Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean

Christina L. Conrath
Virginia Institute of Marine Science
College of William and Mary
1208 Greate Road
Gloucester Point, Virginia 23062
E-mail address: conrath@vims.edu

James Gelsleichter
Mote Marine Laboratory
1600 Ken Thompson Parkway
Sarasota, Florida 34236

John A. Musick
Virginia Institute of Marine Science
College of William and Mary
1208 Greate Road
Gloucester Point, Virginia 23062

Abstract—The northwest Atlantic population of smooth dogfish (*Mustelus canis*) ranges from Cape Cod, Massachusetts, to South Carolina. Although *M. canis* is seasonally abundant in this region, very little is known about important aspects of its biology, such as growth and reproductive rates. In the early 1990s, commercial fishery landings of smooth dogfish dramatically increased on the east coast of the United States. This study investigated growth rates of the east coast *M. canis* population through analysis of growth patterns in vertebral centra. Marginal increment analysis, estimates of precision, and patterns in seasonal growth supported the use of vertebrae to age these sharks. 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 this population: K = 0.292/yr, L_∞ = 123.57 cm, and t_0 = –1.94 years for females, and K = 0.440/yr, L_∞ = 105.17 cm, and t_0 = –1.52 years for males. Males matured at two or three years of age and females matured between four and seven years of age. The oldest age estimate for male and female samples was ten and sixteen years, respectively.

Manuscript accepted 14 June 2002.
Fish. Bull. 100:674–682 (2002).

The smooth dogfish, *Mustelus canis*, is a small shark species found throughout the western Atlantic Ocean from Massachusetts to Florida, and in the northern Gulf of Mexico, including Cuba, Jamaica, Barbados, Bermuda, Bahamas, and southern Brazil to northern Argentina. Smooth dogfish are demersal and typically are found in inshore continental shelf and slope waters (Compagno, 1984). Several discrete populations of smooth dogfish likely exist, separated by large geographic areas; and there appears to be little intermigration between the different populations (Bigelow and Schroeder, 1948). The northwest Atlantic population of smooth dogfish ranges from Cape Cod, Massachusetts, to South Carolina and migrates seasonally in response to changing water temperatures (Bigelow and Schroeder, 1948; Castro, 1983).

Recently, commercial harvest of smooth dogfish has increased on the east coast of the United States. Annual landings were under 80,000 pounds before 1990, over 300,000 pounds in 1990, and increased to around 1 million pounds from 1998 to 2000. In one year (1995) landings exceeded 2.5 million pounds (Fig. 1) (NMFS, 2002). Smooth dogfish have been landed in significant amounts (i.e. over 50 metric tons) in Massachusetts, New Jersey, Maryland, Virginia, and North Carolina (NMFS, 2002).

Sharks are often highly susceptible to overfishing because of life history traits that include slow growth, large adult size, late reproduction, and the production of a few large well-formed young (Hoenig and Gruber, 1990). Because of these characteristics, shark fisheries tend to decline drastically after a short time and take long periods to recover (Holden, 1974). The determination of how increased exploitation will affect a shark population, like that of *M. canis* in the northwest Atlantic Ocean, requires information on the growth and reproductive rates of the species targeted by the fishery. The purpose of this study was to determine the growth rates of smooth dogfish from the northwest Atlantic Ocean by using age estimates derived from vertebral growth-band counts.

Materials and methods

Smooth dogfish were collected from NMFS groundfish and longline surveys, Virginia Institute of Marine Science (VIMS) longline surveys, Grice Marine Laboratory longline surveys, the Massachusetts state trawl survey, and by the Massachusetts Division of Marine Fish-

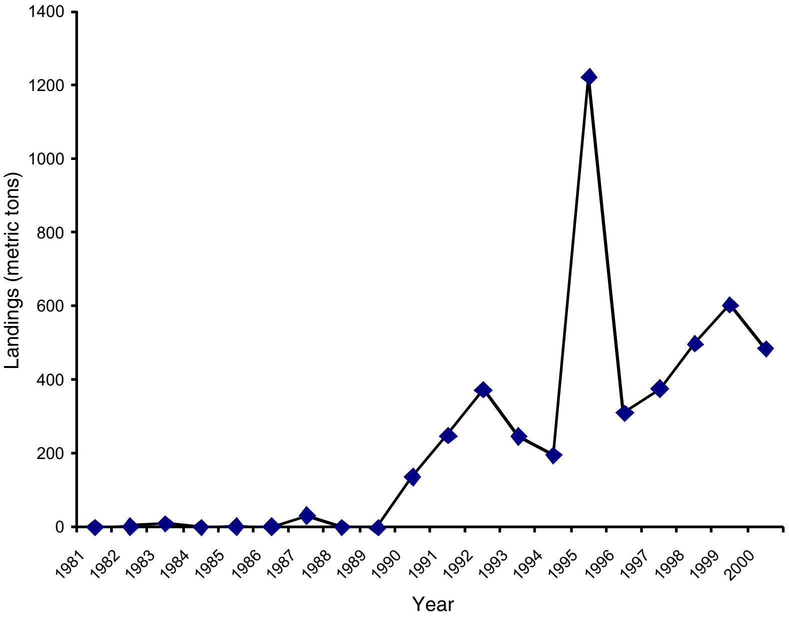

Figure 1

Reported smooth dogfish landings from National Marine Fisheries Service commercial catch statistics for the Atlantic and Gulf states, from 1981 to 2000.

eries (MDMF). Total length (TL), precaudal length (PCL), and male clasper length (CL) were measured, and sex was recorded at the time of collection. A section of the vertebral column containing eight to twelve vertebrae was removed from directly under the first dorsal fin and stored frozen. Reproductive samples were taken from smooth dogfish at this time and maturity state was assessed from these samples.

Vertebral samples were cleaned, soaked in 70% ETOH for 24 hours, and air-dried for 24 hours. Dried vertebrae were sagitally sectioned through the focus with an Isomet rotary diamond saw (Buehler, Lake Bluff, IL). Afterwards, vertebral sections were affixed to microscope slides with mounting medium and polished with wet fine-grit sand paper to a thickness of about 0.5 mm. The vertebrae were viewed under a binocular dissecting microscope with transmitted light.

Vertebral radius was measured from the focus of the vertebra along the axis of the corpus calcarium to the edge of the vertebra (Fig. 2). Total length (TL) was plotted against vertebral radius (VR) to determine if the growth of the vertebra was proportional to somatic growth of the animal and whether the structure was appropriate for estimating growth rate of the animal.

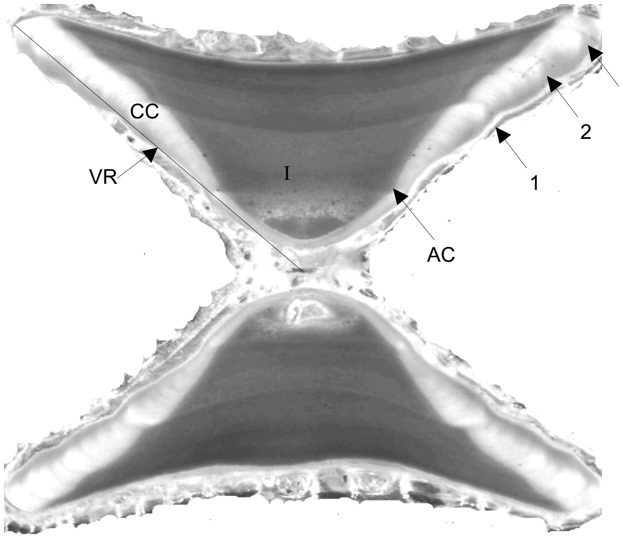

Figure 2

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

Growth patterns of the vertebrae consisted of wide translucent bands separated by narrow opaque bands that extended from the intermedialia to the corpus calcareum (Fig. 2). An angle change—the result of a change in growth rates at this time—was present in the intermedialia approximately 2 mm from the focus of each vertebra and was considered to be a birthmark. Age was estimated by enumerating the narrow opaque bands, which were considered to form annually owing to a slowing or stopping of

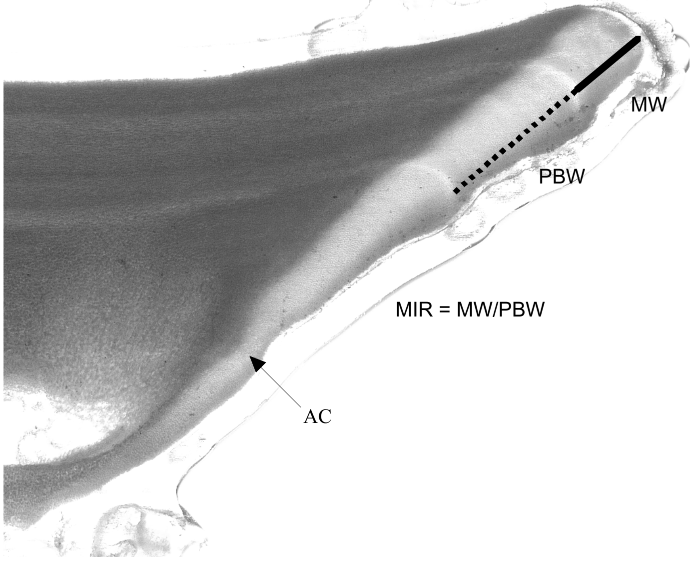

Figure 3

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.

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.

A random sample of twenty vertebrae from each of ten 10-cm size classes (33–132 cm TL) was read independently by two readers, and a chi-square test was used to test for systematic differences between the ages. The number of observations above the main diagonal of a contingency table of reader one's and reader two's ages was compared with the number of observations below the main diagonal to determine if this ratio was significantly different from 1:1. The percent agreement (PA), i.e. the percentage of vertebrae in each length group that were assigned the same ages by both readers, was determined to test for precision between the two readers.

Marginal increment analysis verified the annual nature of the narrow opaque growth bands. The distance from the last opaque 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, Fig. 3). The margin width was divided by the distance to the angle change or birthmark 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 margin width.

The length-at-age data were used to generate a von Bertalanffy growth curve for males and females by using the computer program SigmaPlot (SPSS Inc., 2000) and the Marquardt-Levenberg algorithm to estimate curve-fitting parameters (Press et al., 1986; Marquardt, 1963; Nash, 1979; Shrager, 1970, 1972).

To determine if there was a period of the year when smooth dogfish were growing at a faster rate, the mean total length of age-0 and age-1 smooth dogfish was plotted for each month. For this procedure, we used data from several years and we assumed that every year class followed the same general growth pattern during the first two years of life. The mean monthly length of age-0 animals determined for the 1997 and 1998 cohorts was also calculated. Because we did not collect free-swimming age-0 *M. canis* during May, the largest estimate of birth length (40 cm) was used to minimize the possibility of creating an artificially large growth increment during the summer months.

Results

Vertebrae were collected from 918 smooth dogfish ranging in size from 33 to 132 cm TL. The relationship between TL and VR for males and females was not significantly different (ANCOVA, $P<0.05$); therefore the data for both sexes were combined. The statistically significant relationship ($P<0.001$) between TL and VR was positive and curvilinear (Fig. 4):

$$TL = -0.477(VR)^2 + 17.06\,(VR) + 0.807 \quad [n=833,\ r^2=0.97,\ P<0.001].$$

Of the original 918 vertebral samples, 894 animals were aged and vertebrae from 24 animals were found to be un-

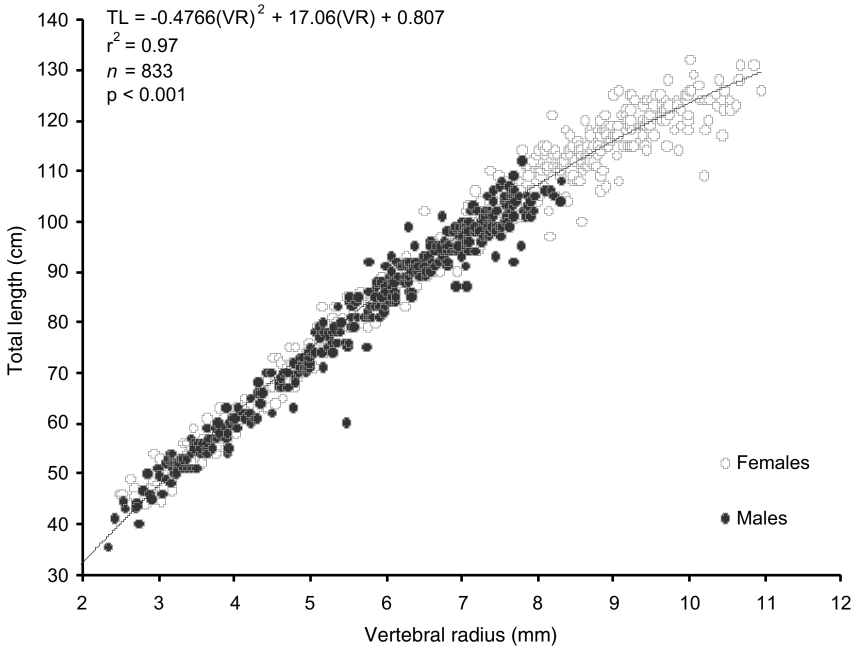

Figure 4

Relationship between vertebral radius (VR) and total length (TL) for *Mustelus canis*.

Table 1

Contingency table of reader one's ages versus reader two's ages, the bold numbers are along the main diagonal (where reader one's age = reader two's age).

		Reader one															
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Reader two	0	**53**															
	1		**19**	2													
	2		1	**19**	1												
	3				**19**												
	4				3	**2**	1										
	5					2	**6**	1									
	6						2	**11**	2								
	7								**14**								
	8									**4**							
	9									1	**2**						
	10									1	1	**1**					
	11										1	2	**2**	1			
	12											1	1	**2**			
	13											2	1		**2**		
	14														**0**	1	
	15															**0**	

readable. To test for precision, a second reader read vertebrae from a total of 185 animals (twenty from each 10-cm size group, except for the 33–42 cm size group [n=9]) and four vertebrae were found to be unreadable. A contingency table of reader one's versus reader two's ages was made and a chi-square test resulted in a $\chi^2 = 3.19$, which was less than the critical value of $\chi^2_{0.05,1} = 3.84$; thus the hypothesis of symmetry was not rejected (Table 1). The overall percent

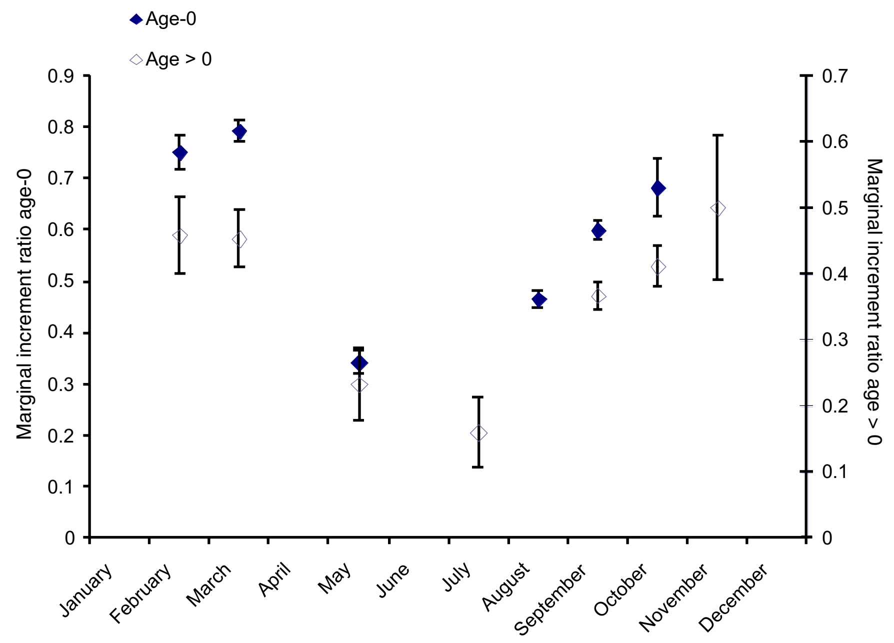

Figure 5

Monthly average marginal increment ratio for male (TL<86 cm) and female (T<102 cm) smooth dogfish (error bars are standard error).

Table 2

Percent agreement (PA) between reader one's ages and reader two's ages for each 10-cm size group.

Size group	Total vertebrae read	No. of vertebrae aged in agreement	No. of vertebrae aged in agreement ±1 year	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

agreement between the two readers was over 84% and the percent agreement within one year was over 96% (Table 2). Agreement within one year was high (over 90%) for all size groups except the largest, where it dropped to 79%.

The largest marginal increments were observed in vertebrae from animals collected in March (Fig. 5). A large drop in marginal width appears to occur in May indicating that band formation most likely occurs 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 dramatically and the difference between margin widths becomes very small, making it difficult to elucidate monthly changes in margin width.

Von Bertalanffy growth parameters were calculated separately for males and females because of the approxi-

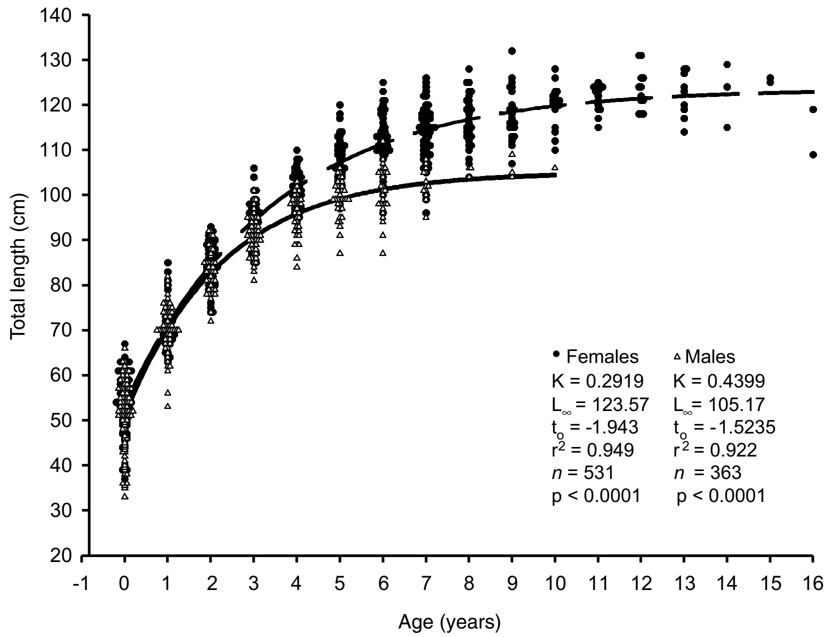

Figure 6

Von Bertalanffy growth function parameters for male and female *Mustelus canis*.

mately 20-cm size difference in both maximum length and length at maturity for males and females. Female growth parameters (Fig. 6) were L_∞ = 123.57 cm, K = 0.2919/yr, and t_0 = –1.9432 years (Table 3). The largest female was 132 cm TL, and 50% of females were found to mature at 102 cm TL and at four to five years of age (Conrath and Musick, 2002). The oldest estimated age for a female smooth dogfish in the study was 16 years and age of the largest female was estimated at nine years old. Male growth parameters (Fig. 6) were L_∞ = 105.17 cm, K = 0.4399/yr, and t_0 = –1.5235 years (Table 3). The largest male in the study was 112 cm TL, and 50% of males were found to mature at 85 cm TL and two to three years of age (Conrath and Musick, 2002). The oldest estimated age for a male smooth dogfish in the study was 10 years, and age of the largest male was estimated at six years old.

The plot of seasonal growth of age-0 and age-1 smooth dogfish indicated a plateau in growth between the months of October and February or March, suggesting slow growth during this period (Fig. 7). There was also a plateau in growth between October and February for both the 1997 and the 1998 cohorts. The mean TL of the 1997 cohort in September 1997 was 51.62 cm (n=31, SE=0.552) and the mean TL of the 1998 cohort in September 1998 was 53.39 cm (n=23, SE=0.579), whereas the mean TL of the 1997 cohort in February 1998 was 57.89 cm (n=18, SE=0.836) and the mean TL of the 1998 cohort in February 1999 was 57.29 cm (n=14, SE=1.605). Assuming a birth length of 40 cm, age-0 animals grew approximately 12–14 cm between May and September and only 4–7 cm between September and February.

Table 3

Von Bertalanffy growth parameters for *Mustelus 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

Discussion

Precision estimates, marginal increment analysis, and seasonal growth patterns justify the use of vertebrae as an aging tool for the North Atlantic population of smooth dogfish. The agreement within one year between two readers was high for all size groups (>90%) with the exception of the largest size class (123–132 cm). 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

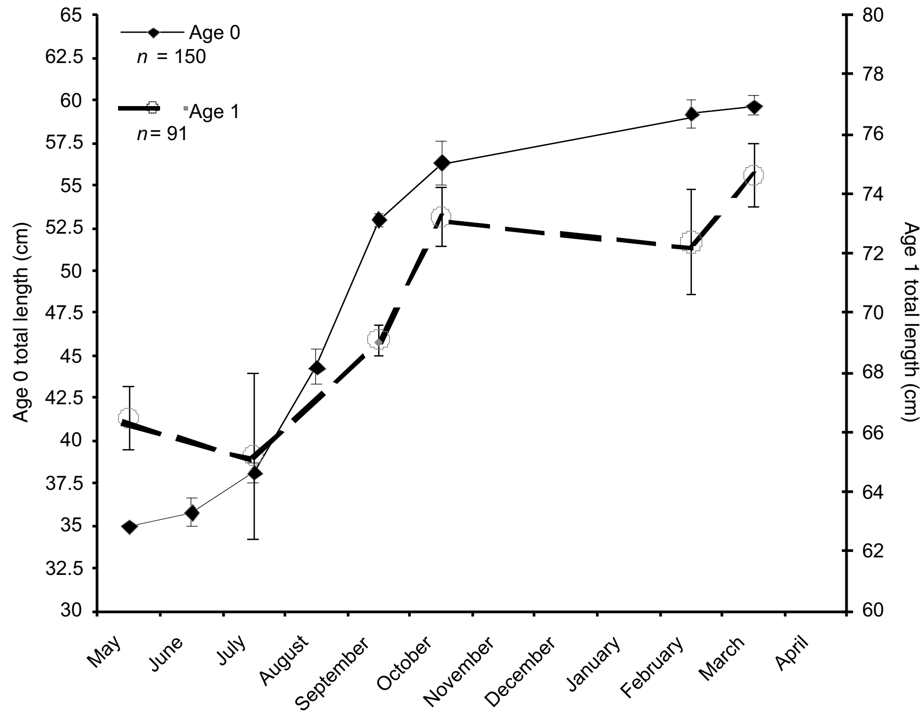

Figure 7

Seasonal growth for smooth dogfish, *M. canis.* Solid line and dashed line show mean size by month of age-0 and age-1 animals (error bars are standard error), respectively.

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

The marginal increment analysis included only animals of length less than or equal to the length of 50% maturity; therefore the annular nature of the growth bands was verified for these length groups only. Although the marginal widths of the largest animals in the population were too small to discern seasonal differences in these widths, we assumed that these animals follow the same patterns of growth throughout their lifespan.

Estimates of seasonal growth indicated that animals in this population experience a plateau in growth during the winter months between October and February or March, at least for the first two years of life. Their major period of growth is during the summer, between March and October. This finding supports the well established conclusion that an opaque band is deposited annually at the time of slowing or cessation of growth during the winter months. Resuming a faster growth rate after February or March supports the conclusion that a growth band becomes visible in the months of April or May.

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 seven to eight 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, but this method has subsequently been discredited for application to sharks by Pratt and Casey (1990).

Rountree and Able (1996) used length-frequency analysis to determine growth rates in young of the year (YOY) smooth dogfish in a New Jersey estuary. YOY animals born in May at 29–38 cm TL reached 55–70 cm TL by October of the same year. We found a slightly slower growth rate: age-0 animals in October 1999 ranged from 53–60 cm with a mean size of 56.3 cm (*n*=6, SE=1.31). We found smooth dogfish grew to a mean of 66.5 cm TL in their first year (size range 61–69 cm, mean size of estimated age-1 May captures, *n*=13, SE=0.924). The majority of smooth dogfish used in this study were collected in Virginia and North Carolina; therefore geographical differences in growth or differences in growth between years may have contributed to the small discrepancy between our results and those of Rountree and Able.

Values of *K* reported from various *Mustelus* species (Table 4) ranged 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 (Tanaka and Mizue, 1979; Yudin and Cailliet, 1990; Francis and Francis, 1992; Moulton et al.,

Table 4

Age and growth parameters for *Mustelus* species.

Species	Sex	K	L_∞	t_0	Age at maturity (yr)	Reference
M. californicus	M+F	0.168	154.4	–1.271	1–4	Yudin and Cailliet (1990)
M. henlei	M+F	0.244	97.7	–1.296	1–4	Yudin and Cailliet (1990)
M. manazo	M	0.695	71.4	–0.734	2–3	Tanaka and Mizue (1979)
	F	0.379	88.6	–1.113	2–3	Tanaka and Mizue (1979)
M. manazo	M	0.120	124.1	–2.59		Yamaguchi et al. (1996)
	F	0.113	134.1	–2.55		Yamaguchi et al. (1996)
M. lenticulatus	M	0.10			5	Francis and Francis (1992)
(Pegasus Bay)	F	0.40				
M. lenticulatus	M	0.16			3.7	Francis and Francis (1992)
(Harakai Gulf)	F	0.42			4.7	
M. antarcticus	M	0.160	155.9	–1.94		Moulton et al. (1992)
	F	0.094	233.6	–2.05		
M. mustelus	M	0.12	1451	–2.14	6–9	Goosen and Smale (1997)
	F	0.06	2049	–3.55	12–15	
M. canis	M	0.440	105.17	–1.524	3	Present study, Conrath and Musick (2002)
	F	0.292	123.57	–1.943	4–5	

1992; Yamaguchi et al., 1996; Goosen and Smale, 1997). Smooth dogfish growth coefficients are at the high end of this range (K=0.4399 for males and K=0.2919 for females). Mean asymptotic length of *M. canis* is at the midrange of reported L_∞ values for *Mustelus* species, which range from L_∞ = 71.4, and 88.6 cm for male and female *M. manazo* (Tanaka and Mizue, 1979) to L_∞=155.9 and 233.6 cm for male and female *M. antarcticus* (Moulton et al., 1992). As in nearly all accounts of age and growth for *Mustelis* species, male and female growth in our study was virtually identical in the first few years, and males have a higher growth coefficient (K) than females due to a plateau in growth at a much smaller size (Table 4). However, Francis and Francis (1992) found that female *M. lenticulatus* grow faster than males but still reach a larger maximum length. Their estimates were based on length-frequency data and they acknowledged that the lack of large females may have affected their estimates of von Bertalanffy growth coefficients.

Our growth coefficients for male and female smooth dogfish were comparably high for a shark population; previously reported K values ranged 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 mature at a relatively young age. These characteristics may make the northwest Atlantic population more productive and possibly more resilient to exploitation than many other shark populations.

Acknowledgments

This project was supported by Wallop-Breaux funds administered by the Virginia Marine Resources Commission. We thank the following individuals, organizations, and vessel crews for their assistance in obtaining samples for this project: J. Galbraith, H. McBride, V. Nordahl, N. Shepherd, A. Howe, J. Loefer, G. Skomal, B. Falterman, R. Kraus, D. Grubbs, K. Goldman, J. Romine, D. Ward, the National Marine Fisheries Service Northeast Fisheries Science Center survey crew, Massachusetts State Fisheries survey crew, scientists at Grice Marine Laboratory and the Massachusetts Division of Marine Fisheries, and the crews of the RV *Albatross IV*, RV *Gloria Michelle*, and the RV *Bay Eagle*.

Literature cited

Bigelow, H. B., and W. C. Schroeder.
1948. Sharks. *In* Fishes of the western North Atlantic, part 1: lancelets, cyclostomes, and sharks (A. E. Parr and Y. H. Olsen, eds.), p. 244–254. Sears Found. Mar. Res. Memoir 1 Yale Univ, New Haven, CT.
Casey, J. G., H. L. Pratt, and C. E. Stillwell.
1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 42:963–975.
Castro, J. I.
1983. The sharks of North American waters, 180 p. Texas A&M Univ. Press, College Station, TX.

Compagno, L. J. V.
1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue, vol 4, part 2. FAO Fish. Synop., p. 404–406. FAO, Rome.

Conrath, C. L., and J. A. Musick.
2002. Reproductive biology of the smooth dogfish, *Mustelus canis*, in the northwest Atlantic Ocean. Environ. Biol. Fishes 64:367–377.

Francis, M. P.
1981. Von Bertalanffy growth rates in species of *Mustelus* (Elasmobranchii: Triakidae). Copeia 1981:189–192.

Francis, M. P., and R. I. C. C. Francis.
1992. Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*). Aust. J. Mar. Freshwater Res. 43:1157–1176.

Goosen, A. J. J., and M. J. Smale.
1997. A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). S. Afr. J. Mar. Sci. 18:85–91.

Hoenig, J. M., and S. H. Gruber.
1990. Life history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranchs as living resources: advances in biology, ecology, systematics, and status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds.), p. 1–16. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.

Holden, M. J.
1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* Sea fisheries research (F. R. Harden Jones, ed.), p. 117–137. J. Wiley and Sons, New York, NY.

Marquardt, D. W.
1963. An algorithm for least squares estimation of parameters. J. Soc. Industrial and Applied Mathematics 11: 431–441.

Moss, S. A.
1972. Tooth replacement and body growth rates in the smooth dogfish, *Mustelus canis* (Mitchill). Copeia 1972: 808–811.

Moulton, P. L., T. I. Walker, and S. R. Saddlier.
1992. Age and growth studies of gummy shark, *Mustelus antarcticus* Gunther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. Aust. J. Mar. Freshwater Res. 43:1241–1267.

Nash, J. C.
1979. Compact mumerical methods for computers: linear algebra and function minimization, 292 p. John Wiley & Sons, Inc., New York, NY.

Natanson, L. J., J. G. Casey, and N. E. Kohler.
1993. Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. Fish. Bull. 93:116–126.

National Marine Fisheries Service.
2002. Commercial fishery statistics. Internet. August 28, 2001. [Available from http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html. Search terms: species: shark, smooth dogfish and shark, dogfish; from: 1980 to 2000; state area: Atlantic and Gulf by state. Access date: 2 June, 2002.]

Pratt, H. L., Jr., and J. G. Casey.
1990. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. *In* Elasmobranchs as living resources: advances in biology, ecology, systematics and status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds.), p. 97–109. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling.
1986. Numerical recipes. Cambridge Univ. Press, Cambridge.

Rountree, R. A., and K. W. Able.
1996. Seasonal abundance, growth, and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary. Fish. Bull. 94:522–534.

Shrager, R. I.
1970. Regression with linear constraints: an extension of the magnified diagonal method. J. Assoc. Computing Machinery 17:446–452.
1972. Quadratic programming for N. Communications of the ACM 15:41–45.

SPSS, Inc.
2000. SigmaPlot 2000 user's quide, 435 p. SPSS, Inc., Chicago, IL.

Simpfendorfer, C. A.
1993. Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori,* from north Queensland, Australia. Environ. Biol. Fishes 36:233–241.

Tanaka, S., and K. Mizue.
1979. Age and growth of Japanese dogfish *Mustelus manazo* Bleeker in the East China Sea. Bull. Jpn. Soc. Sci. Fish. 45:43–50.

Yamaguchi, A., T. Taniuchi, and M. Shimizu.
1996. Age and growth of the starspotted dogfish, *Mustelus manazo*, from Tokyo Bay, Japan. Fish. Sci. 62:919–922.

Yudin, K. G., and G. M. Cailliet.
1990. Age and growth of the gray smoothhound, *Mustelus californicus,* and the brown smoothhound, *Mustelus henlei*, sharks from central California. Copeia 1990:191–204.