and r). Mortality rates estimated for this population using different methods ranged widely, and this is problematic as these values have a large effect on the intrinsic rate of increase of the population (r).

Elasmobranchs are highly susceptible to over exploitation and many studies indicate high fishing pressure will cause these populations to crash (Sminkey and Musick 1996; Cailliet 1992). *Mustelus* species have been found to have higher productivities than many other shark species. In the Australian Southern Shark Fishery which primarily exploits two species, the school shark, *Galeorhinus galeus*, and the gummy shark, *Mustelus antarcticus*, Stevens (1999) finds the gummy shark population to be

exploitable while the school shark is not. The difference in exploitability of the two populations is thought to be due to the higher productivity of the gummy shark as exhibited by their faster growth rates, earlier ages at maturity, and higher reproductive output. Smith et al. (1998) found that two California *Mustelus* species had the highest productivities of 28 shark species studied. In general they found that early maturing small coastal species had the highest productivities and therefore the highest rebound potentials.

GENERAL CONCLUSIONS

As more species fall under regulations in the North Atlantic the possibility of the North Atlantic population of smooth dogfish becoming heavily fished becomes more likely. This study would indicate that management and careful monitoring of the population is necessary to ensure the health of the population and therefore the fishery. The NA smooth dogfish is regularly caught by federal fishery surveys as well as several state surveys and the population could be monitored by abundance indices. Careful monitoring is necessary due to the fact that the mortality rates used in this demographic analysis are estimates and may not truly reflect the mortality of the population. Monitoring of the population and regulation of the fishing mortality will ensure that the population remains healthy

While age, growth, and reproductive studies of this population indicate a fast growth rate and a relatively high fecundity for a shark species, exploitation should still be carefully monitored. Currently this population appears to be only lightly exploited experiencing variable fishing pressure, however it is difficult to determine this accurately as landing data are often inaccurate due to confusion with spiny dogfish landing data. This life table analysis would indicate that while the population most likely could support a commercial fishery there is a potential for the population to crash if fishing mortality is too high. This is an indication that at some point in time the population will need to be managed with some sort of catch and or size regulations imposed on the fishery. To

ensure both the health of the population and the fishery, it is important to consider management measures before the population becomes heavily exploited.

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