

Abstract—Growth parameters were estimated for porbeagle shark (*Lamna nasus*) in the northwest Atlantic Ocean on the basis of vertebral annuli. A total of 578 vertebrae was analyzed. Annuli were validated up to an age of 11 years by using vertebrae from recaptured oxy-tetracycline-injected and known-age sharks. Males and females grew at similar rates until the size of male sexual maturity, after which the relative growth of the males declined. The growth rate of the females declined in a similar manner at the onset of maturity. Growth curves were consistent with those derived from tag-recapture analyses (GROTAG) of 76 recaptured fish and those based on length-frequency methods with measurements from 13,589 individuals. Von Bertalanffy growth curve parameters (combined sexes) were $L_{\infty} = 289.4$ cm fork length, $K = 0.07$ and $t_0 = -6.06$. Maximum age, based on vertebral band pair counts, was 25 and 24 years for males and females, respectively. Longevity calculations, however, indicated a maximum age of 45 to 46 years in an unfished population.

Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean

Lisa J. Natanson

Joseph J. Mello

National Marine Fisheries Service
28 Tarzwell Dr.
Narragansett, Rhode Island 02882

E-mail address (for L. J. Natanson): Lisa.Natanson@noaa.gov

Steven E. Campana

Marine Fish Division
Bedford Institute of Oceanography
P.O. Box 1006
Dartmouth, Nova Scotia
Canada B2Y 4A2

The porbeagle (*Lamna nasus*) is a large pelagic shark in the family Lamnidae that occurs in the cold, temperate waters of the North Atlantic, South Atlantic, and South Pacific oceans. The species extends from Newfoundland to New Jersey in the western North Atlantic (Castro, 1983), and from Iceland and the western Barents Sea to Morocco and the Mediterranean in the eastern North Atlantic (Compagno, 1984). Directed commercial fisheries for porbeagle have existed in the western North Atlantic in both U.S. and Canadian waters since the early 1960s (Campana et al.¹). The fishery collapsed in 1967, apparently from overfishing. Canadian fishermen maintained low and apparently sustainable catches in the 1970s and 1980s, which allowed the stock to rebuild. A renewed fishery for porbeagle began in both the United States and Canada in the 1990s (Campana et al.¹).

Accurate age determinations are necessary for both the assessment and management of the porbeagle shark because they form the basis for calculations of growth and mortality rates, age at maturity, age at recruitment, and estimates of longevity. Aasen (1963), in an early study of porbeagle growth, generated a growth curve for the western North Atlantic population based on analyses of length frequencies from a single year and on vertebral readings of one fish. However, he did not pro-

vide any independent confirmation of the accuracy of his age estimates. Francis and Stevens (2000) used length-frequency analysis to estimate the growth of juvenile porbeagles in the South Pacific. Both of these studies indicated that porbeagle grow relatively rapidly through the first year of life, but only minimal information has been available for older fish.

In view of the history of the porbeagle fishery and the need for accurate biological information for management of this species, an intensive U.S.-Canadian cooperative research program was initiated in 1999 to obtain detailed life-history and population data. This study reports on one portion of this program, specifically, the use of vertebrae to determine age and growth. The vertebral growth readings were validated as annuli on the basis of recaptures of tetracycline-injected and known-age sharks and verified by comparison with growth curves based on tag-recapture and length-frequency analyses.

¹ Campana, S., W. Joyce, L. Marks, P. Hurley, L. J. Natanson, N. E. Kohler, C. F. Jensen, J. J. Mello, and H. L. Pratt Jr. 2000. The rise and fall (again) of the porbeagle shark population in the Northwest Atlantic. Unpubl. manusc. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

Materials and methods

Vertebral aging

Vertebral samples from porbeagle sharks were obtained between 1966 and 1999 on board commercial and research vessels. The majority of samples (97%) were collected after 1990 on Canadian commercial longline vessels. Sampling took place in U.S. and Canadian waters between Massachusetts (NE U.S.) and the Grand Banks (off southern Newfoundland) and all individuals were treated as belonging to the same stock on the basis of tagging data (Campana et al.²). Multiple vertebrae were removed from the area just above the branchial chamber wherever possible; except on commercial vessels where samples were obtained closer to the head. Vertebrae were then stored frozen or in 70% ETOH until processing.

Only samples that had measured fork length (FL—tip of the snout to the fork in the tail, over the body) or total length (TL—tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending downward from the tip of the upper caudal lobe to form a right angle, over the body; Kohler et al., 1995) were used. All lengths reported in this document are over-the-body FL unless otherwise noted. Total length in centimeters (cm) can be converted to FL cm by using the regression equation (Campana et al.¹):

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

One vertebra from each sample was removed for processing. The centrum was sectioned by using a Ray Tech Gem saw with two diamond blades separated by a 0.6-mm spacer. Each centrum was cut through the middle along the sagittal plane and the resulting “bow-tie” sections were stored individually in capsules in 70% ETOH. Each section was digitally photographed with a MTI CCD 72 video camera attached to a SZX9 Olympus stereo microscope by using reflected light. Magnification depended on the size of the section and varied from 4× to 12.5×. Band pairs (consisting of one opaque and one translucent band) were counted and measured from the images by using Image Pro 4 software (Media Cybernetics, 1998). Measurements were made from the midpoint of the isthmus of the full bow-tie to the middle of the opaque growth bands at points along the internal edge of the corpus calcareum (Fig. 1). The vertebral radius (VR) of each centrum was measured from the midpoint of the isthmus to the distal margin of the intermedialia along the same diagonal as the band measurements.

The identity of the birth band in the vertebra was confirmed through comparison of the birth band radius (BR) measurements to vertebral radius measurements of late-term embryos, early young-of-the-year, and late age-0 fish.

The late-term embryo vertebral samples were obtained from the South Pacific porbeagle population, courtesy of Malcolm Francis.³ The assumptions were made that vertebral growth *in utero* was comparable between the two populations and that measurements of the rehydrated dried South Pacific vertebrae were similar to those from wet NW Atlantic preparations.

The relationship between VR and FL was calculated in order to confirm the interpretation of the birth band and to determine the best method for back-calculation of size-at-age data. The FL to VR relationship was curvilinear; therefore, the data were ln-transformed before linear regression. The Fraser-Lee equation of the ln-transformed data was derived for back calculation:

$$\frac{\ln(FL_a) = b + (\ln[FL_c] - b)(\ln radius_a)}{(\ln radius_c)}$$

where a = age;

b = intercept from the FL-VR regression; and

c = capture.

Validation

The accuracy of the vertebral band pair counts as annual indicators was determined by using both known-age recaptures and recaptures of oxytetracycline (OTC)-injected and tagged individuals. Vertebrae from young of the year (YOY) sharks whose FL was measured at both tagging and recapture were used for known-age analyses. Band pair counts were compared with time at liberty to determine band pair periodicity. One hundred and fifty-five porbeagles of various lengths were also tagged and injected with 25 mg/kg of OTC (senior author, unpubl. data). Returned vertebrae from these sharks were examined with reflected UV light for the OTC mark. The number of band pairs distal to the OTC mark were then compared with the number of years at liberty.

Data analysis

Aging bias and precision of annulus counts were examined by using age-bias plots and the coefficient of variation (Campana et al., 1995). Two readers independently counted 100 vertebral sections from which the pair-wise age-reader comparisons were generated.

Von Bertalanffy growth functions (VBGF) were fitted to the length-at-age data by using the following equation (von Bertalanffy, 1938):

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

where L_t = predicted length (cm) at age t ;

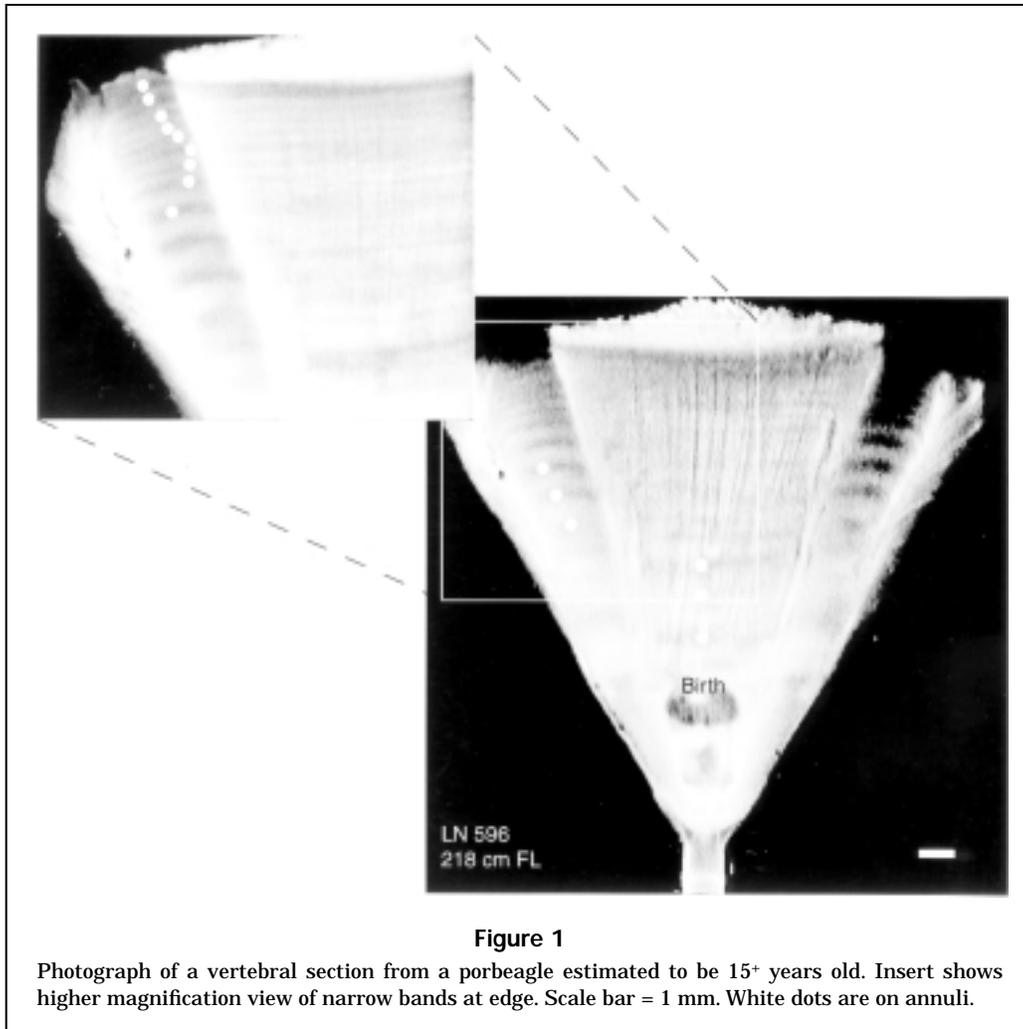
L_∞ = mean theoretical maximum fork length;

K = a growth rate parameter (per yr); and

t_0 = the theoretical age (yr) at zero length.

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

³ Francis, M. 2000. Personal commun. National Institute of Water and Atmospheric Research P.O. Box 14-901, Wellington, New Zealand.



The VBGF was calculated by using the nonlinear regression function in Statgraphics. Locally weighted least squares regression (LOESS) curves were fitted to the FL vs. age data for each sex by using Statgraphics (Manguitics, 1997).

Length frequency

Length-frequency data were obtained from the Canadian International Observer Program operating primarily on the Scotian Shelf, and some data from the Grand Banks. Although the entire data set (1986–98) was analyzed, only data from the most complete year (1991) were used for the final analysis.

Monthly length-frequency histograms were developed for eight months of 1991 for modal analysis. Calculations of mean fork length and annual growth rate for ages 0 and 1 were based on the first two modes of these data, which were easily distinguished and tracked across months.

MULTIFAN (Fournier et al., 1990) was used to estimate the VBGF parameters from the 1991 length-frequency data. The model analyzes multiple length-frequency

distributions by using a maximum likelihood method to estimate the number of age classes present and VBGF parameters L_{∞} and K . An initial systematic search was conducted based on user-supplied K values and age classes. Constraints were placed on the estimates of length at age for the first two age classes. MULTIFAN allows the user to start with a generalized search and then add parameters to further refine the model. The initial search included estimates of K ranging from 0.05 to 0.25 and age classes of 11 through 20. The hypotheses tested were the following: 1) constant length standard deviation for all age classes; 2) variable length standard deviation for all age classes; 3) constant length standard deviation for all age classes with seasonal growth; and 4) variable length standard deviation for all age classes with seasonal growth. A model incorporating constant length standard deviation was fitted first with the additional parameters added sequentially. Results from the four models were compared by using log-likelihood tests following Fournier et al. (1990) and Francis et al. (1999).

The von Bertalanffy growth parameter t_0 was estimated from the equation

$$t_0 = t_1 - a_1, \quad (1)$$

where a_1 = the age estimated by MULTIFAN for the youngest age class at the time it first appeared in the length-frequency samples; and

t_1 = the time elapsed in years between the theoretical birthday and the first appearance of the youngest year class in the samples.

The theoretical birthday was defined as 1 April based on the gestation period and the time of mating (Jensen et al.⁴). The first appearance of the youngest age class in the samples was 1 July.

The model with seasonal growth components required the use of a modified von Bertalanffy equation to incorporate the amplitude and phase of the seasonal growth:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0 + (\phi/2\pi)\sin(2\pi((12t+1)/12) - \phi_2))} \right), \quad (2)$$

where ϕ_1 = amplitude; and
 ϕ_2 = (MULTIFAN phase) + t_1 (from Eq. 1).

Tag-Recapture analysis

Data from three independent tagging studies from the western North Atlantic Ocean were combined for tag and recapture analysis. In the 1960s, 542 porbeagles were tagged and 53 recaptured as part of a Norwegian study of the unfished population. In 1994 through 1996, the Canadian Department of Fisheries and Oceans (DFO) conducted a tagging program in which 256 porbeagles were tagged and 25 recaptured. Between 1979 and 1999, members of the National Marine Fisheries Service's (NMFS) Cooperative Shark Tagging Program tagged 1034 and recaptured 119 porbeagles. Sharks were tagged and recaptured by biologists and commercial and recreational fishermen in the United States and Canada and by biologists in the Norwegian study. All measurements were converted to FL by using the morphometric conversions reported in Campana.¹ Where Norwegian measurements were reported as Aasen's (1963) total length, they were converted to FL with the equation:

$$FL = 0.93 TL.$$

Only those sharks reliably measured at the time of tagging and recapture were used in the analyses. Reliability was based on prior knowledge of the individual's expertise in measuring the shark or on detailed questioning of those individuals as to the method used. The majority of sharks were measured by NMFS biologists or their representatives.

The Gulland and Holt (1959) and Francis (1988a) models were used to generate VBGFs from the tag-recapture data. The Gulland and Holt (1959) method uses graphical interpretation of the recapture data to produce estimates of L_∞ and K . Specifically, annual growth rate (cm/yr) was plotted against average FL (cm) between tagging and recapture to calculate linear regression coefficients. The slope of the line is equal to $-K$ and the x-axis intercept is equal to L_∞ .

The Francis (1988a) method (GROTAG) uses maximum likelihood techniques to estimate growth parameters and variability from tagging data. With this method, a coefficient of variation of growth variability (v), the mean and standard deviation of measurement errors (m and s), and outlier contamination (p), are estimated as well as growth rates at two user-selected lengths (α and β). The reference lengths, α and β , were chosen to lie within the range of tagged individuals. The form of the von Bertalanffy equation becomes

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T} \right], \quad (3)$$

where L_1 = length at tagging;
 ΔL and ΔT = increments in length and time, respectively; and
 g_α and g_β = mean annual growth rates at the arbitrary lengths α and β .

The simplest model, with minimal parameters (α and β), was used initially with additional parameters added to successively increase model complexity. Significant improvement in the model results were determined by using log likelihood ratio tests (Francis, 1988a). The modeling was carried out by using a Solver-based spreadsheet in MS Excel (Simpfendorfer⁵).

The value of t_0 cannot be estimated from tagging data alone; rather it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VB-GF by solving for t_0 such that

$$t_0 = t + (1/K) \left[\ln \left\{ (L_\infty - L_t) / L_\infty \right\} \right], \quad (4)$$

where L_t = known length at age (size at birth);

The t_0 values were calculated from an average size at birth of 67 FL cm (Aasen, 1963) with $t = 0$.

Longevity

Several methods were used to estimate longevity. The oldest fish aged from the vertebral method provides an initial value, but is likely to be underestimated in a fished population. Taylor (1958) defined the life span of a teleost species as the time required to attain 95% of

⁴ Jensen, C., L. J. Natanson, H. L. Pratt Jr., N. E. Kohler, and S. Campana. 2001. The reproductive biology of the porbeagle shark, *Lamna nasus*, in the western North Atlantic Ocean. Unpubl. manuscript. Apex Predators Program, NMFS, 28 Tarzwell Dr., Narragansett, RI 02882.

⁵ Simpfendorfer, C. 2000. Unpubl. data. Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577.

the L_{∞} . Using a wide range of species, Hoenig (1983) calculated the relationship between longevity, t_{max} and the natural mortality rate, M , needed to attain one percent of initial abundance in an unfished population as

$$\ln(M) = 1.44 - 0.982 \ln(t_{max}).$$

However, a relationship based on other species need not be used (Campana et al.²). Assuming a constant instantaneous natural mortality, M , in an unfished population, the following equation applies:

$$\ln(\text{proportion of fish that survive to age } t_{max}) = -Mt_{max}$$

As with Hoenig (1983), this equation was evaluated at a value of 0.01 for the proportion of fish that survive.

Results

Vertebral aging

Vertebral samples from 578 porbeagles were used in our analysis; 283 were males, 292 were females, and 3 were of unknown sex. All vertebrae had distinct band-pair patterns (Fig. 1). The birth mark was indicated by a slight change in angle of the centra and was often the most pronounced first band pair. Subsequent annuli consisted of a pair of alternating opaque and translucent bands that crossed the entire centrum, except in the oldest sharks. Band-pair width decreased with age, narrowing substantially in the oldest individuals (Fig. 1).

The FL-VR relationship was curvilinear (Fig. 2), and although the ln-transformed relationship was not completely linear, it was preferable. Therefore, regressions were calculated based on the ln(FL)-ln(VR) relationship where

$$\ln(\text{FL}) = 0.88 \times \ln(\text{VR}) + 2.96 \quad [r^2=0.94, n=575].$$

There was no significant difference between the regressions of males and females (ANCOVA, $P>0.01$).

The identity and location of the birth band was confirmed through comparison of the BR of all individuals to the VR of YOY and embryos. The mean VR of three late-term embryos ranging in size from 56.1 to 58 cm FL (mean VR=4.3 mm, CI=0.57) was slightly less than the mean BR value of the total sample (mean BR=5.4 mm, CI=0.03 mm, $n=578$). The mean BR those of two early YOY (67.7 and 69.2 cm FL) were also similar to those of the total sample (mean VR=5.3 mm, CI=1.27 mm). The VR of the age-0 individuals ranging in size from 76.5 to 100 cm FL (mean VR=6.2 mm, CI=0.31 mm, $n=16$) was slightly higher (Fig. 2). The placement of the mean BR between the VR of both the YOY and embryos in-

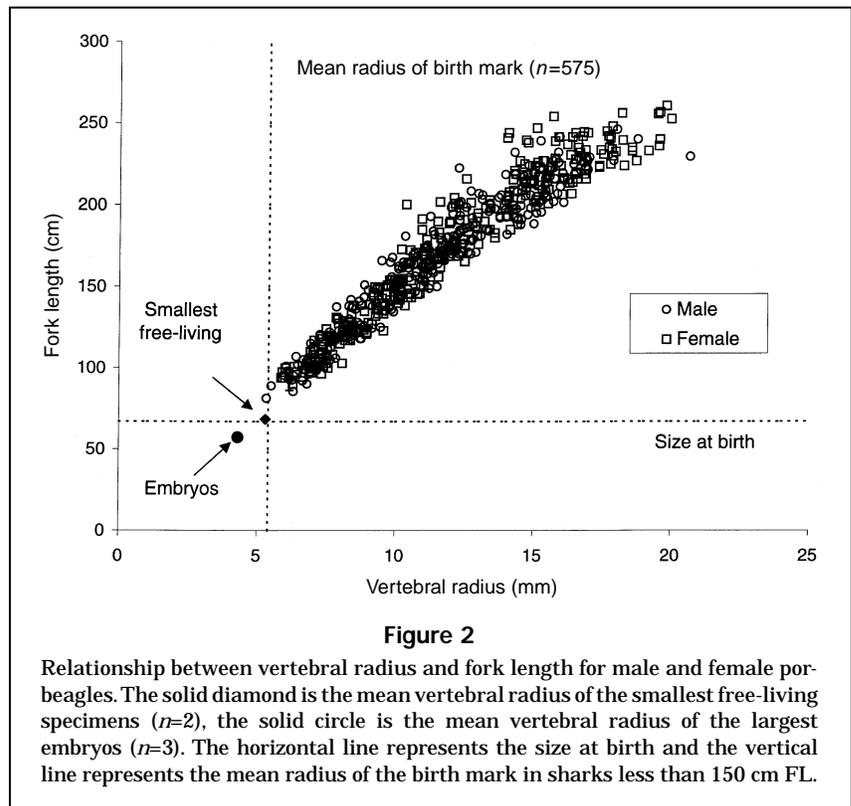


Figure 2

Relationship between vertebral radius and fork length for male and female porbeagles. The solid diamond is the mean vertebral radius of the smallest free-living specimens ($n=2$), the solid circle is the mean vertebral radius of the largest embryos ($n=3$). The horizontal line represents the size at birth and the vertical line represents the mean radius of the birth mark in sharks less than 150 cm FL.

icates that the birth ring was identified correctly. The birth ring radius increased slightly with increasing FL likely because of an increase in the length of the isthmus of the bow-tie section in larger sharks.

Validation

Known-age recaptured porbeagles and OTC-injected recaptured porbeagles returned with vertebrae confirmed the accuracy of the band-pair counts as indicators of age. Six porbeagles tagged as YOY were recaptured after three to five years at liberty (Table 1). Of the four sharks that were recaptured in the spring, all had translucent material at their growing edge. In contrast, the two sharks recaptured in November had a broad opaque zone at the growing edge. In each case, the vertebral band-pair counts matched the expected counts based on time at liberty (Fig. 3). Vertebrae from six OTC-injected sharks were returned after 0.02 to 2.5 years at liberty. All vertebrae showed a distinct fluorescent mark indicating that the OTC was incorporated within six days (0.02 years) of injection (Fig. 3). Two of the OTC-injected sharks were at liberty for over one year and were used for validation. In both cases, the expected number of growth bands was deposited on the vertebrae between the date of injection and the date of recapture (Table 1). The shark at liberty for 2.5 years had 3 full bands after the OTC mark, the last band having formed just prior to capture. The OTC-injected shark at liberty for 1.5 years was an adult (189.8 cm FL) at tagging and was aged, by vertebrae, to be 11 years at recapture. This

Table 1

Tag-recapture data for the OTC-injected and known-age recaptured porbeagles with vertebrae. TFL = fork length at tagging, RFL = fork length at recapture.

	Sample number	Sex	TFL (cm)	RFL (cm)	Date tagged	Date recaptured	Years at liberty	Growth (cm)	No. of bands past birth mark
Known age	LN 207	F	104.0	178.0	10 Nov 1993	23 Apr 1999	5.4	74.0	6
	553	M	85.0	160.0	1 Nov 1994	9 Nov 1999	5.2	75.0	5
	206	M	100.0	153.0	24 Oct 1994	27 May 1999	4.6	53.0	4
	556	F	97.0	154.0	17 Nov 1995	19 Nov 1999	4.0	57.0	4
	185	F	89.7	148.5	17 Nov 1995	29 Mar 1999	3.4	58.8	4
	183	F	94.2	145.0	17 Nov 1995	23 Mar 1999	3.3	50.8	4
								No. of bands past OTC mark	
OTC-injected	LN 171	M	118.0	156.0	16 Sep 1996	30 Mar 1999	2.5	38.0	3
	172	M	189.8	187.0	27 Sep 1997	29 Mar 1999	1.5	-2.8	1+
	473	F	104.0	117.0	15 Apr 1999	21 Nov 1999	0.6	13.0	—
	184	M	147.5	152.0	21 Oct 1998	30 Mar 1999	0.4	4.5	—
	204	M	105.0	95.0	23 Mar 1999	23 May 1999	0.2	-10.0	—
	173	F	96.5	96.0	26 Sep 1997	2 Oct 1997	0.02	-0.5	—

shark had one full band and 83% growth of the next band, based on the size of the last full band. This, along with the YOY known-age individuals, confirmed annulus formation and our band interpretation from birth to 11 years of age. Sharks older than age 11 were assumed to have been aged correctly due to a similar interpretation of the bands.

Data analysis

Comparisons of counts between the two readers indicated no appreciable bias (Fig. 4). The coefficient of variation for age 1+ sharks was approximately 15%. In the absence of bias, this level of precision was considered acceptable; thus the counts generated by one reader for the entire set of vertebrae were used for the analyses.

Length-at-age data showed that males and females grow at similar rates until approximately 170 cm FL, at which point the relative growth rate of the males declines (Fig. 5). The change in relative growth between the sexes coincides with the size and age of male maturity (Jensen et al.⁴). Von Bertalanffy growth functions fitted to the vertebral band-pair count data suggested that males attain a smaller maximum size than females (Table 2). The growth rate of females also declined at size at maturity (approximately 218 cm FL; Jensen et al.⁴). The considerable overlap in size at age between the sexes indicated that the difference in growth rate is minor; therefore subsequent comparisons were made for the sexes combined.

Tag-Recapture analysis

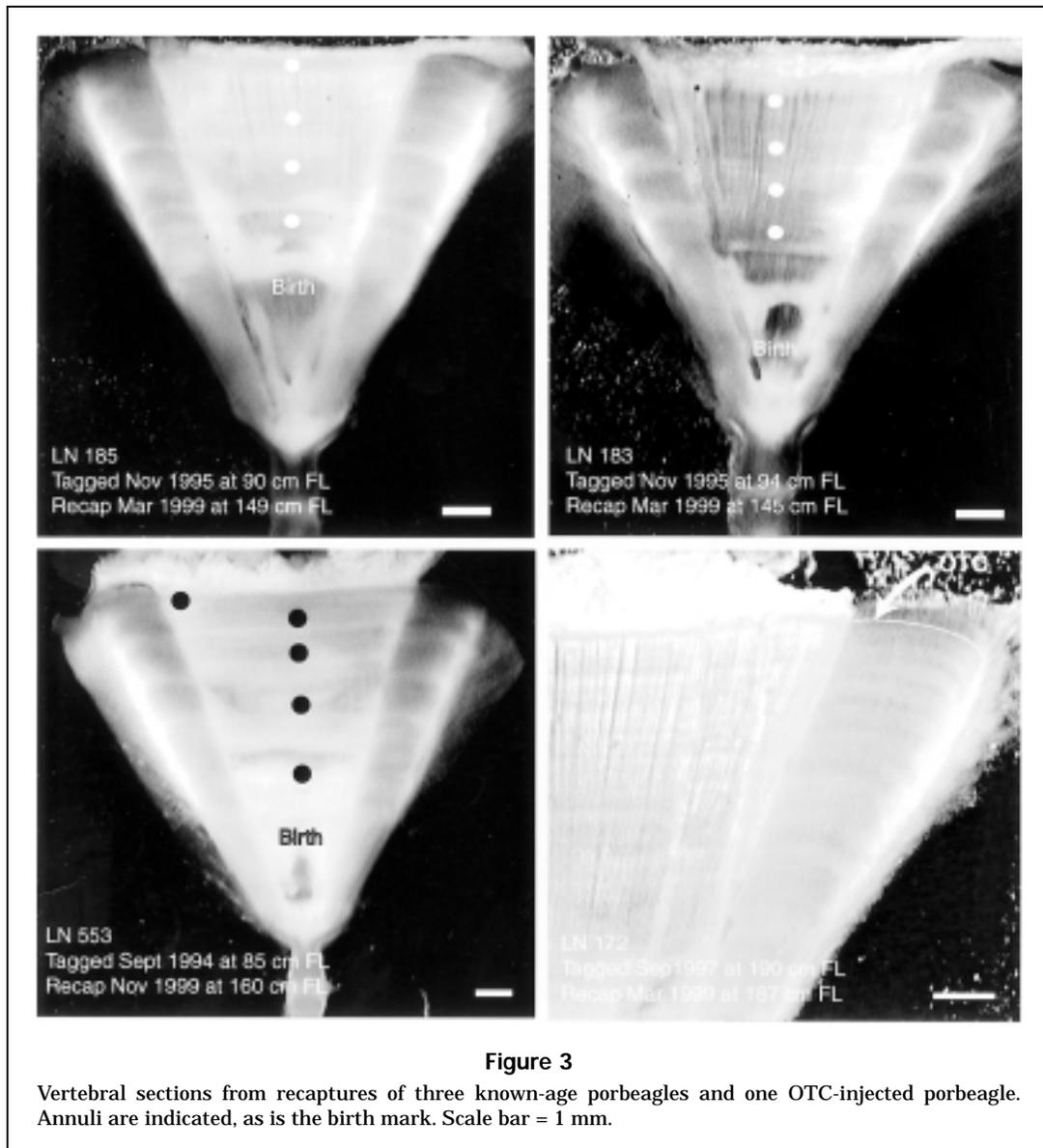
A total of 76 porbeagles was recaptured with sufficient information for tag-recapture analysis. Time at liberty

ranged from 0.02 to 6.0 years and size at tagging ranged from 78 to 204 cm FL. Sharks were tagged and recaptured in all months of the year. Tagging effort was fairly evenly distributed throughout all months, whereas most recaptures were made between March and May (53%). For both tagging and recapture, January and February were represented by the least data (3% and 1% for tagging and recapture, respectively). More tags were released in December than were recaptured (12% of the tags but only 2% of the recaptures). Most tagged sharks were small (74% <150 cm FL) because the majority were opportunistically tagged onboard commercial fishing vessels. Data from 54 sharks at liberty greater than 0.9 years were used in the Gulland and Holt (1959) analysis, whereas all individuals were used for GROTAG (Francis 1988a).

The results of the likelihood ratio tests with GROTAG (Francis, 1988a) demonstrated that the more complex non-linear model with five of the six parameters included was the best fit for these data (model 3, Table 3). The high value of *s* suggests a lack of sufficient information for GROTAG (Francis, 1988a) to distinguish between growth variability and measurement variability (Francis and Mulligan, 1998). The mean annual growth rates at FL= 95 cm and 150 cm were 19.21 cm/yr and 9.52 cm/yr, respectively (Fig. 6). Von Bertalanffy estimates from the Gulland and Holt (1959) and GROTAG (Francis, 1988a) methods produced similar results (Tables 2 and 4).

Length frequency

Analysis of modal length-frequency progressions verified the size at age and growth rate of age-0 and age-1 individuals (Fig. 7). Age-0 fish entered the fishery in July with



a mean length of 85 cm FL and grew to a mean length of 98 cm FL by December. Age-1 individuals had a mean length of 106 cm FL in April, 113 cm FL in July, and 123 cm FL in December, resulting in an annual growth of 25 cm/yr between December and December. Although larger length modes were occasionally visible, only the age-0 and age-1 modes were clear and unambiguous throughout the year.

The MULTIFAN models that best fitted the 1991 data were the most complex, having variable standard deviations in length and variable seasonal growth. The data with sexes combined had 18 age classes, whereas males and females had 16 and 15 age classes, respectively. The MULTIFAN L_{∞} and K von Bertalanffy parameters fell outside the 95% confidence intervals for the tagging and vertebral studies, although the t_0 values did not (Table 2).

These differences are reflected in the VBGF curves as compared with the other methods (Fig. 8). The annual growth rate calculated from the MULTIFAN data was consistent with that of the vertebral and tag-recapture analyses at 150 cm FL (Fig. 6). However, the reliability of the MULTIFAN results is questionable given the large number of age classes in the population. The standard error estimates calculated by MULTIFAN were not reported because they were unrealistically low (Francis and Francis, 1992; Francis and Mulligan, 1998).

Longevity

The maximum ages based on vertebral band pair counts were 25 and 24 years for males and females, respectively. These ages likely underestimate longevity, given the long-

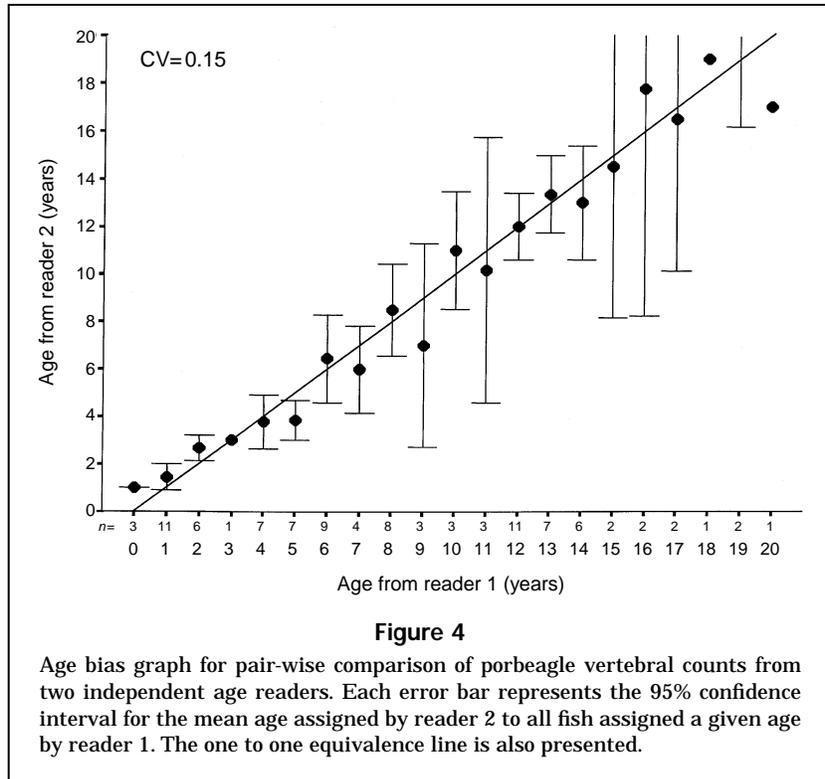


Table 2

Von Bertalanffy growth function parameters and 95% confidence intervals calculated by using vertebral, tag-recapture, and length-frequency methods. Confidence intervals (CI) are not shown for the MULTIFAN parameters. ϕ_1 , ϕ_2 , are seasonal parameters and t_1 is the time (years) between the theoretical birthday and recruitment to the fishery for the MULTIFAN analyses.

Method		L_∞	K	t_0	n	ϕ_1	ϕ_2	t_1
Vertebral	Combined	289.4	0.066	-6.06	576			
	CI	±16.5	0.010	0.71				
	Male	257.7	0.080	-5.78	283			
	CI	±15.6	0.015	0.92				
	Female	309.8	0.061	-5.90	291			
	CI	±26.2	0.013	0.93				
MULTIFAN	Combined	320.1	0.054	-5.33	13,589	0.95	0.76	0.25
	Male	280.2	0.076	-4.42	7142	0.95	0.92	0.25
	Female	419.0	0.039	-5.45	6269	0.95	0.89	0.25
Gulland and Holt (1959)	Combined	212.5	0.172	-2.21	54			
	CI	±31.7	0.089					
GROTAG	Combined	204	0.194	-2.05	76			

term fishery for this species. Taylor's (1958) method, the age at which 95% of the L_∞ is reached, provided a value of 26 years. However, more realistic estimates of longevity take advantage of estimated mortality rates. Given $M=0.10$ (Campana et al.¹), Hoenig's (1983) equation based on multiple species resulted in a longevity estimate of 45 years. The estimate of Campana et al.² was species-inde-

pendent and was calculated by assuming a constant instantaneous rate of mortality = 0.10 in an unfished population. The resulting longevity estimate was 46 years. Each of these methods assumes that M is constant throughout the lifetime of a fish, whereas in fact, it probably increases in sexually mature or senescent fish. Any such increase would result in a lower estimate of longevity. Based on prelim-

Table 3

Log-likelihood function values and parameter estimates for four growth models fitted to porbeagle tagging data by using GROTAG (Francis 1988a). For a significant ($P < 0.05$) improvement in fit, the introduction of one extra parameter must increase λ by at least 1.92 (Francis 1988a). * indicates fixed parameters.

Parameter	Symbol (unit)	Model		
		1	2	3
Log likelihood	λ	-292.04	-291.97	-285.45
Mean growth rates	g_{95} (cm/yr)	19.12	17.92	19.21
	g_{150} (cm/yr)	9.47	8.88	9.52
Measurement error	s (cm)	10.48	10.92	9.43
	m (cm)	0*	0.99	1.00
Outliers	p	0*	0*	0.07

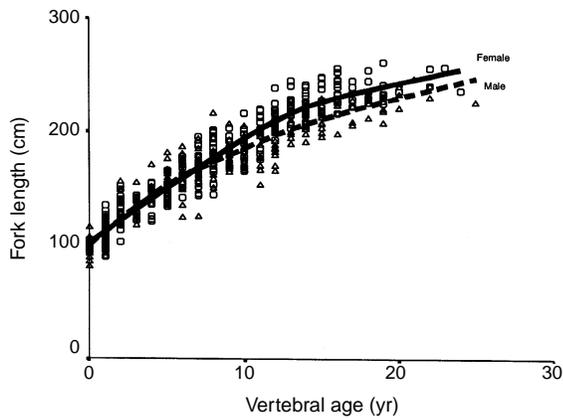


Figure 5

Porbeagle growth data based on vertebral band counts. LOESS curves have been fitted to the data by sex. Open circles represent males, open triangles represent females.

inary results suggesting an increase in female natural mortality rate (to 0.20) at the age of sexual maturity (Campana⁶), longevity would be estimated at 29 years.

Discussion

Age and growth studies of lamnoids have often been confounded because of the continued debate over the periodicity of band-pair formation. Parker and Stott (1965) first

⁶ Campana, S. 2001. Unpubl. data. Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

Table 4

Size at age for the porbeagle (*Lamna nasus*) calculated from von Bertalanffy equations based on tag-recapture, length-frequency, and vertebral data.

Age (years)	Size (cm, FL)			
	Vertebral	MULTIFAN	Tag-recapture	
			Gulland and Holt (1959)	GROTAG
0	95	82	67	67
1	107	94	90	91
2	119	106	109	111
3	130	117	126	127
4	140	128	139	141
5	149	138	151	152
6	158	148	161	161
7	166	157	169	169
8	174	165	176	175
9	181	174	181	180
10	188	181	186	184
11	195	189	190	188
12	201	195	194	191
13	206	202	197	193
14	212	208	199	195
15	217	214	201	197
16	221	220	203	198
17	226	225	205	199
18	230	230	206	200
19	233		207	201
20	237		208	201

suggested that two growth band pairs formed each year (biannual band-pair deposition) in their study of the basking shark (*Cetorhinus maximus*). Pratt and Casey (1983) assumed biannual band-pair deposition for shortfin mako shark, *Isurus oxyrinchus*, based on consistency with length-frequency and tag-recapture analyses. Branstetter and Musick (1994) also suggested biannual band-pair deposition for the sand tiger shark, *Carcharias taurus*, based on marginal increment analysis (MIA) and examination of aquarium-reared sharks. Cailliet et al. (1983, 1985) assumed annual band-pair deposition for Pacific coast shortfin mako and white sharks, *Carcharodon carcharias*, based on marginal increment analysis. Wintner and Cliff (1999) stated that they could not determine band periodicity using marginal increment analysis in the white shark off the coast of South Africa, although one OTC-injected recapture suggested annual deposition. With the exception of Winter and Cliff (1999), direct validation of band periodicity, such as by OTC injection or by known-age tag-recaptures, has not previously been reported in lamnids. Although several studies have attempted validation with MIA (Branstetter and Musick, 1994; Wintner and Cliff, 1999), this technique is not

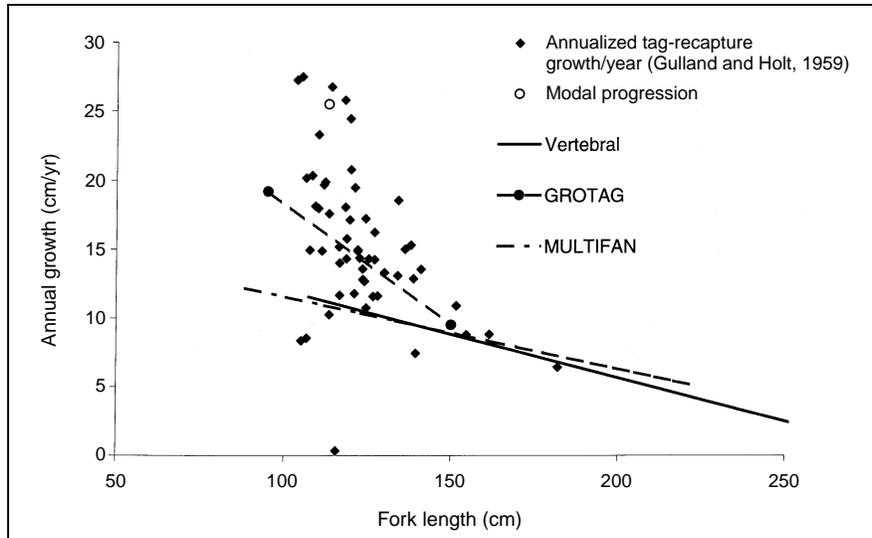


Figure 6
Comparison of the annual growth rate of the porbeagle shark by using multiple aging methods.

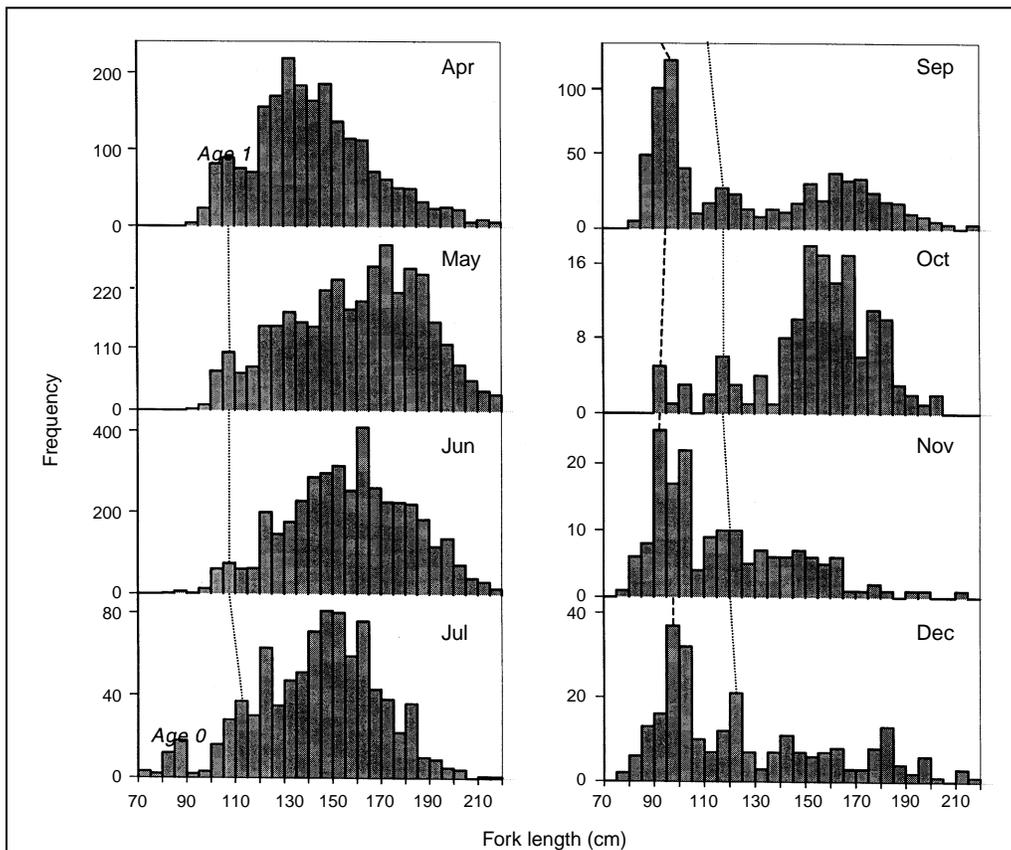
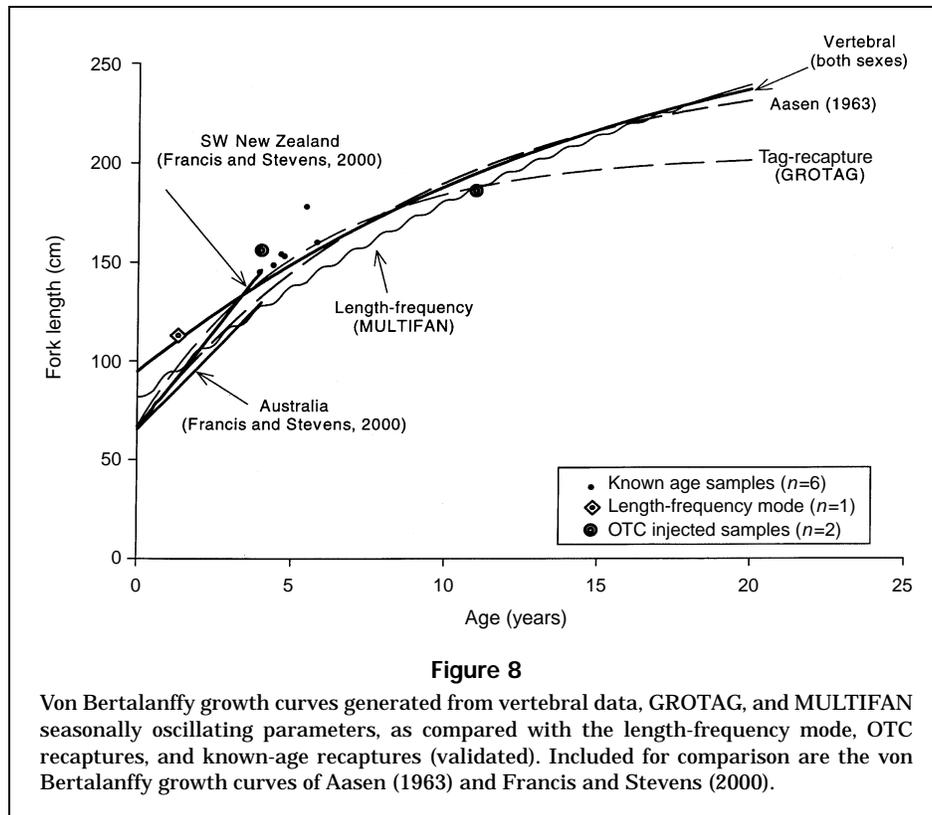


Figure 7
Monthly progressions of age-0 and age-1 length-frequency modes collected by observers in the 1991 Scotian Shelf fishery.



well suited to slow growing species because the narrowness of the bands at the margin makes it difficult to objectively determine marginal growth.

In the present study, we validated annual band-pair periodicity up to age 11 using recaptures of both OTC-injected and known-age porbeagles. Our data clearly indicated that the vertebral band pairs are deposited annually and that the translucent zone is deposited between November and April.

Validation of an annual frequency of band-pair formation confirms Aasen's (1963) interpretation of the vertebral growth zones in the porbeagle. Our size at birth generated from the vertebral bands (95 cm FL), however, was unrealistically high. This may have been due to our sample of age-0 fish being biased towards the faster growing, larger fish that were recruited first into the fishery. The early portion of our growth curve, corresponding to ages 0 and 1, may therefore have been overestimated (Fig. 8).

Francis (1988b) suggested that growth curves derived from age-length and length-increment data were not directly comparable and that the comparison of growth rates at length was more appropriate. The growth rates at L_{150} were similar for all methods, verifying the growth rate at this size. However, the overall growth curves from the different methods were also similar (Fig. 8). The tag-recapture curve shows a more reasonable early growth than the vertebral curve but levels off well below the observed maximum size. The lower L_{∞} and higher K for the tag-recapture method was expected because of the different derivation of the parameters and the absence of recaptured old

sharks (Francis, 1988b). The K and t_0 parameters derived from MULTIFAN are close to those obtained by using vertebral ages, and the scatter in the age readings overlaps the MULTIFAN von Bertalanffy curve (Figs. 5 and 8). Although the MULTIFAN L_{∞} value was slightly higher than that of the vertebral value (Table 2), a difference at the upper end of these curves was not unexpected because length-frequency models are generally considered unreliable for the older age classes where the modes are not easily defined (Francis and Francis, 1992; Francis, 1997; Francis et al., 1999).

Maturity occurs in the porbeagle at 8 and 13 years of age (174 and 218 cm FL, males and females, respectively; Jensen et al.⁴). Growth for both sexes is similar up to the size of male maturity, whereupon, the male growth rate is reduced. Females continue to grow rapidly until the onset of maturity, at which point their growth slows as well (Fig. 5). Owing to this change in growth rate, males reach a smaller maximum size than females; however, the overall growth rate for both sexes is not substantially different. Additionally, the vertebral L_{∞} generated for females is higher than what is being observed in the fishery, suggesting that it has been overestimated and that the combined curve is more appropriate. Aasen⁷ (1963) also found no difference in the growth rate between the sexes although the basis for his conclusion is questionable.

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

Aasen (1963) relied extensively on length-frequency modes to estimate the growth of porbeagle. Although his modes were similar to ours, his interpretation of the age-1 mode differed. Our data indicated that age-0 porbeagle average 85 cm FL in July. Aasen (1963) interpreted this same mode (91 cm FL) as age 1+, thus shifting his ages by one year. Neither Aasen's (1963) modal distribution (his Fig. 4) nor ours, supports the contention that this first mode is age 1+. His classification of these fish as age 1+ was based on size at birth and his opinion that the smallest measured fish were from the age-0 group. There is, however, no mode at this small size. Any age-0 fish born in April and caught between July and September (his sampling period) would certainly be larger than the birth size. Therefore, we feel that these fish represented the faster growing age-0 fish that were large enough to be caught with commercial longline gear. Francis and Stevens (2000) also used length-frequency analysis to estimate the growth rate of porbeagles in the South Pacific. Although their modes were once again comparable to ours, their age 1+ fish were similar in size to our age-0+ fish (Fig. 8). In their view, this first mode represented slow growing age-1 individuals rather than fast growing age-0 individuals. As an alternative explanation, we suggest that the first mode in both the southwest and northeast New Zealand samples represents YOY that have grown during the 4-month sampling period, thus accounting for the apparent absence of individuals close to a birth size. This alternative explanation would also explain why the modal analysis of the Australian sample shows a strong peak at birth and subsequent modes that are similar to ours. If correct, our interpretation of the Francis and Stevens (2000) data would bring their estimates of size at age and growth rate in line with ours. Of course, the comparison of growth rates from such widely separated stocks is difficult, and its value questionable.

Longevity estimates for the porbeagle indicate that they may live for more than 40 years. The maximum time at liberty for any tagged porbeagle is 13 years (Stevens, 1990). The length of this shark when tagged was approximately 120 cm TL (107 cm FL; 1+ years); it was recaptured at an estimated 225 cm FL (age 14+) which would correspond to an age of 16+ years according to our vertebral growth curve. This is substantially less than the oldest observed age from vertebrae (25) and the estimates from the Hoenig (1983) and Campana et al.² methods of 45 and 46 years, respectively.

The growth rate and longevity of the porbeagle are similar to those of other lamnids. Wintner and Cliff (1999) calculated a K value of 0.065 for the white shark from the east coast of South Africa, and Cailliet et al. (1985) estimated a K value of 0.058 for the same species off the coast of California. Both estimates are very similar to the K value of 0.066 calculated for porbeagle in our study. Shortfin mako K values have been estimated at 0.072 (Cailliet et al., 1983) and 0.266 (Pratt and Casey, 1983); however the Pratt and Casey value was based on the assumption that two band pairs were deposited annually. Longevity estimates have ranged between 27 years for the California white shark (Cailliet et al., 1985) and 45 years for the shortfin mako in the Pacific (Cailliet et al., 1983).

Comprehensive age and growth studies of pelagic sharks are difficult to implement because many species are highly migratory and are caught sporadically as part of seasonal fisheries. Thus, aging studies of pelagic sharks have usually been less rigorous than desired, despite the oft-repeated call for age validation (Beamish and McFarlane, 1983; Cailliet et al., 1986, Cailliet, 1990). Previous studies on pelagic species such as the blue shark (Stevens, 1975; Cailliet et al., 1983), white shark (Cailliet et al., 1985), thresher (Cailliet et al., 1983), shortfin mako (Cailliet et al., 1983), pelagic thresher (Liu et al., 1999), oceanic whitetip shark (Lessa et al., 1999), and porbeagle (Aasen, 1963; Francis and Stevens, 2000), have included analyses of ages determined by vertebral or length-frequency analyses (or by both methods), but none of the age interpretations were validated. Wintner and Cliff (1999) used vertebral counts and had one OTC-injected recapture but were unable to provide validation or consistency with other methods. Pratt and Casey (1983) aged the shortfin mako by using four methods (temporal analysis of length-month information, tag-recapture data, length-frequency data, and vertebral band counts) but could not validate their age interpretations. The conclusion that band pairs were deposited biannually was based on vertebrae from four tag-recaptures and consistency between methods. Skomal (1986) aged the blue shark in the western North Atlantic using a combination of vertebral, length frequency and tag-recapture methods for verification. Although Skomal (1986) had two OTC-injected recaptures, they provided conflicting results for validation. The present study is the first that has used validated vertebral band-pair counts in conjunction with length-frequency and tag-recapture analyses to provide consistent and accurate age estimates for a pelagic shark species. We suggest that a similar approach would be useful in studies of other pelagic shark species.

Acknowledgments

We thank Clearwater Fine Foods, Karlsen Shipping, the Atlantic Shark Association, and Stephanie Jane, Inc. for providing access to their fishing vessels. We also thank Andy Kingman, Christopher Jensen, and Warren Joyce for collecting samples. Malcolm Francis kindly provided vertebrae from porbeagle embryos as well as much appreciated knowledge on the procedures associated with MULTIFAN. Colin Simpfendorfer's assistance and spreadsheet were invaluable during the use of GROTAG. Nancy Kohler and Sabine Wintner provided invaluable comments on the manuscript. We are indebted to the thousands of fishermen who voluntarily tag and return tags to us and thus make tagging programs possible.

Literature cited

- Aasen, O.
1963. Length and growth of the porbeagle (*Lamna nasus*, Bonnetterre) in the North West Atlantic. Fisk. Skrift. Ser. Havund. 13(6):20-37.

- Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112:735-743.
- Branstetter, S. and J. A. Musick.
1994. Age and growth estimates for the sand tiger in the north-western Atlantic Ocean. *Trans. Am. Fish. Soc.* 123:242-254.
- Cailliet, G. M.
1990. Elasmobranch age determination and verification: an updated review. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries* (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds.), p. 157-165. U.S. Dep. Commer., NOAA Tech. Rep. 90.
- Cailliet, G. M., L. K. Martin, J. T. Harvey, D. Kusher, and B. A. Welden.
1983. Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. In *Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, bill-fishes, and sharks* (E. D. Prince and L. M. Pulos, eds.), p. 179-188. U.S. Dep. Commer., Tech. Rep. NMFS 8.
- Cailliet, G. M., L. J. Natanson, B. A. Welden, and D. A. Ebert.
1985. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. *Mem. S. Calif. Acad. Sci.* 9:49-60.
- Cailliet, G. M., R. L. Radtke, and B. A. Welden.
1986. Elasmobranch age determination and verification: a review. In *Indo-Pacific fish biology: proceedings of the second international conference on Indo-Pacific fishes* (T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds.), p. 345-360. Ichthyol. Soc. Japan, Tokyo.
- Campana, S. E., M. C. Annand, and J. I. McMillan.
1995. Graphical and statistical methods for determining the consistency of age determinations. *Trans. Am. Fish. Soc.* 124:131-138.
- Castro, J. I.
1983. The sharks of North American waters. Texas A&M Univ. Press, College Station, TX, 180 p.
- Compagno, L. J. V.
1984. FAO species catalogue. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Part 1: Hexanchiformes to Lamniformes. FAO Fish Synop. 125, vol. 4, 250 p.
- Fournier, D. A., J. R. Sibert, J. Majkowski, and J. Hampton.
1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). *Can. J. Fish. Aquat. Sci.* 47:301-317.
- Francis, M. P.
1997. Spatial and temporal variation in the growth rate of elephantfish (*Callorhynchus milii*). *NZ J. Mar. Freshwater Res.* 31:9-23.
- 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.
- Francis, M. P., and K. P. Mulligan.
1998. Age and growth of New Zealand school shark, *Galeorhinus galeus*. *NZ J. Mar. Freshwater Res.* 32:427-440.
- Francis, M. P., K. P. Mulligan, N. M. Davies, and M. P. Beentjes.
1999. Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*. *Fish. Bull.* 97:227-242.
- Francis, M. P., and J. D. Stevens.
2000. Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the southwest Pacific Ocean. *Fish. Bull.* 98:41-63.
- Francis, R. I. C. C.
1988a. Maximum likelihood estimation of growth and growth variability from tagging data. *NZ J. Mar. Freshwater Res.* 22:43-51.
1988b. Are growth parameters estimated from tagging and age-length data comparable? *Can. J. Fish. Aquat. Sci.* 45:936-942.
- Gulland, J. A., and S. J. Holt.
1959. Estimation of growth parameters for data at unequal time intervals. *J. Cons. Int. Explor. Mer* 25:47-49.
- Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 81:898-903.
- Kohler, N. E., J. G. Casey, and P. A. Turner.
1995. Length-weight relationships for 13 species of sharks from the western North Atlantic. *Fish. Bull.* 93(2):412-418.
- Lessa, R., F. M. Santana, and R. Paglerani.
1999. Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic. *Fish. Res.* 42:21-30.
- Liu, K. M., C. T. Chen, T. H. Liao, and S. J. Joung.
1999. Age, growth and reproduction of the pelagic thresher shark, *Alopias pelagicus* in the Northwestern Pacific. *Copeia* 1999(1):68-74.
- Media Cybernetics.
1998. Image Pro 4 software. Media Cybernetics, Silver Spring, MD.
- Parker, H. W. and F. C. Stott.
1965. Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). *Zool. Meded.* 40(34): 305-319.
- Pratt, H. L., Jr., and J. G. Casey.
1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. *Can. J. Fish. Aquat. Sci.* 40(11): 1944-1957.
- Skomal, G.
1986. Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. Master's thesis, Univ. Rhode Island, Kingston, RI, 82 p.
- Statgraphics.
1997. Statgraphics Plus, version 3. Manguistics, Inc., Rockville, MD.
- Stevens, J. D.
1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *J. Mar. Biol. Assoc. U.K.* 55:657-665.
1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. *J. Mar. Biol. Assoc. U.K.* 70: 707-720.
- Taylor, C. C.
1958. Cod growth and temperature. *J. Cons. Int. Explor. Mer* 23:366-370.
- von Bertalanffy, L.
1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* 10:181-213.
- Wintner, S. P., and G. Cliff.
1999. Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. *Fish. Bull.* 97(1):153-169.