Pacific Science (1977), vol. 31, no. 2

Contribution to the Biology of the Whitetip Reef Shark (*Triaenodon obesus*)[1]

JOHN E. RANDALL[2]

ABSTRACT: The whitetip reef shark, *Triaenodon obesus* (Rüppell), is broadly distributed in the tropical and subtropical Indian and Pacific oceans from the Red Sea (type locality) and east coast of Africa to the eastern Pacific. Formerly classified in the Triakidae, it is now regarded as a carcharhinid. It is distinctive in its slender body (depth about 7 in precaudal length), obtuse snout, 43 to 50 teeth in each jaw in at least two functional rows, the teeth with one or two small cusps on each side of the large central cusp, and white tips on at least the first dorsal fin and upper lobe of the caudal fin. It is closely associated with coral reefs and is often seen at rest in caves. There is evidence that this shark has a home cave to which it may return after foraging for food. Although reported to attain a total length of 7 feet (213 cm) or more, the largest of 231 individuals measured by the author and associates was 168 cm total length (135 cm precaudal length). Seven recoveries were made of 124 whitetips tagged at Johnston Island (time at liberty with tags 16 days to 2 years). Two of the tagged sharks were caught in the same area as that in which they were released and the others were taken .3 to 2.9 km from the tagging sites. The growth rate of the tagged sharks, which ranged from 81 to 105 cm precaudal length, varied from 2.1 to 4.2 cm/year. Two captive sharks, 73 and 88 cm precaudal length, grew at the rate of 4 and 2.3 cm, respectively, in the Gulf of Aqaba, Red Sea over a period of 3 years. A whitetip born in captivity in July at a precaudal length of 43.2 cm at Enewetak, Marshall Islands, grew 2 cm in 6 weeks. The stomachs of 56 whitetips were opened; 33 were empty; 17 contained the remains of fishes (those identified were all reef fishes such as scarids and acanthurids); four had eaten octopuses, and two contained both fishes and octopuses. One reference described a diet of xanthid crabs and spiny lobsters. A juvenile whitetip was found in the stomach of a larger grouper (*Epinephelus lanceolatus*); some of the larger sharks such as the tiger and Galapagos sharks are probably more important predators than this grouper. The sex ratio does not deviate significantly from 1 : 1 except for whitetips caught in traps; 65 of 107 trap-caught sharks were males. The smallest mature female *T. obesus* of this study measured 101.2 cm precaudal length (but a smaller size might be expected), and the smallest mature male was 82 cm. Litter size ranges from one to five. Compared to other carcharhinids, *T. obesus* is a relatively placid species which need not be feared by divers unless provoked or attracted by spearfishing (even then aggressive behavior toward man is rare). This shark may cause ciguatera poisoning, especially if the liver is eaten.

THE WHITETIP REEF SHARK (*Triaenodon obesus*) (Figure 1) is one of the three most common sharks on coral reefs of the tropical and subtropical Indo-Pacific region. Like the other two, the blacktip reef shark (*Carcharhinus melanopterus*) and the gray reef shark (*Carcharhinus amblyrhynchos*) (*menisorrah* of many authors), it is a relatively small species well adapted for life in the shallow reef environment. In spite of the abundance of *T. obesus* and the frequency with which it is

[1] Manuscript received 21 May 1976.

[2] Bernice P. Bishop Museum, Post Office Box 6037, Honolulu, Hawaii 96818.

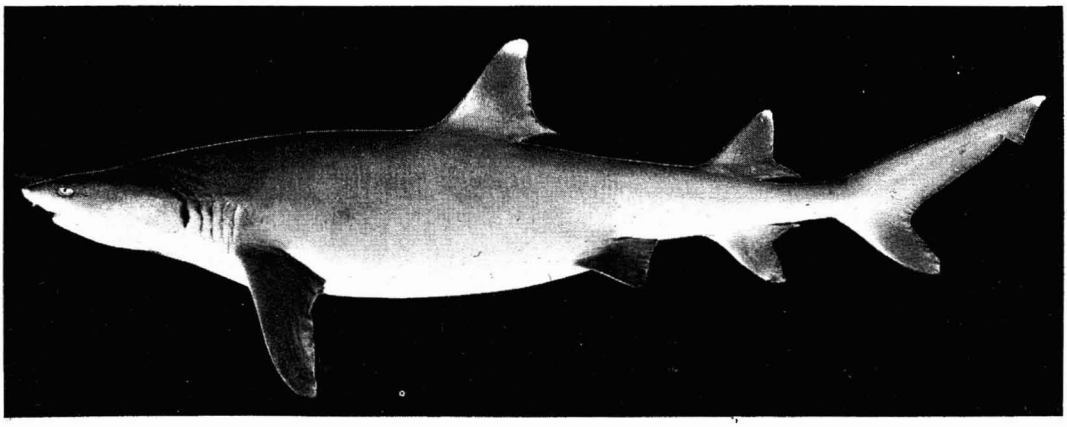

FIGURE 1. Pregnant *Triaenodon obesus*, 121.8 cm precaudal length, 152 cm total length, 23.6 kg (4.55 kg of this weight due to five embryos 40–42.7 cm precaudal length), Tahiti, 27.5 m, 21 September 1967.

encountered by divers, very little has been written about it other than distributional records. The purpose of this paper is to review what is known of the biology of this shark and to present some original data on its life history. These data were assembled incidentally to other projects, as the opportunity arose, beginning December 1966.

CLASSIFICATION

Carcharias obesus was described by Rüppell (1835:64, pl. 18, fig. 2) from a specimen from Jeddah, Red Sea. The choice of the specific name is unfortunate, for *obesus* is a slender species. Klausewitz (1960:291, pl. 42, fig. 1, text-fig. 4) illustrated the holotype and its teeth; it is housed at the Senckenberg Museum, Frankfurt, under number 3149.

Müller and Henle (1837) proposed the genus *Triaenodon*, selecting *obesus* as the type species of the genus. Until recently most authors, including Bigelow and Schroeder (1948), have placed *Triaenodon* in the Triakidae. Gohar and Mazhar (1964*a*), Kato, S. Springer, and Wagner (1967), and Compagno (1973), however, have classified it in the Carcharhinidae. Although the teeth of *Triaenodon* are triakidlike in having small lateral cusps and occurring in more than one functional row, these authors have pointed out that other characters such as the presence of a nictitating membrane rather than a fold, a well-developed precaudal pit, the spiracle minute or absent, a prominent lower caudal lobe, and a scroll-type valvular intestine rather than the spiral form ally this genus with the Carcharhinidae. In addition, Tester and Nelson in Gilbert, Mathewson, and Rall (1967) noted that the distribution of the free neuromasts (pit organs) of *Triaenodon* more closely resembles that of some of the carcharhinids than the Triakidae. Nevertheless, *Triaenodon* is clearly divergent within the family Carcharhinidae.

Four other specific names have been proposed in *Triaenodon: smithii* Müller & Henle, *nigricans* Philippi, *obtusus* Day, and *apicalis* Whitley. Other authors have shown that *smithii* belongs in the West African genus *Leptocharias*, *nigricans* is a teleost fish, and *apicalis* is a synonym of *obesus*. Opinions differ, however, on the status of *obtusus*. Day (1878) described this shark from a single 19-inch (48.3 cm) specimen from Karachi. Bass, D'Aubrey, and Kistnasamy (1975) regarded *obtusus* as a doubtful species, adding that most modern authors treat *Triaenodon* as monotypic; Taniuchi (1975), however, preferred to follow Garman (1913) and Wheeler (1960) in considering it a valid species because the origin of the first dorsal fin is over the inner pectoral edge (hence, notably anterior to *obesus*) and the second dorsal fin is considerably smaller than that of *obesus*. These

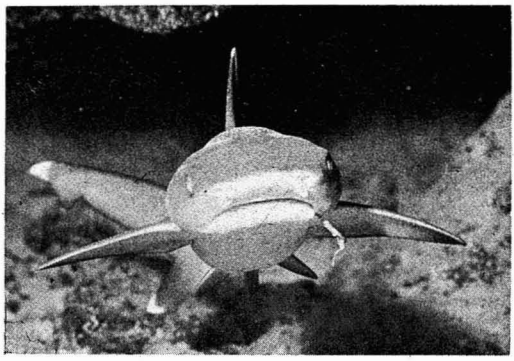

FIGURE 2. Juvenile *Triaenodon obesus* with a fishhook in its mouth at Kwajalein, Marshall Islands. This shark was repeatedly sighted in the same cave for a period of over 1 year. (Photograph by Patricia Bartlett, 14 July 1975.)

differences were specifically mentioned by Day in his description, and they show in his illustration. Nevertheless, a request was made of P. K. Talwar of the Zoological Survey of India in Calcutta to provide measurements from the type specimen (ZSI 2277, a skin now kept in alcohol, which he stated is "about 19 inches total length"). He measured the predorsal distance as 135 mm, whereas the distance from the snout to the inner corner of the pectoral fins is 150 mm. The first dorsal fin base is 61.5 mm compared to 17.5 mm for the length of the base of the second dorsal fin. Day's illustration shows no white tips on any of the fins. Talwar confirmed the absence of these markings though noted that the margin of the tip of the first dorsal is a little lighter in color. The position and relative size of the dorsal fins of *T. obesus* do not differ significantly from young to adult, and the white ends of the fins clearly show in the newborn (Figure 2); thus the differences cannot be attributed to the small size of the specimen of *T. obtusus*. The author therefore agrees with Taniuchi that *obtusus* should be regarded as a valid species.

Fowler (1908:63, fig. 2) described *Eulamia odontaspis* from a specimen 20 7/8 inches (53 cm) in length from an unknown locality "but probably from the Indian Ocean." Fowler (1941) referred his *E. odontaspis* to the synonymy of *Triaenodon obesus*.

Detailed descriptive data of *T. obesus* have been given by several authors, most recently by Taniuchi (1975); this, only a diagnosis is presented here. The proportions are based on adult specimens.

DIAGNOSIS

Body slender, the depth about 7 in precaudal length; head short, its length (to upper end of fifth gill opening) about 4 in precaudal length; head depressed, about twice as broad as deep; snout short and broadly rounded, the length in front of mouth an average of 7 in head length; origin of dorsal fin distinctly posterior to hind edge of pectoral fins, the snout to dorsal origin about 2.2 in precaudal length; height of first dorsal fin about 2.2 in head length; height of second dorsal fin about 3.2 in head length; base of second dorsal fin about three-fourths base of first dorsal fin; pectoral fins of moderate length, the anterior margin about 5.4 in precaudal length; lower caudal lobe prominent, about half as long as upper; no median ridge on back between dorsal fins; eye not large, the horizontal diameter of orbit about 3 in internarial space; nictitating membrane present; nasal flaps large; spiracle minute or absent; total number of upper teeth in outer row of upper jaw 43 to 50 (including two or three small symphyseal teeth); total number of teeth in outer row of lower jaw 43 to 46 (including two or three small symphyseal teeth); teeth in at least two functional rows in jaws; teeth erect medially in jaws, slanting progressively more lateroposteriorly toward rear of jaws; teeth with a small cusp on each side of base of tall slender central cusp, two on each side of lower teeth and two on anteromedial side of upper teeth in about rear half of jaws (except last few small obtuse teeth); skin smooth, the denticles close-set, often slightly overlapping, usually with seven horizontal ridges; precaudal vertebrae 128 to 135; caudal vertebrae 79 to 85 (17 specimens, including one reported by V. Springer and Garrick 1964 and one by Bass, D'Aubrey, and Kistnasamy 1975); color brownish gray, shading to whitish with a yellowish cast ventrally, usually with a few scattered round-

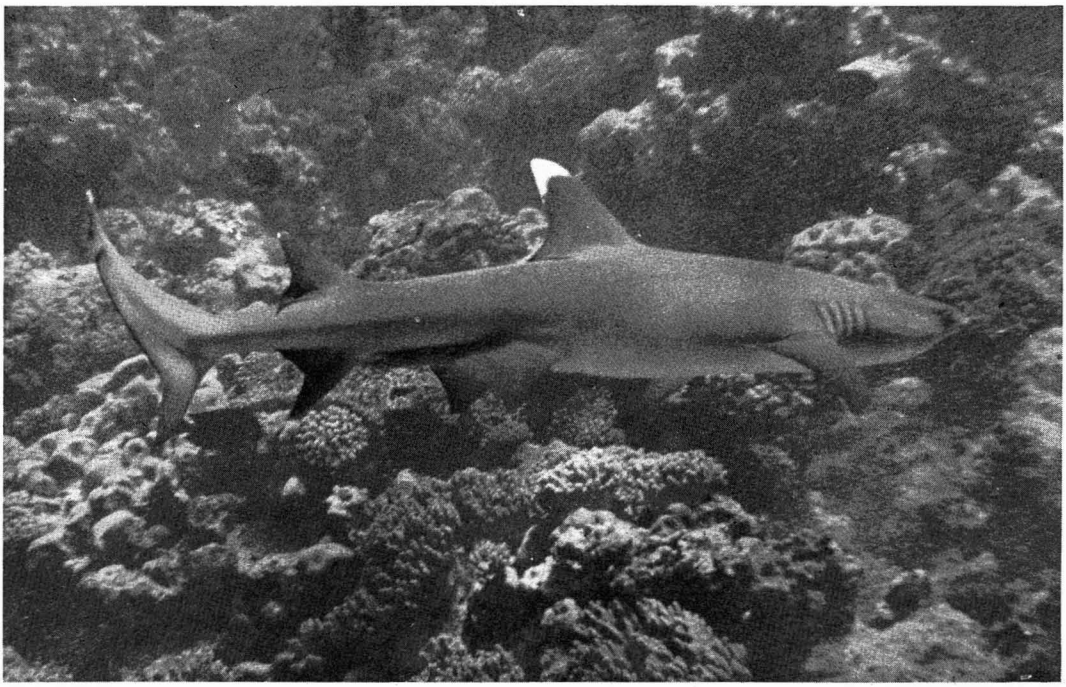

FIGURE 3. *Triaenodon obesus* at Cocos-Keeling Islands. (Photograph by Patrick L. Colin.)

ish dark gray spots (more on ventral half of body than dorsal half); tips of first dorsal and upper caudal lobe white; second dorsal fin and lower caudal lobe often white-tipped; a small whitish blotch may be present near apex on lower side of pectoral fins.

DISTRIBUTION

Triaenodon obesus is very broadly distributed in the Indo-Pacific region from East Africa to eastern Oceania and is also recorded from Cocos Island, Galapagos Islands, and Panama in the eastern Pacific (Snodgrass and Heller 1905; Herre 1936; Kato, Springer, and Wagner 1967). On the east African coast it ranges from the Gulf of Aqaba at the northern end of the Red Sea (Barnes 1973) to northern Natal, South Africa (Bass, D'Aubrey, and Kistnasamy 1975). Elsewhere in the Indian Ocean it is known from India (Bleeker 1853, Day 1878), Seychelles (Playfair 1867, Smith and Smith 1963); Mauritius (Bleeker 1879; Bass, D'Aubrey, and Kistnasamy 1975), Madagascar (Sauvage 1891, Fourmanoir 1961); Mozambique (Smith 1952*a*, *b*), Chagos Archipelago (Wheeler 1953, 1960), Comoro Islands (as *T. apicalis*) (Fourmanoir 1954), Aldabra (Smith 1955), Ceylon (Munro 1955), Tanzania (Wheeler 1959), and Tromelin Island (Bass, D'Aubrey, and Kistnasamy 1975, after Batchelor, personal communication).

Victor G. Springer and associates obtained a specimen of *T. obesus* at Albatross Island, St. Brandon's shoals, during the Smithsonian Institution expedition there in 1976.

William F. Smith-Vaniz (personal communication) noted that *T. obesus* was "rather common" at Cocos-Keeling Islands in the eastern Indian Ocean during an expedition to these islands in 1974. Though no specimens were collected, an underwater photograph by Patrick L. Colin (Figure 3) provides positive identification.

Gerald R. Allen (manuscript) of the Western Australian Museum will report *T. obesus* from Kendrew Island, Dampier Archipelago,

Western Australia (20°20.5′ S; 116°32′ E), based on a sight record of Barry Hutchins of the same institution.

Meyer (1885), Weber (1913), and Munro (1967) have recorded the species from Indonesia and New Guinea. Western and Central Pacific localities include the New Hebrides (Günther 1870), Philippines (Gorgoza 1895, Elera 1895—references from Fowler 1941, Herre 1953), Tahiti (Günther 1910, Bagnis et al. 1972, Randall 1973*b*), Wake Island (Fowler and Ball 1925), Leeward Hawaiian Islands (Fowler and Ball 1925; Pietschmann 1938, Kenyon and Rice 1959), Solomon Islands (Herre 1931), Northern Queensland and Northern Territory, Australia (as *T. apicalis*) (Whitley 1939, 1954), Bonin Islands (Fowler 1941), Phoenix Islands (Schultz 1943), Gilbert Islands (Banner and Randall 1952, Randall 1955), Tuamotu Archipelago (Harry 1953), Marshall Islands (Strasburg, unpublished mimeographed report for the U.S. Office of Naval Research; Schultz and collaborators 1958; Hobson 1963), Taiwan (Teng 1962—reference from Taniuchi 1975), Line Islands (Hobson 1963; Tester and Nelson in Gilbert, Mathewson, and Rall 1967), Johnston Island (Banner and Helfrich 1964; Brock, Jones, and Helfrich 1965), Swain Reef, southern Great Barrier Reef (22° S) (Whitley 1964; head of 110-cm specimen in Australian Museum), Guam (Kami, Ikehara, and DeLeon 1968), Palau Islands (Helfman and Randall 1973), Pitcairn Group (Randall 1973*a*), Takara-jima and Ryukyu Islands, Japan (Taniuchi 1975; Masuda, Araga, and Yoshino 1975).

Taniuchi (1975) stated that he believed that his record of *T. obesus* from Takara-jima (29°9′ N; 129°13′ E) is the northernmost in the world. However, this shark occurs at the northern end of the Gulf of Aqaba in the Red Sea (hence about 29°30′ N); possibly it ranges even farther north in the Gulf of Suez.

The author has collected *T. obesus* at the following localities: Johnston Island; Nuku Hiva, Marquesas Islands; Takaroa and Rangiroa, Tuamotu Archipelago; Tahiti, Moorea, and Tetiaroa, Society Islands; Oeno, Pitcairn Group; Enewetak, Marshall Islands; Ulithi, Caroline Islands; Guadalcanal, Solomon Islands; and Sanganeb Atoll, Red Sea (off coast of Sudan). He has observed but did not collect it at Fanning, Line Islands; Mangareva and Temoe in the Gambier Group, Tuamotu Archipelago; Ducie and Pitcairn, Pitcairn Group; Tubuai, Austral Islands; Ua Pou and Fatu Hiva, Marquesas Islands; Kwajalein, Marshall Islands; Marcus Island (Minami Tori Shima); and Villingili, Maldive Islands. Through the courtesy of William L. Chan and Johnny P. F. Chin he was permitted to see fishes in a large tank at Ocean Park, Hong Kong, before this oceanarium formally opened. Among the residents of this tank was a locally caught subadult *T. obesus*.

The whitetip reef shark has not been reported from Easter Island, and none were observed there by the author during a month of fish collecting and diving in early 1969. Also, none were noted at Rapa, the southernmost island in French Polynesia (27°35′ S), during fieldwork there from 26 January to 17 February 1971.

Bruce A. Carlson of the University of Hawaii (personal communication) has observed the species in the Fiji Islands; he also informed the author that the reference collection of the University of the South Pacific at Suva had two specimens from Viti Levu which had to be discarded due to poor preservation.

Richard C. Wass of the Office of Marine Resources, Government of American Samoa (personal communication), reported that *T. obesus* is common in Samoan waters. He has a specimen from Tutuila in the Marine Resources reference fish collection.

The whitetip reef shark is rare in the principal Hawaiian Islands (Kauai to Hawaii); it is more often sighted off the island of Hawaii than Oahu. None were among the 1727 sharks caught by Tester and associates in the principal Hawaiian Islands in 1967–1969 (Tester, unpublished mimeographed report for the University of Hawaii). The species is common, however, in the Leeward Hawaiian Islands. Fowler and Ball (1925) noted its abundance at Laysan, Lisiansky (and Wake); they stated that many were

always seen in pools and channels of the shore reef. Pietschmann (1938) wrote, "This species seems to be very common in the waters around Pearl and Hermes Reef; at times we could count more than a dozen round our boat." It is evidently common at Midway in view of the observation of Kenyon and Rice (1959); they saw a Hawaiian monk seal (*Monachus schauinslandi*) swimming in the immediate vicinity of a group of 8 or 10 *Triaenodon obesus* at Welles Harbor, adding that the seal showed not the slightest alarm or concern.

HABITAT

As has been noted by several authors such as Klausewitz (1959), *T. obesus* is found within or very near coral reefs. After citing its abundance on the shore reef at Laysan and Lisiansky, Fowler and Ball (1925) wrote, "Not met with at Gardner or Nihoa which lack reef."

This shark is closely associated with the bottom, rarely swimming far above it, and is often seen at rest in caves within the reef (see MOVEMENTS). Its slender supple body enables it to maneuver through narrow crevices and holes in reefs (see FOOD HABITS). Although it may occur at depths of a meter or less, it does not penetrate the very shallow reef and sand flats as readily as does the blacktip reef shark. Fourmanoir (1961), who commented that this shark is encountered only in very clear water, wrote that the usual fishing depths are 8 to 40 m in Madagascar, but sometimes it is caught in as much as 110 m. Taniuchi (1975) listed a specimen from Yomitan, Ryukyu Islands, which was taken with bottom longline gear at a depth of 330 m. He added a question mark to this depth record, however. When asked the reason for the question mark, he replied that there was no doubt about the bottom longline gear being at this depth, as it was confirmed by echo sounder. He simply regarded this depth as "incredible" for the species and suggested that the shark may have been caught when the line was being hauled to the boat. The author believes this is less likely than the capture at 330 m because of the close orientation of *T. obesus* to the bottom and because it is slow to take a bait.

Strasburg (unpublished report), Smith and Smith (1963), Garrick and Schultz in Gilbert (1963), Hobson (1963), and Tinker and DeLuca (1973) have attributed a length of 7 feet (213 cm) or more to *Triaenodon obesus*. Strasburg's and Hobson's remarks on length were based on underwater observations in the Marshall Islands. Hobson stated, "The whitetip was common to a length of 6 ft., with individuals of 7 ft. seen on occasions." The other works mentioned above are compilations, and it is doubtful that these authors measured any individuals of this shark at 7 feet.

Actual measurements of whitetip reef sharks fail to reveal any approaching 213 cm in total length. Fourmanoir (1961) recorded the maximum length of this species from his examination of the catches of fishermen at Madagascar as 165 cm. Bagnis et al. (1972) stated that it rarely exceeds 150 cm. Fowler and Ball (1925) recorded two from Laysan 103.5 and 148.8 cm long and stated, "In the hundred or more specimens seen the size was remarkably uniform. The variation was not more than 20 cm." The largest of 188 specimens measured by the author and associates was 154.7 cm total length. It was a male from Oeno which weighed 27.7 kg. Length-weight data of another 43 specimens taken at Johnston Island in 1964–1965 by personnel of the poisonous fish project of the University of Hawaii, directed by A. H. Banner, included four larger than this; the largest was a male 168 cm in total length which weighed 23.6 kg. The lengths of these 43 specimens may have been taken with a tape laid over the curvature of the sharks and with the caudal fin stretched down to the midlateral position, thus giving greater total length measurements than those made by the author.

For the present study total length was taken as the straight-line measurement from the tip of the snout to a vertical at the posterior end of the upper lobe of the caudal fin in the normal position (i.e., not with the lobe pulled down to the midlateral line).

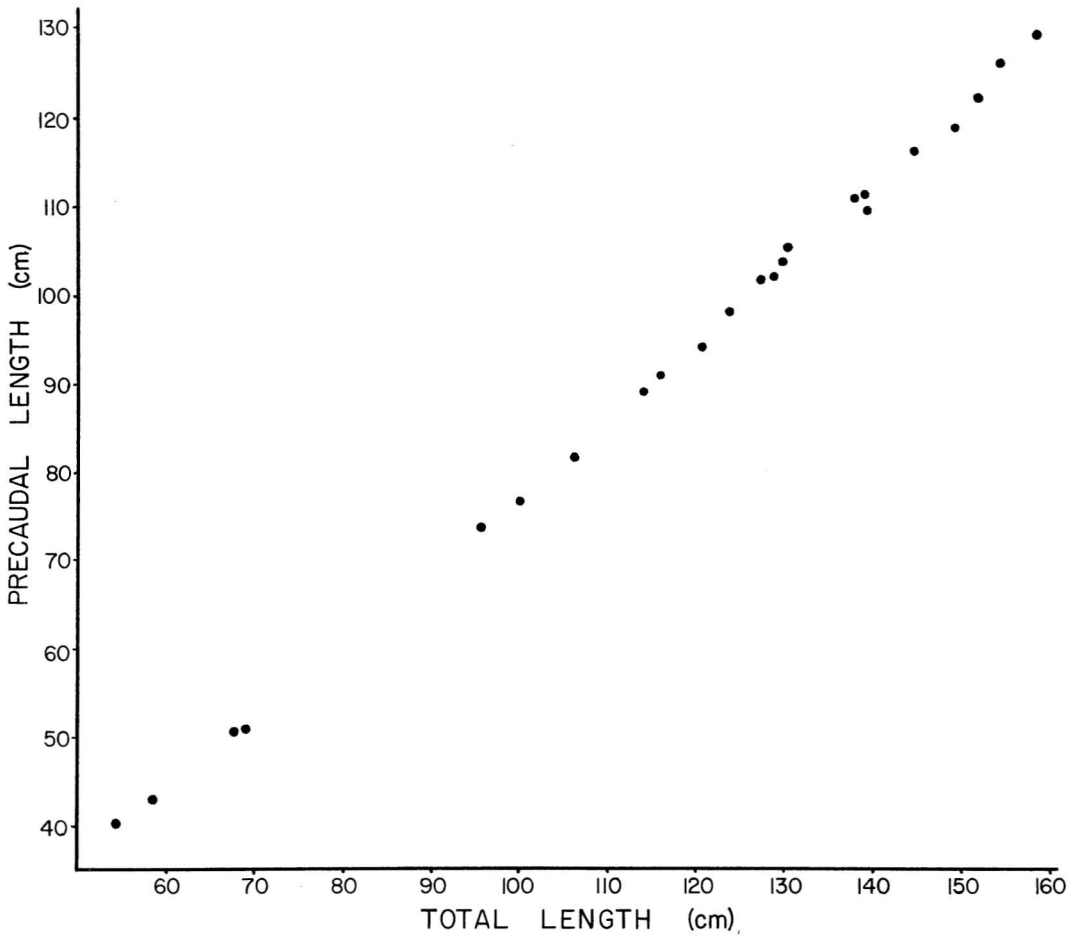

FIGURE 4. Relationship of total length and precaudal length of *Triaenodon obesus*.

The precaudal length (from tip of snout to the pit at the origin of the upper lobe of the caudal fin) is a more precise measurement. This length was used for the tagging study at Johnston Island. Figure 4 provides for the conversion of precaudal length to total length and vice versa. As may be noted, the caudal fin is relatively longer in smaller individuals. On newborn whitetips it is about 27 percent of the total length, whereas in large adults it represents about 20 percent of the total length.

Figure 5 depicts the total length-weight relationship of *Triaenodon obesus*. The weight of embryos within females was subtracted from the mothers' weights before plotting. No difference was noted in the weights of males and females after adjustment had been made for the embryos' weight, so the two sexes were combined for the figure.

GROWTH

During the period of July 1968 to August 1971, the author and associates tagged a total of 124 *Triaenodon obesus* in the lagoon at Johnston Island (16°45′ N; 169°30′ W) (Figure 6). These sharks were taken in fish traps made of steel frames covered with chicken wire which were designed to capture large moray eels (*Gymnothorax javanicus*).

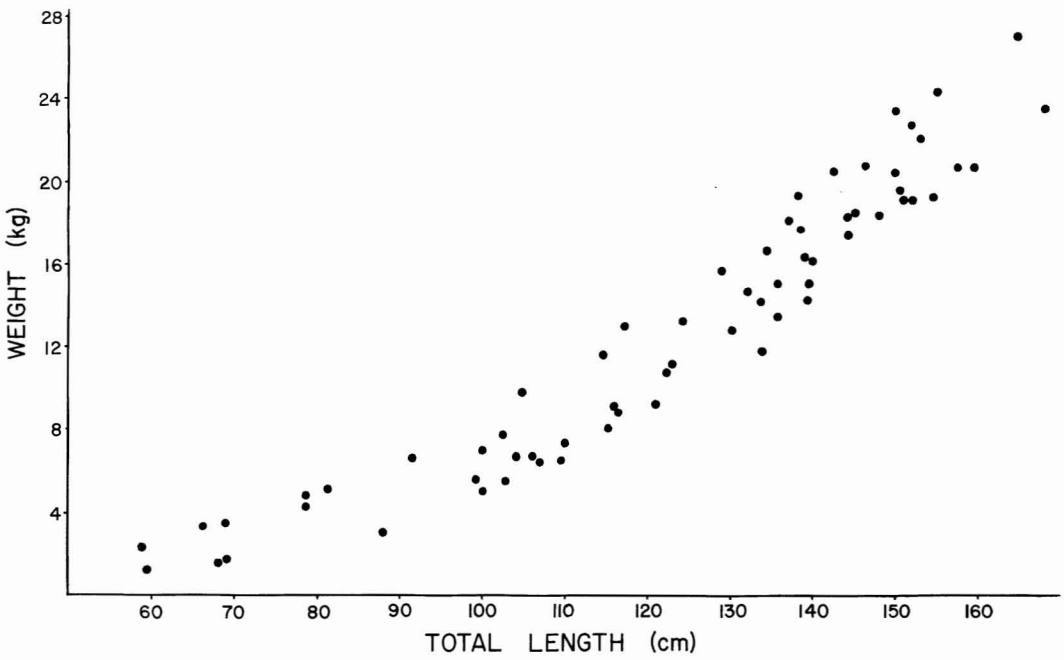

FIGURE 5. Length-weight relationship of *Triaenodon obesus*.

The sharks ranged in precaudal length from 49.6 to 127 cm. The first 16 were tagged in July and August of 1968 (in the back) with dart tags having bright yellow vinyl plastic streamers. One tagged shark of 80 cm precaudal length recovered in April 1969 had only a slight stub of yellow sticking above the skin. Since the streamer bearing the number was missing, the shark was tagged again, this time with a Monel cattle-ear tag clamped to the first dorsal fin. Monel tags were supplied by the American Institute of Biological Sciences through Stewart Springer. They were used for all subsequent whitetip tagging.

A total of seven recoveries were made of *T. obesus* with cattle-ear tags affixed to the first dorsal fin. The first was of the shark that had lost the streamer of its dart tag. It was caught only 16 days after being tagged. Its measurement, which was made after it was frozen, was .5 cm shorter than when it was tagged (probably due to shrinkage from freezing). Data on a second shark, taken 3 months after being tagged, are obviously in error; the precaudal length at recovery was given as 30 inches (76.3 cm), which was 10 cm shorter than the length at tagging; also the locality of recapture was omitted. A third recovery was also made 16 days after release. This shark was released without being remeasured. It was caught a second time more than 10 months later. The data on this recovery and those of two other sharks (one of these was also recovered twice) are presented in Table 1. The extremes in bimonthly averages of sea surface temperatures at Johnston Island are 24.3° and 27.9° C (Brock, Jones, and Helfrich 1965, after Barkley).

The smaller rate of growth of the female shark with tag number 15634 as compared with that of the male with number 15508 might be explained, at least in part, in terms of the larger size of the female. But the even smaller growth rate of the 85.1-cm female with tag number 15502 is clearly at odds with the remaining recovery data. It is not known if there is this much individual variation in growth within the same lagoon or if there was an error in measurement of this shark, or a combination of the two factors.

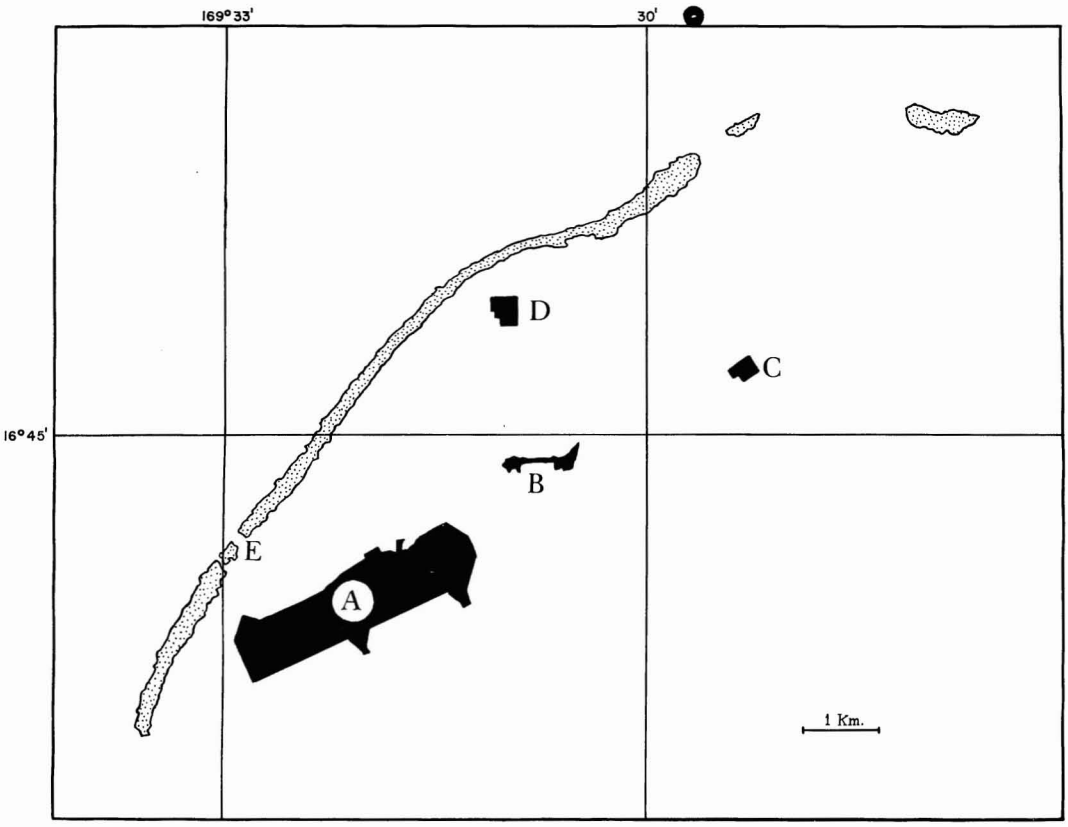

FIGURE 6. Johnston Island. Land masses shown in black: *A*, Johnston Island; *B*, Sand Island; *C*, East Island; *D*, North Island; *E*, small boat passage. Outer reef shown as stippled.

TABLE 1

GROWTH OF TAGGED *Triaenodon obesus* AT JOHNSTON ISLAND

TAG NUMBER	SEX	DATE OF TAGGING	PRECAUDAL LENGTH WHEN TAGGED	DATE OF RECOVERY	PRECAUDAL LENGTH WHEN RECOVERED	GROWTH RATE
15502	Female	27 Jul 1969	85.1 cm	23 Jun 1970	87.0 cm	2.1 cm/year
15508	Male	15 Aug 1969	81.3 cm	10 Jul 1970	85.1 cm	4.2 cm/year
15508	Male	10 Jul 1970	85.1 cm	2 Aug 1971	88.8 cm	4.2 cm/year
15634	Female	10 Jul 1970	105.4 cm	9 Jan 1972	109.2 cm	2.5 cm/year

The longest period of tag retention was nearly 2 years. No recoveries were reported after January 1972. For two of the recoveries, a "festering wound" was noted at the tagging site in the dorsal fin. It is believed that the failure to obtain any recoveries after early 1972 was due to loss of tags.

In July 1972 the author visited the Heinz Steinitz Marine Biology Laboratory of the Hebrew University at Elat, Gulf of Aqaba, Red Sea. Here he saw two *T. obesus*, one a male and the other a female, in a concrete tank measuring 3 by 3 m by 1 m deep. The sharks had been measured by David Fridman when they were introduced to the tank in October 1969. The male then had a precaudal length of 73 cm and the female 88 cm. In October 1972, hence 3 years later,

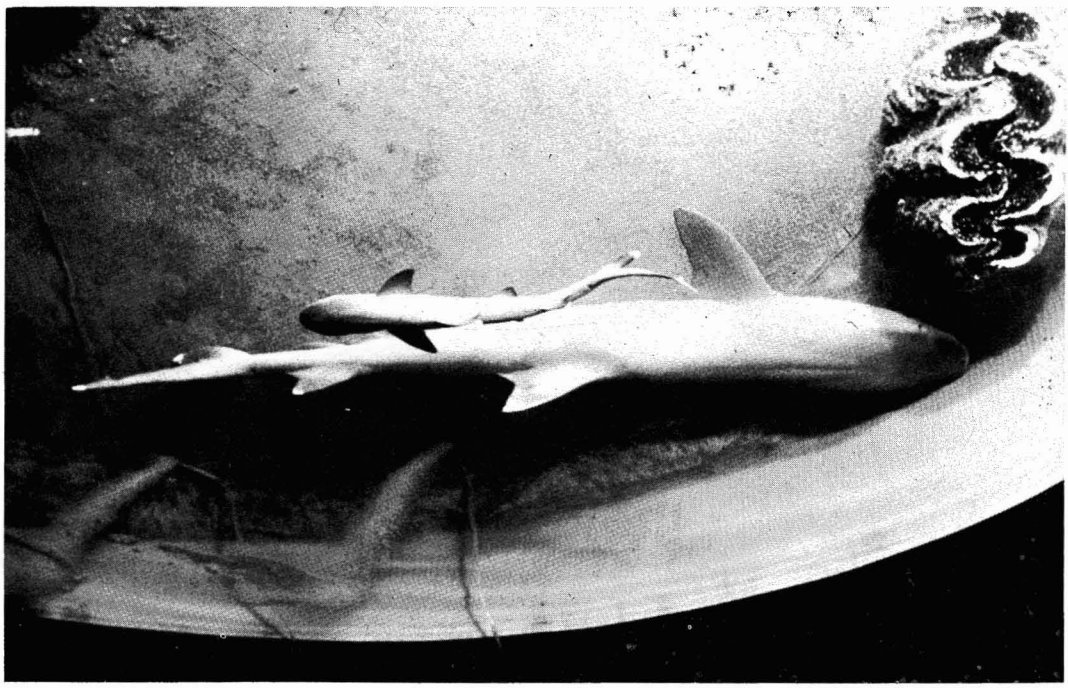

FIGURE 7. Female *Triaenodon obesus* (113 cm precaudal length) and newborn young (43.2 cm precaudal length) in a tank at Enewetak, Marshall Islands. A giant clam (*Tridacna squamosa*) is casting a shadow on the head of the mother shark. (Photograph by Paul M. Allen.)

the sharks were remeasured by Mr. Fridman. The male had grown 12 cm in precaudal length and the female 7 cm. Mr. Fridman stated that the sharks were fed every 2 or 3 days on three to four fishes that measured 10 to 20 cm in length. Water temperatures ranged from 25° to 27° C during the summer months and 21.5° to 23° C during the winter months.

The rate of growth of these two captive sharks was 4 cm per year for the male and 2.3 cm per year for the female. The slower rate of growth of the female might again be explained by its larger size; however, in both this case and that of the sharks of Table 1, the difference in growth rate would seem to be greater than can be explained by differential size alone. Possibly the males have a more rapid growth rate, though there is no reason to expect this. Wass (1973), for example, reported a slightly higher growth rate for captive female sandbar sharks (*Carcharhinus milberti*) than for males.

An exceptional opportunity to obtain data on the early growth of *T. obesus* came on 17 July 1971 when a captive whitetip 113 cm precaudal length at the Enewetak Marine Biological Laboratory (now Mid-Pacific Marine Laboratory) at Enewetak Atoll, Marshall Islands, gave birth to three young (about 2000 hours, birth not witnessed). This shark had been caught in a trap and held in the circular laboratory tank (about 4 m in diameter) for 2 weeks before giving birth. Only one of the three baby sharks survived (the other two were found dead outside the tank soon after birth, their death being a result either of their leaping out or of their having been removed by unauthorized visitors). Figure 7 shows the mother shark and the single surviving young. Paul M. Allen measured this juvenile, a female, the day after its birth at 43.2 cm precaudal length. It was fed daily on fish (it would take food from the hand). By 31 August 1971 it had grown to 45.2 cm. At this time an attempt

was made to transport it alive to Hawaii, but it died enroute. Lagoon water temperatures at Enewetak (lagoon water is circulated through laboratory tanks) vary from about 29° to 30° C in August (Stephen V. Smith, personal communication). The growth rate for this juvenile shark was 1.33 cm per month. If such a rate had continued for an entire year, the annual rate would have been 16 cm. In nature small whitetips probably do not feed daily, and certainly they must expend more energy to obtain food than would a captive individual. Therefore, it is likely that the natural growth rate is less than that of this well-fed juvenile.

The author tried to duplicate Mr. Allen's accomplishment 4 years later when a pregnant female whitetip 111.6 cm in precaudal length was caught off the garbage pier at Enewetak. The female could not be maintained alive, but an embryo 41 cm in precaudal length was removed from one ovary (the other had only one ovum) and was placed in a large plastic-lined pool at the laboratory. The "birth" seemed premature, for the little shark's dorsal fins never became firm but flopped to one side or the other as it swam. It showed no interest in food and rested progressively more often upon the bottom until it died 18 hours later.

Although the data on growth given above are too fragmentary to allow me to attempt to construct a growth curve from young to old adult with any assurance, it is clear that the rate for *T. obesus* is very slow even for sharks (which are generally believed to be slow-growing). Wass (1973) reported an average growth for captive sandbar sharks (a species for which he recorded a maximum precaudal length in Hawaii of 146 cm; hence, not much longer than *Triaenodon*) of 31 cm the first year, 21 cm the second, and 16 cm in the third.

If we were to accept 16 cm as a maximum for the first year's rate for *T. obesus* (from the growth rate of the individual born in captivity), and if it decreased at about the same rate in subsequent years as that of the sandbar shark in Hawaii, the 2nd year's growth might be 11 cm, the third 8. Continuing the same progression, the growth the 4th year might be 6 cm, and in the fifth 4.5 cm. At this time, age 5, our hypothetical shark would be 88.5 cm precaudal length; hence, about the same as three of the four entries of Table 1. Further speculation on age becomes even more difficult due to the lack of knowledge of the growth rate of larger individuals. It seems probable, however, with the expected diminution in rate as a whitetip approaches its maximum size of about 135 cm precaudal length, that it must attain an age of at least 25 years.

MOVEMENTS

It is common knowledge among divers that *Triaenodon obesus* is often found lying at rest on the bottom, often in caves. The sighting of a shark of the same size repeatedly in the same cave naturally leads to the belief that it is the same individual and that the cave may represent a home cave.

One experience at Oeno, Pitcairn Group, serves to point out that more than one whitetip may use the same cave. On 19 December 1970 five *T. obesus* were taken by the author with powerhead and Hawaiian sling spear from a cave in 21 m (Randall 1973*a*). They ranged from 110.5 to 123.8 cm in precaudal length, and all were males. On one dive two were seen together in the cave, but on the other dives only a single shark was present. This was the only cave noted in the vicinity and thus may have been occupied by more sharks than might have been the case if several caves had been available.

To be certain that one is seeing the same individual shark, one should identify it positively by color pattern, some abnormality, or by marking or tagging. Because there is variation in the pattern of dark spots on *T. obesus*, virtually any individual can be identified from a second sighting if the pattern of spots has been committed to memory or if photographs have been taken. The spots are only a little darker than the background color, however, so it is necessary that the shark be seen at rather close range to perceive the pattern.

One opportunity to test the hypothesis

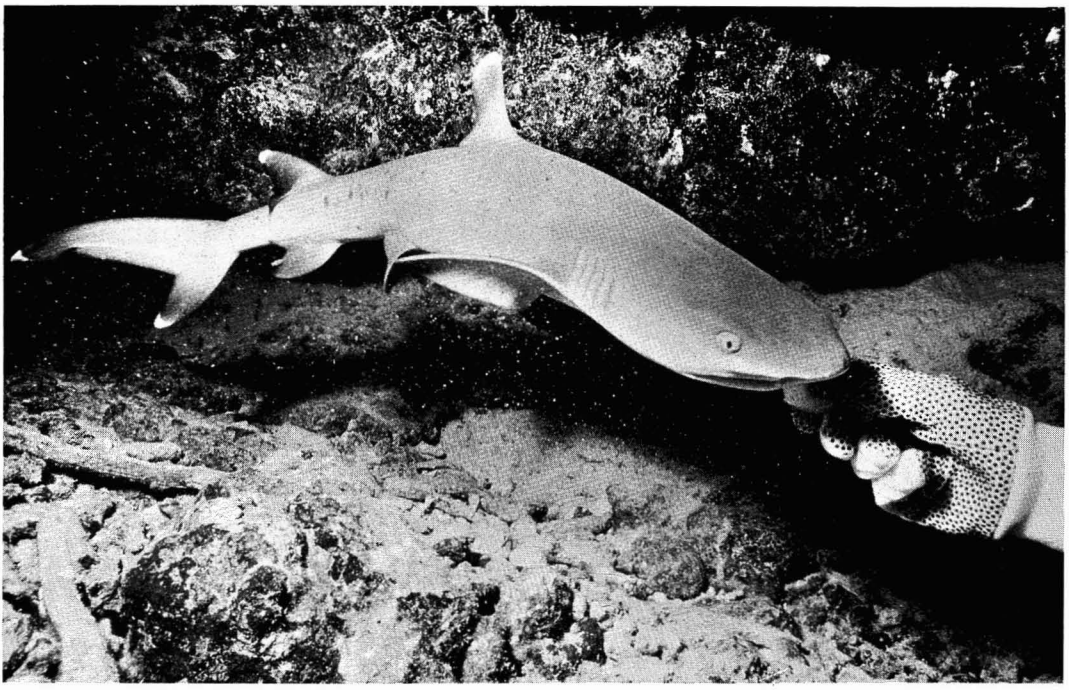

FIGURE 8. Same shark as shown in Figure 2 at same cave taking food from hand of Patricia Bartlett. The pattern of dark spots is different for each individual shark. (Photograph by Nathan A. Bartlett, 18 October 1975.)

that whitetips have a home cave was provided by the observations and photographs of Nathan A. Bartlett and Patricia Bartlett, residents of Kwajalein Atoll, Marshall Islands. On 18 January 1975 the Bartletts observed two whitetips in a cave at a depth of about 5 m on a patch reef in the southern part of the lagoon which is known as K5 from the number of the buoy on the reef. One of the sharks, which they designated as number 1, was small (later they determined the length to be about 58 cm precaudal length by photographing the shark next to a rod marked in inches), the other considerably larger. On 16 February and 1 March they saw what seemed to be the same two sharks at the same cave. On 15 March Mr. Bartlett photographed the smaller shark at the cave. Subsequently this shark was seen on 13 April, 27 April, 25 May (at which time it had acquired a fish hook in the corner of its mouth—Figure 2), 14 June, and 18 July. On the last date the author accompanied the Bartletts to the cave to observe the sharks. An attempt was made to feed the smaller of the two sharks by hand with pieces of fillet of sole (the larger shark was more retiring and remained deep in a recess in the cave). As on previous attempts, this was not successful, though the shark did approach the food in the hand closely. Other fishes such as groupers, however, readily snatched the fillets from the hand, or, in the case of the damselfish *Dascyllus trimaculatus* and other small fishes, nibbled at them. On 2 August the Bartletts succeeded in feeding the number 1 shark directly, and on 9 August and subsequent dates it was photographed taking food from the hand (Figure 8). Other Kwajalein divers soon joined in the feeding, and this seems to have been responsible for an increase in the whitetip population at the cave. By 28 September as many as six sharks (all small except the one larger one that was mentioned above which never took the offering of food) could be seen at one time at the cave. On 21 September the original small shark, which by then had lost the hook

FIGURE 9. The author feeding a juvenile *Triaenodon obesus*. (Photograph by Nathan A. Bartlett.)

in its mouth, was suddenly wary and would not approach the divers. It was noted that it had what appeared to be a knife wound in the side, probably inflicted by a diver unaware that the little shark was approaching him only for a handout of fillet of sole. On 8 April 1976 the author revisited the cave with Mr. Bartlett. At this time there were four small whitetips which freely took food by hand (Figure 9). Between periods of feeding, the four small sharks came to rest on the bottom of the cave. On one occasion one of the sharks lay down across the tail of another, which exhibited no response to the contact. The number 1 shark was not observed at this time, but it definitely was seen on other dives at the cave during the spring. With the advent of feeding one can no longer regard the shark's presence at the cave as a natural occurrence, but it is clear that the cave was its principal daytime locality for the several months prior to its being fed by humans.

As indicated in Table 2, which summarizes the tag recovery data for whitetip reef sharks at Johnston Island (Figure 6), two of the six recoveries were made from the same area as release, one after a period of 16 days, the other after 329 days. The other movements ranged from 300 m to 2.9 km. A movement of 2.9 km is not extensive for a shark and may be within its normal daily range in search of prey.

Donald R. Nelson and Richard H. John-

TABLE 2

MOVEMENTS OF TAGGED *Triaenodon obesus* AT JOHNSTON ISLAND

TAG NUMBER	TAGGING LOCATION	TAGGING PERIOD (DAYS)	MOVEMENT
15361	Small boat channel	16	0.3 km NE
15502	SW edge of North Island	16	None
15502	SW edge of North Island	331	0.6 km E
15508	E of North Island near outer reef	329	None
15508	E of North Island near outer reef	388	2.7 km SW
15634	N of East Island	153	2.9 km E

son (personal communication) have tagged numerous *T. obesus* at Rangiroa, Tuamotu Archipelago, with plastic color-coded dart tags and some with ultrasonic telemetric devices (Nelson 1974) introduced into the stomach with food. They have shown that this species of shark exhibits a strong tendency to possess home caves and to stay within a home area which may be several km^2. They will be reporting their results in detail.

Although there are no data suggesting long migrations by this species, it is clear from its broad distribution that these must occur at least on rare occasions. In view of this shark's apparent close association with coral reefs, it is surprising that this species should have been one that crossed the broad expanse of the Eastern Pacific Barrier. Briggs (1961) listed it among the five sharks that he considered to be shore fishes that occur on both sides of this barrier. If, however, he regards *Galeocerdo cuvier* and *Sphyraena zygaena* as shore fishes, then he should add *Carcharhinus albimarginatus*, *C. altimus*, *C. galapagensis* (Hawaiian records of *altimus* and *galapagensis* by Tester, unpublished report), *C. leucas* (Tuamotu record by Richard H. Johnson, personal communication), *C. limbatus*, and *Odontaspis ferox* (Hawaiian record by Clarke 1972) to his list, thus raising the total to 11. Nine of these 11 are also found in the Atlantic (the Indo-Pacific *Echinorhinus cookei* is now considered as only a variant of the Atlantic *E. brucus*, and the one eastern Pacific record is clearly the *brucus* form—see Bigelow and Schroeder 1948: 527); thus, these sharks may have reached the eastern Pacific when the isthmus of Panama was inundated during the late Pliocene or early Pleistocene.

FOOD HABITS

Triaenodon obesus is well adapted for feeding on reef animals. It moves freely through the interstices of reefs, venturing into cracks and holes that seem too small for a shark of its size to enter. In the lagoon of Onotoa, Gilbert Islands, one was twice observed to wedge its head vertically up to the level of its gill slits into a tight hole in which a speared fish had taken refuge (Banner and Randall 1952). It is able to force itself through the aperture of fish traps so small that there is barely room for its body curled within. Hobson (1963) wrote, "This species was noted as being clumsy and ineffective in attempts at taking baits which were suspended in midwater. However, this same shark was remarkably effective in tracking down and capturing prey which had taken shelter deep in one of the many holes and crevices typical of a coral reef, thus making available to it prey which are beyond the reach of both grays and blacktips."

Gohar and Mazhar (1964*a*) reported partly digested fish in the stomachs of six of eight *T. obesus* collected in the vicinity of al-Ghardaqa, northwestern Red Sea (27° N). One of the sharks of 105 cm length contained an 80-cm eel.

Surprisingly, Fourmanoir (1961) stated that *T. obesus* at Madagascar feeds on crustaceans, mentioning specifically spiny lobsters

and xanthid crabs. One shark of 1 m had in its stomach an intact xanthid of the species *Carpilius convexus*.

The author has opened the stomachs of a total of 56 whitetips ranging from 504 to 1244 mm precaudal length and taken at depths of 1 to 30 m at Enewetak, Marshall Islands (23 individuals), French Polynesia (13), Johnston Island (8), Pitcairn Group (6), Red Sea (3), Caroline Islands (1), and Solomon Islands (1). Thirty-one of these were collected with a powerhead (explosive device on the end of a shaft), 15 by hook and line, and 10 by spearing. Thirty-three (59%) of the stomachs were completely empty; 16 contained the remains of fishes, half of which could not be identified even to major group; four contained octopuses (three of these only as a beak, an indigestible item which is probably regurgitated eventually); two had both fish and octopus remains, and the last had unidentified animal tissue that appeared to be mollusk in origin. There were no crustacean remains.

The fishes identified from whitetip stomachs were: an eel of unknown family (the head was regurgitated by a large whitetip which had been speared as it was being carried to the boat), *Gymnothorax* sp., *Myripristis* sp., *Lutjanus kasmira*, *Abudefduf sordidus*, *Scarus* sp., *Scarus sordidus*, two acanthurids (either *Acanthurus* or *Ctenochaetus*), and a balistid.

The more complete digestion of the stomach material later in the day, generally, would seem to indicate that feeding takes place more at night than during daylight hours. The specimen of the parrotfish *Scarus sordidus*, for example, was taken from the stomach of a whitetip shark 51.2 cm precaudal length (still with umbilical scar) at Tetiaroa, Society Islands, at 1030 hours. The degree of digestion and the vulnerability of scarid fishes at night indicate that this fish was probably captured at night. It measured 180 mm in standard length, which is relatively large prey for so small a shark. It had entered the stomach head first. Digestion of the head and anterior part of the body had progressed to the point where the color pattern was no longer evident, but the posterior part of the fish, which was partly out of the stomach, was readily identifiable from the characteristic bright colors as the terminal male of *S. sordidus*. Parrotfishes enter into a state of torpor resembling sleep at night. A diver can actually pick one up in his hands if no strong tactile stimulation is applied to the fish. If handled at all roughly, however, these fishes exhibit an unconscious escape response of very rapid swimming (propulsion by caudal fin, not pectorals). If a shark contacts a sleeping scarid from the front with mouth agape, the fish's escape response could result only in its driving itself into the shark's stomach.

Some feeding by day evidently occurs. William D. Madden of the Oceanic Institute in Hawaii (personal communication) observed a whitetip about 1 m in total length chase and capture a goatfish (*Parupeneus chrysery-dros*) during daylight hours in the reef tank (diameter at bottom, 12.2 m) of Sea Life Park on Oahu.

Russell E. Miller, a diver at Enewetak, Marshall Islands (personal communication), observed a pair of *T. obesus* at Enewetak during the day which were swimming side by side. One frightened a parrotfish in the direction of the other, which captured it. It is not known if this was a chance occurrence or if such cooperative hunting normally takes place. Certainly it cannot be a common event, for one does not often encounter *T. obesus* swimming in pairs.

Gohar and Mazhar (1964*b*) reported a pregnant female whitetip that survived in captivity for 6 weeks without feeding (see REPRODUCTION).

PREDATORS

Richard C. Wass (personal communication) found a whitetip reef shark about 80 cm in total length in the stomach of a grouper (*Epinephelus lanceolatus*) speared off the northeastern corner of Kusaie, Caroline Islands at a depth of 12 m in July 1973. Also present in the grouper's stomach was a spiny lobster (*Panulirus*) of about .7 kg.

Certain species of sharks are probably

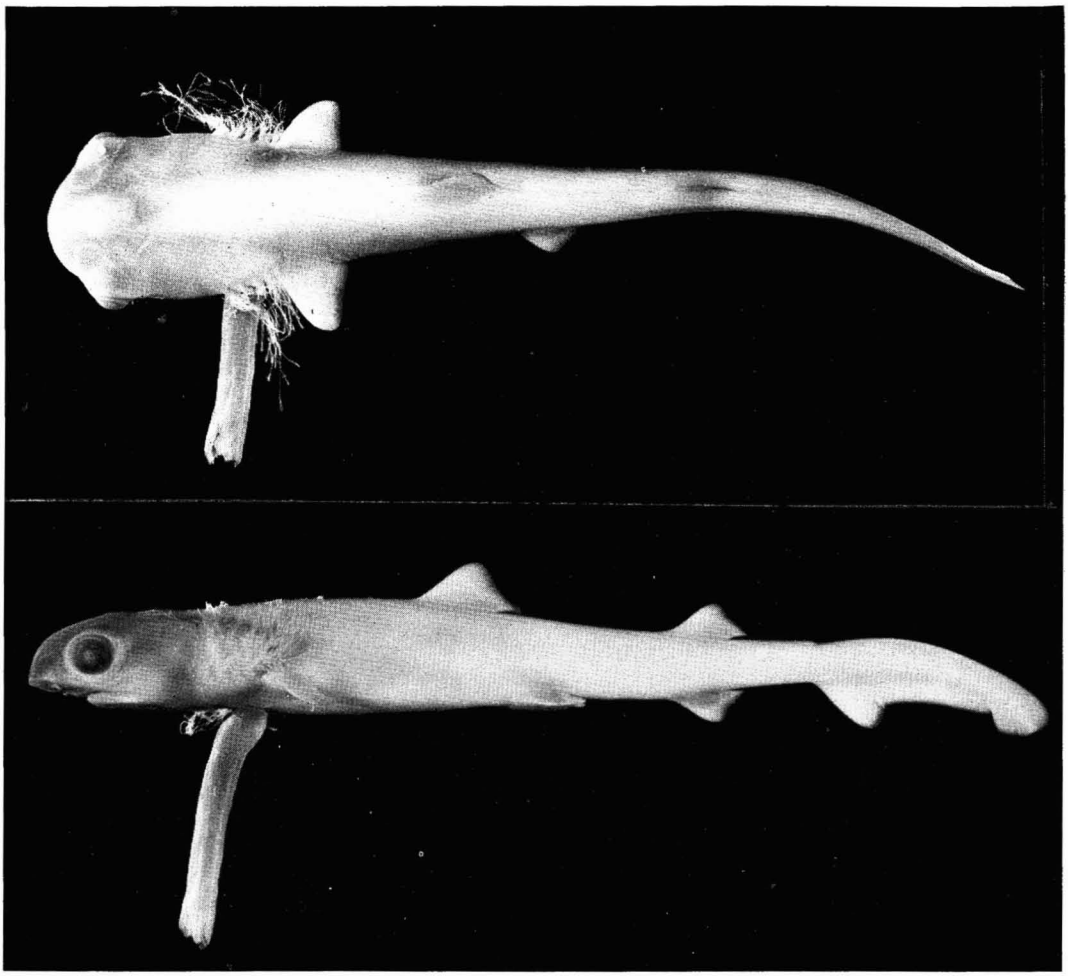

FIGURE 10. Top and side views of an embryo of *Triaenodon obesus* 9.6 cm precaudal length removed from a mother shark of 113 cm precaudal length taken at Sanganeb Atoll off Port Sudan, Red Sea, 8 October 1975.

more important as predators of *T. obesus* than is *Epinephelus lanceolatus* because this giant grouper is relatively rare. As reported by Tester (unpublished report) and other authors, sharks form a significant part of the diet of the tiger shark (*Galeocerdo cuvier*). Though no *T. obesus* have yet been identified from tiger shark stomachs, they probably are eaten by this voracious predator. The author has used adult *T. obesus* as bait to catch *G. cuvier*. Another shark which feeds heavily on elasmobranchs is *Carcharhinus galapagensis* (Tester, unpublished report). Recently the author found a juvenile gray reef shark (*C. amblyrhynchos*) in the stomach of a silvertip (*C. albimarginatus*) at Enewetak Atoll. Because it tends to occur in deeper water generally than *T. obesus*, *C. albimarginatus* would not encounter whitetip reef sharks with the frequency of gray reef sharks; nevertheless, it may be at least an occasional predator of *T. obesus*.

REPRODUCTION

The 56 *T. obesus* mentioned in FOOD HABITS that had been taken by powerhead,

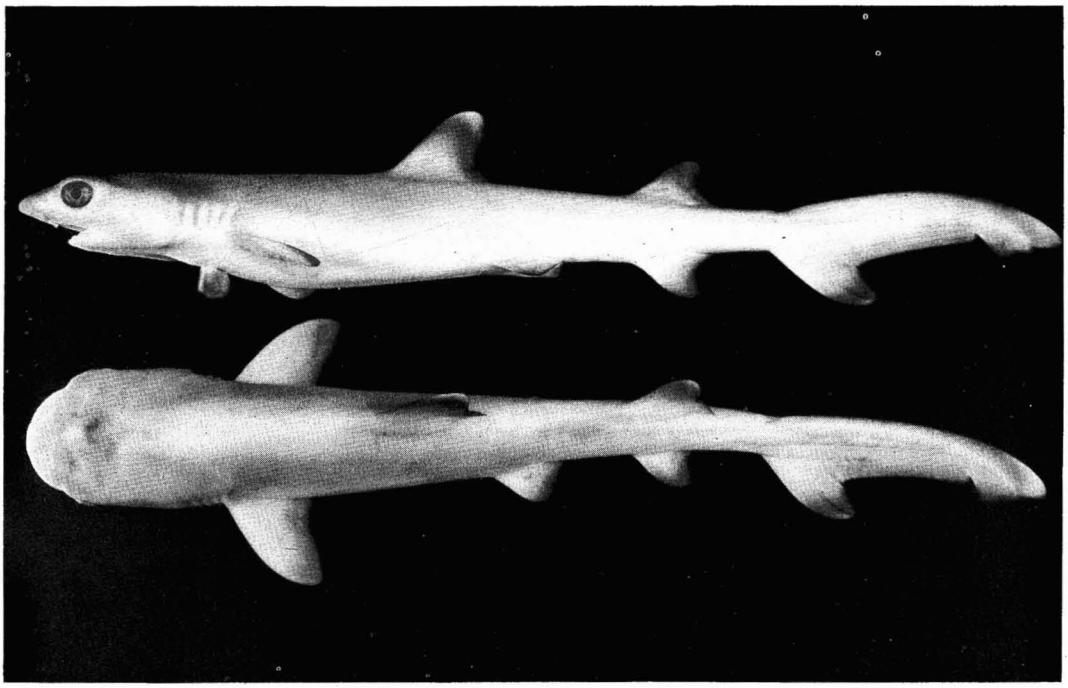

FIGURE 11. Two embryos of *Triaenodon obesus* 18.8 and 18.9 cm precaudal length removed from a mother shark of 109 cm precaudal length taken at Enewetak, Marshall Islands, 31 March 1972.

hook and line, and spear consisted of 25 males and 31 females. The sex was determined for 27 of the embryos removed from the pregnant females; 12 of these were males and 15 were females.

Of the 124 sharks tagged at Johnston Island following their capture in traps, the sex was determined for 107. Surprisingly, 65 of these were males and 42 were females. Perhaps there is a greater tendency for males to enter traps than females.

Fourmanoir (1961) reported that sexual maturity in *T. obesus* is attained at a length of 1 m, that there are two or three embryos per litter, and that their length at birth ranges from 52 to 60 cm.

Gohar and Mazhar (1964*a*, *b*) caught a pregnant female whitetip 146.5 cm total length which weighed 20 kg near al-Ghardaqa, Red Sea, on 7 March 1960. It lived without feeding in a vivarium of loose rock walls at the edge of the sea, which measured 22 by 18 m and was about 1.5 to 3 m deep, for 6 weeks. It was killed after researchers noted that it "had remained motionless in one spot for three days." Two male embryos were found in the right uterus which were 56 and 58 cm long and weighed .87 and .805 kg, respectively, and one female embryo was found in the left uterus which was 55 cm long and weighed 1.13 kg. Each embryo was enveloped by a membrane; each was attached to the yolk sac by a 40-cm placental cord. The relative weight of the liver of the mother shark was only 46 g/kg body weight, compared to 80 g/kg from seven other *T. obesus* that were caught and measured. These authors concluded that the reduction in liver weight may have been due in part to the long period without feeding and in part to the demands of the developing embryos.

Of the 31 female *T. obesus* examined by the author and associates, 13 contained embryos (Figures 10, 11), and another three had developing ova; these 16 sharks ranged from 101.2 to 121.8 cm precaudal length. Eleven other females of a length for which maturity might be expected from Four-

manoir's remark on size at maturity contained no young or obvious ova; these ranged from 81.3 to 108 cm precaudal length. Not all males were checked for maturity, but the four smallest that were measured were 82, 89.3, 90.8, and 98.7 cm precaudal length. The largest immature male measured 81.3 cm.

The 13 pregnant females contained from one to five embryos (average number, 2.77). The largest embryo removed from a female *T. obesus* measured 43.8 cm precaudal length (about 600 mm total length); this was a single male pup from a shark 101.2 cm precaudal length. The second largest embryo was 43.2 cm precaudal length, 59 cm total length, and weighed 1.1 kg. It was the only living embryo in a mother shark of 103.9 cm precaudal length. The other uterus, however, contained a mummified (brown, hard, curled) embryo that measured 11.7 cm precaudal length when straightened. Coincidentally, the precaudal length of the young born in captivity was 43.2 cm (see GROWTH).

Insufficient specimens of mature *T. obesus* have been collected throughout the year to allow us to determine the reproductive season, but there is some indication of it from the examination of 12 mature females collected at Enewetak Atoll, Marshall Islands (11°30′ N; 162°15′ E) and four from Johnston Island (16°45′ N; 169°30′ W). At Enewetak from 2 to 13 December three females contained large ova while a fourth of 109 cm precaudal length (not positively mature) had none. At Johnston Island on 9 January a female of 109.1 cm precaudal length contained four embryos averaging 18.6 cm precaudal length. At Enewetak on 31 March two females were taken, each of which had four embryos (one litter from 13.6 to 14.1 cm precaudal length and the other 17.5 to 18.8 cm). At Johnston from 20 to 27 April one female of 117 cm precaudal length had no ova or embryos, but another of 102 cm contained four young 35.5 to 36.1 cm precaudal length. At Enewetak from 2 to 22 July one whitetip of 113 cm gave birth, and two others (101.2 and 103.9 cm) each had one embryo of a size suggesting that birth was imminent; a fourth shark of 111.6 cm precaudal length contained an embryo 41 cm in precaudal length which lived for 18 hours after having been removed from the mother. Two others (108.8 and 111.8 cm precaudal length) contained no young or obvious ova.

HAZARD TO MAN

Garrick and Schultz in Gilbert (1963) regard *Triaenodon obesus* as "a potentially dangerous species if provoked," but they cite no incidents to support this contention.

If the provocation is spearing, however, the author can support this statement. In March 1976 while snorkeling in a shallow channel (about 1 m) at Enewetak, Marshall Islands, the author spotted an adult male *T. obesus* of about 110 cm precaudal length at rest under a ledge. The shark was struck with a Hawaiian sling spear (no line) just behind the head (a head shot was avoided because a colleague, Roland Bauchot, wished to make a brain dissection of the species). Though severely wounded, the shark emerged from the ledge and swam toward the lagoon. After a chase of more than 100 m, the end of the spear was grasped. The shark then turned and moved strongly toward the author with mouth open. Only by holding firmly to the end of the spear (which bent alarmingly as the shark lunged toward him) was the author able to avoid being bitten. The shark then lunged a second time from the other side, once again with mouth agape. At this time a decision was made to release the spear and retreat.

Triaenodon may on occasions approach a swimmer or diver rather closely. Though this may involve a response of the shark to vibratory stimuli, as of those produced by a struggling wounded fish (Randall in Gilbert 1963; Nelson and Johnson 1976) or to olfactory stimuli (Hobson 1963), it also may come close without any such obvious stimulation. In reference to his fieldwork in the southern Marshall Islands, Strasburg (unpublished report) wrote, "*T. obesus* proved to be of a rather different temperament from *Carcharhinus melanopterus*, the other shark commonly seen at Arno. *T. obesus* was much

more curious about swimmers in the water, and was also quite fearless in approaching them. On several occasions specimens measuring seven or eight feet in length came within a few feet of us as we picked up poisoned fish, and on numerous other occasions they followed us as we swam. No attempts were made, on my part at least, to frighten them by splashing, etc., and as a general rule we sought the safety of a boat or shallow reef when these sharks appeared."

Dr. Raymond Bagnis of the Institut de Recherches Médicales in Papeete, Tahiti, has provided the following accounts of aggressive behavior of *T. obesus*. In about August or September of 1975, J. C. Bourdelon, using SCUBA, had speared two or three fishes at Teahupoo, Tahiti, when a whitetip reef shark of large size suddenly came from behind and bit his leg. Fortunately the wound was not extensive, though five stitches were needed to suture it.

Jack Bennett and Francis Nanai, both professional divers with the Institut de Recherches Médicales, have on several occasions in Tahiti and Tetiaroa had flippers or spearguns bitten by whitetip reef sharks after fishes had been speared. The most frightening episode occurred in Tetiaroa in 1975 after Nanai had speared a carangid fish while skindiving outside the reef. A large *T. obesus* circled a few times and then came directly to him. He pushed it aside, but it kept returning to attack him. He estimated that he made contact with the shark at least 10 times to avoid being bitten.

Paul Watson of Innisfail, Queensland, Australia, had a similar experience while snorkeling on an unnamed outer reef of the Great Barrier Reef about 50 miles south of Lizard Island in April 1975. He speared a "coral trout" of the grouper genus *Plectropomus* of about 12 pounds in weight and began to swim with it back to the boat. A whitetip reef shark 5 to 6 feet in length came over his head from behind, bumping his head in the process, and took a large bite out of the fish. The shark came back for more, but Watson hit it with his speargun. When Watson became tangled momentarily in the cord of the spear, he dropped the gun and the spear, which fell out of sight into a crevice. The shark then came directly at him, attacking about 15 times within 5 minutes. Each time the shark approached he was able to fend it off by pushing up with his hands behind the mouth and ducking beneath it. He managed to free his spear and the remains of the fish from the crevice, and the shark then directed its attention to the grouper.

The above account was provided by Roger C. Steene of Cairns, Queensland, who was in a small boat nearby and heard Watson call for help. He was unable to free the anchor to go to his aid, however, before Watson reached the boat. Both Steene and Watson are experienced divers, and it is unlikely that there was any misidentification of the shark as *Triaenodon obesus*.

Steene wrote, in addition, "On the Great Barrier Reef spearfishermen think of the whitetip as being nonaggressive, although I have seen them do silly, perhaps overinquisitive things when there's blood from fishes around. In a similar incident to Watson's, Cairns diver Arthur Wales was molested by a small (3-foot) whitetip while he had a fish on his spear. He repeatedly hit the shark with his speargun to no avail. The only way the shark could be stopped from biting Wales was when his companion shot and killed the shark at a distance very close to Wales. The attack on Wales occurred on the Barrier Reef at 15°55′ S; 145°42′ E."

It should be emphasized that *T. obesus* is generally a placid species in contrast to other carcharhinids and only on rare occasions can it be provoked or enticed into aggressive behavior.

Probably the greatest threat of the whitetip to man is the possibility of ciguatera poisoning from eating this shark. Banner and Helfrich (1964), noting that the level of ciguatera at Johnston Island had abated, pointed out that the large moray eel *Gymnothorax javanicus* and *Triaenodon obesus* remained toxic. Both of these species were collected as a source of toxin for laboratory studies. Cooper (1964) discussed the problem of ciguatera from the consumption of shark liver in the Gilbert Islands. Though the liver of any large shark may cause poisoning, the

worst offenders are the tiger shark (*Galeocerdo cuvier*) and *T. obesus*. Gilbertese have a great liking for shark flesh, the liver in particular. Cooper added that the flesh of sharks has not been reported as being toxic in the Gilberts. In more highly toxic areas, however, the flesh can be poisonous (as noted by Helfrich, Piyakarnchana, and Miles 1968, the liver of a fish contains more than 50 times the concentration of ciguatera toxin than does muscle tissue). Unable to determine the toxicity of the liver of *T. obesus* because test animals would not eat it with any constancy, Brock, Jones, and Helfrich (1965) used the flesh and found two of 20 specimens toxic at Johnston Island.

ACKNOWLEDGMENTS

The author gratefully acknowledges the assistance of the following in the collecting and tagging of whitetip reef sharks and in providing, pertinent information: Gerald R. Allen, Paul M. Allen, Raymond Bagnis, the late Alan C. Banner, Albert H. Banner, Nathan A. Bartlett, Patricia Bartlett, James A. Brock, Richard E. Brock, Ralph R. Bowers, Bruce A. Carlson, David Erlenkotter, David Fridman, Peter C. Galloway, William Hashimoto, Richard H. Johnson, Phillip B. Lamberson, Daniel W. Lyman, William D. Madden, Rhett M. McNair, Russell E. Miller, Donald R. Nelson, John R. Paxton, Robert P. H. Rutherford, Stephen V. Smith, William F. Smith-Vaniz, Roger C. Steene, Arnold Y. Suzumoto, P. K. Talwar, Toru Taniuchi, Gordon W. Tribble, Richard C. Wass, and Peter J. P. Whitehead.

LITERATURE CITED

BAGNIS, R., P. MAZELLIER, J. BENNETT, and E. CHRISTIAN. 1972. Poissons de Polynesie. Les Editions du Pacifique, Papeete. 368 pp.

BANNER, A. H., and J. E. RANDALL. 1952. Preliminary report on marine biology study of Onotoa Atoll, Gilbert Islands. Atoll Res. Bull. 13. ii + 62 pp.

BANNER, A. H., and P. HELFRICH. 1964. The distribution of ciguatera in the tropical Pacific. Tech. Rep. Hawaii Mar. Lab. 4. iii + 48 pp.

BARNES, A. 1973. Taxonomy and behavior of the genera *Mustelus* and *Triaenodon* (Triakidae, Pisces) of the Mediterranean and Red Seas. M.S. Thesis. Hebrew University, Jerusalem. 108 pp.

BASS, A. J., D. D'AUBREY, and N. KISTNASAMY. 1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. Oceanogr. Res. Inst. (Durban) Invest. Rep. 38. 100 pp.

BIGELOW, H. B., and W. C. SCHROEDER. 1948. Fishes of the western North Atlantic. Sharks. Mem. Sears Found. Mar. Res. 1:57–576.

BLEEKER, P. 1853. Nalezingen op de ichthyologische fauna van Bengalen en Hindostan. Nieuwe Verh. Bataafsch Genoot. Proefonderv. Wijsbegeerte 25:1–164.

———. 1879. Contribution à la faune ichthyologique de l'île Maurice. Verh. K. Akad. Wet. Amsterdam 18:1–23.

BRIGGS, J. C. 1961. The East Pacific Barrier and the distribution of marine shore fishes. Evolution 15(4):545–554.

BROCK, V. E., R. S. JONES, and P. HELFRICH. 1965. An ecological reconnaissance of Johnston Island and the effects of dredging. Hawaii Mar. Lab. Tech. Rep. 5. iv + 90 pp.

CLARKE, T. A. 1972. Collections and submarine observations of deep benthic fishes and decapod Crustacea in Hawaii. Pac. Sci. 26(3):310–317.

COMPAGNO, L. J. V. 1973. *Gogolia filewoodi*, a new genus and species of shark from New Guinea (Carcharhiniformes: Triakidae), with a redefinition of the family Triakidae and a key to the triakid genera. Proc. Calif. Acad. Sci. 39(19):383–410.

COOPER, M. J. 1964. Ciguatera and other marine poisoning in the Gilbert Islands. Pac. Sci. 18(4):411–440.

DAY, F. 1878 (reprinted 1958). The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. William Dawson & Sons, London. xx + 778 pp.

FOWLER, H. W. 1908. Notes on sharks. Proc. Acad. Nat. Sci. Philadelphia 60:52–70.

———. 1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the groups Elasmobranchii, . . . Bull. U.S. Nat. Mus. 100, vol. 13. x + 879 pp.

FOWLER, H. W., and S. C. BALL. 1925. Fishes of Hawaii, Johnston Island, and Wake Island. Bull. Bernice P. Bishop Mus. 26. 31 pp.

FOURMANOIR, P. 1954. Ichthyologie et peche aux Comores. Mém. Inst. Sci. Madagascar, sér. A, 9:187–238.

———. 1961. Requins de la cote ouest de Madagascar. Mém. Inst. Sci. Madagascar, sér. F, 4:1–107.

GARMAN, S. 1913. The Plagiostomia (sharks, skates, and rays). Mem. Mus. Comp. Zoöl. Harvard 36. xiii + 528 pp.

GILBERT P. W., ed. 1963. Sharks and survival. D. C. Heath & Co., Boston. xiv + 578 pp.

GILBERT, P. W., R. F. MATHEWSON, and D. P. RALL, eds. 1967. Sharks, skates, and rays. Johns Hopkins Press, Baltimore. xv + 624 pp.

GOHAR, H. A. F., and F. M. MAZHAR. 1964*a*. The elasmobranchs of the north-western Red Sea. Publ. Mar. Biol. Stn. Ghardaqa, Red Sea 13:1–144.

———. 1964*b*. Keeping elasmobranchs in vivaria. Publ. Mar. Biol. Stn. Ghardaqa, Red Sea 13:241–250.

GÜNTHER, A. 1870. Catalogue of the fishes of the British Museum 8. Taylor & Francis, London. xxv + 549 pp.

———. 1910. Fische der Südsee. J. Mus. Godeffroy 17(9):389–515.

HARRY, R. R. 1953. Ichthyological field data of Raroia Atoll, Tuamotu Archipelago. Atoll Res. Bull. 18. 190 pp.

HELFMAN, G. S., and J. E. RANDALL. 1973. Palauan fish names. Pac. Sci. 27(2):136–153.

HELFRICH, P., T. Piyakarnchana, and P. S. Miles. 1968. Ciguatera fish poisoning. I. The ecology of ciguateric reef fishes in the Line Islands. Occ. Pap. Bernice P. Bishop Mus. 23(14):305–369, 377–382.

HERRE, A. W. 1931. A check list of fishes from the Solomon Islands. J. Pan-Pac. Res. Inst. 6(4):4–9.

———. 1936. Fishes of the Crane Pacific Expedition. Field Mus. Nat. Hist. Publ., Zool. Ser., 21:1–472.

———. 1953. Check list of Philippine fishes. U.S. Fish Wildl. Serv. Res. Rep. 20. 977 pp.

HOBSON E. S. 1963. Feeding behavior in three species of sharks. Pac. Sci. 17(2): 171–194.

KAMI, H. T., I. I. IKEHARA, and F. P. DELEON. 1968. Check-list of Guam fishes. Micronesica 4(1):95–131.

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 pp.

KENYON, K. W., and D. W. RICE. 1959. Life history of the Hawaiian monk seal. Pac. Sci. 13(3):215–252.

KLAUSEWITZ, W. 1959. Fische aus dem Roten Meer. I. Knorpelfische (Elasmobranchii). Senckenbergiana Biol. 40(1/2):43–50.

———. 1960. Die Typen und Typoide des Naturmuseums Senckenberg. 23. Pisces, Chondrichthyes, Elasmobranchii. Senckenbergiana Biol. 41(5/6):289–296.

MASUDA, H., C. ARAGA, and T. YOSHINO. 1975. Coastal fishes of southern Japan. Tokai University Press, Tokyo. 379 pp.

MEYER, A. B. 1885. Catálogo de los peces recolectados en el archipiélago de las Indias Orientales durante los años 1870 á 1873. An. Soc. Españ. Hist. Nat., Madrid 14:5–49.

MÜLLER, J., and F. G. J. HENLE. 1837. Gattungen der Haifische und Rochen, nach ihrer Arbeit: "Ueber die Naturgeschichte der Knorpelfische." Sitzungsber. Ber. Akad. Wiss. Berlin: 1–32.

MUNRO, I. S. R. 1955. The marine and fresh water fishes of Ceylon. Halstead Press, Sydney. xvi + 351 pp.

———. 1967. The fishes of New Guinea. Department of Agriculture, Stock and Fisheries, Port Moresby. xxxvii + 651 pp.

NELSON, D. R. 1974. Ultrasonic telemetry of shark behavior. Naval Res. Rev.: 1–21.

NELSON, D. R., and R. H. JOHNSON. 1976. Some recent observations on acoustic attraction of Pacific reef sharks. Pages

229/239 *in* A. Schuijf and A. D. Hawkins, eds. Sound reception in fish. Vol. 5 of Developments in aquaculture and fishery science. Elsevier, Amsterdam. 288 pp.

PIETSCHMANN, V. 1938. Hawaiian shore fishes. Bull. Bernice P. Bishop Mus. 156. i + 55 pp.

PLAYFAIR, R. L. 1867. The fishes of Seychelles. Proc. Zool. Soc. London: 846–872.

RANDALL, J. E. 1955. Fishes of the Gilbert Islands. Atoll Res. Bull. 47. xi + 243 pp.

———. 1973*a*. Expedition to Pitcairn. Oceans 6(2):12–21.

———. 1973*b*. Tahitian fish names and a preliminary checklist of the fishes of the Society Islands. Occ. Pap. Bernice P. Bishop Mus. 24(11):167–214.

RÜPPELL, E. 1835. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des rothen Meeres. Siegmund Schmerber, Frankfurt am Main. 148 pp.

SAUVAGE, M. H. 1891. Histoire physique, naturelle et politique de Madagascar. Vol. 16. Histoire naturelle des poissons. Imprimerie Nationale, Paris. 543 pp.

SCHULTZ, L. P. 1943. Fishes of the Phoenix and Samoan islands collected in 1939 during the expedition of the U.S.S. "Bushnell." Bull. U.S. Nat. Mus. 180. x + 316 pp.

SCHULTZ, L. P., AND COLLABORATORS. 1958. Fishes of the Marshall and Marianas islands. Bull. U.S. Nat. Mus. 100, vol. 1. xxxii + 685 pp.

SMITH, J. L. B. 1952*a*. A new hound shark from South Africa, and new records. Ann. Mag. Nat. Hist., ser. 12, 5:223–226.

———. 1952*b*. *Carcharhinus zambezensis* Peters, 1852, with notes on other chondrichthyan fishes. Ann. Mag. Nat. Hist., ser. 12, 5:857–863.

———. 1955. The fishes of Aldabra. Part I. Ann. Mag. Nat. Hist., ser. 12, 8:304–312.

SMITH, J. L. B., and M. M. SMITH. 1963. The fishes of Seychelles. Department of Ichthyology, Rhodes University, Grahamstown. 215 pp.

SNODGRASS, R. E., and E. HELLER. 1905. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galapagos islands. Proc. Wash. Acad. Sci. 6:333–427.

SPRINGER, V. G., and J. A. F. GARRICK. 1964. A survey of vertebral numbers in sharks. Proc. U.S. Nat. Mus. 116(3496):73–96.

TANIUCHI, T. 1975. Reef whitetip shark, *Triaenodon obesus*, from Japan. Jpn. J. Ichthyol. 22(3):167–170.

TINKER, S. W., and C. J. DELUCA. 1973. Sharks and rays. Charles E. Tuttle Co., Tokyo. 80 pp.

WASS, R. C. 1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac. Sci. 27(4): 305–318.

WEBER, M. 1913. Die Fische der Siboga-Expedition. E. J. Brill, Leiden. xii + 710 pp.

WHEELER, J. F. G. 1953. Report on the Mauritius-Seychelles Fisheries Survey 1948–1949. Part I. The bottom fishes of economic importance. Fish. Publ., London 1(3):1–57.

———. 1959. Sharks of the western Indian Ocean. I. *Loxodon macrorhinus* M. & H. J. East Afr. Agric. 25(2):106–109.

———. 1960. Sharks of the western Indian Ocean. II. *Triaenodon obesus* (Rüppell). J. East Afr. Agric. 25(3):202–204.

WHITLEY, G. P. 1939. Taxonomic notes on sharks and rays. Aust. Zool. 9(3):227–262.

———. 1954. New locality records for some Australian fishes. Proc. R. Zool. Soc. N.S.W. 1952–53: 23–30.

———. 1964. Fishes from the Coral Sea and the Swain Reefs. Rec. Aust. Mus. 26(5): 145–195.