TAXONOMIC STATUS AND BIOLOGY OF THE BIGEYE THRESHER, *ALOPIAS SUPERCILIOSUS*

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ABSTRACT

This paper reviews the life history, taxonomic status, abundance, distribution and habitat, reproduction, feeding habits, scientific and economic importance, and literature of the bigeye thresher, *Alopias superciliosus*; and presents new information on morphometrics, vertebral counts, tooth counts, denticles, size, age, and growth from 22 specimens. We found *A. profundus* is a junior synonym of *A. superciliosus*, and we have extended the geographic range of the latter to the Mediterranean Sea and New Zealand. *Alopias superciliosus* is a wide-ranging, circumtropical species between the latitudinal limits of 40° north and 40° south.

Thresher sharks (family Alopiidae, genus *Alopias*), instantly recognizable by their tremendously elongated caudal fins (the upper lobe of the caudal fin about as long as the rest of the shark), have been known since antiquity. According to Salviani (1554), Aristotle was familiar with thresher sharks and described their behavior. Bonnaterre (1788) proposed the first valid specific name for a thresher, *Squalus vulpinus* (the common thresher), while Rafinesque (1809) proposed the genus *Alopias* for the same species, which he termed *Alopias macrourus*. More recently Tortonese (1938), Bigelow and Schroeder (1948), and Bass et al. (1975) reviewed the systematics of the genus *Alopias*.

Lowe (1839) described new fishes from Madeira in the eastern Atlantic. Among these was a very brief diagnosis of a new thresher, *Alopecias superciliosus*, which he characterized as follows: "At once distinguished from the only other known species of the genus, *Carcharias vulpes*, Cuv., by the enormous eye and its prominent brow. I have at present only seen a single young example."

This shark, the bigeye thresher, was not mentioned by name in the literature until Fowler (1936) erroneously synonymized it with *Alopias vulpinus* (Bonnaterre 1788). The species was apparently overlooked in the reviews of Dumeril (1865), Günther (1870), Garman (1913), White (1937), and Tortonese (1938). Bigelow and Schroeder (1948) resurrected Lowe's species and gave the first detailed diagnosis and description of *Alopias superciliosus*, based on Floridian and Cuban specimens. Earlier, Grey (1928), Nakamura (1935), and Springer (1943) reported specimens of the bigeye thresher under different scientific names, but all of these writers overlooked Lowe's obscure account. More recently, Cadenat (1956), Strasburg (1958), Fitch and Craig (1964), Kato et al. (1967), Telles (1970), Bass et al. (1975), and Stillwell and Casey (1976) have presented descriptive accounts as well as morphometric, meristic, and other quantitative data on the species.

Thresher sharks are peculiar in that their elongated tails are the only known structure in sharks, other than jaws and teeth and the armed rostrum of sawsharks (Pristiophoridae), that function in killing or immobilizing prey (Springer 1961). An Indo-Pacific orectoloboid, the zebra shark, *Stegostoma fasciatum* (family Stegostomatidae), also has a greatly elongated caudal fin, but is not known to use it as a weapon.

Bigeye threshers are noteworthy in having enormous, dorsally facing eyes and unique head grooves, structures which may reflect specialized habits of the species that differ from the other two species of thresher shark.

The impression gained in most of the taxonomic literature is that *A. superciliosus* is a widespread but rare species. However, the works of Gubanov (1972), Guitart Manday (1975), and Stillwell and Casey (1976) indicate that it can be locally abundant and of importance in pelagic longline fisheries of the west-central Atlantic and northwestern Indian Ocean.

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The purpose of this paper is to bring together the widely scattered information on *A. superciliosus*, summarize its life history, and correct certain inconsistencies in the literature. We present morphometric, meristic, and other quantitative data, including descriptive accounts of specimens from Florida and the central Pacific, compare the bigeye thresher with other species of threshers, and discuss its taxonomic history.

MATERIAL

1. SHG-A2 (S. H. Gruber, private collection); adult female, 356 cm TL (total length), weight 140 kg; Straits of Florida several kilometers east of Miami Beach, Fla.; captured on 29 June 1977 by sport fishermen on a hook baited with squid at 30 m depth in water about 400 m deep. The specimen was photographed, measured, and dissected, and two early fetuses, both eyes, skin patch, and the tail were saved. The jaws were used in a taxidermist's mount and were not available, but the teeth were photographed before the fish was mounted. The fetuses are males, 207 and 213 mm TL.

2. SHG-A7; adult male, 356 cm TL; Straits of Florida several kilometers east of Pompano Beach, Fla.; captured at 1000 h e.d.t. on 4 July 1979 by commercial longliner at 40 m in water about 400 m deep. The specimen was photographed, measured, and dissected. Head, jaws, vertebral column (precaudal), tail, and claspers were saved. The spiral valve was sent to M. Dailey, Long Beach, Calif., for parasite investigation. One eye was sent to G. Hughes, Canberra City, Australia, for retinal study.

3. SHG-A5; adult female, 320 cm TL; Straits of Florida several kilometers east of Miami Beach, Fla.; captured on a longline at 40 m at 2200 h e.s.t., 14 March 1979. The water depth was 350 m. The head was removed, dissected, and saved with the jaws intact.

4. SHG-A6; subadult female, 306 cm TL; caught on same set as no. 3 above.

5. SHG-A3; subadult male, 291 cm TL; Straits of Florida, 35 km east of Palm Beach, Fla.; captured on 24 July 1979 by commercial longliner at 30 m in water about 120 m deep. The specimen was photographed, measured, and dissected, and the jaws, vertebrae, and head saved.

6. SHG-A4; immature male, 150 cm TL; east of Hatteras, N.C.; captured on a longline on 6 May 1979. The specimen was photographed and measured. No parts were saved as the whole shark was used in taxidermy.

7. *Shoyo Maru* voyage 13, SM-9-II-64-3; Nankai Regional Fisheries Laboratory, Japan; immature female, 279 cm TL, weight 62 kg; eastern Central Pacific, lat. 0°38′ N, long. 124°23′ W; captured on a longline on 9 February 1964. The specimen was photographed, measured, and dissected by Susumu Kato[3]; skin, jaws, reproductive organs, eyes, nasal sac, and parasites saved.

8. LJVC-0355 (L. J. V. Compagno, private collection), *Shoyo Maru* voyage 13, SM-11-II-6493; immature female, 287 cm TL, weight 59 kg; eastern Central Pacific, lat. 3°16′ S, long. 128°18′W; captured on a longline on 11 February 1964. The specimen was measured and preserved intact by Susumu Kato (footnote 3), later photographed and dissected by Compagno; skin, jaws, cranium, eyes, vertebral column, and fins saved.

9. *Shoyo Maru* voyage 16, SHO-16-2; 461 cm TL; Mediterranean Sea, lat. 36°39′ N, long. 17°51′ E; captured on a longline on 2 December 1966. Specimen measured by Izumi Nakamura[4] and data presented to Susumu Kato (footnote 3).

10. *Shoyo Maru* voyage 16, SHO-16-22; 2 individuals, 343 and 347 cm TL; lat. 13°36.4′ N, long. 75°34.2′ W; captured on a longline on 4 February 1967. Specimen measured by Izumi Nakamura (footnote 4) and data presented to Susumu Kato (footnote 3).

11. LACM-F-89; no length or sex data; Odawara, Japan, 1968; jaws only, teeth counted by Bruce Welton[5].

12. CAS (California Academy of Science, San Francisco, Calif.) Acc. 1963-X: 7; adult male, 372 cm TL; off San Clemente Is., southern California, 23 July 1963; partly dissected and preserved, jaws dried; previously reported by Fitch and Craig (1964).

13. LACM-F-88; male, presumably adult, 378 cm TL; 25 km ESE of east end of Santa Catalina Is., Calif., 30 June 1967; jaws only, teeth counted by Bruce Welton (footnote 5).

14. LACM-F-90; immature female, ca. 305 cm TL; southern California, probably Santa Mon-

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ica Bay area, 26 October 1966; jaws only, teeth counted by Bruce Welton (footnote 5).

15. Several other examples are listed in the tables on tooth counts but were not otherwise measured or seen.

DISTINCTIVE CHARACTERS

Alopias superciliosus (Figures 1-4) can be immediately distinguished from other threshers by its unique head shape, with lateral grooves

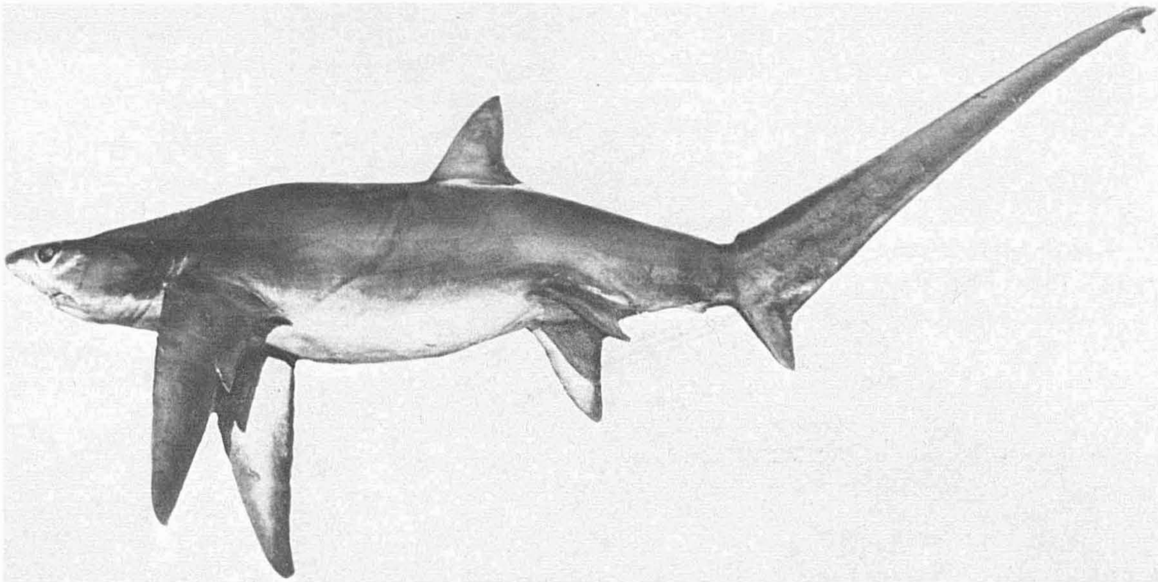

FIGURE 1.—Lateral view of a 356 cm TL, 140 kg female *Alopias superciliosus* (SHG-A2) taken off Miami Beach, Fla. Detailed measurements of this shark are given in Table 1, column 1. The characteristic head grooves are not clearly shown because of the slightly ventral angle of the photograph. Photo: S. Gruber.

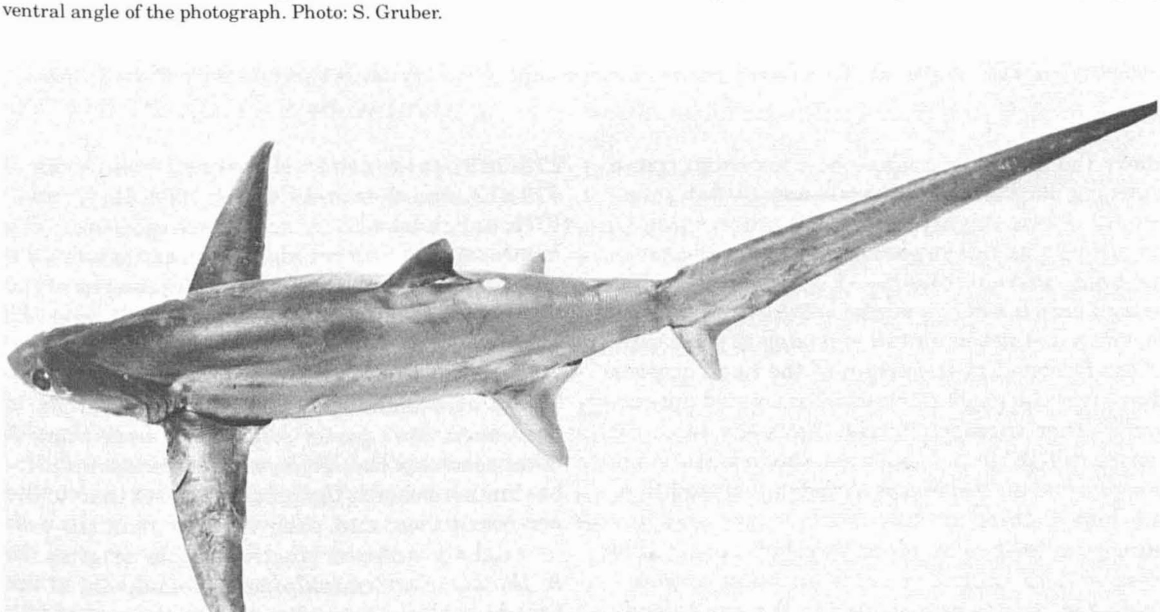

FIGURE 2.—Dorsal view of *Alopias superciliosus* (SHG-A2). The head grooves and upward-looking eyes are more easily seen in this photograph. Photo: S. Gruber.

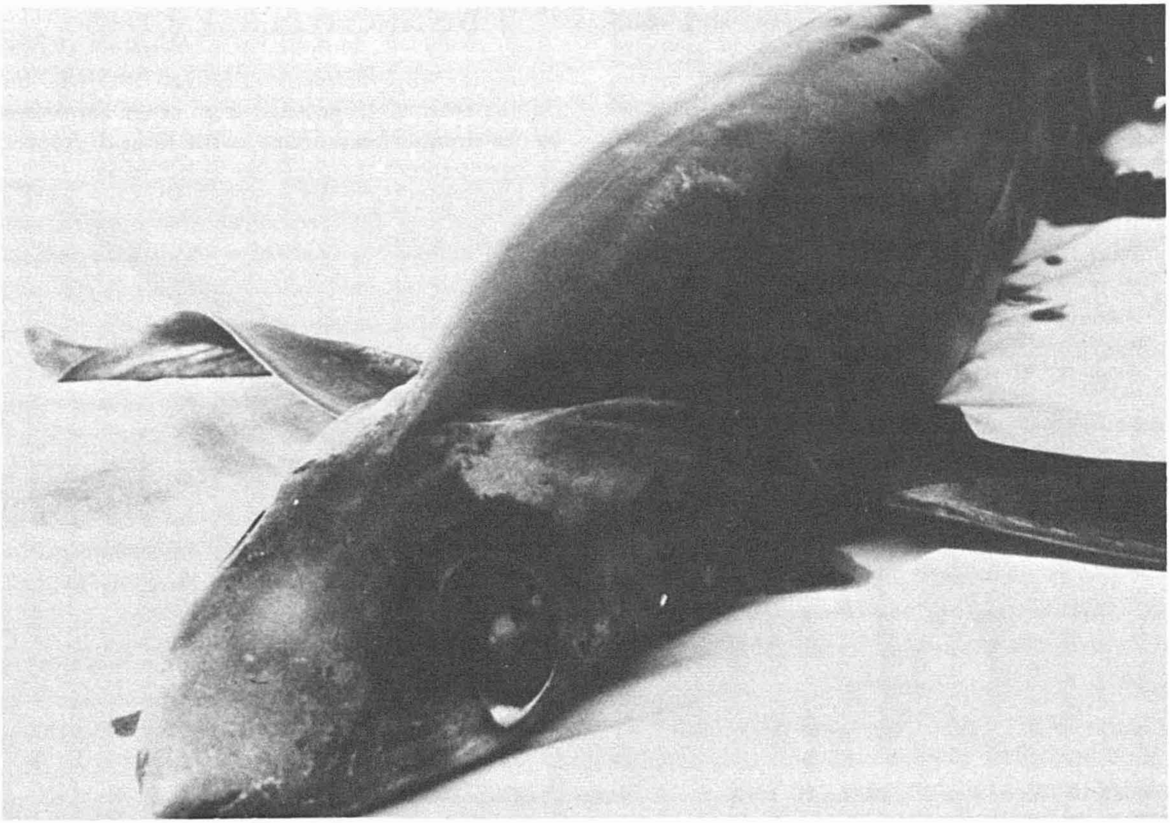

FIGURE 3.—Three-quarter lateral view of the head of a 159 cm TL immature male *Alopias superciliosus* (SHG-A4) showing the head grooves and massive "crest" composed of the epaxial musculature. The characteristic large eyes, bulbous snout and flattened interorbital space can also be seen. The crest and grooves are even more pronounced in mature bigeye threshers. Photo: S. Gruber.

above the branchial region, bulbous snout (more tapering in other threshers), nearly flat interorbital space (highly arched in other species), huge eyes with lids shaped like an inverted pear or keyhole (in individuals >1,300 mm TL) that extend onto the dorsal surface of the head (Figure 4), and a distinct indentation or step in the profile of the forehead at the origin of the head grooves that gives the head a helmeted or crested appearance (other thresher species have the forehead convex or flat but not indented; the indentation is less marked in fetal bigeye threshers). In addition, the bigeye thresher has much larger and less numerous teeth than other threshers, e.g., 24/24 rows or less (32/29 or more in other species). Tooth row groups represented in the adult dentition of the bigeye thresher include anterior and lateroposterior teeth only, without the symphysial or intermediate teeth found in other species. The bigeye thresher has fewer vertebrae, 278-308, than other threshers, which have 339-472 (Springer and Garrick 1964; Bass et al., 1975; unpublished data on all three species). In the monospondylous precaudal region of the vertebral column, the vertebral calcification patterns of the bigeye thresher are simpler than in other species, with fewer radii in the intermedialia and no fusion of their bases (extensively fused in *A. pelagicus*). The first dorsal fin of the bigeye thresher is positioned more posteriorly on the back than in other species of threshers, with the midpoint of its base much closer to the pelvic fin bases than to the pectoral bases, and with its free rear tip over or slightly anterior to the pelvic origins. In *A. pelagicus* and *A. vulpinus* the midpoint of the first dorsal base is usually closer to the pectoral fin bases than to the pelvic bases (occasionally equidistant between pectoral and pelvic bases), and the free rear tip of the first dorsal is far anterior to the pelvic origins.

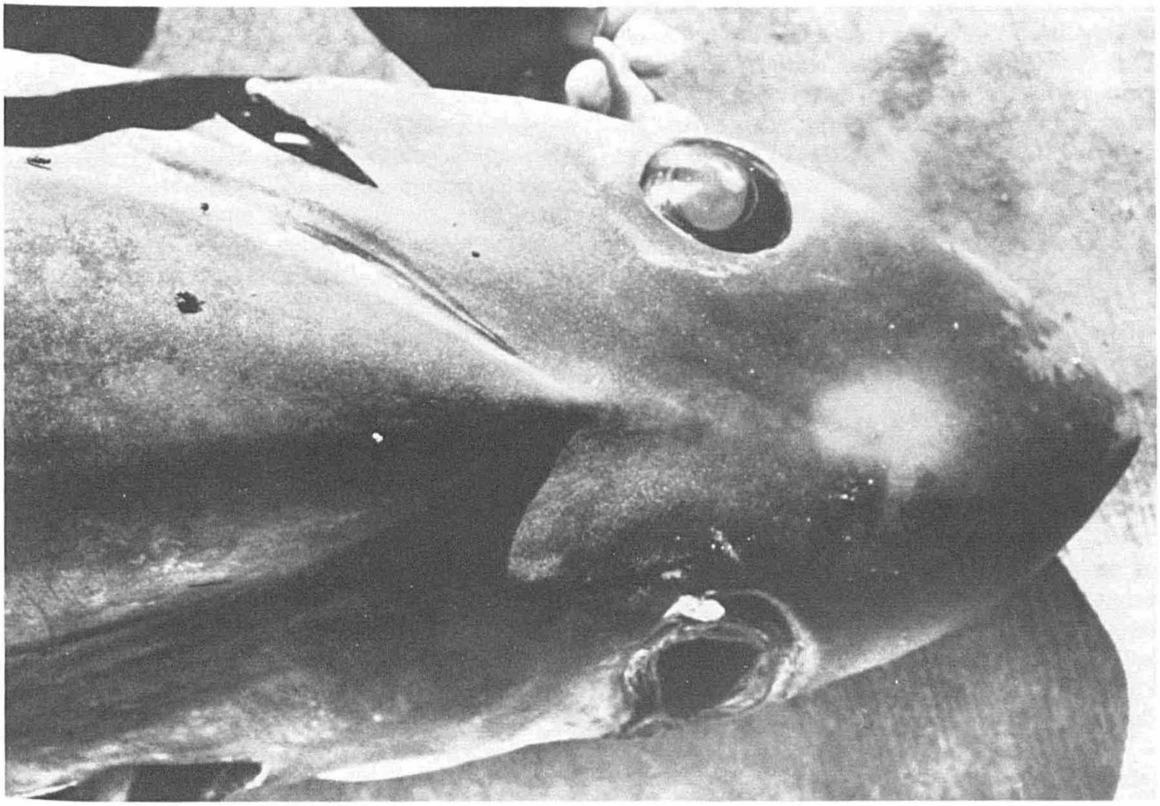

FIGURE 4.—Dorsal view of the head of a 356 cm TL male *Alopias superciliosus* (SHG-A7) showing the head grooves and upward looking eyes. (The lens of the right eye has been removed.) Photo: S. Spielman.

STATUS OF *ALOPIAS PROFUNDUS*

Nakamura (1935) described two new species of thresher sharks, *A. profundus* and *A. pelagicus*, from Taiwan. The thresher sharks were collected at a fish market and capture data were unavailable. Nakamura thought that one of these species lived near the sea bottom and so named it *A. profundus*. He was evidently unaware of Lowe's account of *A. superciliosus*, and only compared his new species with each other. Nakamura concluded that there was insufficient evidence in the literature to determine if either of his two species was equivalent to the wide-ranging "*Alopias vulpes*" (= *A. vulpinus*), and gave this reason as justification in naming *A. profundus* and *A. pelagicus*.

Fowler (1941) listed both Nakamura's species as questionable synonyms of *A. vulpinus* but Bigelow and Schroeder (1948) recognized them as distinct. They noted that *Alopias* can be divided into two groups, one including *A. profundus* and *A. superciliosus*, both with the free rear tip of the first dorsal fin extending to over the pelvic origins and with huge eyes; and the other including *A. vulpinus*, *A. pelagicus*, and the dubious *A. caudatus*, having the first dorsal rear tip well anterior to the pelvic origins and with smaller eyes. Using Nakamura's (1935) account as a source for *A. profundus*, Bigelow and Schroeder (1948) distinguished the two species in the "bigeye" group as follows:

1) "Rear tip of 2nd dorsal terminates considerably anterior to origin of anal; pelvics a little higher vertically than 1st dorsal and a little larger in area; anterior margin of 1st dorsal strongly convex; no lower precaudal pit." *Alopias superciliosus*.

2) "Rear tip of 2nd dorsal terminating over base of anal; pelvics less than 1/2 as high vertically as 1st dorsal and much smaller in area; anterior margin of 1st dorsal only very weakly convex; a precaudal pit below as well as above." *Alopias profundus*.

Several writers, following Bigelow and Schroeder (1948), including Teng (1962), Matsubara (1963), Chen (1963), Garrick and Schultz (1963), Fitch and Craig (1964), and Kato et al. (1967), recognized *A. profundus* as distinct, though Kato et al. suggested that it might be identical to *A. superciliosus*. Bass et al. (1975) synonymized *A. profundus* and *A. superciliosus* because the relative positions of anal and second dorsal fins, relative sizes of first dorsal and pelvic fins, and absence of a lower precaudal pit were, in their opinion, "...highly variable and probably invalid as diagnostic characters," but they did not discuss the matter further. Our analysis of the characters supposedly separating *A. profundus* and *A. superciliosus* leads us to concur with Bass et al. in synonymizing these species.

We have taken Nakamura's (1935) original measurements of *A. profundus* and converted them to precaudal proportions for comparison with other bigeye threshers (Table 1) and find that most of them fall within the range for other specimens identified as *A. superciliosus*. The differences listed by Bigelow and Schroeder (1948) for *A. profundus* and *A. superciliosus* appear to be based on ontogenetic changes and individual variation in a single species, or, in the case of the pelvic

TABLE 1.—Measurements of 13 specimens of *Alopias superciliosus* from the Atlantic, Indian, and Pacific Oceans. All values are proportional to precaudal length (given as unity) except rows 1 and 2 which are in centimeters as indicated.

Item	Original SG-A2 Western North Atlantic Female	Original SG-A7 Western North Atlantic Male	Stillwell and Casey (1975) Western North Atlantic Female	Original SG-A3 Western North Atlantic Male	Original SG-A4 Western North Atlantic Male	Bigelow and Schroeder (1948) Western North Atlantic Male	Telles (1975) Eastern North Atlantic Male	Bass et al. (1975) Western Indian Male	Nakamura (1935) Western North Pacific Female	Strasburg et al. (1958) Central North Pacific Male	Original SM-9-11-64-3 Eastern Central Pacific Female	Original LJVC 0355 Eastern Central Pacific Female	Fitch and Craig (1964) Eastern North Pacific Male
Total length, cm	356	356	340	290.8	159	130	269	363	332	328	279	287	381
Precaudal length, cm	201	199.4	190	150.4	84.5	. 66	152	198	170	167.4	139	144	208
Snout to													
Mouth	085	089	087	094	123	118	079	078	—	061	099	097	076
Eye	080	087	074	096	109	—	—	062	—	—	078	079	—
Pectoral origin	269	286	287	316	328	333	252	265	300	309	320	306	—
Pelvic origin	697	701	702	735	734	716	692	729	729	744	770	716	740
Anal origin	876	930	926	939	976	938	921	—	929	957	—	—	952
1st dorsal origin	535	586	569	603	621	612	562	557	588	595	612	597	600
2d dorsal origin	866	853	874	916	911	903	—	—	894	902	906	903	918
Internarial	027	028	029	031	034	035	—	027	—	029	031	029	026
Mouth:													
Width	070	069	082	076	078	086	086	069	—	082	079	087	072
Height	042	050	051	062	046	051	—	048	—	047	043	046	050
Gills, length:													
1st	045	040	—	—	038	057	—	040	—	049	051	043	057
3d	050	047	—	044	047	055	—	051	—	057	056	048	057
5th	035	046	—	043	050	037	—	045	—	047	045	045	054
Eye (orbit):													
Horizontal	030	029	031	034	047	055	033	031	028	039	034	042	029
Vertical	050	051	048	049	058	—	042	—	044	—	049	050	045
1st dorsal:													
Base	119	117	—	137	101	124	110	112	—	131	122	120	107
Height	129	130	147	144	107	102	128	121	163	147	150	133	152
2d dorsal:													
Base	010	015	—	012	012	018	—	018	—	016	012	015	019
Height	007	—	014	009	009	014	—	007	—	012	010	009	014
Pectoral, anterior margin	343	328	387	380	398	375	356	348	362	393	403	389	324
Pelvic fin:													
Base	164	121	—	169	169	122	—	—	—	—	176	156	155
Height	—	—	—	135	118	—	—	—	—	—	126	128	138
Anal fin:													
Base	017	019	—	016	018	018	018	013	—	025	022	019	022
Height	025	025	—	020	018	020	029	026	—	029	025	031	019
Caudal fin:													
Dorsal lobe	851	792	—	912	905	964	823	864	—	957	1.007	993	839
Ventral lobe	119	118	—	135	132	124	—	127	—	—	137	125	125
Trunk-at-pectoral:													
Height	192	208	—	194	178	178	196	—	—	—	187	181	219
Width	149	135	—	154	160	145	111	—	—	—	151	149	166
Interspace:													
1D-2D	189	171	200	176	189	174	—	—	—	—	191	184	—
2D-caudal	097	072	086	—	—	090	—	128	—	090	094	077	101
Anal-caudal	080	—	052	—	—	037	036	057	—	053	075	054	056

fins, possible misinterpretation of the actual size of these fins in *A. profundus*.

The relative positions of the anal and second dorsal fins vary. The account and illustration of a 130 cm TL *A. superciliosus* from Cuba in Bigelow and Schroeder (1948, figure 5) shows the free rear tip of the second dorsal fin terminating anterior to the anal origin by a distance about equal to the second dorsal base. Nakamura's (1935) illustration of an adult *A. profundus* (pl. 1, figure 1) indicates that the dorsal rear tip extends posterior to the anal base, but his illustration of a fetal *A. profundus* (pl. 2, figure 3) shows that it is about opposite the anal origin. Cadenat (1956, figure 3B-C) illustrated two fetuses of *A. superciliosus* from Senegal, one with the rear tip over the rear end of the anal base and the other with it over the middle of the anal base. Bass et al. (1975, figure 19) pictured a South African specimen of *A. superciliosus* with the tip about over the anal origin. Our 356 cm TL specimen (SHG-A2) from Florida also had the rear tip about opposite the anal origin, but her two fetuses have the rear tip slightly anterior to the anal fin origin. Two specimens from the eastern Central Pacific (SM-9-II-64-3 and LJVC-0355), respectively, had the tip anterior to the anal origin and over the first third of the anal base.

Accounts of bigeye threshers such as those of Springer (1943), Bigelow and Schroeder (1948), Cadenat (1956), Fitch and Craig (1964), Kato et al. (1967), Telles (1970), and Bass et al. (1975), and the specimens examined by us show the pelvic fins to be very large and about the size of the first dorsal fin, but Nakamura's (1935, pl. 1, figure 1) line drawing of an adult female *A. profundus* shows a minute pelvic fin, less than one-fourth of the area of the first dorsal fin. Curiously, the pelvic fins in Nakamura's (pl. 2, figures 3, 4) drawings of a 71 cm fetus of *A. profundus* have the proportions of other bigeye threshers and are about as large in area as the first dorsal fin. Yet Nakamura described the pelvic fins of both adults and fetuses in the same words, "ventral fins moderate" (p. 2, 5). In the absence of pelvic fin measurements in Nakamura's account, we suspect that the unusually small pelvic fins pictured in his adult *A. profundus* may be erroneous and are perhaps due to the difficulties of accurately drawing a large shark, without special techniques and perhaps under trying circumstances (i.e., in a fish market). The drawing of the fetal *A. profundus* seems more accurate and may reflect the writer's ability to study and draw it in his laboratory. Possibly the large adult specimen of *A. pelagicus* sketched by Nakamura (pl. 1, figure 2) was also drawn with undersized pelvics, at least in comparison with the photograph of a specimen by Bass et al. (1975, figure 17), and with photographs and specimens of *A. pelagicus* seen by Compagno. The fetal specimen of "*A. pelagicus*" illustrated by Nakamura (1935, pl. 3) is of no help here as it appears to be a specimen of *A. vulpinus* (unlike the adult).

The supposed differences in the contour of the anterior margin of the first dorsal fin are probably size-related, the contour becoming straighter with increase in size. The adult *A. profundus* pictured by Nakamura (1935) has a nearly straight anterior margin, while in the fetal specimen it is strongly convex. This applies likewise to the 356 cm TL Miami specimen (SHG-A2) of *A. superciliosus* and to the two fetuses taken from her. This change also occurs in *A. vulpinus* (compare the juvenile pictured in Bigelow and Schroeder [1948] with the adult in Bass et al. [1975]) and *A. pelagicus*, as well as some other lamnoid sharks, such as *Isurus oxyrinchus* (Garrick 1967, figure 6).

The lower precaudal pit appears to be variably present or absent in bigeye threshers, as suggested by Bass et al. (1975). The lower pit was present in possibly all of the three adults of *A. profundus*, 332-366 cm TL, studied by Nakamura (1935), though it is not specifically mentioned in his account of a fetal *A. profundus* and not shown in his illustration (pl. 2, figure 1). It was also present in a 372 cm TL adult male from California (CAS-1963-X: 7) studied by Fitch and Craig (1964) but absent in all our Miami specimens and absent in two specimens from the eastern Central Pacific (SM-9-II-64-3 and LJVC-0355). We suspect that the lower precaudal pit is present only in some adult or subadult bigeye threshers, as it has not occurred so far in fetal or very small, free-living specimens. The upper precaudal pit is less well-marked in small specimens than in large subadults and adults.

DESCRIPTIVE NOTES

Proportional measurements of 13 bigeye threshers, including 6 reported by us, are given as proportion of precaudal length in Table 1, rather than total length, as the tail length is apparently quite variable relative to body length. Writers have previously used precaudal length (Fitch and Craig 1964), total length (Bigelow and Schroeder 1948), and fork length (Stillwell and Casey 1976).

The prominent horizontal head grooves (Figures 3, 4) that are characteristic of *A. superciliosus* are present in all specimens we examined, but are better developed in the large subadults and adults than in the two fetuses taken from SHG-A2. The grooves were not indicated in a 130 cm TL, free-living specimen figured by Bigelow and Schroeder (1948); but we suspect that they were overlooked on this shark although we were not able to examine it. Fitch and Craig (1964) first called attention to these grooves in *A. superciliosus* and noted that similar grooves are also found in teleosts, in the swift, mesopelagic louvars (*Louvarus*) and escolars (*Lepidocybium*). They speculated that the grooves might aid in hydrodynamic flow, thus enabling the bigeye thresher to maneuver more rapidly. Head grooves are absent or poorly developed in other species of threshers.

Another characteristic of the bigeye thresher, at least at sizes above 130 cm TL, are the huge, vertically elongated, fleshy orbits, which are expanded onto the dorsal surface of the head and provide the shark with a dorsal, binocular visual field (Figures 4, 5). The eyes, head grooves, and bulbous, elongated snout of *A. superciliosus* give its head a unique, upward-looking, crested or helmeted appearance. The eyelids (Figure 5) apparently change shape with growth, as our two fetuses, and a 130 cm specimen in Bigelow and Schroeder (1948) have relatively enormous, circular lids without the anteroposterior shortening seen in larger individuals such as the 161 cm immature female pictured by Bass et al. (1975). This change in lid shape is also seen though to a lesser degree in *A. pelagicus*, in which fetuses and small, free-living specimens have circular eyelids and adults more vertically oval lids (Compagno unpubl. obs.).

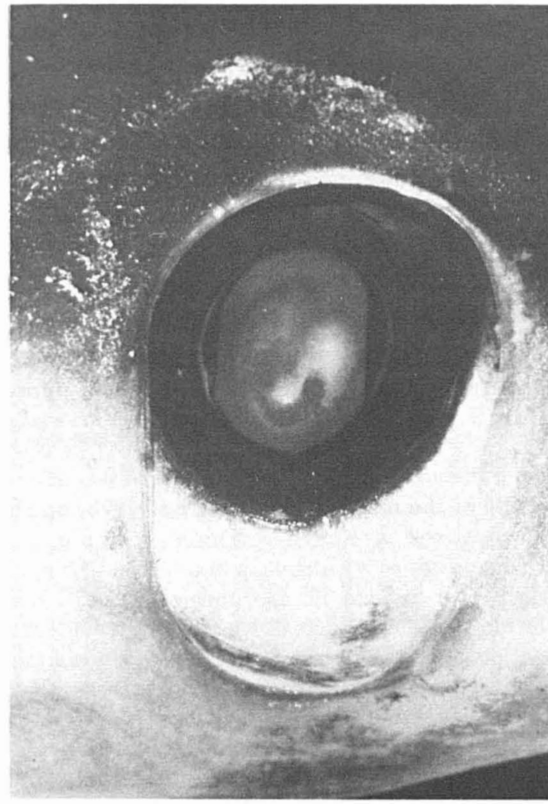

FIGURE 5.—Lateral view of the left eye of *Alopias superciliosus* (SHG-A7) showing the keyhole shape which may be an adaptation for increasing the dorsal binocular fields. The vertical distance between upper and lower eyelid is 101.5 mm. Photo: S. Spielman.

COLOR

The bigeye thresher is often described as gray (Cadenat 1956; Garrick and Schultz 1963; Bass et al. 1975). Bigelow and Schroeder (1948) stated that the bigeye thresher is "Dark mouse gray above and hardly paler below...," but we suggest that this coloration is true for preserved material and not living or freshly killed specimens. Nakamura (1935) noted that a freshly killed bigeye thresher is purple above, and we observed a violet to purplish cast above fading to creamy white below on the body of the 356 cm TL Miami specimen (SHG-A2). S. Kato and I. Nakamura[6] stated that fresh Central Pacific and eastern Atlantic bigeye threshers are purple-brown or gray-brown dorsally, white, grayish or whitish brown below. In the Miami and Central Pacific specimens a metallic silver or silver blue-green sheen was present on the sides at the level of the gills and on the flanks, as in *A. pelagicus* (Bass et al. 1975) and *A. vulpinus* (Compagno unpubl. data). The ventral surface of the paired fins and the caudal fin is oulined in dark gray.

VERTEBRAE

Vertebral counts have been used as an important character in teleost systematics for many

[6]Susumu Kato (see footnote 3) and Izumi Nakamura (see footnote 4), pers. commun. to L. J. V. Compagno, 1978.

years (i.e., Bailey and Gosline 1955) but their importance in shark systematics was recognized only with the surveys by Springer (1964) and Springer and Garrick (1964). We have compiled available vertebral counts for *A. superciliosus* (Table 2), which includes five of our specimens. The counts indicate that bigeye threshers of the eastern Pacific and Indian Ocean have slightly higher caudal and probably higher total vertebral counts than bigeye threshers from the western North Atlantic. Considerable variation is found in caudal counts in *A. vulpinus* from California (230-254, $n = 8$; Compagno unpubl. data) so that larger samples of vertebral counts of *A. superciliosus* from different regions will be needed to confirm possible population differences.

Vertebrae from the monospondylous precaudal region (centra 30-35) were radiographed in a bigeye thresher (LJVC-0355), in longitudinal view to show the calcification pattern. As with most other lamnoid sharks the dorsal, ventral, and lateral spaces of the intermedialia, between the diagonal uncalcified areas of the basalia, are composed of longitudinal calcified plates or radii that are distally bifurcated and interleaved with cartilage (terminology follows Ridewood 1921). In *A. superciliosus* these radii are fewer and less branched than in either *A. vulpinus* or *A. pelagicus*, and are not basally fused into a solid mass as in *A. pelagicus* (Figure 6).

DENTITION

Another quantitative character often used in shark systematics is the number of tooth rows in each jaw. We give dental formulas for 22 bigeye

TABLE 2.—Vertebral counts of *Alopias superciliosus*.

Number[1]	Size cm (TL)	Maturity	Sex	Locality[1]	Counts[1] MP	DP	PC	DC	TC	Source
—	—	—	—	WNA, New York	—	—	102	190±3	295±3	Springer and Garrick (1964)
GH-A6	340	Adult	Male	WNA, Florida			100	203	303	Original
SHG-A2	356	Adult	Female	WNA, Florida	—	—	102	196	298	Original
SHG-A3	241	Subadult	Male	WNA, Florida	—	—	—	191	—	Original
SHG-A7	356	Adult	Male	WNA, Florida	—	—	102	175	[2]278	Original
UMML-8861	—	Fetus	—	WNA, Florida	—	—	102	180	282	Springer and Garrick (1964)
UMML-8861	—	Fetus	—	WNA, Florida	—	—	102	187	289	Springer and Garrick (1964)
MCZ-36155	63	Fetus	Male	WNA, Cuba	—	—	102	181	283	Springer and Garrick (1964)
USNM-197700	369	Adult	Female	ENP, California	—	—	100	204	304	Springer and Garrick (1964)
LJVC-0355	287	Immature	Female	ECP	66	39	105	196	301	Original
—	161	Immature	Male	SWI, S. Africa	—	—	106	202	308	Bass et al. (1975)
—	363	Adult	Male	SWI, S. Africa	—	—	98	—	—	Bass et al. (1975)

[1]Abbreviations: NUMBER: GH, Hubbell collection; LJVC, L. J. V. Compagno collection; MCZ, Museum of Comparative Zoology, Harvard; SHG, Gruber Collection; UMML, University of Miami Marine Laboratory; USNM, United States National Museum of Natural History, Smithsonian Institution. LOCALITY: ECP, eastern-Central Pacific; ENP, eastern North Pacific; SWI, southwestern Indian Ocean; WNA, western North Atlantic. COUNTS: DC, displospondylous caudal centra; DP, diplospondylous precaudal centra; MP, monospondylous precaudal centra; PC, precaudal (MP + DP) centra; TC, total (MP + DP + DC or PC + DC) centra.
[2]Tail of SHG-A7 noticeably shorter; $<49\%$ of the total length.

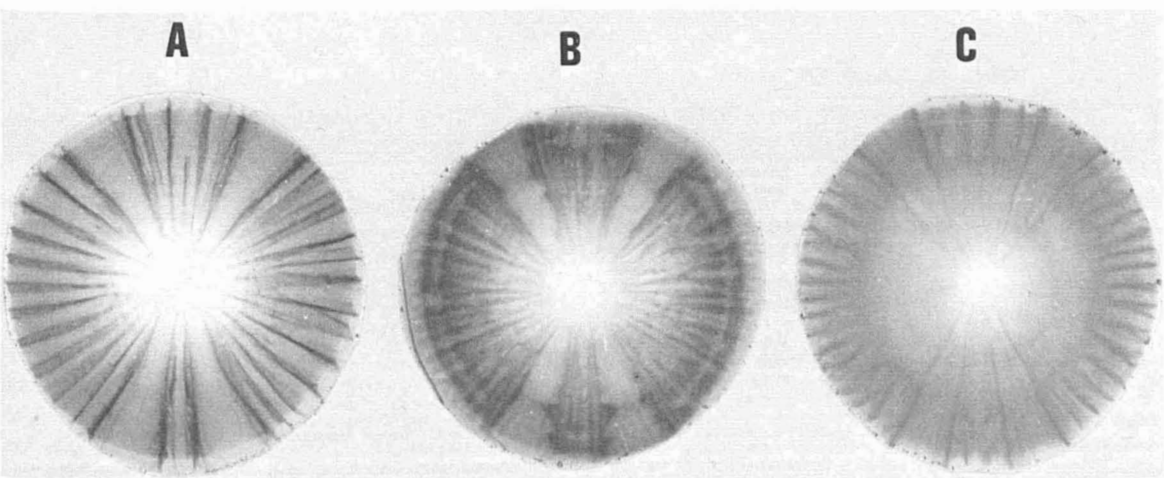

FIGURE 6.—Radiographs in transverse view of the monospondylous vertebral centra of all three *Alopias* species: A, *A. superciliosus*; B, *A. vulpinus*; C, *A. pelagicus*. Note the more simple pattern in *A. superciliosus*. Photo: L. Compagno.

threshers in Table 3, in the form A + B/C + D, where A and B are the numbers of rows in the upper left and right jaw halves, and C and D the numbers in the lower left and right jaw halves. Also presented are total tooth row counts, in the form Ab/Cd, where Ab is the total number of upper rows and Cd the total lower rows. For dental formulas of 10 bigeye threshers the ranges, means, and standard deviations are 11-12 (11.7±0.5) + 10-12 (11.5±0.7)/10-12 (10.8±0.8) + 10-12 (10.7±0.7). For the same number of total counts the ranges, means, and standard deviations are 20-24 (23.2±1.1)/20-24 (21.5±1.4).

Using Applegate's (1965) and Compagno's (1970) terminology for tooth row groups, the dentition of the bigeye thresher can be divided into two rows of anteriors (A) at either side of the symphysis and 8-10 rows of lateroposteriors (LP) on either side and postlateral to them (in both upper and lower jaws, Figure 7). An expanded formula for the bigeye thresher is:

LP9-10 + A2 + A2 + LP8-10/LP8-10
+ A2 + A2 + LP8-10 (Figure 8).

Anterior teeth of threshers differ from lateral and posterior teeth in having narrower crowns relative to their height and more erect cusps, but they are less well differentiated in *Alopias* than in lamnids, odontaspidids, mitsukurinids, and pseudocarchariids. The lateroposterior teeth of the bigeye thresher vary towards the dental band (gradient monognathic heterodonty), becoming smaller, lower relative to width, more oblique-cusped, more convex along the premedial edge, and more deeply notched in the postlateral edge, with the postlateral blade tending to change into cusplets on the more postlateral rows. Posterior teeth are not well differentiated from laterals in the bigeye thresher and are not separated out in the expanded formula; upper intermediate teeth and upper and lower symphyseal teeth are absent.

Teeth in the upper jaw are not markedly different in shape from lowers, but are slightly larger. All teeth are compressed, sharp-edged, and bladelike, and have narrow-based cusps.

Bass et al. (1975) suggested that in *A. superciliosus* the teeth of females are somewhat broader than those of males, reflecting gynandric or sexual heterodonty (dental sexual dimorphism; see Compagno 1970). Comparison of the jaws of an adult female with those of a large adult male (Figures 9, 10) shows that males have teeth (especially the anteriors and more premedial lateroposteriors) with higher, more flexed cusps than females. Gruber and Hubbell[7] (unpubl. data) have examined a number of jaws from male and female

[7]Gordon Hubbell, Director, Candron Park Zoo, Miami, FL 33149.

TABLE 3.—Dental formulas of *Alopias superciliosus*.

Number[1]	Size cm (TL)	Maturity	Sex	Locality[1]	Formula	Total	Source
MCZ-	—	—	—	WNA, Cuba	11 + 11/10 + 10	22/20	Bigelow and Schroeder (1948)
SHG-A2	356	Adult	Female	WNA, Florida	12 + 12/12 + 12	24/24	Original
SHG-A3	290	Subadult	Male	WNA, Florida	12 + 12/11 + 11	24/22	Original
SHG-A4	159	Immature	Male	WNA, North Carolina	12 + 12/11 + 11	24/22	Original
SHG-A5	320	Subadult	Female	WNA, Florida	12 + 11/11 + 11	23/22	Original
SHG-A6	306	Subadult	Female	WNA, Florida	11 + 11/10 + 11	22/21	Original
SHG-A7	356	Mature	Male	WNA, Florida	12 + 12/11 + 10	24/21	Original
GH-A1	—	—	—	WNA, Caribbean	12 + 12/12 + 12	24/24	G. Hubbell (pers. commun.)
GH-A2	381	Mature	Female	WNA, Florida	11 + 11/11 + 11	22/22	G. Hubbell (pers. commun.)
GH-A3	312	Subadult	Female	WNA, Florida	11 + 12/10 + 11	23/21	G. Hubbell (pers. commun.)
GH-A4	342	Mature	Male	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
GH-A5	—	—	—	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
GH-A6	340	Mature	Male	WNA, Florida	12 + 12/11 + 11	24/22	G. Hubbell (pers. commun.)
MBP-	269	Adult	Male	ENA, Portugal	12 + 12/10 + 10	24/20	Telles[2] (1970)
CBAT-	—	—	—	ESA, Angola	11 + 10/11 + 10	21/21	Telles[2] (1970)
—	400	Adult	Female	ENA, Senegal	10 + 8/ 9 + 8	—	Cadenat[3] (1956)
—	161	Immature	Female	SWI, S. Africa	12 + 11/11 + 11	24/22	Bass et al. (1975)
LACM-F-89	—	—	—	WNP, Japan	12 + 11/11 + 11	23/22	B. Welton (pers. commun.)
CAS-1963-X	372	Adult	Male	ENP, California	11 + 11/10 + 10	22/20	Original[4]
LACM-F-88	378	Adult (?)	Male	ENP, California	12 + 12/10 + 11	24/21	B. Welton (pers. commun.)
LACM-F-90	305	Immature	Female	ENP, California	12 + 12/11 + 11	24/22	B. Welton (pers. commun.)
LJVC-0355	287	Immature	Female	ECP	12 + 12/12 + 11	24/23	Original

[1]Abbreviations: CAS, California Academy of Sciences, San Francisco, Calif.; CBAT, Centro Biologia Aquatica Tropica, Lisbon; GH-A, Gordon Hubbell, *Alopias* jaw collection; LACM, Los Angeles County Museum of Natural History, California; LJVC, L. J. V. Compagno collection; MBP, Museu Bocage, Portugal; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts; SHG-A, Samuel H. Gruber, *Alopias* collection. WNA, western North Atlantic; ENA, eastern North Atlantic; ESA, eastern South Atlantic; SWI, southwestern Indian; WNP, western North Pacific; ENP, eastern North Pacific; ECP, eastern Central Pacific.
[2]We doubt that this was a mature adult.
[3]Cadenat (1956) mentioned that 1 or 2 teeth were missing on each side of this specimen.
[4]Fitch and Craig (1964) give 9 + 10/10 + 10 for this specimen, but we found that they apparently missed 3 rows of upper teeth.

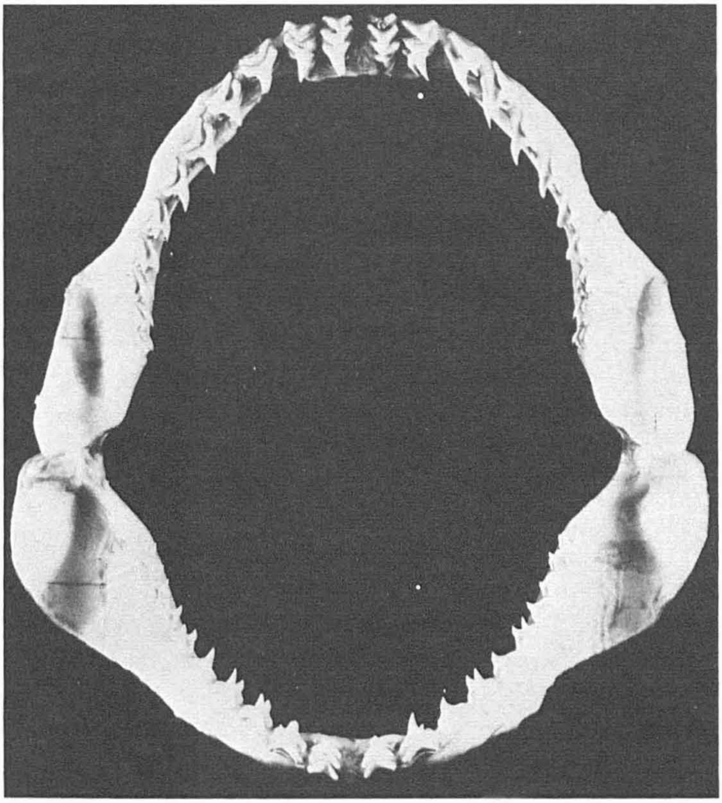

FIGURE 7.—Jaws of 372 cm TL male *Alopias superciliosus* (CAS-Acc. 1963-x: 7). Note the elongated, flexed cusps on the anterior and some lateral teeth which are characteristic of males and shown in detail in Figure 10. Photo: L. Compagno.

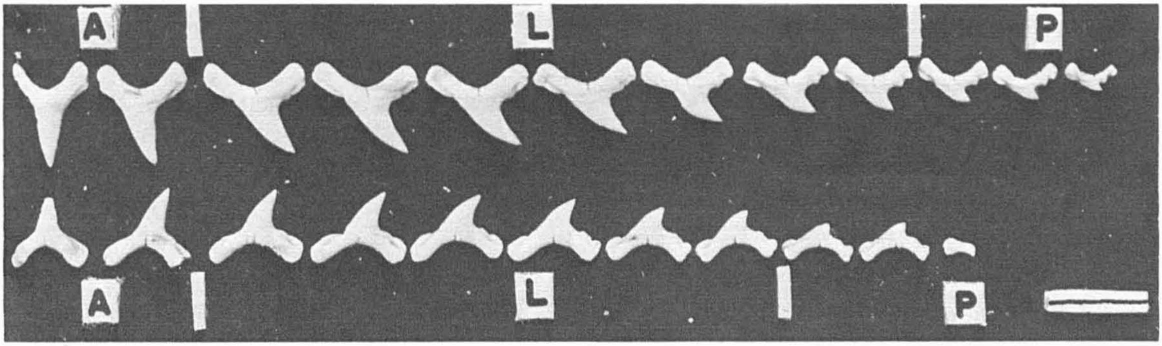

FIGURE 8.—Tooth set from the right side of the jaw of a 278 cm TL female *Alopias superciliosus* (LJVC-0355). A, anterior teeth; L, lateral teeth; P, posterior teeth. Scale mark at lower right is 1 cm. Photo: L. Compagno.

bigeye threshers and have documented this sexual heterodonty. Gynandric heterodonty is found in other sharks (see for example Springer 1964; Springer 1966), and in its ordinary form (teeth larger, more erect, and with larger cusps and often less well developed cusplets in males than in females) may aid the male in holding the female during courtship and copulation (Gruber and Myrberg 1977).

DENTICLES

Samples of skin from the back below the first dorsal fin were removed from three species of threshers (*A. superciliosus*, *A. pelagicus*, and *A. vulpinus*), dried, and examined under the scanning electron microscope to show the structure of their dermal denticles. The lateral trunk denticles of all three species are similar in

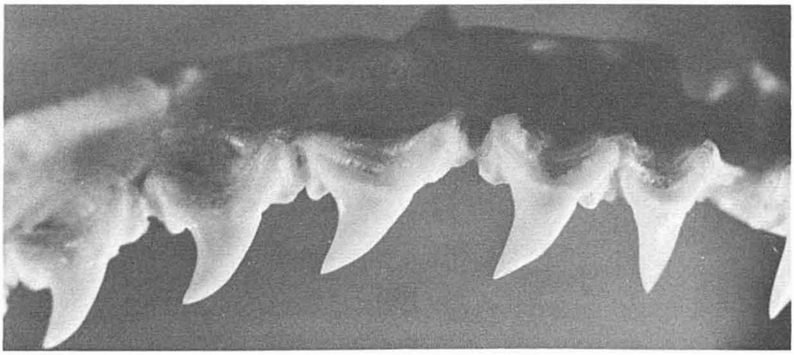

FIGURE 9.—Upper right anterior teeth 1 through 5 of a 381 cm TL female *Alopias superciliosus* (GH-A2) showing that the typical female shape is broader, less sinuous and somewhat flatter than its male counterpart. The cusp height of the 3d anterior tooth was 1.20 cm. Photo: F. Karrenburg.

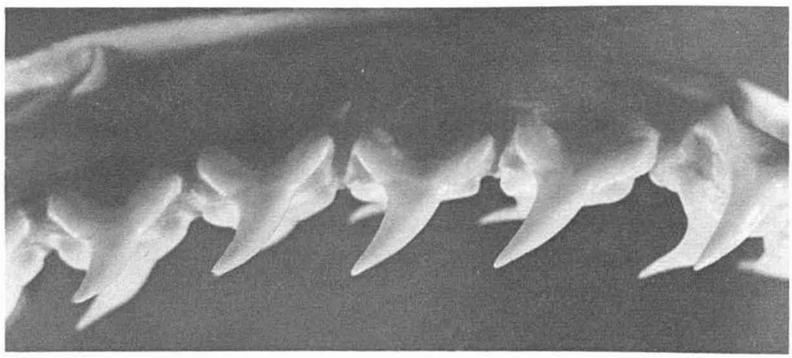

FIGURE 10.—Upper right anterior teeth 1-5 of a 342 cm TL male *Alopias superciliosus* (GH-A4). These elongate, narrrow flexed cusps are typical of males and when compared with the female above one can clearly see the gynandric heterodonty in this species. The cusp height of the third anterior tooth was 1.45 cm. Photo: F. Karrenburg.

having an oval or nearly circular crown with a strong medial ridge and posterior cusp, a pair of weaker lateral ridges, and variably developed lateral cusps (Figure 11). The crowns of these denticles are connected to their bases (buried in the skin) by tall, broad pedicles. The specimen of *A. pelagicus* examined has smaller denticles with less prominent lateral cusps than the two specimens of *A. superciliosus* and three *A. vulpinus* examined.

SIZE

The bigeye thresher grows to a large size as an adult; the heaviest reliably reported was a 284.5 kg female from Cuba (Guitart Manday 1975). Grey (1928) stated that one from New Zealand weighed 640 lb (290 kg). Using the length-weight equation for bigeye threshers given in Guitart Manday (1975)

$$W = 0.1825 \times 10^{-5} L^{3.448534} \text{ or}$$
$$L = 3.448534\,(W/1.825 \times 10^{-6})^{1/2}, \qquad (1)$$

where W is weight in kilograms and L is precaudal length in centimeters; the weight of Guitart Manday's largest bigeye thresher corresponds to a precaudal length of 237 cm and a total length of about 452 cm, while that of Grey's 290 kg bigeye thresher corresponds to a precaudal length of 240 cm and a total length of about 458 cm. Total lengths for these specimens were estimated by averaging the ratio of dorsal caudal and precaudal lengths for 10 specimens of large subadult and adult threshers in Table 1, 270-460 cm TL, which gives $L_{caudal} = 0.908 \pm 0.079$ SD.$L_{precaudal}$.

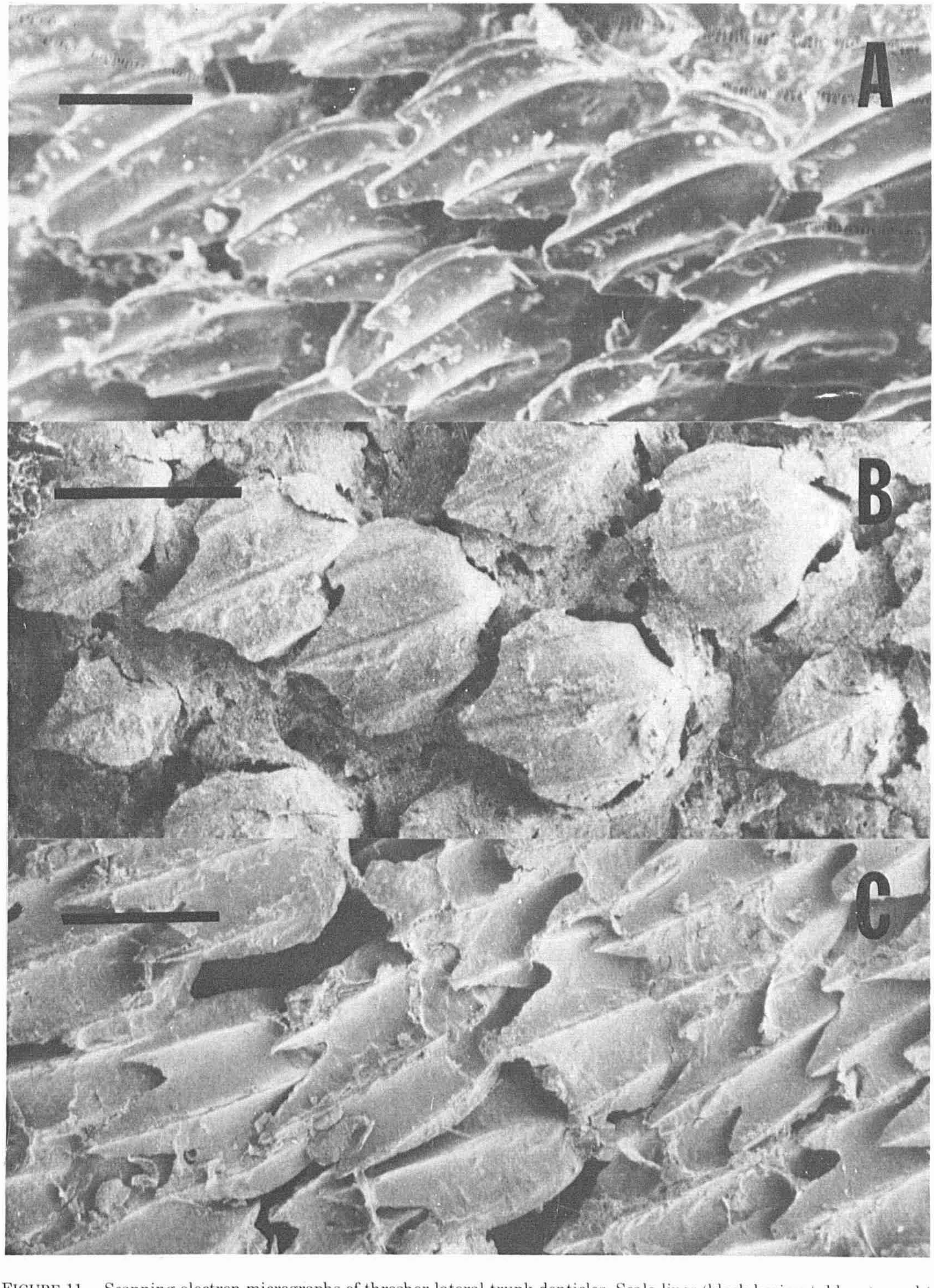

FIGURE 11.—Scanning electron micrographs of thresher lateral trunk denticles. Scale lines (black horizontal bars) equal to 0.1 mm. A, *Alopias superciliosus*, SHG-A2, 356 cm TL adult female. B, *A. pelagicus*, LJVC-0414, 192 cm TL immature male. C, *A. vulpinus*, LJVC-0234, 206 cm TL immature female. Photos: S. Gruber, L. Compagno.

Caudal lengths are variable in the sample mentioned, so that adding and subtracting one standard deviation from the average ratio of caudal to precaudal lengths gives $L_{caudal} = 0.829$ or $0.987\ L_{precaudal}$. Total length given as $L_{total} = L_{precaudal} + 0.908\ (0.829 \text{ or } 0.987)\ L_{precaudal}$. Using the minimum and maximum ratios of caudal to precaudal lengths, Guitart Manday's largest bigeye thresher was estimated to be 434-471 cm long, and Grey's 439-477 cm long.

A bigeye thresher (SHO-16-2) reported by I. Nakamura (pers. commun. to S. Kato[8]) had a precaudal length of 227.2 cm, a dorsal caudal length of 233.5 cm, and a total length (precaudal + dorsal caudal lengths) of 460.7 cm; using Guitart Manday's equation, its precaudal length corresponds to a weight of about 245 kg. Stillwell and Casey (1977) and Cadenat (1956) also measured bigeye threshers of about 4 m TL. However, most adults, especially males, fall below 350 cm TL.

Bigelow and Schroeder (1948) reported a 5.5 m TL bigeye thresher from Cuba, apparently based on data associated with a set of jaws in the collection of Museum of Comparative Zoology, Harvard. It is likely, as Bass et al. (1975) pointed out, that this figure considerably overestimates the maximum size of this shark. The tooth size from Bigelow and Schroeder's (1948) "5.5 m" specimen corresponds almost perfectly to that of a 363 cm TL shark examined by Bass et al. (1975), so that, in the absence of contrary data, the total length of Bigelow and Schroeder's largest specimen should be revised downward to about 360 cm.

The average size of adult females of *A. superciliosus* is larger than males. Guitart Manday (1975) stated that females are always the largest bigeye threshers caught on longlines, many exceeding 250 kg, and averaging 203.8 kg in a sample of eight adults; but males are much smaller, averaging 185.3 kg in a sample of four adults. Stillwell and Casey (1976) reported that 25 females ranged up to 399 cm TL, while the 15 males they examined never exceeded 352 cm TL. However, the mean length of females was only 5 cm greater than that of males. This similarity in average total length resembles a condition noted by Springer (1960) for certain carcharhinid and sphyrnid sharks, in which a small percentage of females in a population grow to a much larger size than most of their sex and species.

[8]Susumu Kato (see footnote 3), pers. commun. to L. J. V. Compagno, 1978.

The longest known adult male bigeye thresher shark was 378 cm TL (LACM-F-88),[9] from off California, and the smallest was 270 cm, from off Portugal (Telles 1970). The longest known adult females are the two of 399 cm TL and about 400 cm TL reported by Stillwell and Casey (1976) and Cadenat (1956) from the western North Atlantic and Senegal, and the shortest two of 355-356 cm from the western North Atlantic (Stillwell and Casey 1976; specimen from Miami, Fla.). The heaviest bigeye thresher reported (Guitart Manday 1975), was a female, presumably mature, and probably over 4.3 m TL (see above).

The smallest free-living bigeye thresher reported to date is a 130 cm TL immature male from off Cuba (Bigelow and Schroeder 1948). Guitart Manday (1975) reported a 144 cm TL free-living individual that weighed 6.7 kg, while Stillwell and Casey (1976) captured a 155 cm TL immature male. We report here a specimen from North Carolina of 159 cm TL. Bigelow and Schroeder (1948) and Osipov (in Gubanov 1979) suggested that parturition occurs in *A. superciliosus* when the fetus attains 64 cm TL, but Cadenat (1956), Nakamura (1935), and Gubanov (1979) reported fetuses respectively at 68, 73, and 100 cm long. Bass et al. (1975) suggested that the most likely size at birth is 100-103 cm TL. Gubanov noted the possibility that larger females might give birth to larger offspring, a possible explanation of the discrepancy of size at birth given by various authors.

Based on available data, the maximum accurately measured total length for *A. superciliosus* is 4.61 m, and weight, 284.5 kg, with total lengths of 4.7-4.8 m and weights of 290+ kg not unlikely. Apparently this species averages smaller in size than at least some populations of *A. vulpinus*, in which females in the western North Atlantic reach 479-549 cm TL; the maximum size for *A. vulpinus* may be over 609 cm TL (Bigelow and Schroeder 1948; Bass et al. 1975).

AGE AND GROWTH

The age of a bigeye thresher has never been determined by standard methods such as analysis of vertebral rings. However, age and growth in other shark species have been investigated by several techniques (i.e., Petersen method, tagging, growth in captivity) and found generally to

[9]Grey's (1928) 4 m bigeye thresher appears to be a male in the published photograph, but the article does not mention the sex.

conform to the von Bertalanffy (1938) model (Wass 1973; Stevens 1975). Holden (1974, 1977) has shown that it is possible, as a first approximation, to obtain parameters for a von Bertalanffy growth curve independently of field data. Using a modification of von Bertalanffy's (1938) basic equation, Holden (1974) rearranged the formula as follows:

$$l_{t+T} - l_t = (L_{\max} - l_t)(1 - e^{-KT}) \qquad (2)$$

where l_t = length at fertilization
l_{t+T} = length at birth
T = gestation period
$L_{\max}$ = maximum observed size
K = growth constant.

We have evaluated these parameters from data given in the literature, and solution of this equation, including generation of the growth curve, was accomplished with computer programs written by Allen (1966).

If Stillwell and Casey (1976) are correct in their assertion in that males mature at 300 cm TL compared with 350 cm TL for females, then time to maturity can be estimated from Figure 12. Assuming parturition in the bigeye thresher at 100 cm (lower curve, Figure 12), then males mature in a little over 3.5 yr while females become sexually active (i.e., reach 350 cm TL) between their fifth and sixth year. Bigeye threshers measuring 4 m TL would be about 10 yr old and the biggest members of this species (480 cm) would be at least 20 yr old.

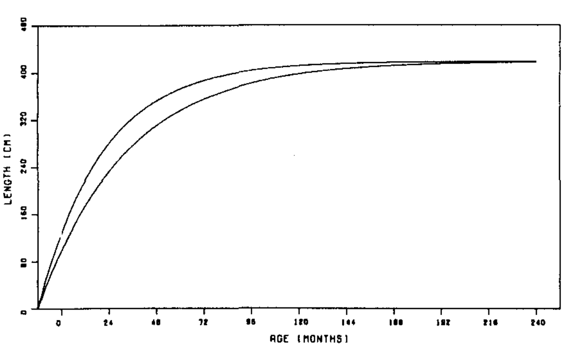

FIGURE 12.—Von Bertalanffy-type growth curve for *Alopias superciliosus*. The curve is based on parameters of: maximum total length of 420 cm; length at birth 100, 130 cm TL and gestation period of 12 months. The lower and upper curves represent a growth rate in sharks born at 100 and 130 cm TL, respectively. If this model is correct, males mature in approximately 3½ yr compared to 4½ yr for females. The largest of these sharks would be between 10 and 20 yr of age.

It should be reemphasized that this curve is but a first approximation since the assumptions of the von Bertalanffy model may not actually be satisfied by growth of the bigeye thresher. Thus this curve cannot substitute for field data and must be validated by independent methods.

No previous attempts have been made to determine the age of a bigeye thresher. We stained a few vertebral centra of the bigeye thresher LJVC-0355—287 cm TL female—from the monospondylous precaudal region (centra 30-31, 33, as counted from the head) using the alizarin technique of LaMarca (1966) and the silver nitrate technique of Stevens (1975), to demonstrate growth rings on the inner surfaces of the calcified double cones. This technique revealed a central clear area surrounded by at least eight dark rings concentric with and interspaced by lighter rings (Figure 13). The clear area is about 14.1 mm across, and the double cone 25.2 mm in horizontal diameter in centrum 33. It is not known if the dark rings are annual (added once a year), but presumably the central clear area represents the maximum size of the fetal vertebral centrum.

A comparison of Figure 12 with the data given in Figure 13 shows that if the rings are annual, the von Bertalanffy model considerably underestimates rate of growth in the bigeye thresher. However, we are not aware of any published work showing that growth rings in the centrum of warm-water sharks are annual. Several temperate water elasmobranchs lay down annual growth rings but the (temperate water) basking shark, *Cetorhinus maximus*, forms a pair of rings each year (Tanaka and Mizue 1979). So in the absence of some confirming data giving the interval between ring formation, we cannot estimate the age of the bigeye thresher by counting circuli in the vertebral centrum.

Beside the length-weight relations developed by Guitart Manday (1975) and Stillwell and Casey (1976), the only other growth data are deductions made by Stillwell and Casey concerning allometry. Based on measurements from 12 adult bigeye threshers (8 males, 4 females) they concluded that head, eye, and mouth dimensions become proportionally shorter as growth proceeds. In contrast, the height of the first dorsal, interspaces between fins, and clasper length all increase. Some differences between males and females in proportional growth were noted in their study.

Data from several sources (Nakamura 1935; Springer 1943; Bigelow and Schroeder 1948;

FIGURE 13.—Centrum 33 from a 287 cm TL, 59 kg female *Alopias superciliosus* (LJVC-0355) treated with the silver nitrate technique of Stevens (1975). This method intensifies the calcified growth rings as shown, for easy visualization. At least 8 and probably 11 dark rings surround a central clear area of 14.1 mm. The external diameter of centrum 33 is 25.2 mm. Photo: L. Compagno.

Cadenat 1956; Bass et al. 1975), but primarily Stillwell and Casey (1976), indicate that males mature at about 300 cm TL, while females mature at a larger size, probably 350 cm TL. To these data are added the observation that all males over 307 cm TL examined by Stillwell and Casey had calcified, elongate claspers, and mature sperm in the epididymis. They noted that a smaller male of 289 cm TL had nearly mature testes.

In contrast, of 13 females examined by Stillwell and Casey (1976), only those over 350 cm TL possessed mature ova and enlarged ovaries. These data support earlier studies indicating that mature (pregnant) females are all larger than about 350 cm TL. Guitart Manday (1975) noted that only the largest females captured in the Cuban fishery were pregnant. Finally, the size of our pregnant female (356 cm TL) agrees with the concept of female maturity at about 350 cm TL.

ABUNDANCE, DISTRIBUTION, AND HABITAT

The early literature on the bigeye thresher seemed to indicate that it is a widely distributed but rare, subtropical to tropical pelagic shark inhabiting relatively deep water. For example, Telles (1970) believed that only 20 bigeye threshers had ever been recorded. Nakamura (1935), Bigelow and Schroeder (1948), Cadenat (1956), and others suggested that *A. superciliosus* was a deepwater species, and Springer (1963) reported that it never approached to within a few hundred meters of the surface. More recent data based on longline catches point to localized concentrations of this species in considerable numbers, especially in the western North-Central Atlantic from off the north coast of Cuba and off North Carolina (Guitart Manday 1975; Stillwell and Casey 1976), and in the northwestern Indian Ocean (Osipov 1968; Gubanov 1972). Enough occur off Cuba to have yielded a total commercial catch for 1975 of 3,400 kg (Guitart Manday[10]). In the western Central Atlantic the species occurs north at least to off New York (Schwartz and Burgess 1975; Stillwell and Casey 1976) and apparently is relatively eurythermic. In the western North Atlantic bigeye threshers are usually caught in waters with the surface temperature from 16° to 25° C, and with longlines fished at a depth from slightly below the surface to 65 m depth where the temperature falls to 14° C (Stillwell and Casey 1976).

The bigeye thresher may be able to maintain body temperatures higher than ambient water temperature (Carey et al. 1971), which may equip it for incursions into colder water. However, like the shortfin mako, *Isurus oxyrinchus*, which is also partly homeothermic, the bigeye thresher is apparently a species preferring warm temperate to tropical waters. From available distributional data the bigeye thresher does not occur in cold temperate waters and apparently has a narrower temperature and latitudinal range than either the blue shark, *Prionace glauca*, or the great white shark, *Carcharodon carcharias*, both of which range from cold temperate seas into the tropics.

[10]Dario Guitart Manday, Institute of Oceanology, Academy of Science of Cuba, Havana, Cuba, pers. commun. to S. H. Gruber, 24 January 1978.

Alopias superciliosus is both neritic and pelagic. Kato et al. (1967) and S. Kato (footnote 8) noted that the bigeye thresher is commonly caught on high-seas longlines far from land, but capture data in Cadenat (1956), Strasburg (1958), Fitch and Craig (1964), Osipov (1968), Guitart Manday (1975), and Stillwell and Casey (1976) indicate that concentrations of the species commonly occur near land and that it occasionally enters coastal and even shallow waters. It also occurs near the bottom in relatively deep water (Nakamura 1935; Fitch and Craig 1964), has been captured at the surface offshore (the Miami specimen), and is known to range to a depth of about 500 m. Prey items taken from stomachs of the bigeye thresher include both midwater and benthic species indicating the habitats visited by the shark (see below for details).

Figure 14 is a map of the known distribution of *A. superciliosus*, including approximate numbers collected. The range as presently known includes the western North Atlantic from off New York to Florida, the Bahamas, Cuba, and the Caribbean to at least Venezuela (Springer 1943; Bigelow and Schroeder 1948; Fitch and Craig 1964; Mago L. 1970; Schwartz and Burgess 1975; Stillwell and Casey 1976; Compagno 1978). It occurs in the western South Atlantic from off southern Brazil (Sadowsky and Amorim 1977); the eastern Atlantic from off Portugal, Madeira, Senegal, possibly Guinea or Sierra Leone, Angola, and the Mediterranean (Lowe 1840; Cadenat 1956, 1961; Williams 1968; Telles 1970; and authors' specimens); the western Indian Ocean from off South Africa, Madagascar, and the Arabian Sea (Fourmanoir 1963; Osipov 1968; Gubanov 1972; Bass et al. 1975); the western Pacific from off Taiwan, possibly Japan, New Caledonia, and New Zealand (Grey 1928; Nakamura 1935; Fourmanoir and Rancurel 1972; and authors' specimens); the central Pacific, north and south of the Hawaiian Islands and between Panama and the Marquesas Islands (Strasburg 1958; S. Kato footnote 8); and the eastern Pacific from off southern California (Fitch and Craig 1964) and in the Gulf of California (Applegate et al. 1979).

REPRODUCTION

Intrauterine development in thresher sharks is ovoviviparous. As in the lamnids and odontaspidids, fetal bigeye threshers are apparently

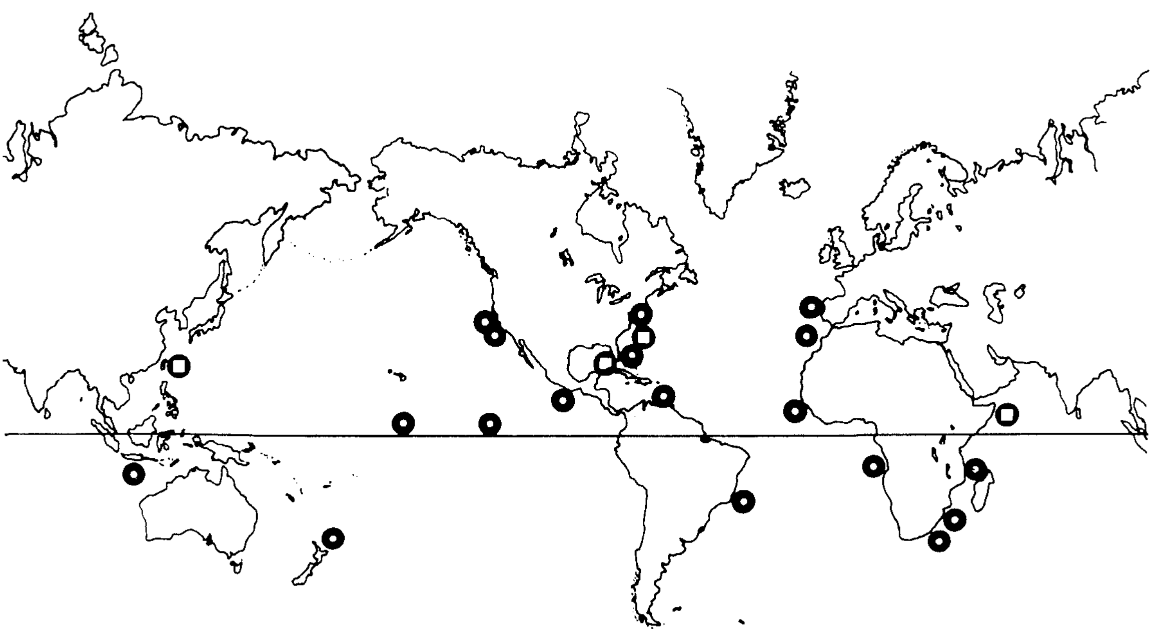

FIGURE 14.—Distribution of *Alopias superciliosus*. The 16 filled circles represent stations where fewer than 10 bigeye threshers were collected. The four filled squares show stations where this shark has been taken in commercial numbers. Several more Bahamian locales reported by the U.S. National Marine Fisheries Service were not included because the scale on the map is too coarse. This chart does not include much of the Soviet or Japanese longline catch, but extends the known distributon of *A. superciliosus* to the Mediterranean and New Zealand.

ovophagous. Horny infertile eggs are deposited in each oviduct and the embryo consumes these as development proceeds (Cadenat 1956; Gubanov 1972). Figures 15 and 16 show the embryos and the infertile eggs removed from the oviducts of specimen SHG-A2. Curiously, Gubanov (1979) claimed that the eggs of the bigeye thresher differ considerably from those of the common thresher. However, the eggs shown in our Figure 11b appear almost exactly like those shown in Gubanov's figure 1. Yet the eggs shown in Gubanov's figure 1 were said to be characteristic of the common thresher only. A possible explanation of this discrepancy is that Gubanov's figures 1 and 2 actually represent nutritive and fertile eggs, which might be similar in both species.

Most sharks do not acquire functional teeth until they reach a size close to that at parturition. However, both of our immature fetuses (Figure 15) had fully functional teeth, which is quite unusual among sharks. Perhaps the early formation of teeth aids the fetal bigeye thresher in cannabalizing potential siblings. Yet, fetal pelagic thresher *A. pelagicus* does not acquire functional teeth until it reaches considerably larger size than our two bigeye thresher fetuses.

As is often the case in odontaspidids and lamnids, the bigeye and other threshers produce only two well-developed offspring per pregnancy. While Guitart Manday (1975) mentioned one or two embryos in each oviduct the usual number is a single fetus in each oviduct (Nakamura 1935;

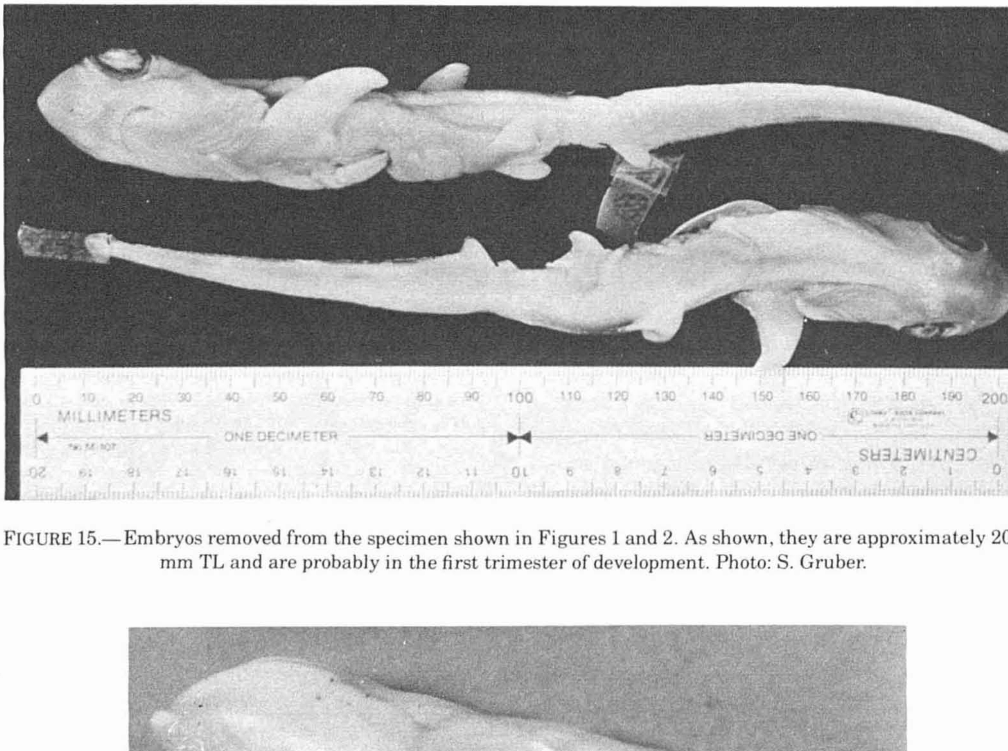

FIGURE 15.—Embryos removed from the specimen shown in Figures 1 and 2. As shown, they are approximately 206 mm TL and are probably in the first trimester of development. Photo: S. Gruber.

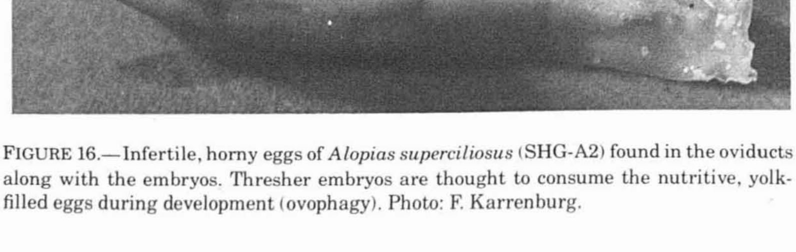

FIGURE 16.—Infertile, horny eggs of *Alopias superciliosus* (SHG-A2) found in the oviducts along with the embryos. Thresher embryos are thought to consume the nutritive, yolk-filled eggs during development (ovophagy). Photo: F. Karrenburg.

Springer 1943; Cadenat 1956; etc.). Since the gestation period is probably 12 mo (Holden 1974), the reproductive capacity of this shark may be said to be relatively low.

Guitart Manday (1975) reported that most large females throughout the year contained embryos. If the reproductive pattern is similar to that of the common thresher (Gubanov 1972, 1979), then mating occurs throughout the year. Not enough data are available for the bigeye thresher to demonstrate seasonality. However, most of the large females examined have been pregnant.

FOOD

Stomach contents of bigeye threshers have been reported in only three studies: Fitch and Craig (1964) obtained some 5 kg of Pacific whiting, *Merluccius productus*, a benthic teleost, from the stomach of their specimen; Bass et al. (1975) reported that a bigeye thresher captured in the protective shark nets along the beach at Durban (hardly deep water) had recently eaten another elasmobranch, perhaps also fouled in the net; Stillwell and Casey (1976) examined the stomachs of 35 bigeye threshers and found over 50% to have food remains—squid was the most common food, composing some 66% of the stomach contents. Other prey included remains of pelagic teleosts, such as scombrids, alepisaurids, clupeids, and istiophorids.

Stomach contents recovered from one of our specimens (SHG-A2) consisted of several eye lenses and two pairs of squid beaks. These were identified by Gilbert Voss[11] as ommastrephid remains, probably from the genus *Illex*. Voss mentioned that *Illex* made up 75-80% of the cephalopod diet of the swordfish, *Xiphias gladius*, caught in the Florida Current.

The food of the bigeye thresher thus consists of small to moderate benthic and pelagic teleost fish, crustaceans, and cephalopds, and as presently known, is restricted to a few species.

PREY CATCHING

According to Springer (1961) the upper caudal lobe of *Alopias* (along with the armed rostrum of the pristiophorids *Pristiophorus* and *Pliotrema*) are the only structures of modern sharks functioning specifically for killing prey (jaws and teeth being used for other purposes in addition to feeding). However, it has not been universally accepted that the tail of thresher sharks is actually used in feeding. In an interesting discussion of this controversy, Lineweaver and Backus (1969) noted that the ichthyologists J. T. Nichols and C. M. Breder doubted that the tail was sufficiently rigid or muscular to kill prey.

Grossly overdeveloped appendages such as the claw of the male fiddler crab, *Uca* sp., often evolve along with elaborate courtship signals, and it is possible that the elongated tail of *Alopias* evolved in the context of a social or species recognition signal. However, field observations support Springer's (1961) concept of the thresher's tail as an offensive weapon for prey capture. One of the first such observations is that of Blake-Knox (1866), who claimed that a common thresher, *A. vulpinus*, used its caudal fin to kill a loon and then consumed the bird. Coles (1915) reported common threshers as feeding in shallow water by throwing fish into their mouth with their caudal fins. Allen (1923) gave a similar detailed description of the feeding behavior of a common thresher. Grey (1928) observed common threshers following baits trolled from a sport fishing boat and striking at the bait with their tails.

Recently, indirect but compelling observations from longline fisheries confirm that threshers use their tail in feeding. Gubanov (1972) reported that 97% of all three thresher species captured were foul-hooked in the upper caudal. This agrees with Stillwell and Casey (1976), who noted that several bigeye threshers were tail-hooked and that two or more baits were often recovered from a captured bigeye thresher's stomach. This suggested to Stillwell and Casey as well as to Gubanov that the live baits were dislodged from the hooks probably by blows from the thresher's caudal fin.

EXPERIMENTAL STUDIES

The bigeye thresher has occasionally been the subject of study unrelated to fishery, natural history, or taxonomic observation. Carey et al. (1971) measured the muscle temperature of a number of freshly captured sharks and teleosts and concluded that, among others, the bigeye thresher is warm-bodied. They described a single vascular heat exchanger which probably makes the storage of heat possible in this species.

[11]Gilbert Voss, Professor of Biology and Living Resources, RSMAS, University of Miami, Miami, FL 33149, pers. commun. to S. H. Gruber, December 1979.

Okada et al. (1969) removed the brain from *A. superciliosus* and compared it with the brains of a number of other sharks in an effort to discern a common structural pattern which might be related to ecology or predatory behavior. They concluded that brain morphology correlates with ecology and behavior rather than with taxonomic similarity since distantly related shark species sharing similar behavior and habitat shared in the development of a number of homologous brain structures. According to Okada et al. the optic tectum of *A. superciliosus* is well developed compared with that of the common thresher and mako, *Isurus*. Perhaps most noteworthy was the size of the cerebellum, which was even larger than the telencephalon. The reverse is usually found (Figure 17). The brain of a 3 m *A. superciliosus* weighed approximately 30 g, some one-third heavier than that of a 3.6 m *A. vulpinus*. The heavier brain of *A. superciliosus* reflects the prominence of the optic lobes. Speculations as to the significance of these structures would be premature because of the paucity of physiological data on shark brains.

Two further studies have used the bigeye thresher as a laboratory subject. Bundschuh and Ballester (1971) tested the serum of 10 shark species including the bigeye thresher for antibodies against human saliva, erythrocytes, and serum. Natural antibodies against human proteins were reported, although the significance of these antibodies was unclear. Finally, Gabeva and Kovaleva (1976) described morphological changes associated with spermatogenesis in the bigeye thresher, and the role of the follicular epithelium of the testes in the process.

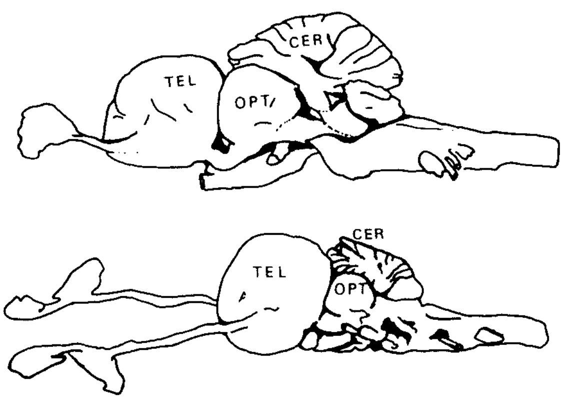

FIGURE 17.—Lateral views of the brains of *Alopias superciliosus* (upper) and *Carcharhinus* sp. (lower) after Okada et al. (1969). Brains have been sketched with telencephalon (TEL) the same size. Note that the optic tectum (OPT) and cerebellum (CER) are relatively much larger in the bigeye thresher.

The dearth of experimental studies on the bigeye thresher points to the difficulty of obtaining fresh material for detailed analysis. Because of this and because the bigeye thresher has never been kept in captivity, it does not ordinarily make a suitable subject for experimental or detailed study.

PARASITOLOGY

The known parasite fauna of the bigeye thresher has been given in five papers: three on gut cestodes and two on external copepods. Dailey (1969) erected the order Litobothridea to include some unusual tapeworms he found in massive infections of the spiral valve of two bigeye threshers collected in southern California. Two worms, *Litobothrium alopias* and *L. coniformis*, were described as new species. Kurochkin and Slankis (1973) further described *L. daileyi* and *Renyxa amplifica* from the spiral valve of bigeye threshers also from the Pacific Ocean. Thus, it would appear that this group of cestodes has evolved along with the Alopiidae and may be restricted to that family. Finally, Heinz and Dailey (1974) reported two cestodes from the stomach of the bigeye thresher: *Sphyriocephalus viridis* and *S. pelorosoma*, the latter a new species.

The only other parasites reported from the bigeye thresher were two new species of copepods: *Pagina tunica* and *Bariaka alopiae*. *Pagina tunicata* was removed from the body surface while *B. alopiae* was taken from the gills (Cressey 1964, 1966). Cressey collected the type-specimen of *B. alopiae* from bigeye threshers captured off Madagascar and South America at stations separated by almost 20,000 km. Because of this great distance Cressey speculated that *B. alopiae* has a specific affinity for the bigeye thresher.

These few species probably do not represent a complete catalogue of parasites infecting the bigeye thresher, but rather are noteworthy examples. If the bigeye thresher is similar to other shark species, it harbors a diverse assemblage of macroparasites including cestodes, nematodes, leeches, copepods, and amphipods.

COMMERCIAL IMPORTANCE

Commercial exploitation of threshers, especially the bigeye thresher, follows two fishery patterns. The first, exemplified by methods of the Japanese and Soviet high-seas pelagic fleet, involves highly mobile longline fishing vessels which actively seek out concentrations of predatory fish associated with small-scale oceanographic processes, such as plankton concentrations, and local circulation patterns (Osipov 1968; Gubanov 1972). While tunas are the major objective of these fisheries, sharks and billfishes are an important bycatch.

Osipov (1968) noted that, in the northwestern Indian Ocean, local circulation patterns produce distinct areas of plankton and fish concentrations in which one or two predatory species predominate. These associations are dynamic both in species composition and time. Thus the concentration of any species in such an area is both spatially and temporally discontinuous and falls off rapidly outside the enrichment cells. As a consequence, fishing vessels must move continuously in the wake of fish schools as concentrations form and disperse.

Osipov (1968) identified three such areas in the Indian Ocean off the Republic of Somalia. In one of these plankton-enriched areas carcharhinid sharks predominated, while the bigeye thresher was the most plentiful shark in another. Taken overall, however, the bigeye thresher amounted to only 12% of the total shark catch. Thus, while the distribution of *A. superciliosus* on the high seas is patchy, they make up a reasonable proportion (over 10%) of the shark catch, at least seasonally.

The bigeye thresher is also commercially important in the short-range pelagic fishery operating off the northwestern coast of Cuba (Guitart Manday 1975, footnote 10). However, the pattern of distribution is quite different from that in the Indian Ocean. Longlines are set year round in the Cuban fishery and 11 shark species are caught in commercially exploitable numbers. Of 11 species, the bigeye thresher is the third most abundant and amounted to some 20% by weight of the total 1973 shark catch. The Cubans have been fishing this species more effectively in recent years and have doubled their catch between 1971 and 1975.

Seasonal distribution is also evident in the Cuban catch records (Guitart Manday 1975). The poorest catches are in March-June. The catch of bigeye threshers gradually increases over the summer and peaks in the fall around September-October, to decline again in the winter.

Bigeye threshers occasionally enter the market when they are caught by sport and commercial anglers fishing for swordfish off southeastern Florida. Since both species are caught at night near the surface in the Florida Current it is not surprising to see several bigeye threshers each year captured by commercial longliners or during the swordfish tourneys. Incidentally, many of these animals are foul-hooked as described above, perhaps reflecting a preference to attack bait with their caudal fins. However, in this fishery the hook is usually attached to a nylon monofilament leader specifically to avoid catching sharks. Thus the low incidence of mouth hooked bigeye threshers could reflect losses due to biting through the leader.

Finally, this species has been captured a few times in gill nets set at moderate depth, to 160 m (Fitch and Craig 1964; Telles 1970; Bass et al. 1975).

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LITERATURE CITED

ALLEN, K. R.
1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23:163-179.

ALLEN, W. E.
1923. Behavior of the thresher shark. Science 63:31-32.

APPLEGATE, S. P.
1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. Los Ang. Cty. Mus., Contrib. Sci. 86, 18 p.

APPLEGATE, S. P., L. ESPINOSA A., L. B. MENCSACA L., AND F. SOTELO M.
1979. Tiburones Mexicanos. Subsecretaria de Educacion e Investigagion Teconologicas, Mexico City, 146 p.

BAILEY, R. M., AND W. H. GOSLINE.
1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Univ. Mich. Mus. Zool. Misc. Publ. 93, 44 p.

BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhinicodontidae. Oceanogr. Res. Inst. (Durban) Invest. Rep. 39, 102 p.

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (Inquiries on growth laws II). Hum. Biol. 10:181-213.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic. Part one, p. 59-546. Mem. Sears. Found. Mar. Res., Yale Univ.

BLAKE-KNOX, H.
1866. Glances into the ichthyology of the county of Dublin. Zool. 1:505-510. [Cited from Lineweaver and Backus (1969).]

BONNATERRE, J. P.
1788. Tableau Encyclopedique et Méthodique des Trois Règnes de la Nature...Ichthyologie. Chez Panckoucke, Paris, 215 p.

BUNDSCHUH, G. VON, AND J. M. BALLESTER.
1971. Agglutination menschlicher Erythrozyten durch Serum verschiedener Haifischarten. Biol. Zbl. 90:321-329.

CADENAT, J.
1956. Note d'Ichtyologie ouest-africaine. XV.—Sur un Requin-Renard nouveau pour la faune d'Afrique Occidentale française *Alopias superciliosus* (Lowe) 1840? Bull. Inst. Fr. Afr. Noire 18 A:1257-1266.
1961. Notes d'Ichthyologie ouest-africaine XXXIV. Liste complémentaire des espèces de poissons de mer (provenant des côtes de l'Afrique occidentale) en collection à la section de biologie marine de l'I.F.A.N. à Gorée. Bull. Inst. Fr. Afr. Noire 23A:231-245.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, K. D. LAWSON, AND J. S. BECKETT.
1971. Warm-bodied fish. Am. Zool. 11:135-143.

CHEN, J. T. F.
1963. A review of the sharks of Taiwan. Biol. Bull. Dep. Biol. Coll. Sci., Tunghai Univ., Ichthyol. Ser. 1, 19:1-102.

COLES, R. J.
1915. Notes on the sharks and rays of Cape Lookout, N.C.. Proc. Biol. Soc. Wash. 28:89-94.

COMPAGNO, L. J. V.
1970. Systematics of the genus *Hemitriakis* (Selachii: Carcharhinidae), and related genera. Proc. Calif. Acad. Sci., Ser. 4, 38:63-98.
1978. Family: Alopiidae. *Alopias superciliosus*. *In* W. Fischer (editor), FAO species identification sheets for fishery purposes, Western Central Atlantic (fishing area 31). Vol. 5, unpaged. FAO, Rome.

CRESSEY, R. F.
1964. A new genus of copepods (*Caligoida*, *Pandaridae*) from a thresher shark in Madagascar. Cah. ORSTOM-Oceanogr. Ser. Nosy Be 2(6):385-397.
1966. *Bariaka alopiae* n. gen., n. sp. (*Copepoda*: *Caligoida*), a parasite on the gills of a thresher shark. Bull. Mar. Sci. 16:324-329.

DAILEY, M. D.
1969. *Litobothrium alopias* and *L. coniformis*, two new cestodes representing a new order from elasmobranch fishes. Proc. Helminth. Soc. Wash. 36:218-224.

DUMÉRIL, A.
1865. Histoire naturelle des poissons ou ichthyologie general. Vol. I and II. Libraire Encyclopedique, Paris, 120 p.

FITCH, J. E., AND W. L. CRAIG.
1964. First records for the bigeye thresher (*Alopias superciliosus*) and slender tuna (*Allothunnus fallai*) from California, with notes on eastern Pacific scombrid otoliths. Calif. Fish Game 50:195-206.

FOURMANOIR, P.
1963. Raies et requins-scie de la cote ouest de Madagascar (ordre des Batoidei). [Bibliogr. Engl.] Cah. ORSTOM-Oceanogr. Ser. Nosy Be 1(6):33-58.

FOURMANOIR, P., AND P. RANCUREL.
1972. Sharks of New Caledonia. [Abstr.] Int. Symp. Oceanogr. South Pac., Wellington, N.Z., 1972, p. 516.

FOWLER, H. W.
1936. The marine fishes of West Africa, based on the collection of the American Museum Congo Expedition, 1909-1915. Bull. Am. Mus. Nat. Hist. 70(1):1-605.
1941. Contributions to the biology of the Philippine archipelago and adjacent regions. U.S. Nat. Mus. Bull. 13(100), 879 p.

GABEVA, N. S., AND T. J. KOVALEVA.
1976. On the morphodynamics of the follicular cells (Sertoli cells) in spermatogenesis of lamellibranchiate fish (subclass Elasmobranchii). (O morfodinamike follikulyatnykh kletok (Kletok Sertoli) spermatogeneze plastinozhabernykh ryb (podklass Elasmobranchii).) Vestn. Univ. Leningr. Ser. Biol. 1(3):50-58.

GARMAN, S.
1913. The Plagiostomia (sharks, skates and rays). Mem. Mus. Comp. Zool. Harvard Coll. 36, 151 p.

GARRICK, J. A. F.
1967. Revision of sharks of genus *Isurus* with description of a new species (Galeoidea, Lamnidae). Proc. U.S. Natl. Mus. 118:663-690.

GARRICK, J. A., AND L. P. SCHULTZ.
1963. A guide to the kinds of potentially dangerous sharks. *In* P. W. Gilbert (editor), sharks and survival, p. 3-60. D. C. Heath Co., Boston.

GREY, Z.
1928. Big game fishing in New Zealand seas. Nat. Hist. 28(1):46-52.

GRUBER, S. H., AND A. A. MYRBERG, JR.
1977. Approaches to the study of the behavior of sharks. Am. Zool. 17:471-486.

GUBANOV, YE. P.
1972. On the biology of the thresher shark [*Alopias vulpinus* (Bonnaterre)] in the Northwest Indian Ocean. J. Ichthyol. 12:591-600.
1979. The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. J. Ichthyol. 18:781-792.

GUITART MANDAY, D.
1975. Las pesquerias pelagico-oceanicas de corto radio de accion en la region noroccidental de Cuba. Acad. Cienc. Cuba Ser. Oceanol. 31, 26 p.

GÜNTHER, A.
1870. Catalogue of the fishes in the British Museum. Vol. 8. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondropterygii, Cyclostomata, Leptocardii in the British Museum. Br. Mus., Lond., 549 p.

HEINZ, M. L., AND M. D. DAILEY.
1974. The Trypanorhyncha (Cestoda) of elasmobranch fishes from southern California and northern Mexico. Proc. Helminth. Soc. Wash. 41:161-169.

HOLDEN, M. J.
1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* F. Hardin-Jones (editor), Sea fisheries research, p. 187-215. Logos Press, Lond.
1977. Elasmobranchs. *In* J. A. Gulland (editor), Fish population dynamics, p. 187-215. Wiley, Lond.

KATO, S., S. SPRINGER, AND M. H. WAGNER.
1967. Field guide to eastern Pacific and Hawaiian sharks. U.S. Fish Wildl. Serv., Circ. 271, 47 p.

KUROCHKIN, YU. B., AND A. J. SLANKIS.
1973. Novye predstavitele i sostav otryada Litobothridea Dailey, 1969 (Cestoidea). (New representative and composition of the order Litobothridea Dailey, 1969 (Cestoidea).) [In Russ.] Parazitologiya (Leningr.) 7(6):502-508.

LAMARCA, M. J.
1966. A simple technique for demonstrating calcified annuli in the vertebrae of large elasmobranchs. Copeia 1966: 351-352.

LINEWEAVER, T. H., AND R. H. BACKUS.
1969. The natural history of sharks. J. B. Lippincott Co., Phila., 256 p.

LOWE, R. T.
1840. On new species of fishes from Madeira. Proc. Zool. Soc. Lond. 8:36-39.

MAGO L., F.
1970. Lista de los Peces de Venezuela incluyendo un estudio preliminar sobre la ictiogeografia del país. Minist. Agric. Cria. Of. Nac. Pesca. Caracas, Venezuela, 283 p.

MATSUBARA, K.
1963. Fish morphology and hierarchy. Part 1. 2d ed. Ishizaki-Shoten, Tokyo, 789 p.

NAKAMURA, H.
1935. On the two species of the thresher shark from Formosan waters. Mem. Fac. Sci. Agric. Taihoku Imp. Univ. 14:1-6.

OKADA, Y., M. AOKI, Y. SATO, AND H. MASAI.
1969. The brain patterns of sharks in relation to habit. J. Hirnforsch. 11:347-365.

OSIPOV, V. G.
1968. Some features of the distribution of tuna and other pelagic fishes in the northwestern Indian Ocean. (Nekotorye osobennoste raspredeleneya Tunstov i drugekh pelagechekikh ryb v severo-zapadnoii chasti Indiiskogo Okena.) (Transl. in Probl. Ichthyol. 8:22-28.)

RAFINESQUE, C. S.
1809. Caratteri di alcuni nuovi generi e nuovi specie di animali e piante della Sicilia. Sanfilippo, Palermo, 105 p.

RIDEWOOD, W. G.
1921. On the calcification of the vertebral centra in sharks and rays. Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci. 210:311-407.

SADOWSKI, V., AND A. F. DE AMORIM.
1977. Sobre a composicao de fauna dos esqualos pelagicos do Brasil. Cienc. Cult., Supl. Resumos 29(7):792.

SALVIANI, l.
1554. Aquatiluim animalium historiae Liber Primus, cum eorumdem Formis, Aere Excuis. Romae Medicinam Profitente Auctore, Romae, 256 p.

SCHWARTZ, F. J., AND G. H. BURGESS.
1975. Sharks of North Carolina and adjacent waters. N.C. Dep. Nat. Econ. Resour., 57 p.

SPRINGER, S.
1943. A second species of thresher shark from Florida. Copeia 1943:54-55.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61:1-38.
1961. Dynamics of the feeding mechanism of large galeoid sharks. Am. Zool. 1:183-185.
1963. Large sharks of the Florida-Caribbean region. *In* P. W. Gilbert (editor), Sharks and survival, p. 96-124. D.C. Heath Co., Boston.
1966. A review of the western Atlantic cat sharks Scyliorhinidae, with descriptions of a new genus and five new species. U.S. Fish Wildl. Serv., Fish. Bull. 65:581-624.

SPRINGER, V. G.
1964. A revision of the carcharhinid shark genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. Proc. U.S. Natl. Mus. 115:559-632.

SPRINGER, V. G., AND J. A. GARRICK.
1964. A survey of vertebral numbers in sharks. Proc. U.S. Natl. Mus. 116:73-96.

STEVENS, J. D.
1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). J. Mar. Biol. Assoc. U.K. 55:657-685.

STILLWELL, C. D., AND J. G. CASEY.
1976. Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic. Fish. Bull., U.S. 74:221-225.

STRASBURG, D. W.
1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 58:335-361.

TANAKA, S., AND K. MIZUE.
1979. Studies on sharks—XV Age and growth of Japanese dogfish *Mustelus manazo* Bleeker in the east China Sea. Bull. Jpn. Soc. Sci. Fish. 45:43-50.

TELLES, A. M.
1970. Presence de *Alopias superciliosus* (Lowe) dans les mers du Portugal. Remarques sur les *Alopias* (Selachii) recents et fossiles. Arq. Mus. Bocage 11(19):363-378.

TENG, C. Y.
1962. Classification and distribution of the Chondrichthys of Taiwan. Privately published, Taipei, Taiwan, 304 p.

TORTONESE, E.
1938. Intorno agli squali del genere *Alopias*. Boll. Mus. Zool. Anat. Comp. Univ. Torino 46-III(78):1-7.

WASS, R. C.
1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac. Sci. 27:305-318.

WHITE, E. G.
1937. Interrelationships of the elasmobranchs with a key to the order Galea. Bull. Am. Mus. Nat. Hist. 74(2):25-138.

WILLIAMS, F.
1968. Report on the Guinean Trawling Survey, Volume 1. Gen. Rep. Organ. Afr. Unity, Sci., Tech. Res. Comm., 828 p.