Abstract—Age and growth estimates for salmon sharks (*Lamna ditropis*) in the eastern North Pacific were derived from 182 vertebral centra collected from sharks ranging in length from 62.2 to 213.4 cm precaudal length (PCL) and compared to previously published age and growth data for salmon sharks in the western North Pacific. Eastern North Pacific female and male salmon sharks were aged up to 20 and 17 years, respectively. Relative marginal increment (RMI) analysis showed that postnatal rings form annually between January and March. Von Bertalanffy growth parameters derived from vertebral length-at-age data are L_∞=207.4 cm PCL, k=0.17/yr, and t_0=−2.3 years for females (n=166), and L_∞=182.8 cm PCL, k=0.23/yr , and t_0=−1.9 years for males (n=16). Age at maturity was estimated to range from six to nine years for females (median precaudal length of 164.7 cm PCL) and from three to five years old for males (median precaudal length of 124.0 cm PCL). Weight-length relationships for females and males in the eastern North Pacific are W=8.2×10^{-05}×$L^{2.759}$ (r^2=0.99) and W=3.2×10^{-06}×$L^{3.383}$ (r^2=0.99), respectively. Our results show that female and male salmon sharks in the eastern North Pacific possess a faster growth rate, reach sexual maturity earlier, and attain greater weight-at-length than their same-sex counterparts living in the western North Pacific.

Growth and maturity of salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific, and comments on back-calculation methods

Kenneth J. Goldman

Alaska Department of Fish and Game
3298 Douglas Place
Homer, Alaska 99603
E-mail address: ken_goldman@fishgame.state.ak.us

John A. Musick

College of William & Mary, School of Marine Science
Virginia Institute of Marine Science
Route 1208, Greate Road
Gloucester Point, Virginia 23062

The salmon shark (*Lamna ditropis*) is a large apex predator inhabiting the coastal and oceanic waters of the North Pacific Ocean, most commonly ranging from 65°N latitude to 35°N in the west and to 30°N in the east (Strasburg, 1958; Neave and Hanavan, 1960; Compagno, 1984, 2001; Blagoderov, 1994; Nagasawa, 1998). It is found individually and in large aggregations at sea-surface temperatures of 5°C to 18°C and has a depth distribution ranging from the surface to at least 150 m (Compagno, 1984, 2001). The salmon shark is a highly opportunistic predator, feeding on a wide variety of prey and sharing the highest trophic level of the food web in boreal and temperate North Pacific waters with marine mammals and seabirds (Brodeur, 1988; Nagasawa, 1998). Adult salmon sharks typically range in size from 180–210 cm precaudal length (PCL; = 200–260 cm total length, TL) and can weigh up to 220 kg (Tanaka, 1980; JAMARC, 1980; Nagasawa, 1998). Reported lengths of 300 cm TL and greater and weights exceeding 450 kg are unsubstantiated.

Salmon sharks are migratory in nature. North-south migrations have been documented on both sides of the North Pacific; northern movements occur in spring and southern movements are occur in autumn (Iino, 1939; Kosugi and Tsuchisaki, 1950; Gorbatenko and Cheblukova, 1990; Balgaderov, 1994; Nakano and Nagasawa, 1994). However, this species is present in boreal waters throughout the year (Goldman and Human, in press; Weng et al., 2005). Salmon sharks tagged with satellite transmitters have shown an extremely wide range of movements throughout the eastern North Pacific—movement as far south as southern California and Hawaii (Weng et al., 2005). To date, however, no salmon shark has been recorded moving across the Pacific, but such movements are suspected to occur (Nakano and Nagasawa 1996; Goldman and Musick, in press; Weng et al., 2005)

Sexual segregation is relatively common in sharks; however an extremely large sex ratio difference exists in salmon sharks across the North Pacific basin (Sano, 1962; Nagasawa, 1998; Goldman and Musick, in press). The western North Pacific (WNP) is male dominated and the eastern North Pacific (ENP) is female dominated. Male dominance in the WNP and female dominance in the ENP increase with increasing latitude. Larger sharks range farther north than smaller individuals, and

southern catches generally occur in deeper waters (Nagasawa, 1998; Goldman and Musick[1]).

Shark catches in Alaska waters have been reported to be as high as those from Washington, Oregon and California combined (Camhi, 1999), and there is concern over the amount of shark bycatch being taken (Gaichas[2]). In 1997, state managers closed commercial shark fishing in Alaska state waters and imposed conservative sport-fishing limits (1 shark per person per day, 2 per year) that legally encompass federal waters too. Federal managers are currently addressing elasmobranch management issues (Goldman, 2001).

Because of the ever-increasing importance of providing accurate and timely life history parameters to foster responsible management efforts, we had two main objectives in our study. The first was to estimate growth parameters and the age and length at sexual maturity of salmon sharks in the ENP. The second was to compare our results to those previously published on salmon sharks from the WNP to elucidate any existing variability in the life history parameters of this highly sexually segregated population. Lastly, because of the small number of samples for female juvenile age classes, a small overall sample size for males, and the fact that samples (for both sexes) were not obtained for each month, we applied several back-calculation methods to our data (see Cailliet and Goldman, 2004 and Goldman, 2004) and provide a demonstration and brief discussion on the importance of choosing an appropriate back-calculation method.

Materials and methods

Salmon shark vertebrae were obtained from numerous sources and locations ranging geographically from southern California to Kodiak Island (n=182) between 1997 and 2002. The majority of samples came from research cruises in the Gulf of Alaska (GOA) and Prince William Sound (PWS), by accompanying sport-fishing vessels on salmon shark trips in the GOA and PWS, and from Alaska Department of Fish and Game (ADF&G) port samplers. Vertebral samples collected from British Columbia to southern California came from incidental catches and recently beached animals.

Precaudal, fork, and total length (PCL, FL, and TL) were measured on a straight line and recorded along with date, location, and sex (and clasper length in males). Samples provided by additional sources included at least one of the necessary straight-line measurements, date and location of capture or wash-up, and sex. Weights were obtained from 20 females ranging from 67.1 to 213.4 cm PCL, and 7 males ranging from 69.5 to 187 cm

PCL. The power function, $W = aL^b$, was fitted to the data (in SigmaPlot, vers. 6.0, SPSS Inc., Chicago, IL), where W = weight (kg) and L = length (cm PCL). Specimens weighed had been collected from southern California to Alaska. A likelihood ratio test was used to determine whether differences between female and male weight-length parameters were significant or if a single set of parameters described the data better (Kimura, 1980; Quinn and Deriso, 1999; Haddon, 2001) (SAS, vers. 8.0, SAS, Cary, NC). A 20- to 25-cm section of vertebrae was removed from directly in front of the first dorsal fin (above the gills) and stored frozen. We used PCL measurements to make direct comparisons with previously published salmon shark age and growth data from the WNP. Linear regression equations, based on our samples, were developed for converting PCL to FL and TL.

Vertebral samples were thawed, cleaned of excess tissue, separated into individual centra and stored in 70% ethyl alcohol for at least 24 h. Centra were sagittally sectioned immediately adjacent to the center of the focus and then cut again approximately 1.5 mm off-center by using an Isomet rotary diamond saw (Buehler, Lake Bluff, IL). The sections were pressed between two pieces of Plexiglas (to prevent warping), air-dried for 24 h under a ventilation hood, and then mounted onto microscope slides with a mounting medium. After drying, sections were polished with wet fine grit (320-, 400-, and 600-grit) sand paper to approximately 0.5 mm and air-dried. Sections were viewed by using a binocular dissecting microscope with transmitted light.

Centrum radius (CR) and distance to the outer margin of each ring were measured to the nearest 0.001 mm along a straight line from the central focus to the center of the outer margin of the corpus calcareum (Fig. 1A) using a compound video microscope with the Optimus image analysis system (Media Cybernetics, vers. 6.5., Silver Spring, MD). PCL was plotted against CR to determine the proportional relationship between somatic and vertebral growth.

A banding pattern was readily distinguishable in sectioned centra; wide bands were separated by distinct narrow opaque bands. This pattern occurred on both arms of the corpus calcareum and extended across the intermedialia. Each pair of wide-narrow bands was considered a growth cycle; the narrow opaque bands, hereafter referred to as "rings," were counted (Fig. 1A). An angle change in the intermedialia and a ring on the corpus calcareum were present approximately 5 to 6 mm from the focus of each centrum and were considered to represent a birthmark. The "prebirth ring" reported by Nagasawa (1998) was present in most specimens just prior to the birthmark but was not counted nor measured (Fig. 1A).[3] A distinct notch was usually

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present along the inside edge of the corpus calcareum at each ring, providing an additional aging feature, particularly in sections where the cut excluded the radials of the intermedialia (Fig. 1B). Annulus measurements were made from the origin of a wide band to the outer margin of the adjacent narrow band.

Two readers independently aged all centra two times in blind, randomized trials. This procedure allowed the calculation of within-reader precision, and between-reader precision twice. When there was a disagreement between readers, a final age determination was made by both readers viewing the centrum together. Percent agreement ($PA = [No.\ agreed/No.\ read] \times 100$), and percent agreement plus or minus one year (PA [±1 yr]) were calculated for length groups of 10 cm to test for precision. The criticism of percent agreement as a measure of precision has been that it varies widely among species and ages within a species (Beamish and Fournier, 1981; Campana, 2001). The criticism regarding variation among species is irrelevant because one is only interested in the particular species one is aging (i.e., these particular species are not compared among other species), but the criticism regarding variation of ages within a species is not only relevant, but is true. There is, however, validity in using percent agreement with individuals grouped by length as a test of precision because it does not rely on ages (which have been estimated), but rather on lengths, which are empirical values (Goldman, 2004; Cailliet and Goldman, 2004). Ages could be used if, and only if, all age classes have been validated.

The most commonly used methods for evaluating precision among age determinations have been the average percent error (APE) technique of Beamish and Fournier (1981) and the modification of their method by Chang (1982). However, Hoenig et al. (1995) have demonstrated (using the Beamish and Fournier, 1981, data) that there can be differences in precision that these methods obscure because with the APE it is assumed that the variability among observations of individual fish can be averaged over all age groups and that this variability can be expressed in relative terms. Also, APE indices do not result in values that are independent of the age estimates, do not test for systematic differences, and do not distinguish all sources of variability (such as differences in precision with age) (Hoenig et al., 1995). Good APE values appear to tell us only which reader was less variable, not which was better or if either was biased, which is more critical in knowing whether reliable ages can be produced and replicated (i.e. is the error within and between readers due to random error or a systematic bias).

Campana et al. (1995) stated the importance of a separate measure for bias, and Hoenig et al. (1995) and
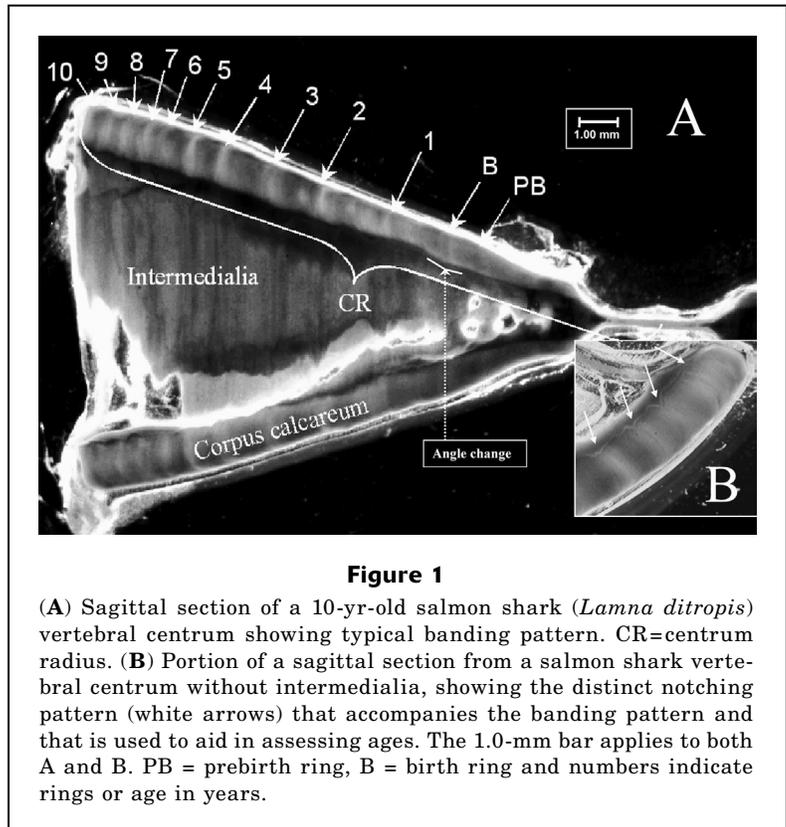
Figure 1

(**A**) Sagittal section of a 10-yr-old salmon shark (*Lamna ditropis*) vertebral centrum showing typical banding pattern. CR=centrum radius. (**B**) Portion of a sagittal section from a salmon shark vertebral centrum without intermedialia, showing the distinct notching pattern (white arrows) that accompanies the banding pattern and that is used to aid in assessing ages. The 1.0-mm bar applies to both A and B. PB = prebirth ring, B = birth ring and numbers indicate rings or age in years.

Evans and Hoenig (1998) suggested testing for systematic differences between readers using chi-square tests of symmetry to determine whether differences are systematic (biased) or due to random error. These are statistically rigorous and effective methods for detecting bias (Campana, 2001) and were conducted in the present study. These techniques place all age values in contingency tables and test the hypothesis that values in a given table are symmetrical about the main diagonal (Hoenig et al., 1995; Evans and Hoenig, 1998). They can also be set up to test among all individual age classes or groups of age classes (Hoenig et al., 1995). The test statistic (the chi-square variable) will tend to be large if a systematic difference exists between the two readers.

A relative marginal increment (RMI) analysis was used to verify the temporal periodicity of ring formation in the vertebrae. This is a standardized marginal increment analysis whereby the margin, or growth area of a centrum from the last narrow growth ring to the centrum edge, is divided by the width of the last fully formed growth increment (Branstetter and Musick, 1994; Conrath et al., 2002). Resulting RMI values were compared to the month of capture. This analysis was performed on immature and mature sharks separately and combined. Age-zero animals were not included (because they have no fully formed increments).

The von Bertalanffy growth function was fitted to the vertebral age-at-length data for salmon sharks from the ENP with a nonlinear least squares regression algorithm ("nls" in S-Plus, Professional Release 1, Math-

soft Inc., Seattle, WA) to estimate parameters. The von Bertalanffy growth function is

$$L_t = L_\infty \left[1 - \exp\left(-k(t - t_0)\right)\right],$$

where L_t = length at age 't';
 L_∞ = asymptotic or maximum length;
 k = the growth coefficient; and
 t_0 = age or time when length theoretically equals zero.

Growth parameters were estimated for the sexes separately and combined. A likelihood ratio test was used to determine whether differences between female and male growth parameters were significant or if a single set of growth parameters described the data better (Kimura, 1980; Quinn and Deriso, 1999; Haddon, 2001) (SAS, vers. 8.0, SAS, Cary, NC).

Back-calculation is a method for describing the growth history of each individual sampled, and numerous variations in methods exist (see Francis, 1990, for a thorough review and Goldman, 2004, for a description and application to elasmobranchs). Back-calculations estimate lengths-at-previous-ages for each individual and should be used if sample sizes are small and if samples have not been obtained from each month (Goldman, 2004; Cailliet and Goldman, 2004). Cailliet and Goldman (2004) stated "the proportional relationship between animal length or disk width and the radius of the vertebral centrum among different length animals within a population is used as a basis for empirical relationships regarding population and individual growth, as is the distance from the focus to each annulus within a given centrum." Hence, choosing the appropriate method (based on the relationship between animal length or disk width and the radius of the vertebral centrum) is critical if back-calculated data are to be used for obtaining accurate life history parameter estimates from growth function models. Because smaller size classes were not well represented in our female sample and because our male sample size was small, lengths at previous ages were back-calculated from centrum measurements for both sexes and fitted with the von Bertalanffy growth function.

The relationship between CR and PCL for ENP salmon sharks was used to determine the most appropriate method for back-calculating previous length-at-age. To our knowledge, however, no studies on elasmobranch fishes have examined multiple back-calculation methods for statistical or biological accuracy in relation to vertebral sample data. To that end, four different proportion methods were used and compared with our sample length-at-age data. We first applied the standard Dahl-Lea direct proportions method (Carlander, 1969):

$$L_i(L_c / CR_c) \times CR_i, \qquad (1)$$

where L_i = length at ring 'i';
 L_c = length at capture;
 CR_c = centrum radius at capture; and
 CR_i = centrum radius at ring 'i'.

Next, we applied two modified versions of the Dahl-Lea method that use parameter estimates from the specific linear and quadratic fits that described the PCL-CR relationship. The linear-modified Dahl-Lea method (Francis, 1990) is

$$L_i = L_c \times \left[(a + bCR_i)/(a + bCR_c)\right], \qquad (2)$$

where 'a' and 'b' are the linear fitted parameter estimates. The quadratic-modified Dahl-Lea method (Francis, 1990) is

$$L_i = L_c \times \left[(a + bCR_i + cC_i^2)/(a + bCR_c + cCR_c^2)\right], \qquad (3)$$

where 'a,' 'b,' and 'c' are the quadratic-fitted parameter estimates.

Ricker (1992) applauded Francis's (1990) back-calculation review paper, but like Campana (1990) suggested that the point of origin of proportional back-calculations should be related to a biologically derived intercept (i.e., length at birth). We, therefore, also applied Campana's (1990) "size-at-birth-modified" Fraser-Lee equation:

$$L_i = L_c + \left[(CR_l - CR_c) \times (L_c - L_{Birth})/(CR_c - C_{Birth})\right], \quad (4)$$

where L_{Birth} = length at birth; and
 CR_{Birth} = centrum radius at birth. (Based on Tanaka, 1980, 62.5 cm PCL was used for L_{Birth}.)

Von Bertalanffy growth parameter estimates were obtained from all individual and mean back-calculated length-at-age, and from a combination of back-calculated lengths-at-age and our sample data. A likelihood ratio test was used for all scenarios to determine whether differences between female and male growth parameters were significant or if a single set of growth parameters described the data better (Kimura, 1980; Quinn and Deriso, 1999; Haddon, 2001) (SAS vers. 8.0, SAS, Cary, NC). Back-calculated length-at-age results from all four methods were examined to see which best reflected our vertebral sample data.

The reproductive tracts of 64 female and 14 male salmon sharks were examined visually to assess their reproductive status. Females ranged in size from 71 to 209 cm PCL, and males ranged from 63 to 187 cm PCL. Clasper lengths were obtained from 12 of the males (from 91 to 187 cm PCL). Gross analysis of reproductive tracts and maturity determinations were made according to the methods of Pratt (1988), Gilmore (1993), Pratt and Tanaka (1994), Hamlett (1999) and Hamlett and Koob (1999).

Median precaudal length-at-maturity (MPCL) was determined by first coding female ($n=64$) and male ($n=14$) maturity data into binary form, with 0=immature and 1=mature. The binary data were fitted with a logistic regression model ("GLM" in S-Plus, Professional Release 1, Mathsoft Inc., Seattle, WA). The median precaudal length-at-maturity was then estimated as

$MPCL = -a/b$ (a=intercept, b=slope) (Mollet et al., 2000; Neer and Cailliet, 2001; Conrath and Musick, 2002; Conrath, 2004). To estimate percent maturity by length for the ENP salmon shark population, the 'a' and 'b' estimates (from the "GLM" model) were substituted into the equation; *percent mature* $= 100 \times [(e^{(a+b \times length)})/(1+e^{(a+b \times length)})]$, and plotted against *PCL*. A nonparametric bootstrap (n=1000 replications) was conducted with S-Plus and 95% confidence limits were obtained from the 2.5th and 97.5th empirical percentiles.

Sperm storage in the oviducal gland has been documented in several shark species (Pratt, 1993). Oviducal glands were taken from six mature females, ranging in size from 180 to 192 cm PCL, caught in PWS waters in late July and late August, to determine the presence or absence of sperm. Samples were initially fixed in 10% formalin. Samples were rinsed extensively to remove fixative and then stored in 70% ethanol. Cross-sections along the entire length of each gland were trimmed, dehydrated in a graded series of ethanol, cleared in a limonene-based solvent, infiltrated with paraffin, and embedded in paraffin blocks. Serial sections (5 um) were prepared by using a rotary microtome, mounted onto poly-L-lysine-coated slides, dried, deparaffinized, rehydrated, and stained by using standard Harris hemotoxylin and eosin in order to examine general cellular detail (Hinton, 1990). Sections were examined for the presence of sperm by using a compound microscope at magnifications ranging from 100× to 1000×.

Results

Length and weight equations

One hundred sixty-six of the 182 salmon sharks in this study were female, resulting in a F:M sex ratio of 10.4/1. Although females dominated our sample, the following equations for converting PCL into FL and TL appear to work equally well for both sexes.

$FL = 1.08 \times PCL + 6.91$ (r^2=0.99; n=138)
$TL = 1.15 \times PCL + 15.19$ (r^2=0.97; n=133).

Weight-length relationships for female and male salmon sharks we sampled in the ENP were $W = 8.2 \times 10^{-05} \times L^{2.759}$ (r^2=0.99, n=20) and $W = 3.2 \times 10^{-06} \times L^{3.383}$ (r^2=0.99, n=7) respectively, and $4.4 \times 10^{-05} \times L^{2.875}$ (r^2=0.99) for the sexes combined. A likelihood ratio test showed that separate equations for each sex describe the data better than a single equation for the sexes combined (χ^2=12.1; df=3; P<0.01).
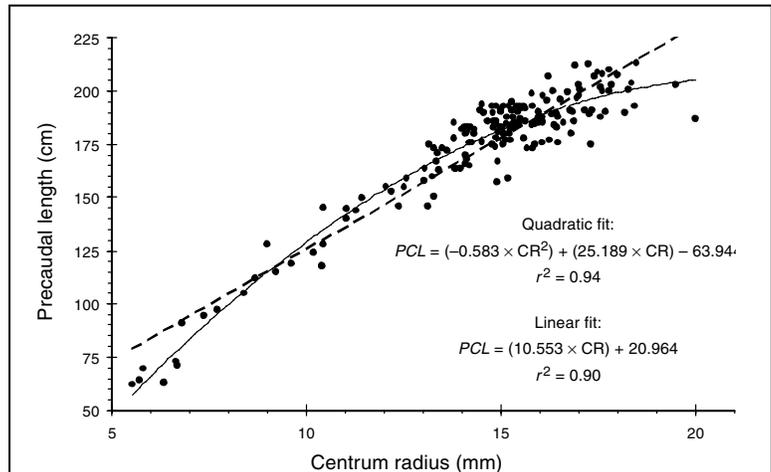
Figure 2

Relationship between centrum radius and precaudal length for eastern North Pacific salmon sharks (*Lamna ditropis*) showing significant fits given by linear and quadratic equations (sexes combined, n=182). PCL = precaudal length, CR = centrum radius.

Vertebral analysis

There was a slight curvilinear relationship between centrum radius (CR) and shark PCL (Fig. 2). A linear regression gave a significant fit to the data ($PCL = (10.553 \times CR)+20.964$; r^2=0.90; P<0.0001); however, a quadratic equation produced a slightly better fit ($PCL = -63.944 + (25.189 \times CR) - (0.583 \times CR^2)$; r^2=0.94; P<0.0001) and a t-test showed the third parameter to be statistically significantly different from zero (t=10.32; df=181, P<0.0001). However, it was necessary to compare the mean back-calculated results from Equations 1 through 4 with the mean sample PCL data to see if the slightly better statistical fit of the quadratic equation translated into better biological accuracy for modeling growth.

Percent agreement (PA) among readers was 68.1% for the first set of blind reads and 72.0% for the second set, and the within-reader PA was 79.7% for reader one (the lead author) and 75.3% for reader two. Percent agreement (±one yr) was >95% for all reader comparisons. Agreement between and within reader age assessments was 100% until age 7 or 8, depending on the reader comparison. When grouped by 10-cm length increments, percent agreement was 100% for sharks ≤160 cm PCL, and 100% ±1 yr for sharks ≤180 cm PCL (Table 1). (PA and PA ±1 for length groups were virtually the same for both sets of between-reader comparisons, but slight differences occurred above 160 and 180 cm PCL, respectively.) The chi-square tests of symmetry gave no indication that differences between and within readers were systematic rather than due to random error (χ^2 test, P>0.05 in all cases).

Relative marginal increment (RMI) analysis showed that postnatal rings form annually between January and March. The smallest relative margins occurred in

Table 1

Percent agreement (PA) and PA ± one year, from the second set of "reads," for eastern North Pacific salmon sharks (*Lamna ditropis*) when placed into 10-cm precaudal length (PCL) groups.

PCL (cm)	Total no. read	No. agreed upon	No. agreed upon ±1	PA	PA ±1
60–70	5	5	5	100	100
70.1–80	2	2	2	100	100
80.1–90	0	—	—	—	—
90.1–100	4	4	4	100	100
100.1–110	1	1	1	100	100
110.1–120	5	5	5	100	100
120.1–130	3	3	3	100	100
130.1–140	1	1	1	100	100
140.1–150	6	6	6	100	100
150.1–160	9	9	9	100	100
160.1–170	11	8	11	72.7	100
170.1–180	30	22	30	73.3	100
180.1–190	55	38	53	69.1	96.4
190.1–200	34	22	32	64.7	94.1
200.1–210	12	4	10	33.3	83.3
>210	4	1	3	25.0	75.0
n	182	131	175	—	—
Percent agreement	—	—	—	72.0	96.2

February and March, followed by a consistent increase in RMI, and the largest relative margins occurred in December and January. There was no difference in this trend when immature and mature sharks were examined separately; therefore all ages classes were combined (Fig. 3).

Vertebral age-at-length data from 166 female salmon sharks provided von Bertalanffy parameters of L_∞=207.4 cm *PCL*, k=0.17/yr, and t_0=−2.3 years (Fig. 4). When the von Bertalanffy growth function was fitted to the quadratic-modified Dahl-Lea back-calculations for females, the life history parameters were similar to those produced from the sample length data (Table 2). Vertebral age data from 16 males provided von Bertalanffy parameters of L_∞=182.8 cm PCL, k=0.23/yr, and t_0=−1.9 years (Fig. 4). Back-calculated lengths-at-age for male salmon sharks, either with or without sample data included, provided slightly lower k coefficients (=0.20), but similar L_∞ and t_0 parameters (Table 2). Vertebral age data for the sexes combined (*n*=182) provided von Bertalanffy parameters of L_∞=204.5 cm PCL, k=0.18/yr, and t_0=−2.2 years. A likelihood ratio test showed that separate von Bertalanffy growth models describe the data better for each sex than one model with the sexes combined (χ^2=29.1; df=3; P<0.001).

The quadratic-modified Dahl-Lea method (Eq. 3) represented most accurately the mean sample precaudal
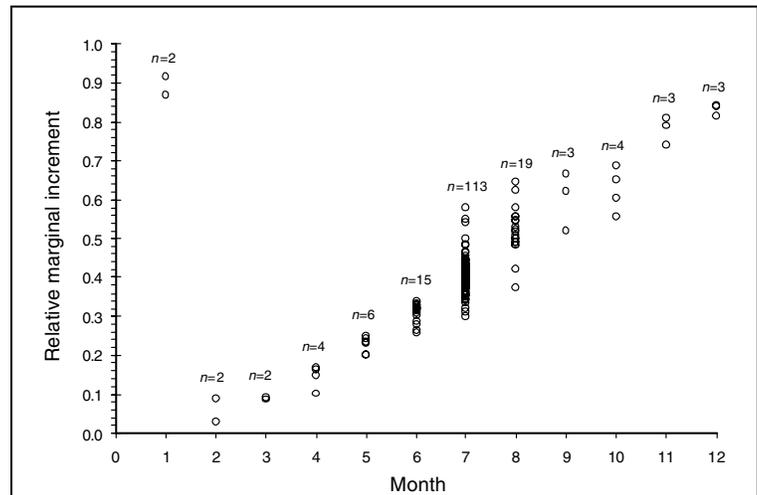
Figure 3

Results of relative marginal increment analysis showing that annulus formation occurs between January and March (*n*=176).

length-at-age data. It produced mean back-calculated lengths-at-age within 4.2 cm of mean sample lengths-at-age for female salmon sharks >120 cm PCL and within 8.8 cm for females <120 cm PCL (Fig. 5A). When applied to males, Equation 3 produced mean back-calculated lengths-at-age within 10 cm of mean sample lengths-at-age for sharks <120 cm PCL and >150 cm

Table 2

Von Bertalanffy growth parameters for female, male, and sexes combined for salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific. Numbers in parentheses are standard errors. * = not independent.

	L_∞	k	t_0
Eastern North Pacific (present study)			
Females			
Vertebral sample data (*n*=166)	207.4 (2.5)	0.17 (0.01)	−2.3 (0.2)
Back-calculations (*n*=1814*)	205.3 (0.9)	0.18 (0.002)	−2.0 (0.03)
Mean back-calculation (*n*=21*)	210.0 (1.1)	0.17 (0.004)	−2.1 (0.09)
Back-calculations with sample data (*n*=1980*)	206.0 (0.8)	0.18 (0.002)	−2.0 (0.03)
Males			
Vertebral sample data (*n*=16)	182.8 (3.7)	0.23 (0.03)	−1.9 (0.3)
Back-calculations (*n*=161*)	183.9 (2.0)	0.20 (0.008)	−2.0 (0.1)
Back-calculations with sample data (*n*=177*)	184.2 (1.9)	0.20 (0.008)	−2.0 (0.1)
Combined			
Vertebral sample data (*n*=182)	204.5 (2.4)	0.18 (0.01)	−2.2 (0.2)
Western North Pacific (Tanaka, 1980)			
Females			
Vertebral sample data	203.8	0.14	−3.9
Males			
Vertebral sample data	180.0	0.17	−3.6

PCL. In between those lengths, however, the deviation from mean sample length-at-age increased to 16.5 cm (Fig. 5B). (The larger deviations for males were likely the result of the small sample size.) Lee's phenomenon did not occur in either sex with the quadratic-modified Dahl-Lea method.

Of the 64 female salmon shark reproductive tracts examined, 55 were fully mature, and 11 of the 14 males examined were mature. Mature female reproductive tracts consisted of a well-developed right ovary (the only functional ovary in lamniform sharks) containing various sizes of ova, large oviducts and oviducal glands, and expanded, heavily striated uteri with thickened walls. In stark contrast, the right ovary from immature female reproductive tracts was considerably smaller and had no signs of developing ova, the oviducal gland was virtually indistinguishable from the oviduct, and the uteri were extremely small, thin-walled, flaccid and completely smooth. Additionally, the epigonal organ in mature females was large and extended $^2/_3$ the length of the uteri, whereas in immature females it was small and generally did not extend much past the anterior end of the uteri. No females examined were of an "intermediate" reproductive nature. Mature male reproductive tracts consisted of large well-developed testes, a thick epididymis leading to a coiled ductus deferens, rigid (fully calcified) claspers and well-developed siphon sacs. Immature male reproductive tracts consisted of small testes that were partially embedded in the epigonal organ, thin epididymis and straight ductus deferens, nonrigid claspers and poorly developed siphon sacs.

Estimated median precaudal length-at-maturity (MPCL) for ENP female and male salmon sharks were 164.7 cm PCL and 124.0 cm PCL, respectively (Fig. 6). The smallest mature female observed was 164.0 cm PCL, and the largest immature female observed was 176.5 cm PCL (however, all other immature females were ≤163 cm PCL). None of
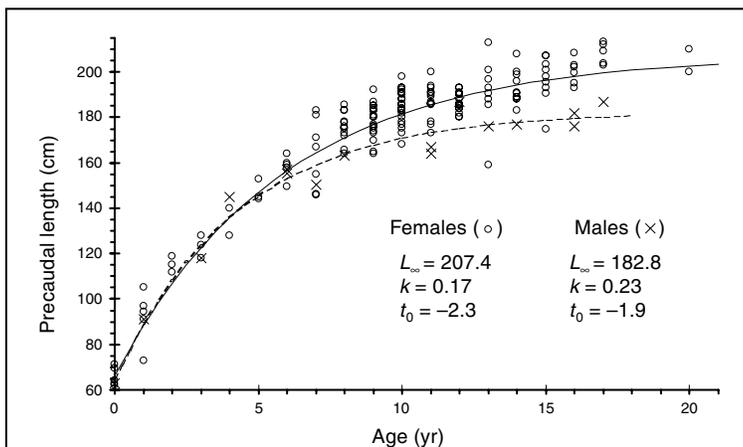
Figure 4

Von Bertalanffy growth curves fitted to female (*n*=166) and male (*n*=16) vertebral sample data for eastern North Pacific salmon sharks (*Lamna ditropis*). Estimates for parameters of the von Bertalanffy growth function are summarized.

Table 3

Mean ages and precaudal lengths (PCL) for eastern North Pacific salmon sharks (*Lamna ditropis*) by location. CA = California; seAK = southeast Alaska.

|	Females			Males		
	CA to seAK	Alaska	Combined	CA to seAK	Alaska	Combined
Age (yr)						
Mean	2	11	10	3	12	9
Range	0–5	5–20	0–20	0–7	6–17	0–17
PCL (cm)						
Mean	103.6	184.7	175.0	113.5	171.9	153.7
Range	62.2–153	144.8–213.4	62.2–213.4	63–150.5	155.4–187	63–187
n	20	146	166	5	11	16

the oviducal glands sampled from mature females contained spermatozoa. The smallest mature male observed was 155.4 cm PCL, and the largest immature male was 91.0 cm PCL. Based on age estimates from vertebral sample data, ages at MPCL range from 6 to 9 yr for females and from 3 to 5 yr for males. Ninety-five percent confidence limits (for percent mature) were very narrow for females <155 cm PCL and >172.5 cm PCL and for males <107.5 cm PCL and >132.5 cm PCL. The wide vertical confidence intervals around the calculated estimates of MPCL (Fig. 6) were caused by not having many observations for lengths around the estimated MPCL in the sample.

Age-length composition in the Eastern North Pacific

The mean age and length composition of ENP salmon sharks was latitude dependent (Table 3). Sharks between 0 and 7 yrs old, ranging from 62.2 to 153 cm PCL, were collected from southern California to southeast Alaska, with smaller individuals found in the southern part of that range. Sharks between 5 and 20 yrs old, ranging from 144.8 to 213.4 cm PCL, were collected from southeast Alaska up into the Gulf of Alaska, Prince William Sound, and the Bering Sea.

Discussion

Vertebral growth significantly increased with somatic growth (Fig. 2), which, along with the reliability of the RMI analysis
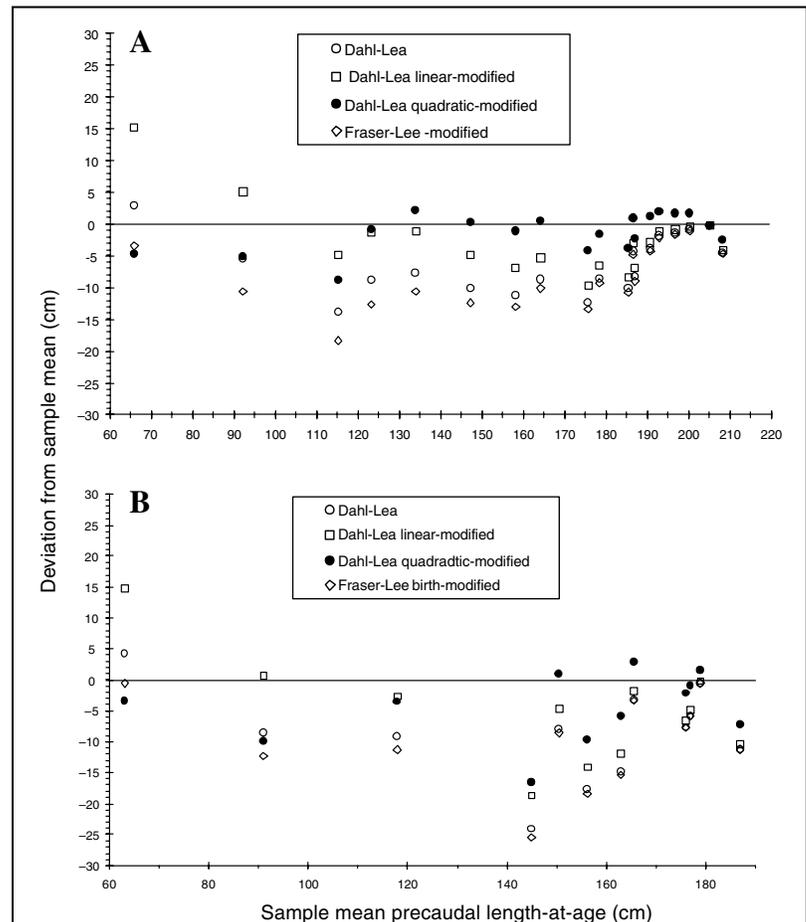
Figure 5

Mean deviation, from mean sampled precaudal length, of four proportional back-calculation methods for (**A**) female, and for (**B**) male eastern North Pacific salmon sharks (*Lamna ditropis*). Data points represent mean back-calculated lengths-at-age. An *x*-axis point on the zero line extending from the y-axis would represent zero deviation from the sample mean length-at-age.

Figure 6

Percent versus precaudal length curves for eastern North Pacific female (heavy lines) and male (light lines) salmon sharks (*Lamna ditropis*) with 95% confidence bands on percent mature. Diamond and circle show estimates of median precaudal length at maturity (MPCL) for females and males respectively. Confidence bands (dotted lines) are 2.5th and 97.5th empirical percentiles obtained by bootstrapping.

(Fig. 3), demonstrates that vertebral growth patterns are a reliable indicator of age in salmon sharks. Precision was high between and within readers with limited differences (Table 1) that were attributable to random error. These results provided us with a high degree of confidence in the age assessments determined from the von Bertalanffy growth model (with vertebral sample data), and hence in the resulting life history parameter estimates.

Tanaka (1980) and Nagasawa (1998) stated that salmon sharks produce one ring per year, but a RMI analysis was not provided in their studies. Our RMI analysis verified an annual periodicity of banding patterns for salmon sharks, ranging from 73 cm to 213.4 cm PCL and encompassing ages 1 to 20 for females and ages 1 to 17 for males. The major period of growth occurs from May through November, slowing some as January approaches (Fig. 3). A brief cessation, or extreme slowing, of growth (ring formation) occurs between January and March, and growth increases again in April–May. Although we were able to examine specimens from every month of the year, additional samples from December through April would enhance RMI precision.

The similar von Bertalanffy growth parameter estimates generated from female vertebral sample data, back-calculated data, and the combination of the two indicated that sample size was sufficiently large and encompassed the known size range of the species. Von Bertalanffy parameters for males would have been improved with a larger sample size that would have reduced the difference between values of '*k*' from vertebral sample and back-calculated data (Table 2). More samples would likely have had little influence on L_∞ for

either sex because salmon sharks close to maximum length were examined in the present study. It is possible that the discrepancy between female and male sample sizes could have influenced the outcome of the likelihood ratio test. However, with the differences in observed maximum length (and estimated L_∞) between the sexes and the small standard errors associated with the male von Bertalanffy estimates (Table 2), it is unlikely that an increased male sample size would have altered the test result.

The error associated with back-calculated length *versus* the actual length at a given age has been a focal point of papers by Campana (1990), Francis (1990) and Ricker (1992) and prompted our evaluation of several proportional back-calculation methods. There was a statistically valid reason for using the quadratic-modified Dahl-Lea (Eq. 3) over the linear-modified Dahl-Lea (Eq. 2) (see "Results" section); however, the only way to cross-compare all four back-calculation methods in a biologically meaningful way was to apply all of them to the vertebral sample data. Both modified Dahl-Lea equations were more accurate in representing the mean sample length-at-age data than the standard Dahl-Lea or the size-at-birth-modified Fraser-Lee equations (Fig. 5, A and B). However, the quadratic-modified Dahl-Lea was the best predictor of prior length-at-age (i.e., best resembled our vertebral sample length-at-age data). Although these back-calculation results are, of course, dependent on the assumption that growth has not significantly changed over time, and are applicable only to salmon sharks, they demonstrate the importance of choosing the appropriate method to minimize error, which results in a greater ability to accurately model growth. Accurate growth parameters will result in more accurate demographic parameters and stock assessments, leading to more responsible management. Even greater confidence could be achieved if animals collected in the past were available because they would allow a direct comparison of size-at-age then and now in order to verify that the growth rate for the salmon shark has not changed.

Our results show that salmon sharks in the ENP attain their maximum size at a faster rate (*k*) than those from the WNP (Table 2). We were unable to test the statistical significance of these differences because neither Tanaka (1980) nor Nagasawa (1998) provided point estimates and standard error values for their WNP data. There were, however, significant resultant biological differences present. Both female and male salmon sharks reach first age at sexual maturity approximately 2 years earlier in the ENP than in the WNP. Female salmon sharks in the WNP mature between 8 and 10 years of age (Tanaka, 1980; Nagasawa, 1998). From the reproductive tracts examined, we found that female salmon sharks in the ENP reach sexual maturity between ages 6 and 9. Although age at first maturity was earlier in the ENP, length at maturity appears to be similar; 160–180 cm PCL in the WNP, and a MPCL = 164.7 cm PCL in the ENP (Fig. 6). Male salmon sharks in the WNP mature at approximately

5 years of age and 140 cm PCL (Tanaka, 1980; Naga-sawa, 1998). From our small sample size, the logistic method provided an estimate that male salmon sharks in the ENP mature between the ages of 3 and 5, and MPCL=124.0 cm PCL (Fig. 6). Clasper lengths did not enhance the ability to determine male length at sexual maturity because specimens around the calculated MPCL were not sampled. Although the MPCL for males indicates a smaller length at maturity, our confidence in the accuracy of the male MPCL estimate (due to sample size) is low (Fig. 6).

The lack of spermatozoa in any of the oviducal gland samples analyzed is not surprising considering no lamniform shark examined to date has shown evidence of sperm storage (Pratt, 1993). However, specimens we examined were specifically chosen from the time period of late July through late August when mating was likely to have been taking place (Goldman and Human, 2005; Goldman and Musick, in press). A larger sample size taken through that time period and extending through September may resolve the question better regarding the suspected residence time of sperm in the oviducal gland of lamniform sharks—a residence time that is probably only a few days timed with actual mating activity (Pratt, 1993). The large number of eggs produced to feed oophagous young (Wourms, 1977; Gilmore et al., 1983; Gilmore, 1993) could have "flushed" any stored sperm out of the oviducal gland (Pratt, 1993).

In the WNP, salmon sharks are born in the spring of the year and pups range in length from 60 to 70 cm PCL (Tanaka, 1980; JAMARC, 1980; Nagasawa, 1998). Litter size in the WNP is up to 5 pups, and the ratio of male to female is 2.2:1 (Tanaka, 1980). Our data support a similar timing for pupping and for length at birth in the ENP, but no pregnant females were taken during the course of our research and therefore information on litter size and pup sex ratio is not available for the ENP.

Nagasawa (1998) characterized salmon shark growth through age ten as follows; after birth, "they grow to between 90 and 105 cm PCL by the next spring ... subsequent annual growth is 10–15 cm per year up to age-4 fish." He stated, in addition, that females and males attain an average length of 173 cm PCL and 163 cm PCL, respectively, by age 10. Our data indicated that the average growth rate (cm per year) for salmon sharks in the ENP is very similar to the rate in the WNP through age 4. By age 5, ENP females are growing at a considerably faster rate than WNP females, reaching an average of 185.4 cm PCL by age 10 (Table 4). Male salmon sharks in the ENP appear to begin outgrowing their WNP counterparts by age 4 (Table 4). Salmon shark longevity appears to be similar in the ENP and WNP. Maximum observed age for females in our study was 20, whereas it was 17 in the WNP (Tanaka, 1980); however, maximum observed age for males was only 17, whereas it was 25 for the WNP. We were unable to obtain samples of male salmon sharks at or near maximum age because of our small sample size.

Salmon sharks in the ENP and WNP attain the same maximum length (about 215 cm PCL for females and about 190 cm PCL for males). However, WNP salmon sharks take longer to reach a given length than those in the ENP (Table 4). Additionally, the weights for the same length females and males are considerably different except at male maximum length, which appears to be equivalent to females of similar length. Our data indicate that the weight-at-length differences between ENP and WNP salmon sharks begin at approximately 110 cm PCL for females, and at 140 cm PCL for males (Fig. 7, A and B). Although a greater sample size could enhanced precision and may alter the equations presented in the present study to some degree, the data show that weight-at-length is particularly greater for adult salmon sharks in the ENP than in the WNP. As with the von Bertalanffy growth models, it is possible that the discrepancy between female and male sample sizes may have influenced the outcome of the likelihood ratio test. However, the sample-size discrepancy was not as large as with the growth curve data and standard errors were small for both sexes; therefore it is unlikely that an increased male sample size would have altered the test result.

Although season and size at birth appear to be similar for salmon sharks in the ENP and WNP, the locations where females pup are different. A salmon shark pupping and nursery ground exists along the transitional boundary of the subarctic and central Pacific currents (Nakano and Nagasawa, 1996). Our data indicate that a second pupping and nursery ground exists, ranging from southeast Alaska to the northern end of Baja California, Mexico (central California being the most common area for ages zero and one [see Table 3]). Ages zero through 5 were caught only between southern California and southeast Alaska, and ages 5 and above were caught only in Alaska waters. The latitudinal size segregation observed in the ENP indicates that pregnant females may move south along the California coast to give birth in the spring.

The high degree of sexual segregation across the Pacific Basin (Nagasawa, 1998; Goldman and Musick, in press), along with the age- and length-dependent latitudinal distribution are important factors in pursuing responsible management and conservation of the salmon shark. Although latitudinal migrations and movements are documented in this species (Iino, 1939; Kosugi and Tsuchisaki, 1950; Tanaka, 1980; Balgaderov, 1994; Nakano and Nagasawa, 1994; Weng et al., 2005), they are still poorly understood. Similarly, although trans-Pacific movements have been inferred from fisheries bycatch data (Goldman and Musick, in press), there has yet to be documentation of individuals moving across the North Pacific. However, the degree of the sexual segregation by itself (in regard to finding a mate) would seem to indicate that movements across the Pacific are likely.

Another critical element for successful management of salmon sharks is stock structure, which is not well understood at this time; however a study of population

Table 4

Mean precaudal length (PCL) at age for salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific (ENP and WNP). Ranges (or individual lengths for some males) are given for sharks from the present study.

Age	Females WNP* mean PCL	Females ENP mean PCL	Females ENP range	Males WNP* mean	Males ENP individual or range
0	62.5	65.9	62.2–71.1	62.5	63.0
1	97.5	92.1	73.0–105.0	97.5	91.0
2	110.0	115.3	112.0–119.0	110.0	—
3	122.5	123.3	118.0–128.0	122.5	118.0
4	135.0	134.0	128.0–140.0	135.0	145.0
5	141.3	147.3	144.0–153.0	139.7	—
6	147.7	158.1	149.7–164.0	144.3	155.4–157.0
7	154.0	164.1	145.9–183.0	149.0	150.5
8	160.3	175.7	164.0–185.4	153.7	163.0
9	166.7	178.4	164.0–192.0	158.3	—
10	173.0	185.4	168.0–198.0	163.0	—
11	177.4	187.0	173.0–200.0	164.2	164.0–176.0
12	181.8	186.7	180.0–193.0	165.3	187.0
13	186.2	190.8	159.9–213.0	166.5	176.0
14	190.6	192.9	183.0–208.0	167.6	177.0
15	195.0	196.7	175.0–207.1	168.8	—
16	199.4	200.1	193.0–208.3	169.9	176.0–182.0
17	203.8	208.3	203.0–213.4	171.1	187.0
18	—	—	—	172.2	—
19	—	—	—	173.4	—
20	—	205.1	200.0–210.2	174.5	—
21	—	—	—	175.7	—
22	—	—	—	176.8	—
23	—	—	—	178.0	—
24	—	—	—	179.1	—
25	—	—	—	180.3	—

* Mean length-at-age for WNP calculated from information in Nagasawa (1998), L_∞ was used as mean length at age 17 for females and as mean length at age 25 for males.

genetics is currently underway. Current information from the western and central North Pacific implies that salmon sharks constitute a single stock, but there is no current information for the Japan Sea or the eastern North Pacific (Sano, 1962; Tanaka, 1980; Blagoderov, 1994; Nagasawa, 1998). New technologies such as archival and pop-up satellite transmitters should provide documentation of movements and migrations (Weng et al., 2005) and key information as to whether regional or international conservation and management plans are needed.

Stock structure may be an important factor in the differential growth rates between ENP and WNP salmon sharks. However, ecological differences between the ENP and WNP could also be responsible for the observed differences. Young salmon sharks appear to move from temperate waters of the U.S. west coast into the Alaska Gyre and the Gulf of Alaska as they approach adulthood, which is when their growth rate begins to exceed that of their WNP counterparts. These waters are extremely productive (Strub et al. 2001), and abundant food resources may be the key factor in the differences in growth rate, age-at-maturity, and weight-at-length observed between ENP and WNP salmon sharks.

A high degree of variability exists in the periodicity of ring and growth band formation within and among taxonomic groups of elasmobranchs, and much of the variation observed in several lamniform sharks has not yet been explained (Branstetter, 1990; Branstetter and Musick, 1994; Wintner and Cliff, 1999). For example, Cailliet et al. (1983) stated that shortfin mako sharks (*Isurus oxyrinchus*) from the Pacific appear to form growth rings annually, whereas Pratt and Casey (1983) stated that Atlantic specimens appeared to produce two
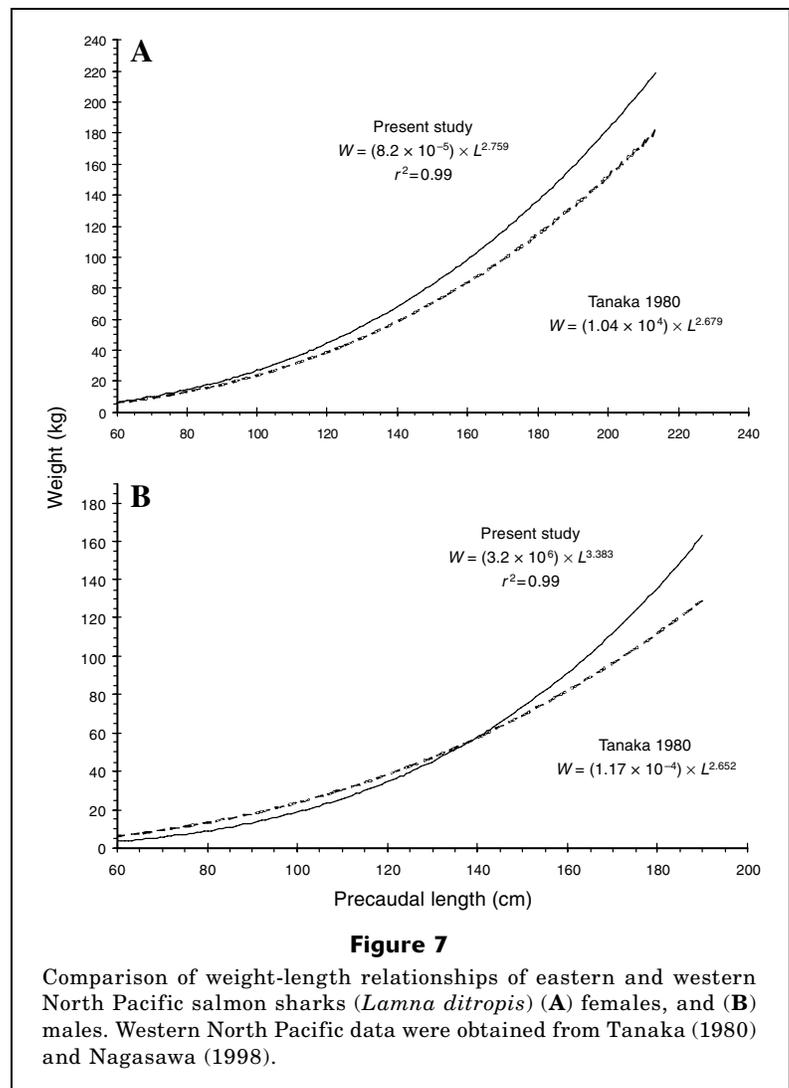
rings per year. However, validation of single annual ring (band pair) deposition has now been demonstrated from recaptures of oxytetracycline(OTC)-injected mako sharks (Natanson et al., in press), as well as with a new technique where bomb radiocarbon is used to validate ages in long-lived sharks (Campana et al., 2002; Ardizzone et al., in press).

Lamnid sharks are endothermic (Carey et al., 1985; Lowe and Goldman, 2001), and prior to the Campana et al. (2002) and Ardizzone (in press) radiocarbon studies, it appeared that lamnid sharks might possess fairly high growth rates (growth coefficient, *k*) compared to other sharks, particularly those that grow to a large size (Musick, 1999). However, with mako sharks now appearing to have a growth coefficient around 0.072/yr (sexes combined)(Cailliet et al. 1983), the validation of porbeagle shark (*Lamna nasus*) age and growth (*k*=0.06 and 0.08/yr for females and males, respectively) (Natanson et al. 2002), and estimates of white shark (*Carcharodon carcharias*) growth coefficients ranging from 0.058 to 0.071/yr (for sexes combined)(Cailliet et al., 1985; Wintner and Cliff, 1999; Malcolm et al. 2001), salmon sharks appear to be the species that possess the higher growth rates (Tanaka, 1980; present study). Salmon sharks are not only endothermic, but also appear to be homeothermic (i.e., defend a specific body core temperature regardless of ambient temperature) (Goldman et al., 2004). This uncommon physiological trait for a shark, combined with a diet that includes many lipid-rich species (e.g., salmonids), may influence the growth rate of this species, but endothermy does not appear to be correlated with faster growth rates in lamnid sharks (Goldman, 2002).

The most recent demographic analysis has indicated that salmon shark populations in the eastern and western North Pacific are stable at this time (Goldman, 2002) and current research is beginning to assess standing stock and population numbers, as well as examine the stock structure of salmon sharks in the eastern and western North Pacific in order to further responsible management of the species. The differences in growth rates and strong sexual segregation across the North Pacific basin and an unknown rate of current bycatch complicate management of this species.

Acknowledgments

Figure 7

Comparison of weight-length relationships of eastern and western North Pacific salmon sharks (*Lamna ditropis*) (**A**) females, and (**B**) males. Western North Pacific data were obtained from Tanaka (1980) and Nagasawa (1998).

Mary, School of Marine Science, Virginia Institute of
Marine Science. This article is dedicated to the life and
memory of Philip Goldman, compassionate human being
and dedicated father.

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