

Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction

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Received 18.5.1990

Accepted 26.9.1991

Key words: California, Elasmobranchs, Exploitation, Fisheries, Life history, Tagging, Triakidae

Synopsis

The age, growth, and sexual maturation of the leopard shark, *Triakis semifasciata*, from central California were studied. Growth band counts in vertebral centra of 162 leopard sharks produced von Bertalanffy growth curves with L_{∞} , K , and t_0 parameters of 1536 mm, 0.082, and -2.31 , respectively, for both sexes combined. The L_{∞} value for females (1602 mm TL) was slightly but insignificantly higher than for males (1499 mm TL), but the K and t_0 values were almost identical. Seasonal changes in size modes of young-of-the-year leopard sharks, centrum edge characteristics, and growth and tetracycline mark-recapture from the field were used to validate annual deposition of vertebral centrum band pairs. Sexual maturity was evaluated by the gonads and presence of sperm and eggs; males mature at 7 yr and at about 63% of asymptotic length, and females mature at 10 yr, and at about 72% of asymptotic length. This slow growth, late maturity, and relatively low fecundity may increase their susceptibility to over-exploitation.

Introduction

Elasmobranchs have become important fishery resources worldwide, yet many aspects of their ecology suggest that they may be susceptible to over-exploitation (Holden 1974, 1977). For most elasmobranchs, including those commercially fished, very little essential information on their life histories is available (Compagno 1984). In general, those studied exhibit relatively slow growth rates, late age at sexual maturity, and low fecundity (Holden 1973, 1974, 1977, Holden & Vince 1973, Ketchen 1975, Jones & Geen 1977a).

Establishing the temporal periodicity of growth

zone deposition in calcified body parts is essential to the complete understanding of fish growth (Beamish & McFarlane 1983, Cailliet et al. 1986, Cailliet & Radtke 1987). Various authors have postulated that these growth zones are deposited annually, but few critical tests of this hypothesis have been accomplished, especially for elasmobranchs (Brown & Gruber 1986, Smith 1984, Beamish & McFarlane 1985, McFarlane & Beamish 1987). Inaccurate estimates of ages result in very serious errors in the management and understanding of fish populations (Beamish & McFarlane 1983).

The leopard shark, *Triakis semifasciata*, is one of the commercially and recreationally important

shark species from California. It is distributed commonly in bays and nearshore water from Mazatlan, Mexico to Oregon, including the Gulf of California (Miller & Lea 1972, Castro 1983, Eschmeyer et al. 1984, Ebert 1986). Individuals obtain a maximum size of 1981 mm total length (Miller & Lea 1972). This shark is primarily a benthic feeder (Ackerman 1971, Russo 1975), and like many shark species, its diet varies with size and season (Compagno 1984).

Little is known about age determination or growth of the leopard shark. Determination of age of elasmobranchs is hampered by the lack of calcareous otoliths and cycloid or ctenoid scales. Several alternate methods of age determination have been developed for elasmobranchs (reviewed by Cailliet et al. 1983a, 1986). The most promising method is analysis of the growth bands deposited in calcified structures such as dorsal spines and vertebral centra. This approach, with a resin-embedding and sectioning process, was used by Smith (1984) to verify growth bands in tetracycline-labelled vertebrae. Prior to this, the only age determination technique applied to the leopard shark to date was size frequency analysis (Ackerman 1971).

Part of our study was initiated in 1979 at Moss Landing Marine Laboratories (MLML), California, to develop age determination techniques for use in producing a reliable growth curve, and to describe the size- and age-specific reproductive capabilities of the leopard shark in Elkhorn Slough, California. In the same year, a tagging study was initiated in San Francisco Bay, California by the National Marine Fisheries Service (NMFS), to determine if vertebral growth zones in leopard sharks formed annually. Using the first 12 oxytetracycline (OTC) marked and recaptured fish from the first three years of the NMFS study, the annual deposition of the growth zones was confirmed (Smith 1984). Also, other aspects of the population dynamics and fishery biology from this tagging study have been evaluated (Smith & Abramson 1990). Subsequent information from recaptured sharks from the NMFS study are updated herein, and combines with the results of the MLML study to produce more complete information on the growth and reproduction of this species.

Materials and methods

Leopard sharks were collected between March 1979 and June 1981 from Monterey and San Francisco Bays, California. Otter trawl and gill net samples in Monterey Bay, and hook and line catches at several angling contests (e.g. Herald et al. 1969) and power plant entrainment in Elkhorn Slough provided most (65%) of the specimens. Additional sharks were obtained from the San Francisco Bay NMFS tag-recapture study (Smith 1984, Smith & Abramson 1990).

Total length (TL) precaudal length (PCL), and girth to the nearest mm, and weight, to the nearest g, were recorded from each specimen. A section of 12 vertebrae was typically removed from below the origin of the first dorsal fin and frozen. For many specimens, clasper length (CL) was measured to the nearest mm and the reproductive tract was examined. Stage of development and the external outline of the Wolffian ducts (vas deferens) were recorded to assess reproductive condition in males (Pratt 1979). Sperm smears were examined microscopically to verify the presence of mature sperm. For females, the number and size of eggs in the ovaries were recorded, and newly fertilized eggs or embryos were counted, measured and sexed. Oviduct dimensions and degree of vascularization were also recorded. Females suspected of aborting young had oviduct vascularization and dimensions corresponding to observations for pregnant females.

To make the calcium-rich rings on the vertebral centra more visible, we first used a modified silver nitrate staining technique (Stevens 1975, Cailliet et al. 1983a), then used resin-embedding and sectioning techniques (Humason 1972, Smith 1984). A substitution reaction of silver for a calcium salt (usually a carbonate, phosphate or chloride) provided distinct silver-impregnated bands which became markedly dark after illumination under ultraviolet light.

To expose anterior and posterior centrum surfaces for staining, and to make the dimensions of each centrum uniform, the neural and haemal arches were cut away and the notochord remnants and

connective tissue were removed from each vertebra. For this procedure, the centra were immersed in bleach for 10–75 min, depending upon centrum size. The centra were rinsed thoroughly in distilled water and then soaked in concentrated formic acid for four min. Rinsed centra then were placed in 1% silver nitrate and exposed to ultraviolet light from 3–15 min until bands became discernible. Bound silver was fixed following a brief immersion in 5% sodium thiosulfate and non-specific background color was removed by a water rinse. Tetracycline-marked centra from the tag-recapture study were never stained, because the process involves decalcification and would have removed the fluorescent mark.

The staining technique resulted in highly visible bands near the center of the centrum surface, but the closely spaced bands near the centrum margin of larger sharks were not easily seen (Fig. 1). Also, larger centra required longer exposure to silver nitrate stain, which increased the resolution of central growth zones, but decreased the resolution of the peripheral bands. Therefore, all vertebrae were embedded in clear polyester casting resin and sectioned longitudinally at their widest diameters (Smith 1984). Sections (0.5 mm thick) were mounted on microscope slides with clear enamel and examined under a dissecting microscope at $25\times$ magnification with transmitted lighting.

Centrum diameter (CD) was plotted against TL of the shark. A least-squares linear regression analysis was used to test the hypothesis that CD increased with body size (TL). This is a requirement if centrum growth is to represent the growth of the shark.

The concentric bands differed from those described by Cailliet et al. (1983a) in that there were no fine rings within them. Two kinds of bands occurred: those which appeared transparent with transmitted light (poorly calcified), and those which were silver-nitrate stained and appeared black (highly calcified). The latter bands were initially assumed to be more heavily mineralized and to represent summer growth on the centrum (Jones & Geen 1977b). In the sections, only opaque bands that appeared in the corpus calcareum (see Brown

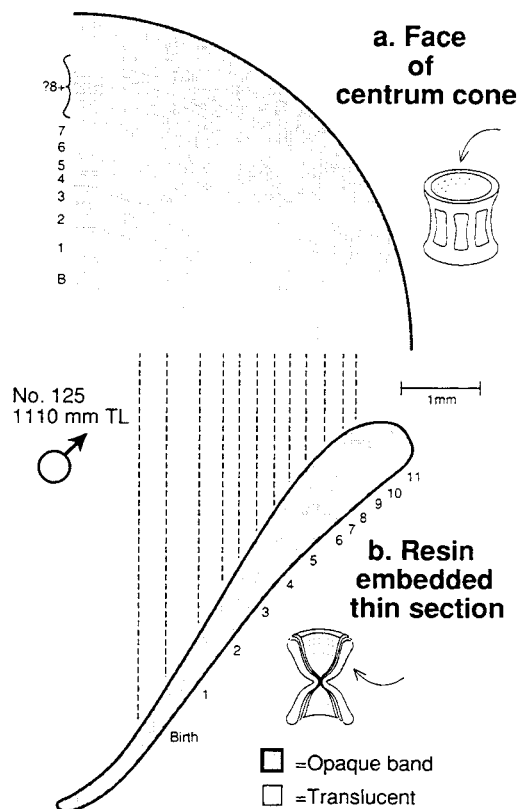


Fig. 1. Diagram comparing surface and thin-section band counts from the vertebral centrum of a male leopard shark (1110 mm TL): a – the anterior surface of the whole centrum stained with silver nitrate, showing 8 band pairs; b – an antero-dorsal thin section of the same centrum, showing 11 distinct bands.

& Gruber 1986) were counted (Fig. 1). Therefore, band counts refer to a complete pair of translucent and opaque bands.

Several centra from each specimen were processed to make sure that clearly stained specimens were available for study. To ensure precise, non-biased results, vertebral band counts were made without knowing specimen size, sex, or time of year collected. A consensus was reached among the two or three estimates of zone counts between readings.

Centra from 32 randomly chosen specimens were aged independently by two readers. Three

indices of band count precision were calculated: (1) average percent error (APE), measures the average deviation of each reading from the means of all readings of each section (Beamish & Fournier 1981); (2) percent error (D; Chang 1982), is calculated by dividing the coefficient of variation (V) of readings by the square root of the number of times each fish is aged (R), then multiplying this figure by 100. Chang (1982) suggested that D was a better estimator of precision because it is unbiased and consistent over all samples; and (3) the percent of the readings that agreed by $\pm 1, 2, 3$, etc. bands among all counts for the particular sample in question, also presented as a histogram of the percent agreement.

The von Bertalanffy growth function (VBGF; Bertalanffy 1938) was fitted to all the size and age data using FISHPARM (Prager et al. 1987). This program implements Marquardt's (1963) algorithm for least-square estimation of non-linear parameters. Standard errors and 95% confidence intervals were calculated for each of the three VBGF parameter (L_{∞} , K, and t_0). The VBGFs were calculated for both sexes combined and for each sex separately. Von Bertalanffy growth curves were plotted only for combined sexes. To substantiate the temporal periodicity of growth band deposition in vertebral centra, corroborative evidence was obtained from three sources. First, changes in size modes of young-of-the-year (YOY) leopard sharks were compared to the growth curve predicted from the VBGF from all aged specimens. YOY were collected in the spring and summer of 1979 through 1981 by otter trawl in the tidal creeks of Elkhorn Slough (Barry 1983). The first newborn (approximately 250 mm TL, with a slight umbilical scar remaining) leopard sharks to be caught in these collections indicated that birth occurred in May and June of each year, an observation previously made by Ackerman (1971). Starting in June, size modes were identified as means of individual TLs, and could be followed easily from month to month. Mean lengths and standard deviations were plotted on the growth curves from all aged specimens. The position of mean length on the X axis (i.e., number of bands) was based on the number of months between size modes and the assumption that one

pair of bands was deposited per year. These two curves were compared visually.

The second source of verification was the analysis of centrum edge type over different seasons. After silver nitrate staining, the centrum edges for all specimens collected in the Monterey Bay area between 1979 and 1981 were characterized as being opaque (highly stained) or translucent (lightly stained). We collected specimens from as many months of the year as possible to detect seasonal variation in the nature of the peripheral band. However, due to the large number of samples taken from the shark derbies, more samples were available in the summer. The number of opaque and translucent edges were plotted by season to assess temporal variation in edge deposition patterns.

The third source of evidence came from the tag-recapture study, which provided size data over a known time increment for individual recaptured sharks, and an oxytetracycline (OTC) mark in each centrum. Between 26 July and 13 September 1979, 948 leopard sharks were collected off Hunters Point in south San Francisco Bay, with a 183 m longline rigged with an average of 150 baited hooks, and fished on the bottom at depths of 15–20 m. Prior to release, TL and PCL were recorded, and each fish was given an interperitoneal injection of OTC at a dosage rate of approximately 25 mg per kg BW, to mark the most recent growth zone in the vertebral centra (Gruber & Stout 1983, Smith 1984). Sex and general physical condition of each fish were recorded and seriously injured fish were not tagged. A plastic tag (Kato & Carvallo 1967) was applied to the first dorsal fin and the shark was released at the capture location. The fin tags were imprinted with a legend that described the reward and recapture processing instructions (Smith 1984).

Every effort was made to obtain accurate measurements and vertebrae from recaptured sharks. If any doubt arose regarding the reliability of a measurement, it was not used. Centra from recaptured sharks were embedded and sectioned (0.5–0.6 mm; Smith 1984) and stored in the dark to prevent loss of OTC fluorescence. Sections were mounted on slides and examined under a dissecting

microscope at 12 or 25 \times magnification, using transmitted substage light alternately with reflected ultraviolet (UV) light to discern the band patterns and numbers in relation to the OTC mark (Smith 1984).

The number of growth zones distal to the OTC mark was plotted against the time, in portions of years, that each shark had been at large. A least-squares linear regression analysis was performed on these data. The null hypothesis that the slope (b) of the relationship between number of bands and time was equal to one, a situation occurring if one opaque and one translucent band were deposited each year, was tested using a two-tailed *t* test (Zar 1974).

Growth of individual recaptured sharks was plotted against time-at-large on the von Bertalanffy growth curve derived from centrum band counts. Here, the size and estimated age-at-recapture served to place each fish on the curve. The time-at-large determined the distance on the X axis (number of bands), and the size-at-tagging determined the slope. These lines were compared visually with the size-at-age data from the centrum readings.

In addition, average growth rate (cm year⁻¹) was calculated for tagged sharks at liberty for one or more years. When these growth increments are plotted against the length-at-capture, the slope provides an independent estimate of *K*, and the intercept is an independent estimate of the asymptotic length, *L*_∞ (Gulland 1983). There are at least two assumptions necessary to use this technique: (1) growth rates based on varying time intervals are representative of growth over the entire time interval (in our data set, years-at-large averaged 3.8 yr and ranged from 1 to 8 yr); and (2) the relationship between growth rate and length-at-capture is linear and statistically significant.

We also used length and time-at-large to provide information on the growth of the tagged portion of the population. In this approach, the age-at-recapture and the difference between capture and recapture lengths were used in two computer programs that estimate parameters of the VBGF. The first was a von Bertalanffy subroutine of the curve-fitting program FISHPARM (Prager et al. 1987), which uses length-at-age data. The second was the

program BGC4 (by P.K. Tomlinson, in Abramson 1971), which estimates the parameters *K* and *L*_∞ using length-at-tagging, length-at-recapture, and time-at-large. This program fits the equation:

$$l_{t + \text{delta } t} = l_t e^{-K \text{delta } t} + L_{\infty} (1 - e^{-K \text{delta } t}); K > 0,$$

where *l*_{*t*} is the length at tagging, *l*_{*t* + delta *t*} is the length at recapture, and delta *t* is time-at-large. The third parameter, *t*₀, cannot be estimated using tag-recapture data alone.

Results from these two programs were compared with those from the other techniques. The growth coefficient (*K*) and asymptotic length (*L*_∞) calculated from growth in the field were compared to the equivalent values from the age- and length-at-recapture length data. If our age estimates and length measurements at time of tagging are accurate, both values should be similar.

In addition, growth curves obtained from observed growth of the NMFS tagged sample and untagged central California sample were compared to discern possible effects of tagging and/or OTC injection on growth. Because the tagged sample represented only fish of an intermediate size, the growth curve was generated using only fish within the size range of those aged recaptures in the NMFS study (610–1220 mm TL). To facilitate a visual comparison of the two curves, the BGC4 curve, which only describes growth in TL over annual increments and not by age, was situated along the X axis by positioning the starting length of the curve (610 mm TL) at a band count (estimated age) of 3.5 yr, which is the average we obtained for fish of this size aged from vertebrae.

Using the reproductive information obtained from dissected specimens, the size and estimated age at which male and female leopard sharks mature was assessed. For males, clasper length (CL) was plotted against TL, and the length at which CL began to rapidly rise provided an indication of first maturity. Presence of active spermatozoa and coiling of the vas deferens were used to further categorize sharks and were compared with size and age estimates. Similarly, female sexual maturity was demonstrated when the width and degree of vascularization of female oviducts indicated either re-

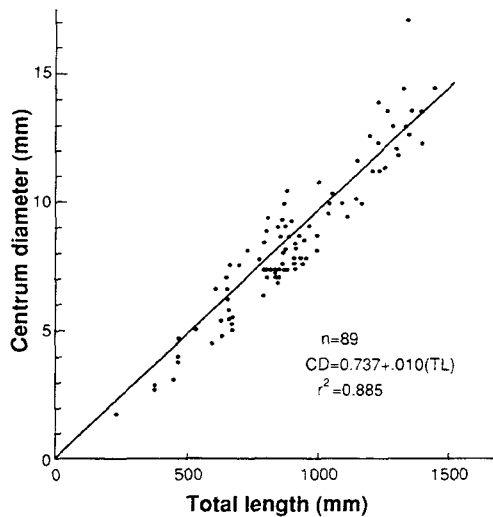


Fig. 2. Relationship between total length (TL) and centrum diameter (CD) of the leopard shark, with sexes combined.

cent birth or embryo abortion, or the oviducts contained fertilized eggs or embryos.

Results

The relationship between TL of the shark and centrum diameter was linear and significant (Fig. 2; $r^2 = 0.89$, $p < 0.001$). Thus, the centra grew proportionately to shark length over all size classes sampled, making this structure useful for age analysis. Ages were estimated using vertebral centra from 85 male and 77 female leopard sharks collected in central California. These sharks ranged from 226 to 1450 mm TL, and had from 0 to 24 bands. The largest shark was estimated to be 19 years old and the oldest shark (24 bands) was a male of 1364 mm TL.

Precision of band counts was relatively high between two readers (Fig. 3). D and APE were 4.9% and percent agreement within ± 2 yr was 90.7%. This set of comparative readings included specimens of widely ranging sizes and age estimates (from 5 to 24 yr). Thus, the error measured was most likely due to difficulties defining criteria among widely varied numbers, sizes, and spacing

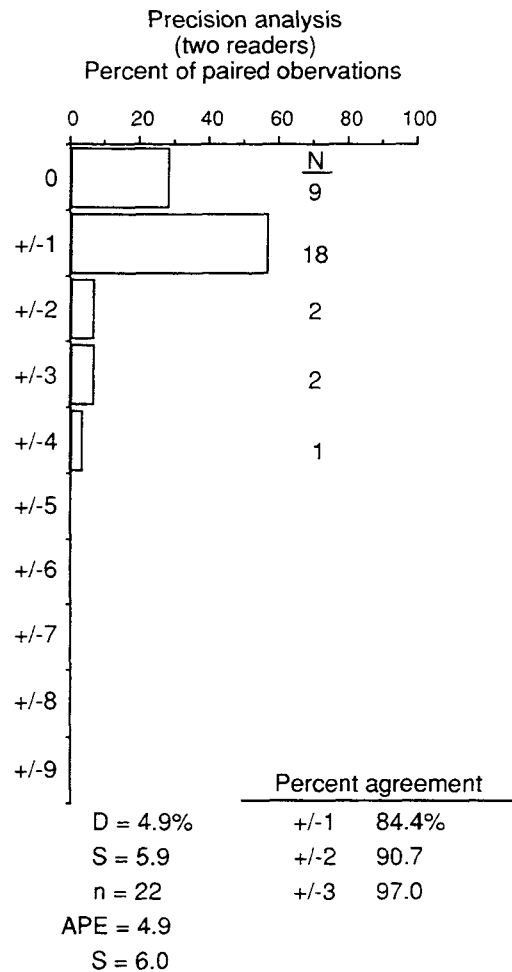


Fig. 3. Precision of age estimate of the leopard shark, with both sexes combined. Histogram represents the difference (as the percent of paired band counts differing by 1, 2, 3, etc. years) between two readers. The proportion of counts which agreed within a certain number of band counts is listed under 'percent agreement', and D, APE, and S are percent error, average percent error, and their standard deviations, respectively (Beamish & Fournier 1981, Chang 1982). The letter n represents the number of samples (centra) aged during this comparison, while N is the number of comparative readings of those centra.

of growth bands. However, because percent agreement was high and usually within 2 years or less, a consensus was always reached.

The VBGC determined for combined sexes of leopard shark had a growth coefficient (K: Ricker

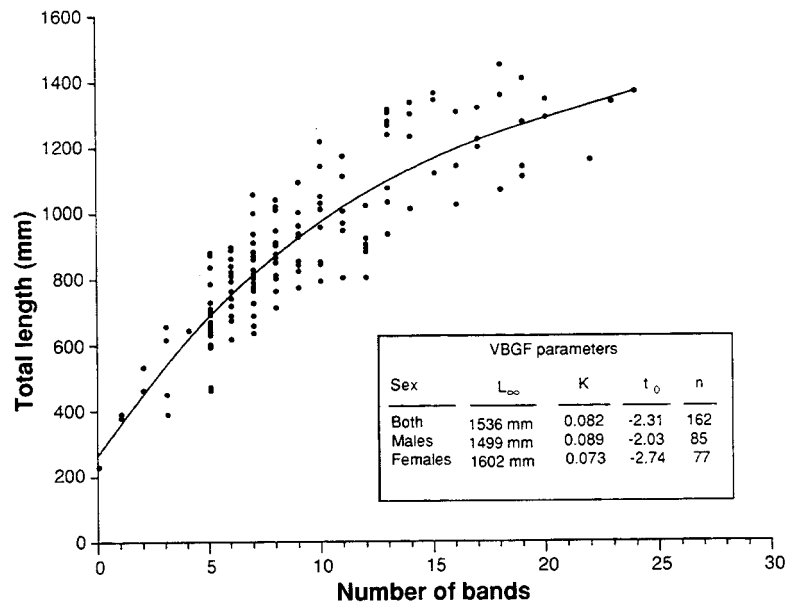


Fig. 4. Von Bertalanffy growth function (VBGF) for 162 leopard sharks of both sexes, collected in central California waters, in which the number of bands was estimated using the silver nitrate staining and thin-sectioning technique on vertebral centra. VBGF parameters and sample sizes for combined and separate sexes are given in the insert.

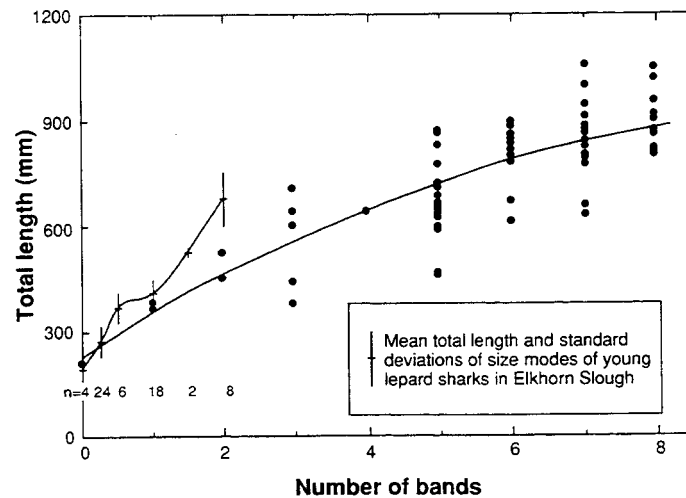


Fig. 5. Growth of young-of-the-year (YOY) leopard sharks, with a line connecting mean length of size modes during the first two years. VBGF for the first 4 years is plotted for comparison. Data for YOY sharks are taken from collections between 1979 and 1981 in Elkhorn Slough (Barry 1983).

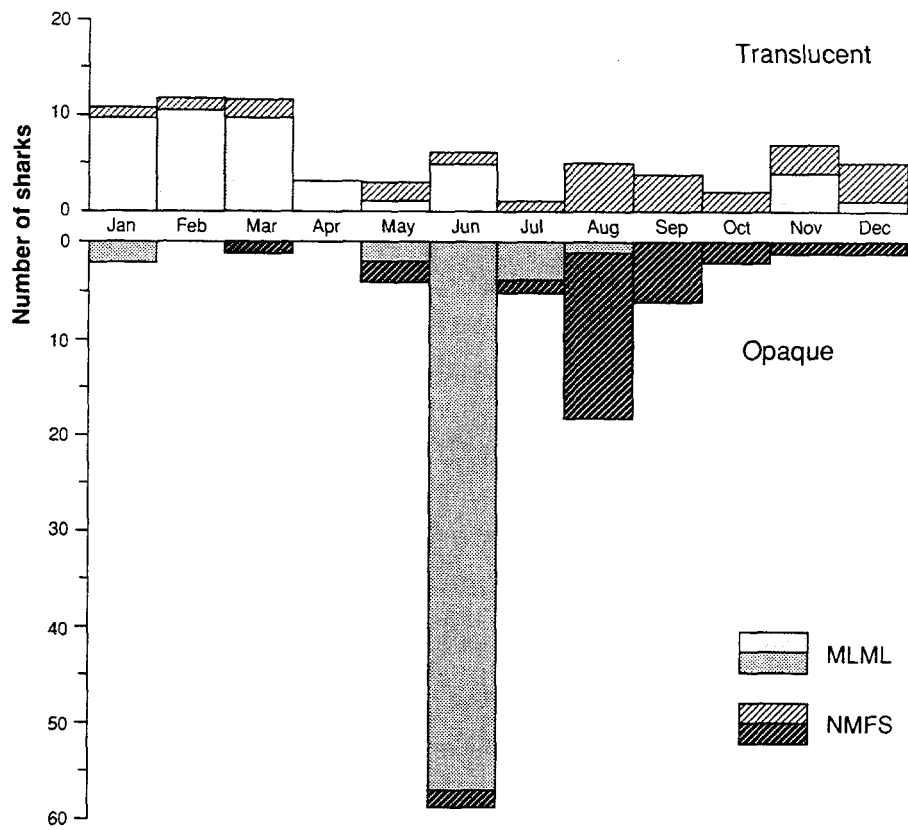


Fig. 6. Centrum edge characteristics by month, with seasonal alternation of peripheral zones from opaque in summer months to translucent in winter months. Those sharks taken from Monterey Bay and Elkhorn Slough are labelled 'MLML', and those taken from San Francisco Bay are labelled 'NMFS'.

1975) of 0.082 and produced a curve that steadily approached the calculated asymptotic length (L_{∞}) of 1536 mm (Fig. 4). This curve appeared to closely match the observed data, judging from the low standard errors of 102.5 mm for L_{∞} and 0.014 for K . The asymptotic length was less than the maximum reported size of leopard sharks (1981 mm TL: Miller & Lea 1972), but was close to the maximum size of those collected in Elkhorn Slough (1515 mm TL: Ackerman 1971). The size at 0 bands was approximately 260 mm TL, which agrees with known size-at-birth (Ackerman 1971). The estimated age at zero size (t_0) was -2.31 yr, a figure which could be partly of statistical rather than biological significance.

The VBGF parameters, determined for separate

sexes, suggest that females ($n = 77$) attain a slightly larger asymptotic TL ($L_{\infty} = 1602$ mm) than males ($n = 85$; $L_{\infty} = 1499$ mm TL), but that males grow faster ($K = 0.089$) than females ($K = 0.073$). However, these differences were not statistically significant.

Size mode analysis of YOY leopard sharks collected monthly in Elkhorn Slough produced a growth trend which was similar to that determined from band counts during the first year, but which was faster than the VBGF during the second year (Fig. 5). Numerous problems arise when interpreting such modal trends, including delineation of modes, emigration of year classes, differential growth of individuals, and underrepresented sizes in the samples. However, it appears that modal

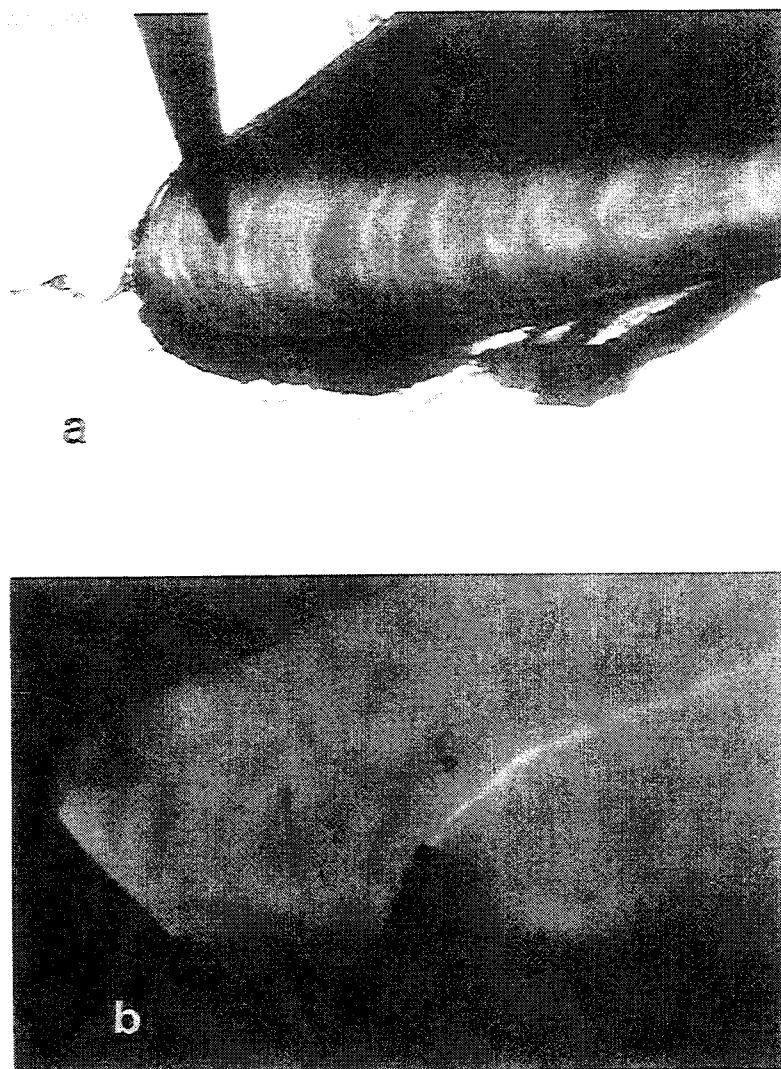


Fig. 7. OTC marks (pointer) and two typical band patterns outside these marked bands in the thin section of leopard shark centra: a – 4 relatively narrow bands distal to the OTC mark, from specimen # 497, a male shark that grew from 108 to 111 mm TL in 4.8 years and was estimated to be 19 years old at recapture; b – 7 relatively broad bands distal to the OTC mark, from specimen # 280, a female that grew from 98.6 to 122 mm in 7.3 years and was estimated to be 17 years old at recapture. The photographs were produced using : a – transmitted incandescent illumination; and b – ultraviolet light alone.

analysis agrees with band counts for the first year of the leopard shark's life, and supports the annual periodicity of growth band deposition in vertebral centra of YOY sharks.

The nature of the peripheral zone on the cen-

trum edge varied predictably with season (Fig. 6). Opaque peripheral bands occurred mainly on centra from sharks captured in late spring through summer, while translucent peripheral bands primarily occurred in centra from sharks collected

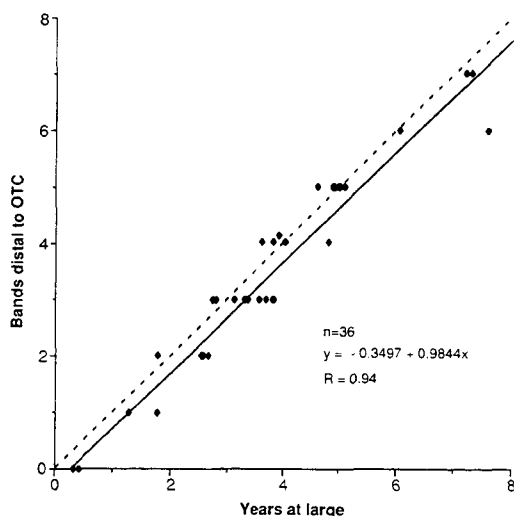


Fig. 8. Number of band counts distal to the OTC mark versus the number of years the specimen was at large. This relationship is significant and linear ($r = 0.94$, $p > > > 0.001$), and had a slope which was not statistically different from one ($p < < < 0.001$; Zar 1974). The dotted line represents a perfect 1:1 relationship with a slope of 1.0 and the solid line is the one that fits the data.

mostly in fall and winter months. From the 116 specimens collected in Monterey and San Francisco Bays, 67 had opaque edges while 49 had translucent ones.

There were 104 tagged sharks recaptured in the 8 yrs after tagging. From these, 51 vertebral samples were obtained for ageing. Reliable growth information (i.e., length at tagging and recapture) was available for 61 specimens, of which 56 were at liberty for one year or more. Sufficient OTC uptake was found in 36 specimens, allowing a reading of the number of bands distal to the OTC mark and a comparison with time-at-large. The male:female ratio of recaptures was 53:47, exactly the same as that at tagging.

Two general patterns of zone formation were noted (Fig. 7). In the first pattern, a group of relatively narrow bands were obvious outside of the OTC mark (Fig. 7a). The second pattern consisted of more widely spaced bands (Fig. 7b). These patterns were generally associated with the relatively slow or fast growth, respectively, of the individual shark.

There was a significant, linear correlation between the number of bands distal to the OTC and the number of years at large (Fig. 8; $r = 0.94$; $n =$

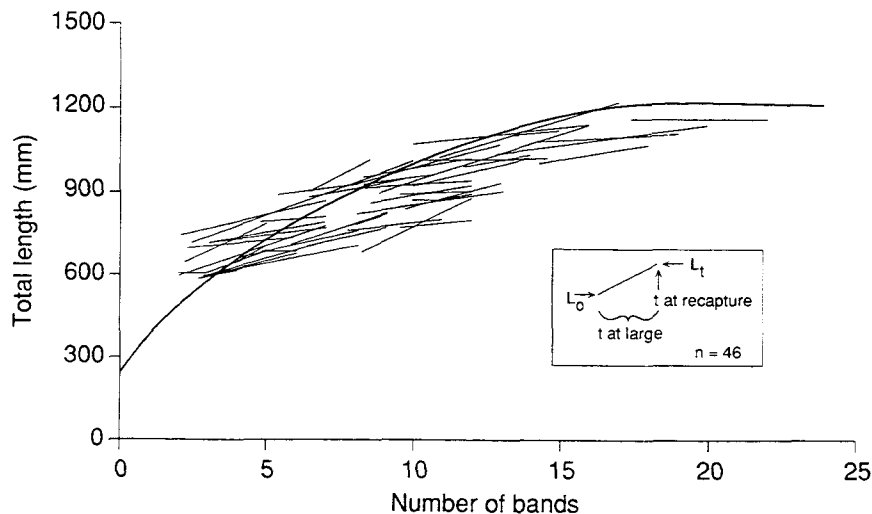


Fig. 9. Growth of 46 tagged and recaptured male and female leopard sharks. Each line is the result of tag-recapture information on size, age at recapture, and time at large from sharks tagged in San Francisco Bay by Smith (1984).

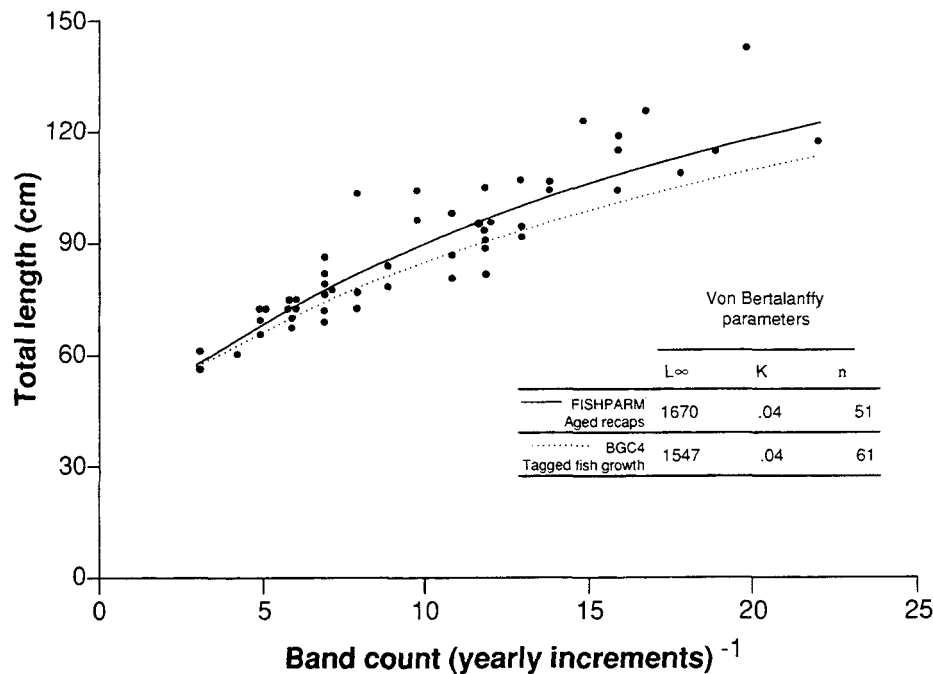


Fig. 10. VBGFs generated from vertebral band count and length of leopard shark at time of recapture (FISHPARM: solid line), and from interim growth of sharks between tagging and recapture (BGC4: dashed line).

36; $p \gg 0.001$). Time-at-large prior to recapture ranged from 0.32 to 7.6 years, and the number of bands distal to the OTC mark ranged from 0 to 7, for specimens which ranged in size from 59 to 116 cm TL at time of original capture. The observed slope of this relationship ($b = 0.984$) was not significantly different from the expected value of 1 ($p \gg 0.001$). These results confirm the hypothesis that one pair of vertebral growth bands is produced per year in this species.

Changes in TL of the 46 leopard sharks for which there were lengths at capture and recapture, time-at-large, and age estimates, corresponded well with the growth curve generated by the VBGF from centrum band counts (Fig. 9). Individual growth rates and time-at-large varied a great deal, but the majority of individual growth lines had slopes which closely approximated the curve.

There was considerable variation in average annual growth rate (cm yr^{-1}) among the 56 recaptured fish at liberty for 1 year or more, resulting in a

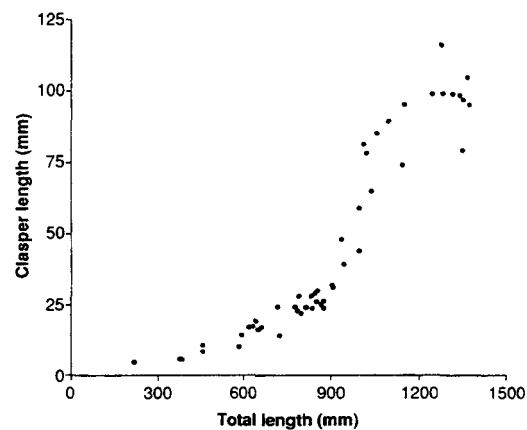


Fig. 11. Relationship of clasper length (CL) to total length (TL). The abrupt increase in CL between 1000 mm and 1200 mm TL coincides with maturation of spermatozoa and vas deferens of 16 specimens.

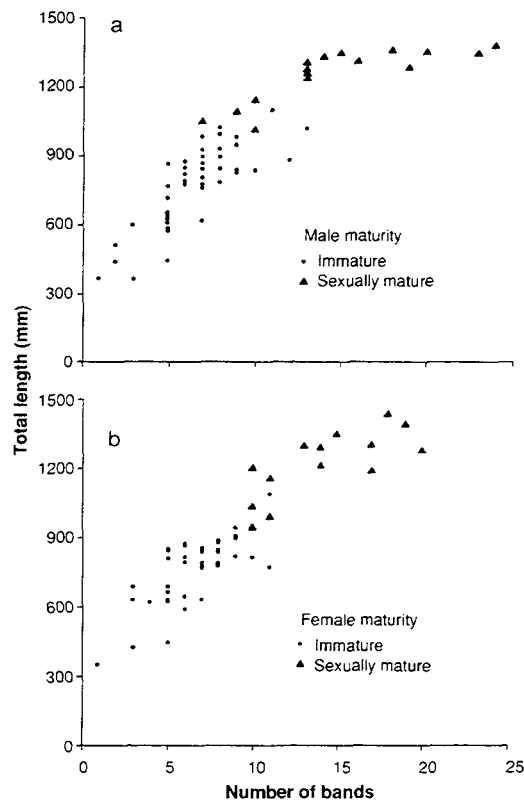


Fig. 12. Length-at-age estimates and sexual maturity information for separate sexes of leopard sharks. Maturity designation given in insert: a – male maturity was based upon developmental status of claspers, presence of mature spermatozoa, and coiling of the vas deferens; b – female maturity was based upon the developmental status of ovaries and oviducts.

statistically insignificant correlation coefficient between annual growth rate and length at capture (cm). Because of this variability, predicted by Sainsbury (1980), Gulland's (1983) annual incremental growth technique, when applied to the leopard shark growth data, was inappropriate. It is interesting, however, that the larger sharks tended to have slower annual growth rates and that the asymptotic length and growth coefficient values predicted by this method ($L_{\infty} = 1508$ cm TL, and $K = 0.029$, respectively) compared favorably with estimates using other methods.

Three of the recaptured sharks did not grow at all, 27 grew between $0.1\text{--}2.0$ cm yr^{-1} , 21 between

$2.1\text{--}4.0$ cm yr^{-1} , while only 5 grew more than 4.1 cm yr^{-1} . The overall average annual growth rate was 2.14 cm yr^{-1} , with females averaging 2.3 (range $0\text{--}5.9$; $n = 32$), and males averaging 2.0 cm yr^{-1} (range $0.2\text{--}4.9$; $n = 24$).

The VBGFs calculated from (1) aged sharks and length-at-recapture using FISHPARM, and from (2) interim growth of tagged and recaptured sharks only using BGC4, produced growth curves and parameters which were very similar (Fig. 10). The values for K (0.04) obtained by the two methods were identical, indicating strong agreement between observed growth and growth calculated from estimated age-at-length alone. However, these K values were only half of those produced from the age-at-length analysis of the entire data set (Fig. 4: $K = 0.082$), indicating that growth of tagged fish might be slower. The values for L_{∞} (1670 and 1547 cm TL, respectively) were also similar, both to each other and to those produced by the entire data set (Fig. 4: $L_{\infty} = 1536$ mm TL). These apparent differences were not statistically significant due to the large standard errors associated with K and L_{∞} values from both data sets.

Length and age of leopard sharks at time of sexual maturation differed only slightly between sexes. Males first become mature at approximately 1000 mm TL as evidenced by the rapid increase in CL at that size (Fig. 11), the maturation of spermatozoa identified in sperm smears of 16 sharks, and the subsequent development of the vas deferens in all specimens over 1000 mm TL. The youngest mature male in our sample had 7 vertebral bands (Fig. 12a). The oldest and largest male in our sample was 1364 mm TL and had 24 bands. In contrast, the youngest male was 226 mm TL but had 0 bands.

Females attained maturity at approximately 1050 mm TL (Fig. 12b). The oldest, but not largest, female in our sample was 1290 mm TL and had 20 bands, while the youngest was 375 mm TL and had one band. The youngest mature female in our sample had 10 vertebral bands. At TLs greater than 1100 mm, all females collected showed signs of either recent birth or embryo abortion (based upon width and degree of vascularization of oviducts), or were pregnant, with oviducts containing embryos.

Discussion

In this study, several independent methods of processing vertebral centra and counting band pairs produced very similar results within specific size ranges, thus satisfying the criteria defined by Wilson et al. (1983). In addition, the precision analysis (Fig. 3) concluded that percent agreement was high and error low. Indeed, our D and APE values (4.9) were considerably lower than those found in equivalent age precision analyses on *Mustelus manazo*, another triakid species which is more difficult to age (Cailliet et al. 1990: D = 6.8–8.9) and on *Prionace glauca*, a carcharhinid species in which reader and sample processing technique caused high variability in counts (Tanaka et al. 1990: D = 6.1–21.9).

The growth of elasmobranch skeletons has been considered to be a determinate process of deposition, in which no resorption of minerals occurs (Applegate 1967, Simkiss 1974, Cailliet et al. 1983a). The significant correlation found between TL and CL (Fig. 2) supports this contention, and agrees with Tanaka & Mizue's (1971) and Taniuchi et al.'s (1983) studies of *Mustelus manazo*. The variability found in this relationship may, however, be related to resorption of minerals in small amounts or at variable times in the life of the shark. Indeed, radioisotope composition in different parts of the centra of four elasmobranch species, including the leopard shark, was not useful in assessing growth; this was attributed to a violation of the assumption of no resorption of minerals (Welden et al. 1987).

The age and size data for leopard sharks fit the von Bertalanffy growth equation well. However, computation of VBGF parameters for combined and separate sexes (Fig. 4) resulted in asymptotic TL estimates that were well below the maximum observed length (1981 mm TL: Miller & Lea 1972). These discrepancies may be attributable to the lack of specimens greater than 1450 mm TL, a problem similar to that of Tanaka & Mizue (1971) in their study of *Mustelus manazo*. The goodness of fit of data to the VBGF can seriously influence the growth model parameters obtained (Cailliet et al. 1990). Individual leopard sharks rarely attain the

maximum size. In fact, most adults are smaller than 1600 mm TL (Compagno 1984). Also, the asymptotic TL is not necessarily the largest recorded, but rather represents the mean size of the oldest group of fish.

The VBGF asymptotic length was slightly higher for females, yet the growth coefficient was higher for males (Fig. 4), suggesting that females may get larger but grow more slowly, a situation commonly found in other species of sharks (Compagno 1984). However, a larger sample size, with better representation of all size classes, is necessary before this question can be adequately assessed statistically (Cailliet & Tanaka 1990).

For the leopard sharks in this study, the growth coefficient (K) was 0.082 for combined sexes, a value below the range of 0.1 to 0.2 predicted by Holden (1974) from ratios of length at birth to maximum observed length. However, Holden (1974) had assumed a gestation period of two years for *Triakis barboursi*, which is considerably longer than the commonly assumed gestation period of 10–12 months for *Triakis semifasciata* in California (Ackerman 1971, Smith & Abramson 1990). The estimated gestation periods of seven species of the triakid genus *Mustelus* range from 10–13 months in duration with corresponding K values between 0.22 and 0.53, based upon extrapolation from embryonic growth (Francis 1981).

Mean sizes of modes of YOY leopard sharks provide a standard by which to compare mean sizes predicted by growth curves derived from band counts (Fig. 5). The greatest agreement between predicted and observed sizes occurred among smaller, younger sharks, because they are born in predictable habitats, are easier to sample, and there is less variation in size-at-age in these younger individuals than in older ones (Ackerman 1971, Cailliet et al. 1983a, 1986). Model analysis indicated a slightly faster growth rate in the second year than that predicted by the VBGF. This could be explained if more than one age class was included in this larger size mode. One additional explanation for this difference in growth rates could be the lack of small specimens in our sample of centra, thus negatively influencing the accuracy of our early growth estimates from size mode analysis.

However, Ackerman's (1971) analysis of YOY size frequencies was based upon a larger sample and resulted in identical estimates of mean sizes of the first four year classes.

The seasonal variation in centrum edge characteristics of the leopard sharks also supported the annual band formation hypothesis (Fig. 6; see also Smith 1984). Vertebrae from sharks captured from June through August generally had opaque edges, while sharks captured from November through April had non-stained, translucent edges. It is unknown whether the opaque zones contain more calcium and phosphate, as in the spiny dogfish (*Squalus acanthias*; Jones & Geen 1977b), and the common thresher (*Alopias vulpinus*) and gray reef (*Carcharhinus amblyrhynchos*) sharks (Cailliet & Radtke 1987). From the centrum edges of three species of *Mustelus*, one pair of translucent and opaque bands was discerned for each year, therefore supporting annual deposition (Tanaka & Mizue 1971, Yudin & Cailliet 1990). The marginal band may be obscured by connective tissue (Holden & Vince 1973, Roussouw 1984, Smith 1984). However, techniques used in the present study provided easily discernible edges for observation.

Seasonal and annual variation in the deposition of the material in the centrum edges are influenced by changes in food consumption and availability, environmental factors, or endogenous growth rhythms that differentially affect uptake of elements from water (Jones & Geen 1977b), and exchange of calcium between the circulatory and skeletal system (Welden et al. 1987). It is difficult to determine which of these factors influence the centrum edge formation in the leopard shark.

Many studies of field-tagged and recaptured elasmobranchs have reported growth information (for reviews, see Cailliet et al. 1986, Cailliet 1990), but often this growth information is not related to vertebral band counts. We were able to obtain such information, because reliable data on interim growth were available for 94% of our sharks aged at recapture.

The occurrence of two patterns of band deposition (Fig. 7) and the relationship of these patterns with body growth (Fig. 6, 8) indicate that there is a relationship between the number, width, spacing,

and opacity of bands and body growth. These two patterns also were described in spine sections for the spiny dogfish from a recent tag-recapture study (Beamish & McFarlane 1985, McFarlane & Beamish 1987).

The rates of growth that were derived from changes in body size over known periods of time (Fig. 9) also indicate that the growth equation derived from age estimates of centra is accurate. While some sharks did not grow at all, and others grew more slowly or faster, most of them grew approximately as the VBGF model predicted. Inaccurate measurements could have accounted for some of the discrepancies between observed and predicted growth rates. Fish growth could also have been influenced by capture handling, tagging, and OTC injection.

The most likely explanation of any discrepancies between individual growth rate and that estimated by the VBGF is that growth rates vary considerably with response to environmental conditions. High individual growth variation is not unusual in sharks (Thorson & Lacy 1982), and was noted in two populations of *Mustelus manazo* (Tanaka & Mizue 1971, Taniuchi et al. 1983, Cailliet et al. 1990). Growth rates of individual tagged slit-eye sharks (*Carcharhinus albomarginatus*, now *Loxodon macrorhinus*; Compagno 1984) of almost identical lengths ranged from -23 cm to $+20.8$ cm year⁻¹ (Kato & Carvallo 1967). Captive *Heterodontus portusjacksoni* exhibited extreme variation in growth rates (McLaughlin & O'Gower 1971). Age at length also varied widely for *Galeorhinus japonicus* (Tanaka et al. 1978) and *Prionace glauca* (Cailliet et al. 1983b, Tanaka et al. 1990).

We have demonstrated that the stained and sectional vertebral centra of leopard sharks offer a good method for growth analysis. In addition, we have provided convincing verification and validation to support the hypothesis that centrum bands are annually deposited (Smith 1984). This evidence ranges from size frequency analysis of YOY, to seasonal centrum edge analysis and tag-recapture and OTC-marked growth data from the field.

Our data support the hypothesis that leopard sharks, like many elasmobranchs, exhibit late maturation (Fig. 11, 12). Females were observed to

mature at ages between 10 and 15 years, 1050 to 1350 mm TL, and 0.72 to 0.93, respectively of their asymptotic length. Males mature between 7 and 13 years, 1000 to 1050 mm TL and 0.63 to 0.66 of their asymptotic length. These values are slightly lower than Ackerman's (1971), in which the smallest mature female was 1180 mm TL, but normal size of maturity was around 1200 mm TL. *Galeorhinus zyopterus* matures after 9 years (Holden 1977) and *Squalus acanthias* matures after 14–23 years (Ketchen 1972, 1975, Holden 1973, Jones & Geen 1977a), or longer (Beamish & McFarlane 1983). All of these estimates agree with Holden's (1974) suggestion that female elasmobranchs, in general, attain sexual maturity at 0.6–0.9 of their asymptotic length. In contrast, male elasmobranchs mature at a smaller size than females (Hisaw & Abramowitz 1938, Springer & Lowe 1963, Teshima et al. 1971, Tanaka & Mizue 1971, Francis & Mace 1980), as evidenced by rapid increase in CL (Clark & von Schmidt 1965).

The leopard shark has a relatively slow growth rate, matures relatively late in life, and has a low fecundity of 7–36 offspring per female during each year-long reproductive season (Ackerman 1971). An estimated longevity of 25–30 years (Smith 1984), however, is considerably higher than the 13–16 years suggested by Ackerman (1971) from size frequency analysis. All of these life history features contribute to the suggestion that they are susceptible to over-exploitation.

Acknowledgements

Many people contributed to the successful completion of this project. Jim Barry, Dave Ebert, Kevin Hill, Michael Kelly, Linda Martin, Lisa Natanson, Dan Reed, Kate Yudin, Bruce Welden, and Patty Wolf aided in the field collections. The Pajaro Valley Rod and Gun Club allowed us to sample during several shark derbies, and many fishermen cooperated by returning tags and recaptured sharks. Jim Brennan, Bill Hayden, Lynn McMasters, Guillermo Moreno, and Mary Yoklavich helped with computer graphics and photographs. Norm Abramson, Margaret Bradbury, Joe Crim, Michael Foster,

and Mary Yoklavich read and edited the manuscript. Jim Harvey and Jim Barry loaned us their laptop computer and printer, respectively, allowing GMC to revise the manuscript during recuperation from surgery at his parents' home. This work is a result of research sponsored in part by NOAA, National Sea Grant College Program, Department of Commerce, under grant numbers 04-8-M01-189 and NA 80AA-D-00120, project numbers R/F-54, R/NP-1-11C, and R/F-81, through the California Sea Grant College Program, and in part by the California State Resources Agency. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

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