THE BIOLOGY OF THREE PELAGIC SHARKS FROM CALIFORNIA WATERS, AND THEIR EMERGING FISHERIES: A REVIEW

GREGOR M. CAILLIET
Moss Landing Marine Laboratories
P.O. Box 223
Moss Landing, California 95039

DENNIS W. BEDFORD
California Department of Fish and Game
245 West Broadway
Long Beach, California 90802

ABSTRACT

The rapid growth of a drift gill net fishery for pelagic sharks off southern California has caused concern among fishery biologists because elasmobranchs tend to have slow growth and low reproductive rates. The primary targets of this developing fishery are the common thresher shark, *Alopias vulpinus,* and the bonito shark, *Isurus oxyrinchus.* Not marketed, but also taken in large numbers, is the blue shark, *Prionace glauca.* From 1976 through 1981, annual shark landings increased from 360 to over 1575 metric tons (MT). During the same period, the drift gill net fleet grew from 15 to 200 vessels. During 1982, thresher shark landings alone exceeded 1059 MT. Bonito shark landings reached nearly 231 MT. We report our results to date on the age, growth, and reproduction of these three pelagic species.

Ages between 0 and 15 years were estimated for 167 thresher sharks ranging from 360 to 5733 mm total length (TL). Male thresher sharks mature at 3330 mm TL, and females at 2600 to 3150 mm TL. Age at maturity ranges from 3 to 7 years. Females give birth to 4 pups annually. Little is known about stock distribution or abundance.

Ages between 0 and 17 years were estimated for 44 bonito sharks ranging from 900 to 3210 mm TL. Bonito sharks mature at 1800 mm TL. The number of offspring reportedly varies between 2 and 16. Ages between 0 and 9 years were estimated for 130 blue sharks ranging from 280 to 2521 mm TL. Blue sharks reach maturity at 2200 mm TL. The number of offspring may be as high as 82. Because of the limited area over which the current southern California fleet operates, and the lack of information concerning the distribution and stock structure of these three pelagic species, the future of the southern California gill net fishery cannot be predicted.

RESUMEN

El rápido incremento de la pesca de tiburones pelágicos en el sur de California, usando trasmallos, ha causado preocupación a los biólogos pesqueros, ya que estos Elasmobranquios presentan un crecimiento lento y un índice de reproducción bajo. Esta pesquería se enfoca principalmente al *Alopias vulpinus* (pez zorro), *Isurus oxyrinchus* (marrajo), capturándose también un número elevado de *Prionace glauca* (tintorera), aunque estos últimos no se cotizan todavía en el mercado. Desde 1976 hasta 1981, los desembarcos de tiburones aumentaron de 360 hasta más de 1575 toneladas métricas. Durante este período, la flota que utiliza trasmallos aumentó de 15 a 200 embarcaciones. Los desembarcos de *Alopias vulpinus* sobrepasaron las 1059 Tm. en 1982, mientras que *Isurus oxyrinchus* llegaba a las 231 Tm.

Se incluyen los resultados obtenidos sobre la edad, crecimiento y reproducción de estas especies de tiburones. 167 ejemplares de *Alopias vulpinus* incluían peces de menos de un año y de hasta 15 años de edad, con tallas de 360 hasta 5733 mm de longitud total (LT). Los machos de *Alopias vulpinus* maduran a los 3330 mm de longitud, y las hembras entre los 2600 mm y 3150 mm de longitud total. La edad que tienen al alcanzar la madurez sexual oscila entre 3 y 7 años. Las hembras producen 4 crias cada año. Se conoce poco sobre la distribución y abundancia de las poblaciones de esta especie.

44 *Isurus oxyrinchus* oscilaban entre edades de menos de un año y 17 años, con tallas de 900 mm hasta 3210 mm de longitud total. *Isurus oxyrinchus* madura cuando alcanza 1800 mm de longitud total. El número de crias que producen al año varía entre 2 a 16.

Se obtuvieron 130 *Prionace glauca* con tallas de 280 a 2521 mm de longitud total, y edades entre menos de un año y 9 años. Las tintoreras alcanzan su madurez sexual a los 2200 mm de longitud total. El número de crias puede ascender a 82 por año.

Debido a que la zona cubierta por la flota que actualmente opera en aguas del sur de California es muy limitada, y la carencia de información sobre la distribución y estructura de las poblaciones de estas tres especies pelágicas, no se puede predecir el futuro de la pesquería con trasmallos que está operando en el sur de California.

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INTRODUCTION

During the last few years, commercial fishing for pelagic sharks has increased rapidly in California's coastal waters. Historically, sharks were used primarily for their oils and for reduction (Byers 1940) and for the vitamins in their livers (Frey 1971). Today, however, their principal use is for human food. In 1977 a new fishery began to develop off the coast of southern California. Long gill nets, drifted near the surface in deep offshore waters, were used successfully to land pelagic sharks. Recent increases in the retail demand for fish had led wholesale buyers to look for new sources, and shark meat looked promising to many. Wholesalers began to pay a good price for sharks, creating a new and attractive market for commercial fishermen. The new shark fishery grew rapidly.

Fishery biologists began to express some concern over the rapid expansion of the commercial shark fleet. Historically, shark fisheries have tended to decline soon after their initial success, principally because of the relatively slow growth and reproductive rates that seem to characterize elasmobranchs as a group (Holden 1973, 1974, 1977). Perhaps the new pelagic shark fisheries might also be subject to a similar decline. Unfortunately, there was little life-history information (generally considered an effective prerequisite for management) available on any of the main pelagic shark species. Aging techniques had not been evaluated for any of the three pelagic sharks being fished in California, and very little was known of their reproductive biology. This kind of information could prove critical in the development of management measures. We have been working for several years toward a better understanding of the biology of these species, particularly in regard to age, growth, and reproduction.

We here describe the California pelagic shark fishery, both in terms of fishing methodology and historical development. We then review what is currently known about the biology of these most important species.

DESCRIPTION OF THE FISHERIES

The southern California drift gill net fleet targets on pelagic sharks (the common thresher, *Alopias vulpinus*; the bonito or short-fin mako, *Isurus oxyrinchus*; and the blue shark, *Prionace glauca*) and swordfish (*Xiphius gladius*) in the deeper waters surrounding the Channel Islands chain.

The basic gear includes a hydraulically driven spool or drum on which the net may be rolled. The spool is most often located on the stern of the vessel. The net is constructed of nylon twine, and the mesh sizes of nets used in this fishery may range from 8 inches (20.3 cm) to 20 inches (50.8 cm) stretched. Mesh sizes of 14 inches (35.6 cm) and 16 inches (40.6 cm) seem to be favored. Most nets range from 10-20 fathoms (18.3-36.6 m) in depth, and may be as long as 1000 fathoms (1828.8 m).

When fished, the drift gill net hangs vertically in the water column, stretched between a buoyant corkline on one side, and a lead line on the other (Figure 1). The entire net is suspended by a series of floats attached at intervals of about 10 fathoms (18.3 m). The floats are attached to the corkline via extension lines, usually ranging from 1-3 fathoms (1.8-5.5 m) in length. As a result, the net is suspended beneath the surface commensurate with the length of these extensions. While fishing is underway, the boat remains attached to the net at one end. Attached to the opposite end of the net is a buoy on which a strobe light and radar reflector are mounted.

Drift net fishing operations are conducted during nighttime hours. Until 1982, drift net fleet activities extended from south of Point Conception to the Mexican border. In the summer of 1982, drift gill net operations began to expand northward to Morro Bay. Currently, a few vessels are fishing on an exploratory basis as far north as Monterey Bay. Drift gill net op-

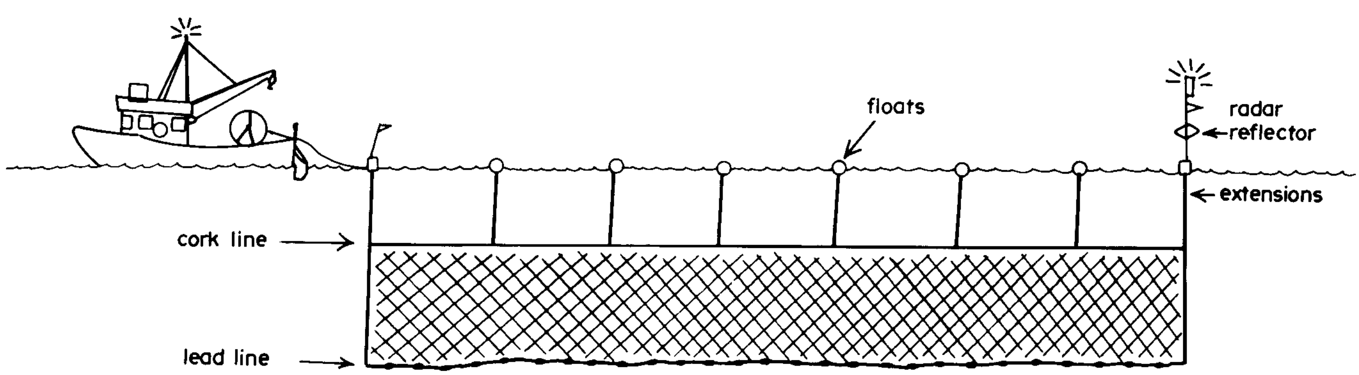

Figure 1. Drift gill net in operation.

erations north of Point Conception are severely limited by sea conditions.

The drift gill net fleet has undergone rapid expansion from 15 participating vessels in 1977 to the current level of about 200. Aside from the dramatic increases in the ex-vessel price of common thresher and bonito sharks, the discovery that large-mesh drift gill nets provided an efficient method of taking swordfish served to fuel that expansion.

Landings of various shark species in California have historically been little more than incidental byproducts of other fisheries. Until recently, the only exception was the soupfin shark fishery, which began in 1937 (Byers 1940) and continued for a period of approximately ten years (Figure 2). Even so, it was not the shark's flesh which prompted this fishery. It was the high concentration of vitamin A in the soupfin's enormous liver that led to the demand for this species. When vitamin A was synthesized in a laboratory following the end of World War II, the soupfin fishery collapsed just as suddenly as it had begun (Ripley 1946).

During the 1970s, the rising cost of red meat and growing public awareness of health benefits from decreasing one's animal fat consumption probably contributed to the increase in consumer demand for fresh fish. As this demand grew, wholesale fish dealers began to look for new sources of fish protein. An interest in sharks was renewed, this time for their food value. Over the period from 1976 to 1981, shark landings increased from 391 MT (800,000 lbs) to nearly 1600 MT (3,500,000 lbs) annually (Table 1).

In addition to drift gill nets, at least one vessel out of San Pedro has targeted on the blue shark using longline with 2-m stainless steel leaders baited with anchovy or squid. This process allows these sharks to be cleaned immediately after live capture, and prevents the flesh from becoming unpalatable as the fish's high urea content rapidly decomposes in the dead blue sharks.

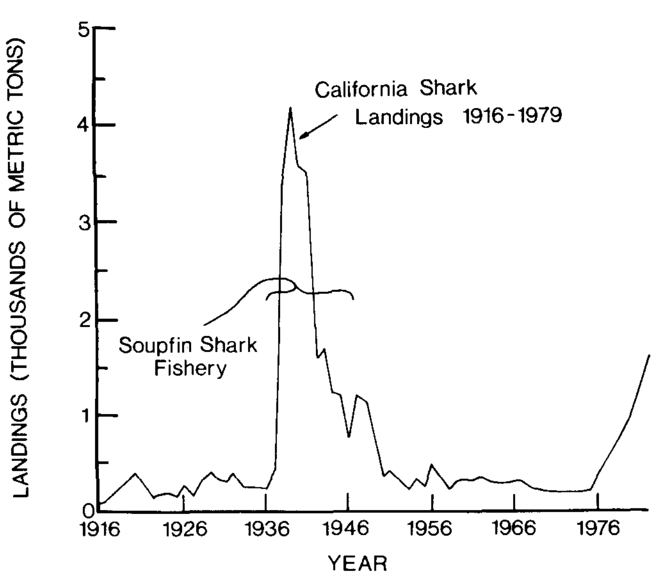

Figure 2. Annual landings of sharks (all species) in California.

DRIFT GILL NET FLEET MONITORING

In September 1980, a program was established for direct observation of on-board activities and catch of the drift gill net fleet. California Department of Fish and Game personnel boarded certain fishing vessels before they left port, and remained on those vessels during entire fishing trips. While aboard, the observers kept a complete record of activities pertaining to all interactions between crew members and marine life. Additionally, the observers gathered biological information on the size, age, sex, and reproduction of the target species.

Between October 1980 and November 1982, 17 different drift gill net vessels were observed during 53 separate fishing trips, for a total of 270 nights of fishing. These observations represent approximately 3% of the fleet's fishing activity. The limited and nonrandom number of observable vessels and observations restricts statistical inferences that might be made about the fleet as a whole. However, we are confident that our observations of the drift gill net fleet are representative. To support this assertion, we make the following points:

1. This fishery targets on pelagic species that are not uniformly distributed around the entire fishing ground. When a group of fish is located in an area, the fleet, generally moving as a unit, converges on that specific area.
2. The major components of the fishing gear and the methodology behind its use are well standardized throughout the fleet.
3. The catch of marketable species from observed vessels closely parallels the reported catch from unobserved vessels. This has been verified by comparison of wholesale market receipts.

TABLE 1
Shark Landings in All of California from 1976 to 1981

Year	Landings (metric tons)
1976	391
1977	580
1978	748
1979	1,006
1980*	1,488
1981	1,599

*Preliminary information.

AGE, GROWTH, AND REPRODUCTION STUDIES

For this portion of the study, most blue shark specimens were collected between September 1974 and October 1977 in Monterey Bay, California, by longline and hook and line. Most collections of common thresher and bonito sharks, and several specimens of blue shark were obtained from commercial fisheries in southern California, and from the California Department of Fish and Game's pelagic gill net observer program. Additional preserved specimens of all three species were obtained from several California museums.

All sharks were measured (mm), weighed (kg), and their sex and reproductive status was noted, if possible. The main measurements used were total length (TL), fork length (FL), and alternate length (AL, the distance between the origin of both dorsal fins). All length measurements were converted to total length for uniformity using conversion factors based upon measurements from our own specimens and from the literature (Bigelow and Schroeder 1948; Applegate 1967). To estimate total length from alternate length and fork length (all in mm), we used $TL = (5.73 \times AL) - 54.29$, and $TL = 1.85 \times FL$, respectively.

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. For details on processing and cleaning the vertebrae, see Cailliet et al. (in press, a). The aging technique used for blue sharks was modified from a procedure attributed to Von Kossa, in 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. A dissecting microscope with illumination focused laterally on the centrum was used to count bands. The cleaned centra from the common thresher and bonito sharks were X-rayed with a Hewlett-Packard Faxitron Series X-ray system (Model No. 43805N) and 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.

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). The parameter estimates 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 bonito sharks, because the data set consisted of only 44 fish. For the bonito shark, we also used the logistic growth equation (Ricker 1979).

As an initial evaluation 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 superimposed over these the means and standard deviations of the sizes categorized into each age division by band counts. Visually, we then compared these mean sizes with modes in the size-frequency distribution.

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

The reproductive biology of the common thresher sharks from waters off California was examined during at-sea observations of the pelagic shark fleet. Estimates of size at maturity for males and females, length of the gestation period, and litter size were made[1].

Common Thresher Shark (**Alopias vulpinus**)

Fisheries statistics. Prior to the use of open-water drift gill nets, landings of thresher shark were incidental in hook and line, purse seine, and nearshore gill net fisheries. When the first experiments with offshore drift nets were started in 1977, approximately 15 part-time gill netters landed 59 MT (129,000 lbs) of thresher shark. The years following have seen a dramatic increase in the landings of this pelagic species (Table 2). Thresher sharks are caught off southern California from spring to fall (Figure 3).

We have attempted to characterize fishing pressure on the thresher shark stock through two indirect means: analysis of length-frequency data, and examination of the trends of catch per unit of effort (CPUE). Length-frequency data illustrate the size

[1]Bedford, D. B. Sexual maturity and fecundity in the common thresher shark (*Alopias vulpinus*) off southern California. Manuscript, 10 pages.

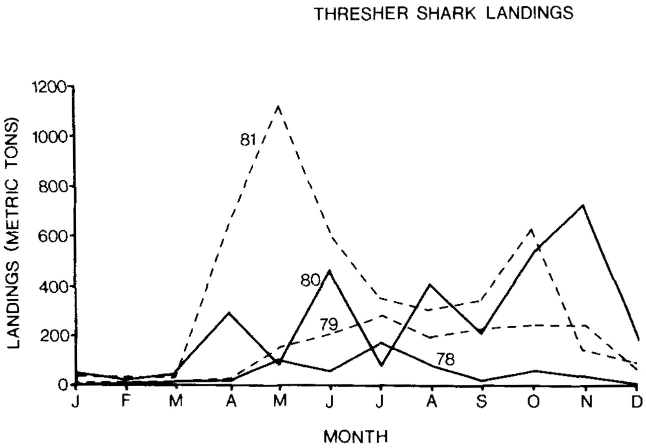

Figure 3. Monthly landings of thresher shark by drift gill net.

structure of the segment of the population that is vulnerable to capture. Length-frequency curves prepared for the 1981 and 1982 seasons based on market sampling in San Diego, San Pedro, Santa Barbara, and Morro Bay (Figure 4) indicate no obvious size-structure shifts, but the two-year time series is too short to allow resolution of trends.

CPUE data provide a measure of the relative density of the available population. We assume that the density of fish on the fishing grounds is an index of the magnitude of the total population. An index of CPUE has been prepared for the seasons 1977-82 using the number of landing receipts listing any thresher shark as an indicator of a completed trip (Figure 5). One trip is considered one unit of effort.

This index, based on landing receipts, is very crude. However, if the population was in immediate danger of depletion, even a tenuous index such as this one might illustrate that danger through a rapid decrease in both total catch and CPUE. On the other hand, the early years of a fishery are a period of learning and gear improvement, and this may obscure

TABLE 2
Thresher Shark Landings by the Drift Gill Net Fleet and the CPUE Indices

Year	Thresher (metric tons)	Number receipts	CPUE (MT/trip)
1977	59	349	0.17
1978	137	433	0.32
1979	334	745	0.45
1980	638	880	0.73
1981	895	1632	0.55
1982*	994[1] (1059)[2]	1851[1]	0.54

*Preliminary
[1]through September
[2]through December

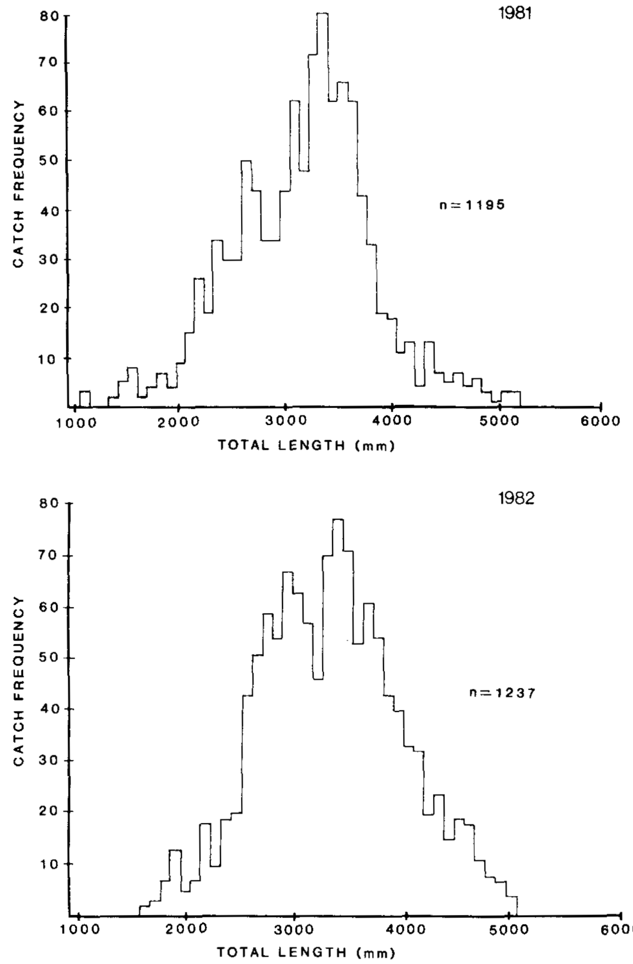

Figure 4. Length-frequency histogram of thresher shark landings.

actual trends in abundance. Neither length-frequency data nor trends in CPUE yet show apparent impacts of the fishery on this migratory shark species.

Distribution. The common thresher shark is an inhabitant of most temperate and subtropical waters, including the Pacific, Atlantic, and Indian oceans, and the Mediterranean and Red seas (Bigelow and Schroeder 1948; Roedel and Ripley 1950; Miller and Lea 1972; Gubanov 1978). In the eastern Pacific, the thresher shark has been reported from Vancouver Island to Chile, although it seems likely that the stocks are discontinuous across the equatorial regions. One survey of Pacific oceanic sharks indicated that the thresher is abundant in nearshore waters only, but may make long-range movements (Strasburg 1958).

Age and growth. For age determination, 167 common thresher sharks were 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 1450 mm

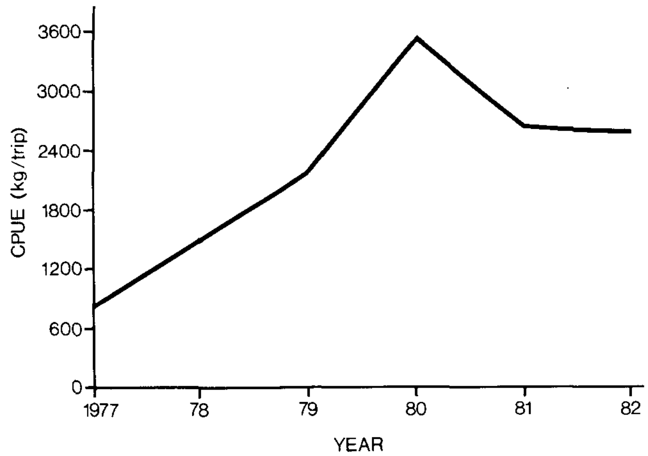

Figure 5. Catch per unit of effort for thresher shark.

TL to adults up to 5733 mm TL. Because common threshers are reported to reach maximum lengths of 6096 mm TL (Bigelow and Schroeder 1948) to 7600 mm TL (Hart 1973), our sample does not contain sufficient representatives of the larger size classes. However, Hart (1973) reports that 13- to 16-foot (3800-4900 mm TL) specimens are "common" in the northeastern Pacific, and therefore our sample includes representatives of the locally occurring larger size classes of this species.

The X-radiography technique was used to age common thresher sharks because it enhanced bands well, and many vertebrae could be processed easily in a short time. The von Bertalanffy growth curve for the 143 aged common thresher sharks ranging between 360 and 5733 mm TL rose gradually and began to level toward the estimated asymptotic length (L_∞) of 6509 mm TL for both sexes combined (Figure 6), which is only 14% smaller than the maximum reported length (6500 mm TL), and within the size range of the commonly occurring largest specimens collected in the Pacific (Strasburg 1958; Hart 1973). Females were estimated to reach a longer length (6360 mm TL) than males (4927 mm TL). The two oldest fish aged had 15 bands and measured 5102 and 5389 mm TL, and the youngest were eight embryos ranging between 360 and 1605 mm TL, having no bands. Unfortunately, sexes were unknown for most of the fish examined, because they were taken cleaned from fish markets.

Our estimate of size at birth, derived from the von Bertalanffy growth model (1580 mm TL), was slightly higher than reported smaller sizes of free-living young, which can be as small as 1168 mm TL (Bigelow and Schroeder 1948) and range up to around 1500 mm TL (Hixon 1979). One explanation for this difference is that our aging technique is not precise enough to distinguish time intervals smaller than one year. Another might be that different stocks living in differing oceanic conditions might exhibit different reproductive characteristics. In fact, this appears to be true when comparing size at birth and number of offspring reported by Gubanov (1978) for Indian Ocean speci-

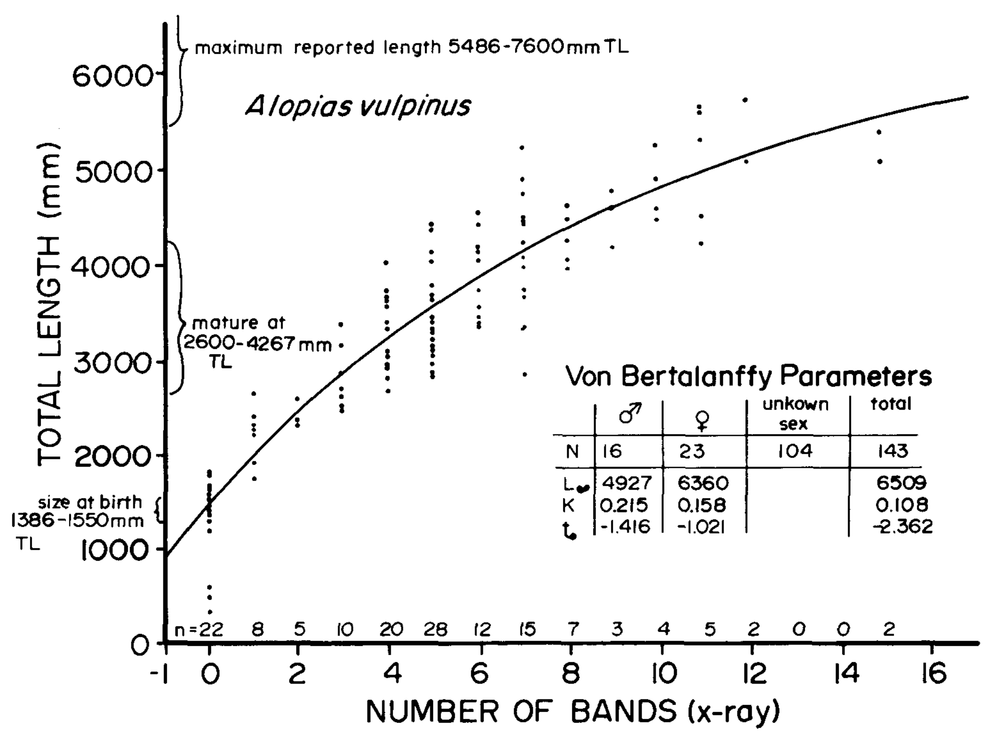

Figure 6. Von Bertalanffy growth curve for 143 common thresher sharks collected in California waters and aged using X-radiography. Dots represent individuals of both sexes. Von Bertalanffy parameters for males, females, and the total sample are given in the insert. References used for size at birth, size at maturity, and maximum reported size include Bigelow and Schroeder (1948), Roedel and Ripley (1950), Hixon (1970), Miller and Lea (1972), Hart (1973), and Gubanov (1978).

TABLE 3
Estimates of Age (Number of Bands), Length, and Weight for Thresher Sharks from the Eastern Pacific Ocean

Age estimate (yrs)	Total length (mm)	Dressed weight (kg)
1	1981	15.9
2	2446	28.7
3	2954	48.9
4	3234	63.1
5	3569	83.1
6	3870	104.2
7	4140	126.1
8	4383	148.0
9	4601	169.4
10	4797	190.5

mens and those examined by Bedford (see Reproduction, below).

Because most length data in the literature were reported as total lengths, yet most field work could only measure fork length or alternate length, we converted all measurements to total lengths. The average dressed weight (kg) from sample data from southern California, when combined with estimates of total length at age (Figure 6), yields Table 3.

Mortality. At present, there are no estimates of natural or fishing mortality rates for the thresher shark in the Pacific Ocean. Natural mortality is assumed to be quite low, because thresher sharks are born alive, and are already about 1500 mm TL at birth. As a result, predation upon juvenile threshers is likely to be minimal. Even food does not seem to be an immediate problem for newborn threshers. At birth, their stomachs are often distended by a mass of yolk material consumed while still in the uterus (Bedford[2]).

Reproduction. Common thresher shark females range in length at reproductive maturity from 2600 mm TL in the Indian Ocean (Gubanov 1978) to 3150 mm TL in the Pacific Ocean (Strasburg 1958) and 4267 mm TL in the Atlantic Ocean (Bigelow and Schroeder 1948). Using the length of the inner margin of the claspers versus total length, we estimated that males off southern California reach maturity at about 3330 mm TL. These three lengths at maturity represent sharks ranging between 3 and 7 years old (Figure 6). Using our asymptotic length of 6509 mm TL, we found that common threshers apparently mature at a size between 39% and 66% of this length, overlapping somewhat with Holden's (1977) generalization of 60% to 90%. However, if we use the maximum reported size of 7600 mm TL, these sharks mature at between 34% and 55% of their maximum length.

From observations aboard drift gill net vessels, we found that thresher sharks in the northeastern Pacific appear to pup annually from March through June. Because gestation appears to last about nine months, mating most likely takes place around July and August. A pregnant female will typically carry four young (Bedford[3]). In our observations off southern California, we found that all mature females examined during the early spring were pregnant. The numbers of males and females in the population off southern California appear to be equal.

[2]See footnote 1 on page 60.

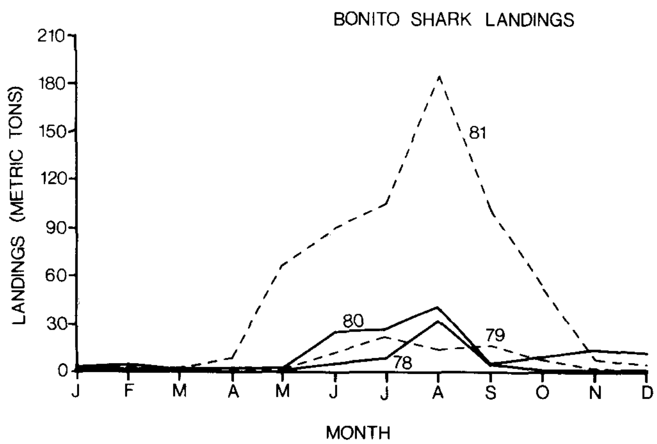

Figure 7. Monthly landings of bonito shark by drift gill net.

Migration. Adults are pelagic and considered to be highly migratory. Large numbers of threshers taken off the coast of California carry Japanese longline hooks, indicating an origin outside the U.S. Fishery Conservation Zone. Both adult and subadult threshers seasonally congregate in inshore waters of southern California; the greatest concentrations occur during spring and summer.

Stock structure and status. Differences in size at maturity, and in the number of offspring for Indian Ocean threshers reported by Gubanov (1978), for a thresher from the tropical central Pacific as reported by Strasburg (1958), and for those occurring off southern California suggest that separate stocks exist. Alternatively, these differences may simply reflect different physical conditions and forage levels.

Bonito Shark (Isurus oxyrinchus)

Fishery statistics. The bonito shark is considered one of the more palatable sharks, resulting in a relatively high ex-vessel price of \$.23-\$.45/kg (\$.50-\$1.00/lb). By comparison to the other targeted species of the drift gill net fishery, the average bonito shark is quite small, weighing in at only 9-14 kg (20 to 30 lbs). Thus the bonito shark is considered a "welcome incidental," rather than a true target.

[3]See footnote 1 on page 60.

TABLE 4
Annual Landings of Bonito Shark (1978-82)

Year	Metric tons landed
1978	12.4
1979	16.0
1980	27.6
1981	125.7
1982*	187.8

*Through September.

Bonito shark landings have increased over the last five years in a manner similar to thresher landings (Table 4). But in the last two years landings of bonito shark have increased even beyond that which could be attributed to effort increases for the thresher shark, suggesting either fluctuations in availability or increased targeting.

At least two recent changes in the drift gill net fishery may have contributed to this sudden increase in bonito shark landings. First, there has been the anomalously warm water off southern California during the 1981 and 1982 seasons. Bonito sharks are known to have a distribution within the warmer ocean waters of the Pacific. Second, the legalization of drift gill net use in the swordfish fishery (Bedford and Hagerman 1983) may have played a role. Catch records for bonito shark (Figure 7) indicate peak seasonal availability between thresher shark (Figure 3) and swordfish.

Distribution. The bonito shark is an inhabitant of the warm and temperate oceans of the world (Bigelow and Schroeder 1948). In the eastern Pacific, it has been reported from Chile to the Columbia River, including the Gulf of California (Miller and Lea 1972). The bonito shark is pelagic, and may be found from nearshore to open-ocean waters.

Age and growth. Few specimens (50) of the bonito shark were available from the 1978-82 commercial catches and museum collections. The smallest specimen was a free-living 900-mm TL male, and the largest a 3210-mm TL female. Although this size range does not approach the largest individuals reported worldwide (3962 mm TL; Bigelow and Schroeder 1948; Roedel and Ripley 1950), nor the largest individual found off California (3507 mm TL; Applegate 1977), it is representative of the normal size range off California (2134-2438 mm TL; Roedel and Ripley 1950).

Both age determination techniques enhanced bands, but the X-radiography technique was used to age bonito sharks in this study because it was faster. The von Bertalanffy growth curve for the 44 bonito sharks we aged demonstrates a relatively slow growth rate that levels off at an asymptotic length of only 3210 mm TL (Figure 8). The oldest fish was estimated to have 17 bands, and was our largest individual (3210 mm TL), with exactly the same length as our estimated asymptotic length. In addition, the estimated asymptotic length is only 9% less than the maximum California reported length of 3507 mm TL (Applegate 1977), but is 16% less than the largest Indian Ocean specimen (3800 mm TL; Gubanov 1974), and 19% less than the maximum world size of 3962 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 4081 mm TL (Figure 8), which is only 3% higher than the reported maximum sizes worldwide. The differences between the curves produced by these two methods 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 improve the curves.

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 bonito sharks (Figure 8). Garrick (1967) examined two embryos 605 mm TL, and one free-living male measuring 705 mm TL, whereas the smallest free-living shark examined by Gubanov (1978) was 900 mm TL, and by Strasburg (1958), 1251 mm TL. The mean size for one-year-old bonito sharks corresponds to the first size mode in sharks collected.

Reproduction. Bonito sharks reportedly do not mature until they reach lengths of 1800 mm TL (Gubanov 1978), 1828 mm TL (Bigelow and Schroeder 1948), or up to 2800 mm TL (Stevens 1983), which corresponds to a minimum age of about 7-8 years (Figure 8). Thus they reach maturity at a size that is only 56% to 87%, or 44% to 69% of the asymptotic lengths estimated by the von Bertalanffy and logistic growth models, respectively. They reach maturity at a size which is only 51% of the maximum length reported off California, and 45% of the maximum world size, both below Holden's (1977) generalization of 60% to 90%. The number of pups born to a bonito shark appears to range from 2 to 16 per birth (Bigelow and Schroeder 1948; Gubanov 1978; Stevens 1983). The length of gestation and the seasonality of pupping are unknown.

Blue Shark (Prionace glauca)

Fishery statistics. During our 270 night observations of the drift gill net fleet, equal numbers of blue sharks and thresher sharks were caught. Catch rates as

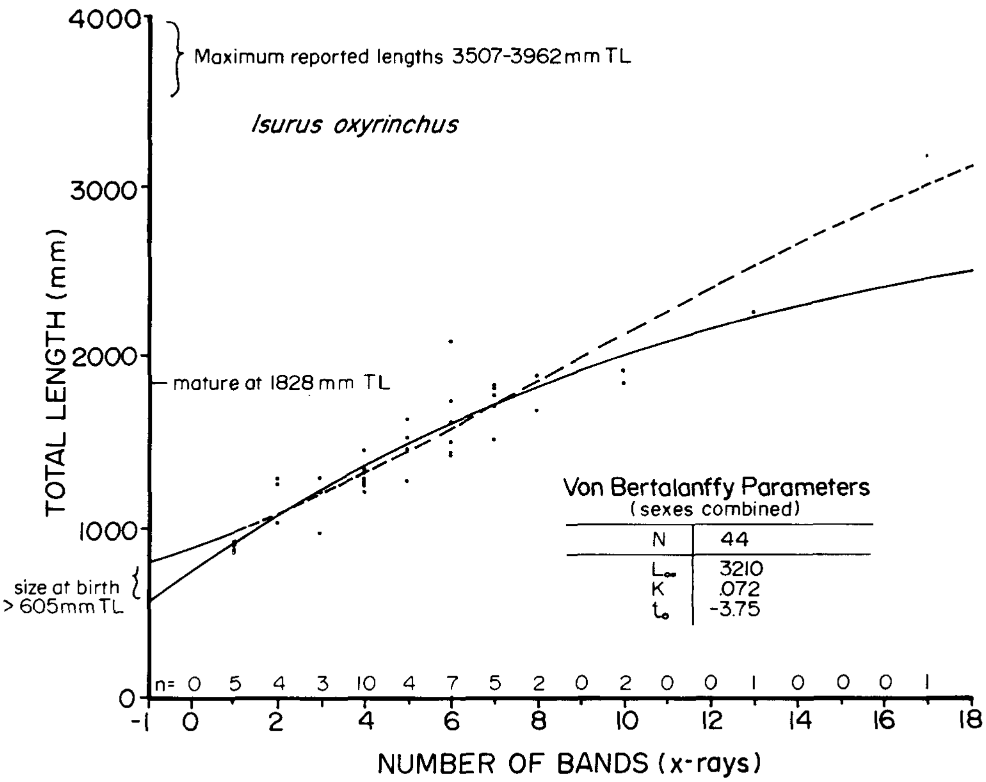

Figure 8. Von Bertalanffy (solid line) and logistic (dashed line) growth curves for 44 bonito sharks collected in California waters and aged using X-radiography. Sexes were combined because of small sample size, and von Bertalanffy parameters are for all 44 specimens. Reported size at birth, size at first maturity, and maximum size are from Bigelow and Schroeder (1948), Roedel and Ripley (1950), Garrick (1967), Applegate (1977), and Gubanov (1978).

high as 15,000 fish could contribute substantially to the income of commercial fishermen, except that unresolved spoilage problems render this fish unmarketable. Once wrapped in a gill net, these fish suffocate. Blue sharks must be bled, dressed, and cooled down while still freshly caught; otherwise the urea within the tissue begins to change to foul-smelling ammonia. Because the nets are left in the water overnight, by the time some blue sharks are retrieved they may have been dead long enough for this type of spoilage to have ruined the flesh for food purposes.

As with other shark species, there is a growing market demand for blue sharks, but not those caught by drift gill nets. An experimental longline fishery off southern California has proven successful in both capturing and processing blue sharks so that a high-quality marketable product results.

At this time, no one can predict with any certainty whether the high catch rates by the drift gill net fleet could result in a serious depletion of blue sharks. It seems advisable that the wastage be minimized, if that is possible. The most promising solution—larger mesh sizes—has been recognized by some commercial fishermen since this fishery first developed, but a trade-off situation exists because larger mesh sizes are also less efficient in capturing the targeted species. A second important potential solution involves the hanging distance of individual meshes along the corkline of the net; i.e., whether the net hangs fully stretched or loosely, creating a bagging effect. A fully stretched net captures fewer blue sharks, but the same trade-off exists as with mesh size. The escapement characteristics of both mesh size and hanging distance require further exploration.

Distribution. The blue shark inhabits all the temperate and subtropical seas of the world. It is abundant in both nearshore and open-ocean waters, and may be the most common of all the pelagic sharks (Strasburg 1958; Beckett 1970; Stevens 1976).

Age and growth. We caught a total of 120 blue sharks by longline in Monterey Bay between 1974 and 1977, and obtained an additional 42 specimens from museum collections and the commercial catch in southern California over a wider range of years. The Monterey Bay collections produced specimens ranging from 958 to 2045 mm TL, and fish smaller and larger than these sizes were added from the additional sources. The resulting size range was between 300 and 2705 mm TL. Because blue sharks are born at approximately 400 mm TL, and reach a reported maximum size of about 3962 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 2600 mm TL are quite rare in eastern North Pacific waters (Strasburg 1958).

Both silver nitrate and X-radiography produced clear bands, but the silver nitrate technique was chosen to age blue sharks because it was the first technique available; it worked consistently well; and 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 aged blue sharks ranging between 280 and 2521 mm TL rose steeply, and leveled at an estimated TL of 2655 mm for both sexes combined (Figure 9). Males were estimated to reach a larger asymptotic size (2953 mm TL) than females (2419 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 2450-mm TL male that had nine bands; the youngest were two near-term embryos between 350 and 400 mm TL, having no bands.

The male asymptotic length was close to that of the largest common specimens collected in the Pacific

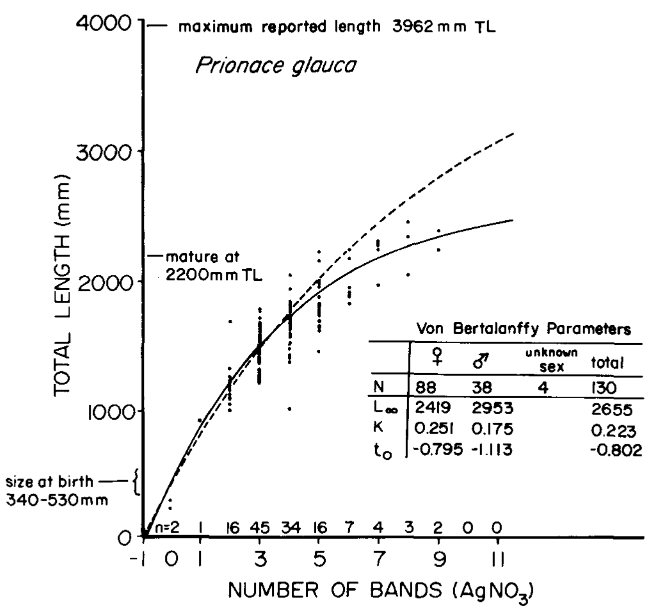

Figure 9. Von Bertalanffy growth curve for 130 blue sharks collected in California waters. Age was estimated using silver nitrate. Dots represent individuals of both sexes. Von Bertalanffy parameters for males, females, and the total sample are given in the insert. Dashed growth curve is based on Stevens (1975), and references used for size at birth, size at maturity, and maximum size were Bigelow and Schroeder (1948), Strasburg (1958), Hart (1973), Gubanov (1978), and Pratt (1979).

(around 3100 mm TL; Strasburg 1958), but was considerably smaller than the largest reported blue shark (3962 mm TL; Bigelow and Schroeder 1948). With additional larger specimens, our estimate of asymptotic length might increase. This would agree more with the maximum reported size, unless Pacific blue sharks do not grow comparably to those in the Atlantic.

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. With larger and older fish, the correspondence weakened, probably because of (1) small sample size, (2) mixing of several age classes into a larger size class because of different individual growth rates, or (3) slower growth rates in general.

Stevens (1975), using size frequencies and the silver nitrate technique on centra of 81 blue sharks of both sexes off England, 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 five and six years of age were higher. Stevens (1976), from tag-recapture size information, estimated growth at approximately 320 mm per year for sharks between 800 and 2040 mm TL, which is higher than our average estimate of about 210 mm per year 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 in California blue sharks may be a bit less than in those found off England. 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 3950 and 4230 mm TL, respectively. Both are considerably higher than the asymptotic length we derived from observed sizes and ages (2655 mm TL for both sexes combined; Figure 9). Because Stevens's counts of bands on two centra from our study were identical, his estimate of yearly growth rates from recaptured blue sharks (Stevens 1976) corresponds with our growth curve up to about 2000 mm TL. Stevens's (1975) size and age data fit within the range of observations we have found for similar age classes, the only differences between these two studies occurring in the small sample of larger fish. Blue sharks living under different oceanic conditions could exhibit different growth characteristics.

Total length (mm) and weight data from the central

TABLE 5
Estimate of Age (Number of Bands), Length, and Weight for Blue Sharks from the Pacific Ocean

Age estimate (yrs)	Total length (mm)	Weight (kg)
1	878	3.1
2	1234	8.9
3	1518	17.2
4	1745	26.5
5	1927	36.2
6	2072	45.5
7	2189	54.0
8	2282	61.5
9	2357	68.1
10	2416	73.2

Pacific by Strasburg (1958), when combined with estimates of total length at age, yield Table 5.

Reproduction. According to Pratt (1979), the blue shark reaches maturity at approximately 2200 mm TL, which, according to our age estimates, is six or seven years 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.

The blue shark is viviparous, with its embryos having a well-developed yolk sac placenta attached to the uterine wall of the mother (Pratt 1979). The number of pups in a litter is large for an elasmobranch—as many as 135 (Gubanov and Grigor'yev 1975). Gestation lasts from 9 to 12 months.

Migration. Blue sharks are highly migratory. A large number have been tagged in the Atlantic, and trans-Atlantic migrations have been reported (Casey 1979). Some sharks tagged off the northeastern coast of the United States have been recovered as far away as the eastern Atlantic and Mediterranean. One equatorial crossing has been reported. It is likely that the Pacific population also migrates considerable distances.

GENERAL DISCUSSION

Many problems arise in estimating age and growth patterns of large and mobile organisms. It is difficult to obtain sufficient samples of all size classes, because of high cost and the time involved. The size and activity of these fishes make them difficult to measure accurately. Because cleaned market fish are often used, 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. The resultant growth curves are generally supported by size at birth and by asymptotic or maximum length information. A major objective is to understand the periodic nature of the band formation in shark centra. Even when tag-recapture length information is available, interpretations are often limited by the accuracy and precision of the measurements (Pratt and Casey, in press). There are promising techniques available, such as tetracycline marking, histology, centrum edge characteristics, and natural radioactive geochronologues (see Cailliet et al., in press b) which, applied to these species in more large-scale and comprehensive sampling programs, could 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 the bonito or the common thresher shark. Because the upper lobe of the common thresher's tail constitutes almost half of its total length, it is more conservative to compare weight of these fishes. The common thresher and bonito sharks range up to about 454 kg maximum (Bigelow and Schroeder 1948; Applegate 1977), whereas the largest blue shark ever taken probably weighed about 181 kg (Bigelow and Schroeder 1948; Strasburg 1958). Considering tail length, size at birth exhibits a similar trend. Blue sharks range between 340 and 630 mm TL at birth; bonito sharks range between 705 and 900 mm TL; and common threshers range between 1386 and 1552 mm TL (Bigelow and Schroeder 1948; Garrick 1967; Gubanov 1978; Pratt 1979). Size at maturity, which varies considerably among individuals, appears similar for all three of these species. The blue shark ranges in length at maturity from 1800 to 2500 mm TL, common threshers from 2600 to 4267 mm TL, and bonitos from 1800 to 1828 mm TL (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 bonito sharks.

There is an apparent trend for fecundity to be lower in the largest species among these, although information on their reproduction is relatively sparse. Blue shark fecundity estimates range from 23 to 135 per female (Tucker and Newnham 1957; Gubanov and Grigor'yev 1975; Gubanov 1978; Pratt 1979), whereas the best estimates for bonitos are between 2 and 16 (Bigelow and Schroeder 1948; Gubanov and Grigor'yev 1975; Gubanov 1978; Stevens 1983), and for common threshers 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 months. Our growth curve supports this contention. One of us (Bedford) estimates that gestation in the thresher sharks lasts about 9 months. Virtually nothing is known about the gestation period of the bonito shark.

In conclusion, our preliminary data and the available literature indicate that these three pelagic sharks attain large sizes and exhibit relatively slow 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, depending upon their population abundance, distribution, and migration patterns. However, this conclusion may be countered by our estimate of a relatively early age of reproductive maturity. More extensive samples of all sizes over a wider geographical range, an equal representation of sexes, and more detailed demographic analyses including age, growth, and reproduction need to be conducted before definitive statements can be made about the life histories of these species. Then, perhaps, the fisheries can be predicted and satisfactorily managed.

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