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Preliminary Studies on the Age and Growth of Blue, *Prionace glauca*, Common Thresher, *Alopias vulpinus*, and Shortfin Mako, *Isurus oxyrinchus*, Sharks from California Waters

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ABSTRACT

Two methods of enhancing growth bands on vertebral centra—silver nitrate impregnation and X-radiography—have proven to be successful when used on centra from 130 blue, *Prionace glauca*, 143 common thresher, *Alopias vulpinus*, and 44 shortfin mako, *Isurus oxyrinchus*, sharks. Bands were counted and measured, and these data were used to construct growth curves based on the von Bertalanffy and logistic growth models. The problems of verification of these counts, and validation of the periodicity of band formation, have been identified and are discussed in relation to the growth curves generated for each of these three species. Our results and other available information indicate that these elasmobranchs grow relatively slowly, reaching their asymptotic lengths at 20 yr of age for blue sharks, and between 45 and 50 yr for shortfin mako and common thresher sharks. They have a large size but relatively early age of first reproductive maturity, and low fecundities. This combination of traits could make them susceptible to overfishing.

INTRODUCTION

Commercial fishing for elasmobranchs is increasing rapidly in California. For example, the United States Department of Commerce (1978-80) reported that blue shark, *Prionace glauca*, landings in San Pedro, Calif., have increased from virtually nothing in 1978 to over 188,000 lb in 1980. Similar trends have occurred for common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks. Landings of common thresher and shortfin mako increased from 15,500 lb and 1,129 lb in 1978 to 994,000 lb and 62,000 lb, respectively, in 1980. Thus, commercial fishing of these three species has increased over the past few years, and they now comprise over 87% of the total shark landings in San Pedro. Historically, sharks were used primarily for their oils, for reduction (Byers 1940), and for the vitamins in their livers (Frey 1971). Today, however, their principal use is for food.

A major problem that arises with this increased commercial use of elasmobranchs is the lack of life history information necessary to ensure effective management. For example, age determination has not been evaluated sufficiently for the majority of elasmobranchs in California, and, therefore, such critical information as age at first maturity is not known.

The usual means of age determination in bony fishes, by examining scales, otoliths, or bones, are not applicable to elasmobranchs. However, the evidence that does exist indicates that growth rates in sharks may be slow, compared with many teleosts, with size at first sexual maturity estimated at approximately 60 to 90% of the asymptotic length (Holden 1977). Because of these growth and reproductive traits, intensive fisheries directed toward subadults could deleteriously affect the total population size of sharks very quickly, assuming a close relation between stock and recruitment (Holden 1973, 1974, 1977). Without information on size and age at which reproduction first occurs, effective management measures, such as setting size restrictions, would be difficult to implement.

Recently, several techniques have been used to estimate ages of elasmobranchs by counting bands laid down concentrically in their vertebral centra (Stevens 1975; Cailliet et al. 1983). However, nothing has been done to estimate age or growth of blue, common thresher, and shortfin mako sharks in California waters. Therefore, our objectives in this study were to use recently developed techniques to enhance growth bands on centra for these three west coast pelagic sharks, make estimates of age based on counts from these structures, and construct preliminary growth curves. Finally, because these pelagic sharks appear to range widely over the oceans (Strasburg 1958), very little information has been gathered that could validate the presumed annual nature of bands in their vertebral centra. We attempted to use what little information was available on their size and reproduction to evaluate our growth curves.

MATERIALS AND METHODS

Most blue sharks were collected between September 1974 and October 1977 in Monterey Bay, Calif., by longline and hook and line using 2 m stainless steel leaders baited with either anchovy or squid. Most collections of common thresher and shortfin mako sharks and several specimens of blue sharks were obtained from commercial fisheries in southern California and from the California Department of Fish and Game pelagic gill net observer program. Additional preserved specimens of all three species were obtained from several California museums.

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All sharks were measured and weighed and their sex and reproductive status noted, if possible. The main measurements used were total length (TL), fork length (FL), and alternate length (AL, the distance between the origins of both dorsal fins). All length measurements were converted to total length for uniformity using conversion factors based upon measurements from the literature (Bigelow and Schroeder 1948; Applegate 1977) and from our own specimens. For age determination, a section of the vertebral column was removed, usually just anterior to the first dorsal fin, because this appears to be the area where vertebrae are largest and most calcified (Ridewood 1921). However, in some cases, such as common threshers collected from fish markets, we could only obtain caudal vertebrae from carcasses. Each section, usually consisting of 8-12 vertebrae, was frozen in a plastic bag or was stored as long as several months in 50% isopropyl alcohol until it was analyzed.

For all three species, a piece of the defrosted vertebral column was cleaned using a combination of steps. First, the haemal arch and lateral processes were removed, and most of the connective tissue was picked off with forceps to expose the surface of the centra. Then, several centra were soaked for approximately 5 min in distilled water, followed by air drying or by soaking in bleach to further facilitate the removal of connective tissue from the centrum. For larger centra, a longer soaking time was needed, and immersion intervals ranged from 5 to 30 min. The centra of the blue sharks were then soaked in a concentrated solution of formic acid for 2 to 4 min to remove any remaining traces of bleach and to etch the centrum surface. For the centra of common thresher and shortfin mako sharks that were X-rayed, the formic acid treatment was not necessary. Centrum diameters (millimeters) were measured for each specimen of common thresher and shortfin mako, and the relationship between centrum diameter and total length of the fish was determined with regression analysis. This has already been done for blue sharks by Stevens (1975). All statistical inferences were made with a significance level of $\alpha = 0.05$.

The ageing technique used for blue sharks was modified from a procedure attributed to Von Kossa (Stevens 1975). This basically involved replacing the calcium salts in the centrum with silver, providing distinct silver-impregnated bands, which become quite dark after illumination under ultraviolet light. After cleaning, these centra were rinsed in distilled water for approximately 15 min, then immersed in a 1% silver nitrate solution, and immediately placed in a chamber where they were illuminated by an ultraviolet light source. The length of light exposure ranged from 3 to 15 min, depending upon centrum size. The centrum was then rinsed again in distilled water to remove excess silver nitrate. A dissecting microscope, with illumination focused laterally on the centrum, was used to count bands. Because staining clarity can be inconsistent, several centra from each specimen were stained and counted by two or three different readers for replicate analysis. Once a concensus was reached regarding these counts on the newly stained centra, they were soaked in a 5% sodium thiosulfate solution for 2 to 3 min. This procedure removed excess silver and fixed the chemical substitution. Because fixation also eradicated the very narrow rings, counts were made before and after fixation to estimate this bias. The final step was storage in 70% iospropyl alcohol. Also, the radius, defined as the distance from the center of the focus to the outer edge of each light band, was measured so they could be compared with similar measurements made by Stevens (1975).

The cleaned centra from the common thresher and shortfin mako sharks were X-rayed using a Hewlett-Packard[3] Faxitron Series X-ray system (Model No. 43805N) with Kodak Industrex M film (Readypack M-2). These X-radiographs were viewed through a dissecting microscope using transmitted light from below.

For both of these techniques, procedures for counting the concentric lines were standardized. We defined any concentric line found on a centrum as a "ring." We further defined "band" as a group of rings (Cailliet et al. 1983). Two kinds of bands occurred: Those that were transparent (translucent, see Glossary) with transmitted light and those that were more opaque. In silver nitrate impregnated centra, opaque bands appeared black, and in X-rays they were white. We assumed that these bands were more heavily mineralized and represented summer growth on the centrum (Jones and Geen 1977). To insure the accuracy of band counts, at least two observers made independent counts of the opaque bands on each centrum. If these initial counts did not agree and additional readings did not result in a concensus, the centrum was not used for age analysis.

For simplicity and the widest applicability of this preliminary age information, we fit our data on age and length for all three species to the von Bertalanffy (1938) growth equation using methods for calculating the parameters L_∞, k, and t_0 from Allen (1966), Gulland (1969), and Everhart et al. (1975). Those parameters producing the best fit (least mean square error) from one of these methods were then selected to plot the growth curve for each species. These parameters were calculated for all individuals of each species combined and separately for male and female blue and common thresher sharks. Sexes were not separated for shortfin mako sharks, because the data set consisted of only 44 fish. Growth was characterized for all three species by plotting individual total lengths (TL) against estimated ages, and by plotting the predicted von Bertalanffy growth curve based upon the parameters L_∞, k, and t_0 for combined sexes. For the shortfin mako, we also used the logistic growth equation (Ricker 1979).

As an initial approximation of the temporal periodicity of band formation, we plotted size-frequency histograms of all specimens of each species collected during the entire study period and plotted above these the means and standard deviations of total length at estimated ages based on band counts. Visually, we then compared mean size at estimated age with the corresponding modes in the size-frequency distribution.

For the blue shark, we compared our growth curve with information presented for North Atlantic blue sharks by Stevens (1975, 1976), and we sent two of our centra to him for independent band counts. Our shortfin mako shark growth data were compared with those presented by Pratt and Casey (1983) for the same species in the western Atlantic Ocean. For all three species, we also compared the size and age at birth, first maturity, and the maximum size reported in the literature with those values estimated from our growth curves to gain insight into the accuracy of our counting methods.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS AND DISCUSSION

Blue Shark

We caught a total of 120 blue sharks between 1974 and 1977, with an additional 42 specimens coming from museum collections and the commercial catch in southern California taken over a wider range of years. The Monterey Bay collections produced specimens ranging from 958 to 2,045 mm TL, and fish smaller and larger than these sizes were added from the additional sources. The resulting size range collected was between 300 and 2,705 mm TL (Fig. 1). Because blue sharks are born at approximately 400 mm TL and reach a reported maximum size of about 3,962 mm TL (Bigelow and Schroeder 1948; Tucker and Newnham 1957; Strasburg 1958; Miller and Lea 1972; Hart 1973; Pratt 1979), our sample sizes are low for the smallest and largest size classes. Although the blue shark is known to make extensive, sexually segregated migrations (Strasburg 1958; Beckett 1970; Stevens 1976), our samples suggest that the larger individuals are uncommon off central California, or are not as vulnerable to commercial gear. Even with extensive collecting efforts, blue sharks over 2,600 mm TL are quite rare in northeast Pacific waters (Strasburg 1958).

Both silver nitrate and X-radiography produced clear bands (Urist 1961; Cailliet et al. 1983), but the silver nitrate technique was chosen to age blue sharks (Fig. 2), because it was the first technique available and it worked consistently well; it was also used by Stevens (1975) on this species. Because we counted bands in centra and not the finer rings, all counts taken before fixing in sodium thiosulfate were identical to those taken immediately after.

The von Bertalanffy growth curve for the 130 blue sharks we aged, which ranged between 280 and 2,521 mm TL, rose steeply and leveled at an estimated TL of 2,655 mm for both sexes combined (Fig. 3). Males were estimated to reach a larger asymptotic size (2,953 mm TL) than females (2,419 mm TL), but as in Stevens' (1975) study, there were insufficient samples to recognize significant differences in male and female growth rates. The oldest fish in our sample was a 2,450 mm TL male that had nine bands, while the youngest were two near-term embryos that had no bands and were between 350 and 400 mm TL.

The male asymptotic length was close to that of the largest specimens commonly collected in the Pacific (around 3,100 mm TL; Strasburg 1958), but was considerably smaller than the largest reported blue shark (3,962 mm TL; Bigelow and Schroeder 1948). Extrapolating from our von Bertalanffy growth curve for combined sexes, a fish at the asymptotic length of 2,655 mm TL would be approximately 20 yr old. With additional larger specimens, our estimate of asymptotic length might increase, and this would agree more with the maximum reported size, unless Pacific blue sharks do not grow comparably with those in the Atlantic. Until larger specimens are obtained, the maximum age attained by the blue shark will remain unknown.

Our estimate of size at birth (435 mm TL), derived from the von Bertalanffy growth curve, was between the reported sizes of free-living young (340 and 530 mm TL; Bigelow and Schroeder 1948; Tucker and Newnham 1957; Strasburg 1958; Hart 1973; Pratt 1979). Also, the mean sizes of the younger age classes corresponded to the size modes of blue sharks collected (Fig. 1). With larger and older fish, this relationship deteriorated, perhaps due to our small sample size or mixing of several age classes into a larger size class due to different individual growth rates and slower growth rates in general.

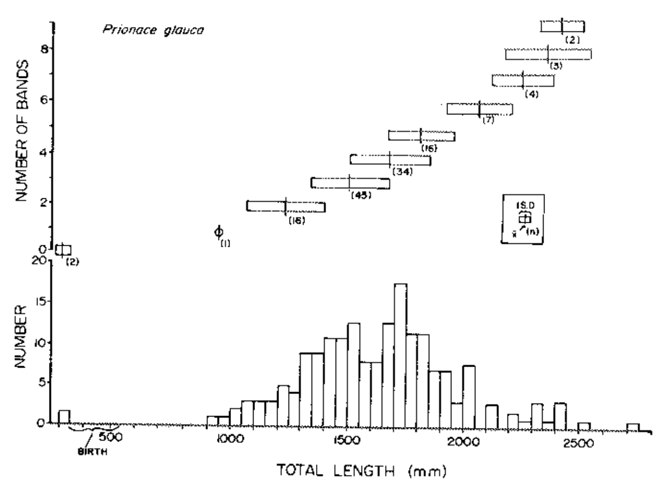

Figure 1.—Size-frequency histogram of blue sharks collected from California waters used for age determination, with the means (vertical lines) and standard deviations (horizontal bars) of the lengths of all fish placed in a single age category shown above the pertinent size-frequency axis. Sample sizes are in parentheses.

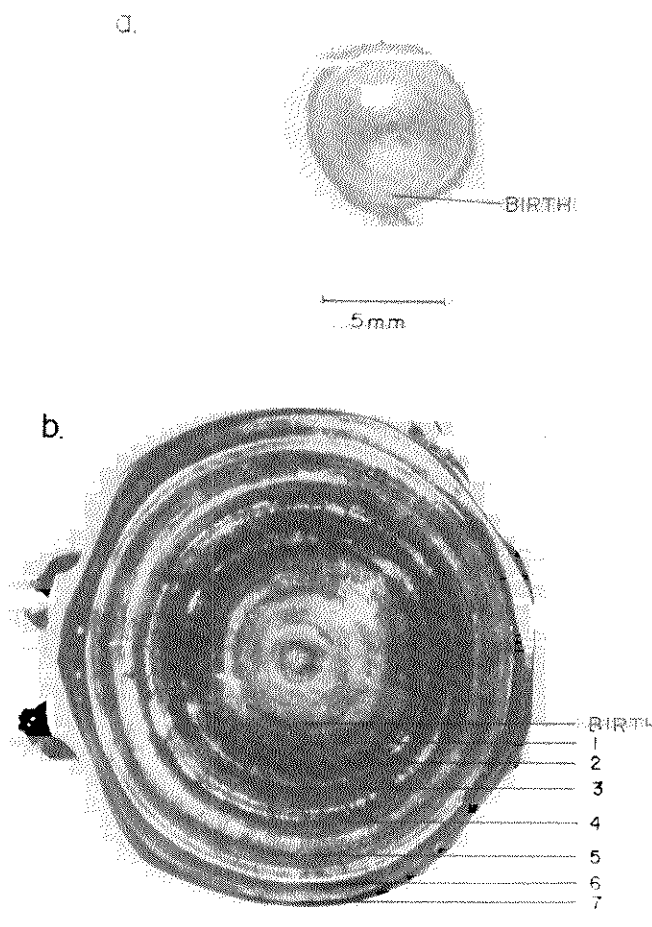

Figure 2.—Centra from blue sharks treated with silver nitrate. (a) From a small (972 mm TL) free-living male, centrum diameter 7 mm, estimated age 0 + ; and (b) from an adult male (2,401 mm TL), centrum diameter 24 mm, estimated age 7.

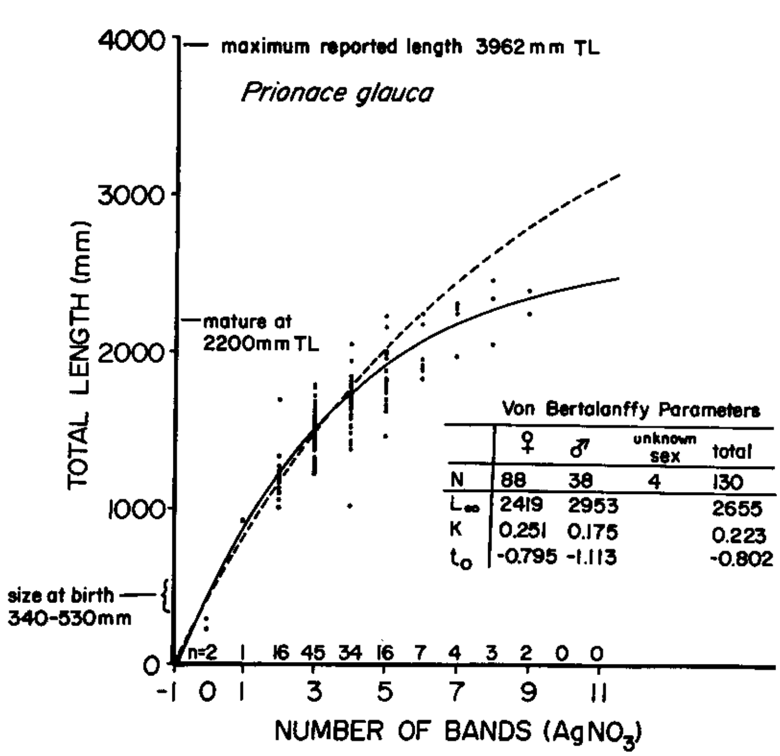

Figure 3.—Von Bertalanffy growth curve for 130 blue sharks collected in California waters where age was estimated using silver nitrate. Dots represent individuals of both sexes, and von Bertalanffy parameters for males, females, and the total sample are given in the insert. Dashed growth curve is based on Stevens (1975) and references used for size at birth, size at maturity, and maximum size are given in text.

Stevens (1975), using size frequencies and the silver nitrate technique on centra of 81 blue sharks of both sexes from the eastern North Atlantic, produced a von Bertalanffy growth curve that corresponds to ours for the first three or four age classes, but his estimates of mean length of sharks between estimated ages 5 and 6 were higher. Stevens (1976), from tag-recapture size information, estimated growth at approximately 320 mm/yr for sharks between 800 and 2,040 mm TL, which is higher than our average estimate of about 210 mm/yr taken from the growth curve for similarly sized blue sharks. Also, our measurements of radii in centra were somewhat smaller at higher band counts than those of Stevens (1975), providing further evidence that the growth rates of blue sharks off California may be a bit less than those found in the eastern North Atlantic. Stevens (1975) used both his centrum band counts and Aasen's (1966) size-frequency data to generate growth curves and to estimate asymptotic lengths for both sexes combined of 3,950 and 4,230 mm TL, respectively, which are both considerably higher than the asymptotic length we derived from observed sizes and ages (2,655 mm TL for both sexes combined; Fig 3.). The counts of bands on two centra sent to Stevens were identical to those made by us. In addition, his estimate of yearly growth rates from recaptured blue sharks (Stevens 1976) corresponds with our growth curve up to about 2,000 mm TL, and his (1975) size and age data fit within the range of observations we have found for similar age classes. Therefore, we feel that the differences between these two studies could partly be due to the methods used to calculate the von Bertalanffy growth parameters. For blue sharks, we followed the methodology of Allen (1966), while Stevens (1975) used the Ford-Walford plot to calculate asymptotic length. Of course, blue sharks living under different oceanic conditions could exhibit different growth characteristics.

According to Pratt (1979), the blue shark reaches maturity at approximately 2,200 mm TL, which, according to our age estimates, is 6 or 7 yr of age. Thus, blue sharks become reproductively mature at about 56% of their maximum reported size and 83% of our estimated asymptotic length. This conforms to Holden's (1977) generalization that most elasmobranchs become mature at about 60 to 90% of their asymptotic lengths. However, using the estimated age of 20 yr at asymptotic length, blue sharks first become sexually mature at an age that is only 30 to 35% of their projected life span.

Common Thresher Shark

A total of 167 common thresher sharks was collected from the southern California gill net fishery and museum collections. The specimens ranged in size from embryos of 360 mm TL and free-living juveniles of about 1,450 mm TL to adults up to 5,733 mm TL (Fig. 4). Because common threshers are reported to reach maximum lengths of 6,096 mm TL (Bigelow and Schroeder 1948) to 7,600 mm TL (Hart 1973), our sample does not contain sufficient representatives of the larger size classes. However, Hart (1973) reported that 13- to 16-ft (3,800-4,900 mm TL) specimens are "common" in the northeastern Pacific, and, therefore, we have some representatives of the locally occurring larger size classes of this species. As with blue sharks, the common thresher shark is thought to make large-scale migrations, and their distribution patterns will influence the sizes available at any one location (Strasburg 1958).

Although both techniques produced clear bands, the X-radiography technique was chosen to age common thresher sharks, because it worked consistently well and many vertebrae could be easily processed in a short time (Cailliet et al. 1983). Bands were most easily seen in X-radiographs of centra from small common thresher sharks; however, with larger sharks, the banding patterns at the outer edge of the centra were slightly more difficult to identify and count (Fig. 5). A significant ($r^2 = 0.90$; $P < 0.01$) linear relationship was found between total length and diameter of caudal centra in common thresher

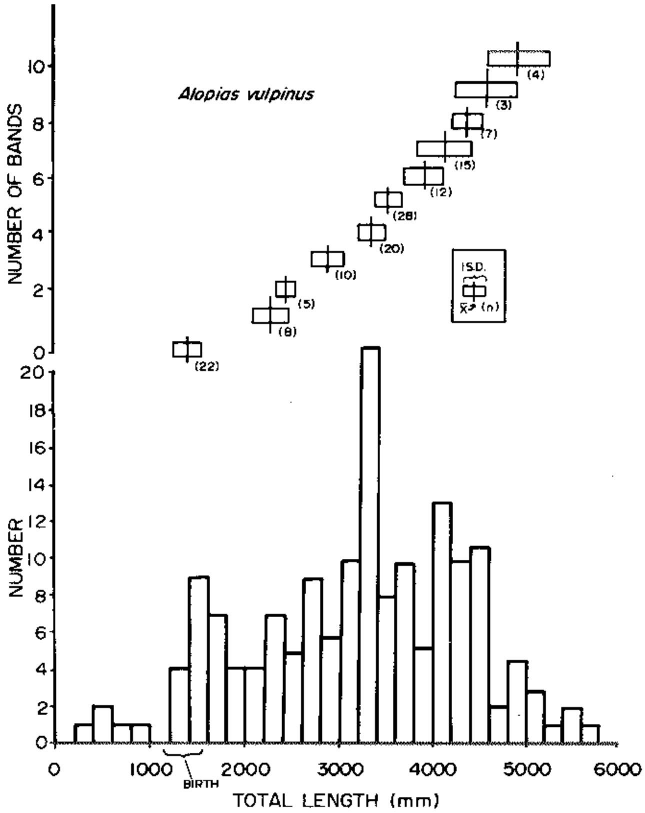

Figure 4.—Size-frequency histogram of common thresher sharks collected from California waters and used for age determination. Means (vertical lines) and standard deviations (horizontal bars) of the lengths of all fish placed in a single age category are shown above the pertinent size-frequency axis. Sample sizes are in parentheses.

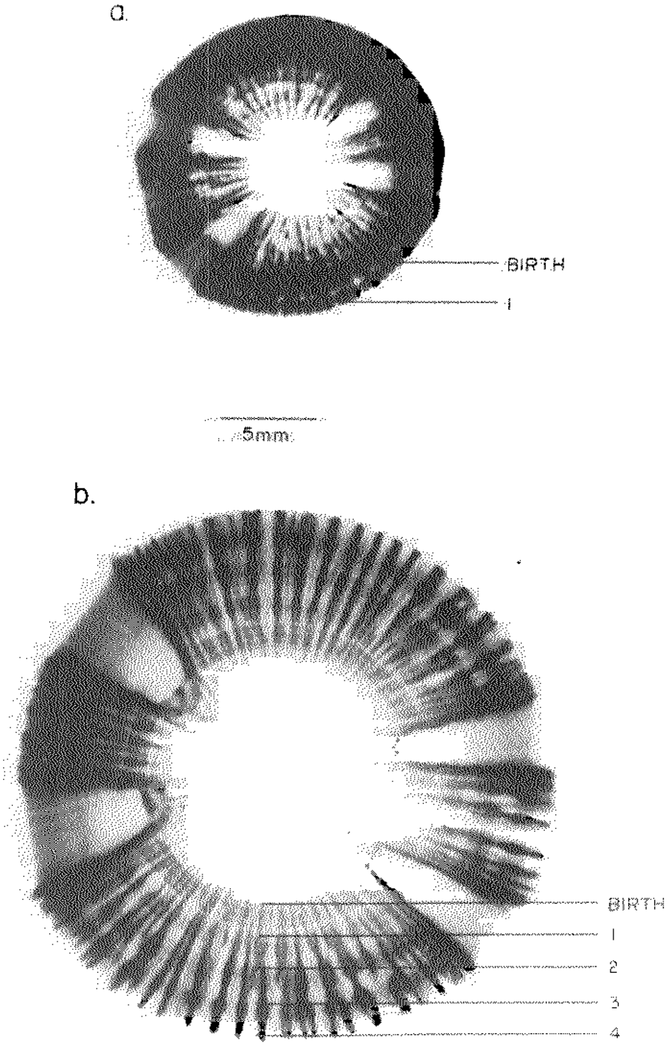

Figure 5.—X-radiographs of centra from common thresher sharks. (a) From a small (1,751 mm TL) free-living male, centrum diameter 15 mm, estimated age 1; (b) from an adult (unknown sex) which measured 3,349 mm TL, centrum diameter 28 mm, estimate age 4.

sharks (Fig. 6). Thus, in future studies, back calculation could prove useful in generating growth curves.

The von Bertalanffy growth curve for the 143 common thresher sharks we aged, which ranged between 360 and 5,733 mm TL, rose gradually and began to level toward the estimated asymptotic length (L_∞) of 6,509 mm TL for both sexes combined (Fig. 7). Females were estimated to reach a longer length (6,360 mm TL) than males (4,927 mm TL). The two oldest fish aged had 15 bands and measured 5,102 and 5,389 mm TL, and the youngest were eight embryos ranging between 360 and 1,605 mm TL, having no bands. Unfortunately, sexes were unknown for most of the fish examined because they were taken from fish markets and had already been cleaned.

The combined asymptotic length from the von Bertalanffy growth curve was 6,509 mm TL, which is only 14% smaller than the maximum reported length (7,600 mm TL), and within the size range of the commonly occurring largest specimens collected in the Pacific (Strasburg 1958; Hart 1973). Using our growth curve, a fish at the asymptotic length of 6,509 mm TL would be close to 50 yr old. Using this approach is questionable, because there are problems associated with the von Bertalanffy growth model, and because we have not collected any specimens near this size. Thus, the maximum age attained by the common thresher shark can be hypothesized, but remains unknown.

Our estimate of size at birth, derived from the von Bertalanffy growth model (1,580 mm TL), was slightly higher than

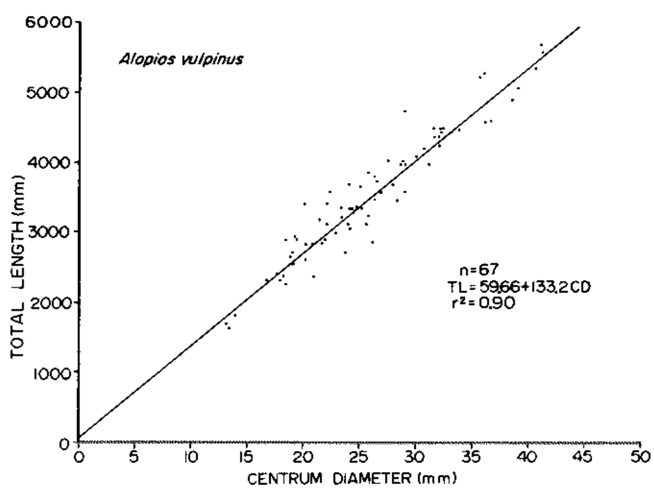

Figure 6.—Regression of the caudal centrum diameter and total length of 67 common thresher sharks.

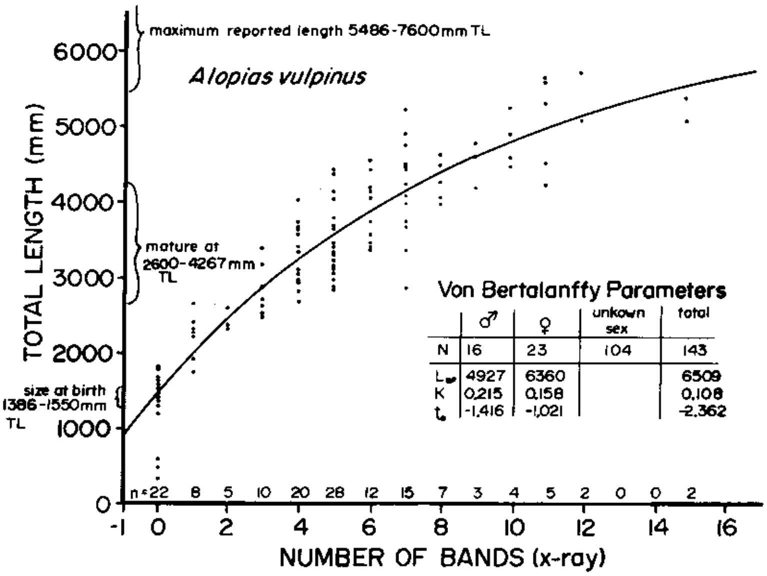

Figure 7.—Von Bertalanffy growth curve for 143 common thresher sharks collected in California waters and aged using X-radiography. Dots represent individuals of both sexes, and von Bertalanffy parameters for males, females, and the total sample are given in the insert. References used for size at birth, size at maturity, and maximum reported size are given in text.

reported smaller sizes of free-living young, which can be as small as 1,168 mm TL (Bigelow and Schroeder 1948), and range up to around 1,500 mm TL (Hixon 1979). One explanation for this difference is that our ageing technique is not precise enough to distinguish time intervals smaller than 1 yr. The mean size of the youngest age class is represented by a single size mode (Fig. 4) and several other mean sizes of younger age classes correspond to size modes, even though our sample was relatively small and nonrandom.

Common thresher shark females range in length at first reproductive maturity from 2,600 mm TL in the Indian Ocean (Gubanov 1978), 3,150 mm TL in Pacific waters (Strasburg 1958), 4,267 mm TL in the Atlantic (Bigelow and Schroeder 1948), and 4,625 mm TL off southern California (Bedford[4]). Bedford (footnote 4), using clasper length versus total length information, estimated that males off southern California first reach maturity at about 3,330 mm TL. These three lengths at first maturity represent sharks which we estimated to range between 3 and 8 yr old (Fig. 7). Using our asymptotic length of 6,509 mm TL, common thresher sharks apparently mature at a size that is between 39 and 71% of this length, which conforms with Holden's (1977) generalization of 60 to 90%. However, if we use the maximum reported size of 7,600 mm TL, these sharks mature at between 34 and 61% of their maximum length. Using age at first maturity versus projected oldest age, the figures would be much lower, reaching maturity at between 6 and 16% of their life span. An increased number of observations on older and larger sharks need to be obtained before a more definitive statement can be made.

Shortfin Mako Shark

Few specimens (50) of the shortfin mako shark were available from the commercial catches between 1978 and 1982 and museum collections, the smallest being a free-living 900 mm TL male and the largest a 3,210 mm TL female (Fig. 8). Although this size range does not include the largest individuals reported worldwide (3,962 mm TL; Bigelow and Schroeder 1948; Roedel and Ripley 1950), nor the largest individual found off California (3,507 mm TL; Applegate 1977), it is representative of the normal size range off California (2,134-2,438 mm TL; Roedel and Ripley 1950).

As with thresher sharks, both age determination techniques enhanced bands, but the X-radiography technique was used to age shortfin mako sharks in this study, because it was faster (Cailliet et al. 1983). Most X-radiographs of centra from shortfin mako sharks were easily assigned ages (Fig. 9), but occasionally outer bands were difficult to discern. We also prepared and read other vertebrae from difficult specimens with silver nitrate for collaboration.

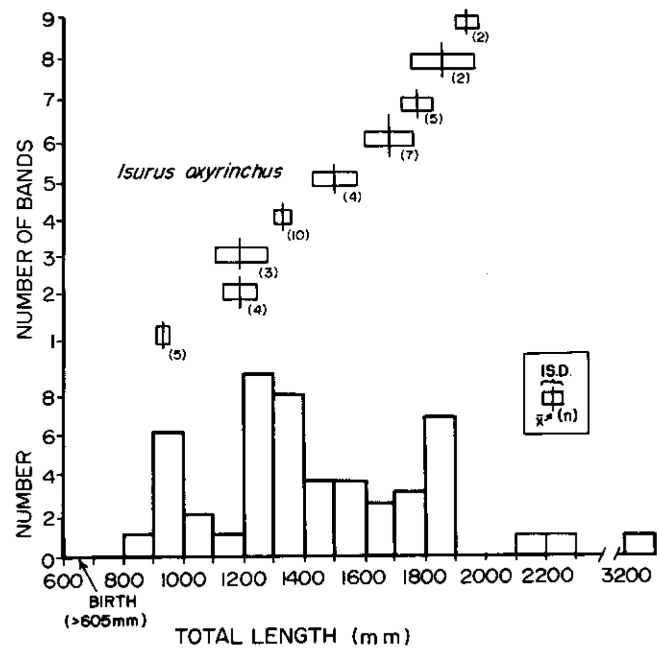

Figure 8.—Size-frequency histogram of shortfin mako sharks collected from California waters and used for age determination. Means (vertical lines) and standard deviations (horizontal bars) of the lengths of all fish placed in a single-age category are shown above the pertinent size-frequency axis. Sample sizes are in parentheses.

[4]D. Bedford, Biologist, California Department of Fish and Game, 245 West Broadway, Long Beach, CA 90802, pers. commun. 1982.

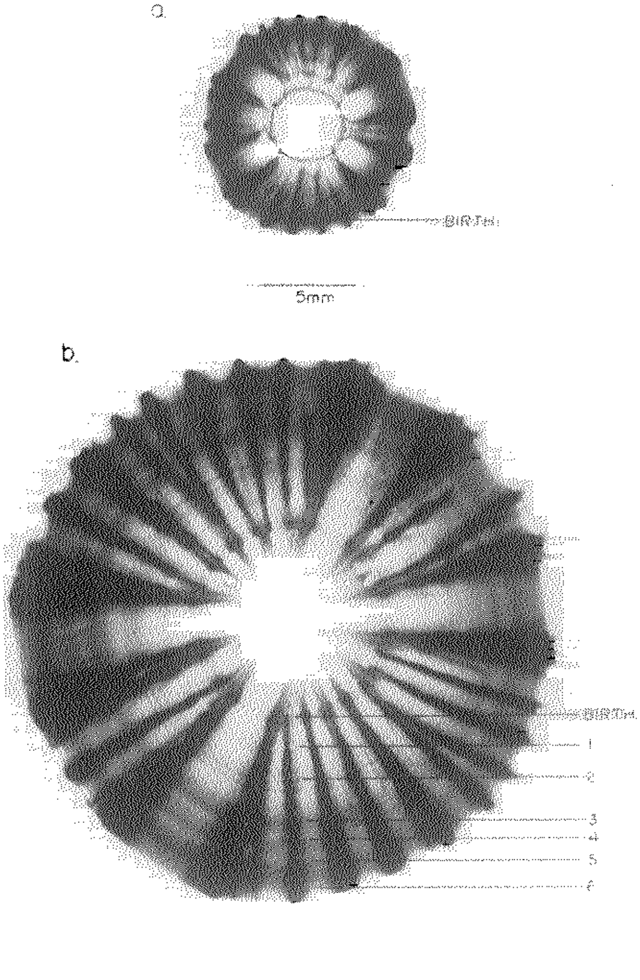

Figure 9. – X-radiographs of centra from shortfin mako sharks. (a) From a small (920 mm TL), free-living male, centrum diameter 11 mm, estimated age 0 + ; (b) from an adult female (2,110 mm TL), centrum diameter 26 mm, estimated age 6.

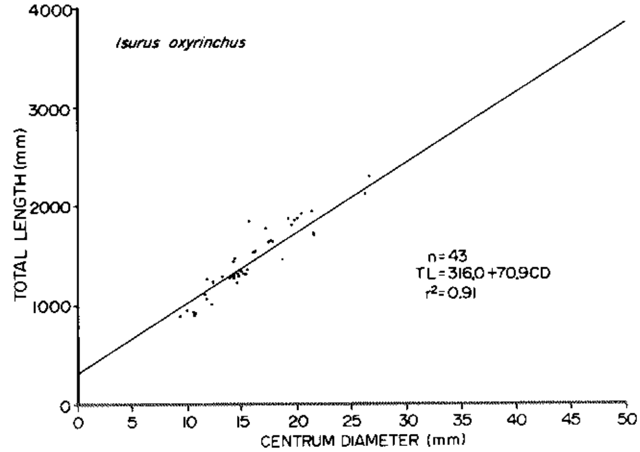

Figure 10.—Regression of centrum diameter and total length of 43 shortfin mako sharks.

A significant (r^2 = 0.91; P < 0.01) linear relationship was found between total length of shortfin makos and the diameter of their centra (Fig. 10). Thus, in future studies of Pacific shortfin mako sharks, back calculation, a technique used on Atlantic shortfin mako sharks by Pratt and Casey (1983), will be possible.

The von Bertalanffy growth curve for the 44 shortfin mako sharks we aged demonstrates a gently sloping curve which levels off at an asymptotic length of only 3,210 mm TL (Fig. 11). The oldest fish was estimated to have 17 bands and was our largest individual (3,210 mm TL), exactly the same length as our estimated asymptotic length. This age estimate indicates that this specimen was considerably younger than the von Bertalanffy growth model predicted. In addition, the estimated asymptotic length is only 9% less than the the maximum California reported length of 3,507 mm TL (Applegate 1977), but

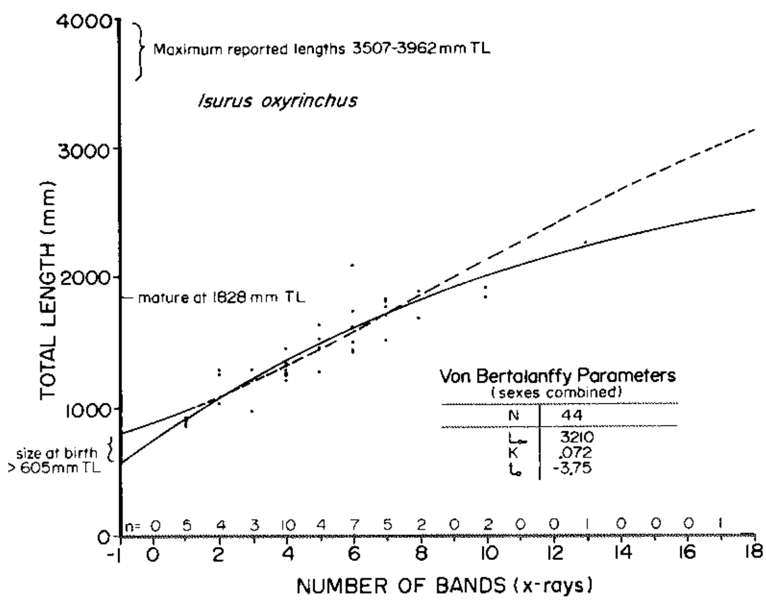

Figure 11.—Von Bertalanffy (solid line) and logistic (dashed line) growth curves for 44 shortfin mako sharks collected in California waters and aged using X-radiography. Sexes were combined due to small sample size, and von Bertalanffy parameters are for all 44 specimens. References used for size at birth, size at first maturity, and maximum size are given in text.

is 16% less than the largest Indian Ocean specimen (3,800 mm TL; Gubanov 1974) and 19% less than the maximum world size of 3,962 mm TL (Bigelow and Schroeder 1948; Roedel and Ripley 1950; Miller and Lea 1972). Using the logistic growth equation on the same data produces a different curve and a more reasonable estimate of asymptotic length of 4,081 mm TL (Fig. 11), which is only 3% higher than the reported maximum sizes worldwide. The differences between the curves produced by these two growth models may be due to their differential sensitivity to the ages assigned to the smallest and largest individuals; hence, increased samples of these size classes should clarify the shape of the curves.

The only other study of growth in the shortfin mako shark was performed by Pratt and Casey (1983) and suggested a growth rate for Atlantic shortfin makos that was approximately twice as fast as our data suggest. They based their growth information on size frequency (N = 848) and length-month analysis (N = 175), tag-recapture length estimates (N = 27), and back calculations from band counts in vertebral centra (N = 109). Their growth rates, based upon size frequency analysis for smaller (and therefore younger) size classes, conformed more to our estimated growth curve than for the larger (older) size classes. This is probably due to the difficulty in accurately and precisely delineating size modes in larger fishes, which are often comprised of several age classes (Ricker 1979).

Pratt and Casey (1983) reported an overall mean growth rate of 25.3 cm/yr based on their tag-recapture analysis of 27 shortfin mako sharks from the northwest Atlantic but considerable variation of this estimate was evident (SD = 41.2). This Atlantic shortfin mako growth rate was about twice as fast as the growth of this species we describe from California waters (overall mean from mean total lengths at successive ages, Fig. 8, of 12.9 cm/yr, SD = 8.5). This discrepancy could be related to differences in habitat and environmental conditions or differences in sample size or ageing methodology used in each of these studies; however, it is interesting to note that the growth rate reported by Pratt and Casey (1983), based on their back calculations from counts of bands on centra, would be similar to ours if each pair of bands from their fish were interpreted as an annual event.

Our estimates of size at birth, derived from either the von Bertalanffy or the logistic growth curves, agree with the scanty information available about the smallest, free-living shortfin mako sharks (Fig. 11). Garrick (1967) examined two embryos that were 605 mm TL, and one free-living male which measured 705 mm TL, while the smallest free-living shark examined by Gubanov (1978) was 900 mm TL, and that by Strasburg (1958) was 1,251 mm TL. The mean size for 1-yr-old shortfin mako sharks corresponds to the first size mode in sharks collected, while the next 3 yr correspond to a single mode (Fig. 8). Extrapolation to the age at which these sharks reach asymptotic lengths estimates longevity to be about 45 yr, based upon both growth models.

Shortfin mako sharks reportedly do not mature until they reach a length of 1,800 mm TL (Gubanov 1978) to 1,828 mm TL (Bigelow and Schroeder 1948), which corresponds to our estimated age of 7-8 yr (Fig. 11). Thus, shortfin makos reach first maturity at a size that is apparently only 56 to 57%, or 44 to 45% of the asymptotic lengths estimated by the von Bertalanffy and logistic growth models, respectively. They reach first maturity at a size that is only 51% of the maximum length reported off California, and 45% of the maximum world size, both below Holden's (1977) generalization. If age at first maturity and the predicted age (45 yr) at which asymptotic length is reached are used, the figures would be much lower, with predicted maturity at between 15.5 and 17.8% of their life span.

LIFE HISTORIES

Many problems arise in estimating age and growth patterns of large and mobile organisms, which need to be considered in relation to our findings (Brothers 1983). It is difficult to obtain sufficient samples of all size classes, due to the high cost and the time involved. The size and activity of these fishes make them difficult to measure accurately. Because market fish are often used and are usually cleaned, a conversion from an available shorter dimension, such as the distance between origins of both dorsal fins to our standard unit of measure (TL), may cause some errors in estimating size. However, the techniques we have developed and applied to delineate bands in centra of these three species have provided consistent results, and the resultant growth curves are generally supported by size at birth and asymptotic or maximum length information. A major objective is to understand the periodic nature of the band formation in shark centra. Even where tag-recapture length information is available, interpretations are often limited by the accuracy and precision of the measurements (Pratt and Casey 1983). There are promising techniques available (Cailliet et al. 1983) which, when applied to these species in more large-scale and comprehensive sampling programs, may increase our understanding of their growth processes.

Our preliminary findings on age and growth, coupled with the literature on size and reproductive characteristics, indicate that these three pelagic species, which often occur together in coastal areas around the world, differ in their life histories. The blue shark is generally smaller than either the shortfin mako or the common thresher sharks. Because the upper lobe of the common thresher shark's tail comprises almost half of its total length, it is more appropriate to compare the weight of these fishes. The common thresher and shortfin mako sharks range up to about 454 kg maximum (Bigelow and Schroeder 1948; Applegate 1977), while the largest blue shark ever taken probably weighed about 181 kg (Bigelow and Schroeder 1948; Strasburg 1958). Considering tail length, size at birth also exhibits a similar trend. Blue sharks are between 340 and 530 mm TL at birth, while shortfin makos range between 705 and 900 mm TL, and common threshers 1,386 and 1,552 mm TL (Bigelow and Schroeder 1948; Garrick 1967; Gubanov 1978; Pratt 1979). Size at first maturity, which varies considerably among individuals, appears to be similar for all three of these species. The blue shark ranges in length at first maturity from 1,800 to 2,500 mm TL, while the values for common threshers and shortfin makos are 2,600 to 4,265 mm TL, and 1,800 to 1,828 mm TL, respectively (Bigelow and Schroeder 1948; Gubanov 1978; Pratt 1979). Relative to ultimate maximum size or age, the blue shark reaches maturity later than either the common thresher or shortfin mako sharks.

There is an apparent trend for fecundity to be less in the larger of these three species, although the available information on their reproduction is relatively sparse. Blue shark fecundity estimates range from 23 to 135 per female (Tucker and Newnham 1957; Gubanov 1978; Pratt 1979), while the best estimates for shortfin makos are between 2 and 10 (Bigelow and Schroeder 1948; Gubanov 1978), and for common threshers are between 2 and 4 (Bigelow and Schroeder 1948; Strasburg 1958; Hixon 1979). There is very little information about the gestation period for pelagic elasmobranchs. Pratt (1979) estimated that blue shark embryos reach full term in 9 to 12 mo. Our growth curve supports this contention. Virtually nothing is known about the gestation period of the other two species, but Bedford (footnote 4) has estimated gestation to be 9 mo long in common thresher sharks off southern California.

In conclusion, our preliminary data and the available literature indicate that these three pelagic sharks attain large sizes, have gradual growth rates, long life spans, and relatively low but variable fecundities. Therefore, as first postulated by Holden (1973, 1974, 1977), it is quite possible that this combination of life-history traits could make these species susceptible to overfishing. However, this conclusion may be countered by our estimate of a relatively early age of first reproductive maturity. More extensive samples of all sizes over a wider geographical range, an equal representation of sexes, and more detailed analysis of age, growth, and reproduction need to be conducted before definitive statements can be made about the life histories of these species. Also, more needs to be known about their population abundance, distributions, and migration patterns. Only when this information is available will we be able to accurately predict the future of these fisheries, and perhaps satisfactorily manage them.

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