

DIEL BEHAVIOR OF THE TIGER SHARK,
GALEOCERDO CUVIER, AT FRENCH FRIGATE
SHOALS, HAWAIIAN ISLANDS.—

Adult tiger sharks, *Galeocerdo cuvier*, are among the largest aquatic predators in tropical and subtropical reef communities and are well known for their euryphagic diet (Ikehara, 1960, 1961; Tester, 1969; Fujimoto and Sakuda, 1972; Taylor and Naftel, 1978). However, the majority of information on the daily movement patterns of this shark comes from anecdotal field observations. For example, in Caribbean waters tiger sharks were considered nocturnal because they were rarely observed at the surface during the day but often captured on set lines (Randall, 1967) or encountered near fishing operations (Springer, 1943), at night. While tiger sharks inhabit the tropical waters of Florida throughout the year (Springer, 1963), some individuals migrate northward in the summer months along the western Atlantic coast as far as Woods Hole, Mass. (Big-

elow and Schroeder, 1948). Limited data from conventional tagging studies in Hawaiian waters indicate that tiger sharks may restrict movements within a geographic area for at least part of the year (Tester, 1969).

Much still remains to be learned of the diel activity patterns of tiger sharks. Herein, we present results of the first telemetric study on this predator and provide detailed data on the daily spatial requirements of a free-swimming adult tiger shark in its natural environment.

Study area and methods.—French Frigate Shoals is located in the center of the Hawaiian Archipelago, approximately 900 km northwest of Honolulu, Oahu (Fig. 1). The area was chosen because it offered a topography conducive to day and night operations of a small tracking boat and an abundance of sharks. In addition, it lies within the Hawaiian Island National Wildlife Refuge and presents a natural reef ecosystem relatively undisturbed by human activity. The shoal consists of a shallow reef on the north and east (windward) sides with a deeper leeward shelf (approximately 20–40 m deep) that extends westward to the reef drop-off. There are 13 small sand islands scattered on the reef and one basalt island, La Perouse Pinnacle, near the center of the shoal.

A high-power, long-range ultrasonic transmitter was developed to monitor the activity patterns of adult tiger sharks. Tags incorporated a modified version of the circuitry described by Ferrel et al. (1974), and transmitted at frequencies near 32 kHz. The cylindrical package was 25 cm long, 4 cm in diameter and weighed 440 g in air. Pulse intervals were controlled by a resistive depth sensor sensitive from 0 to 140 m and adjusted to rates ranging from 0.5 to 1.5 pulses/second, respectively. Signals were monitored with a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. Absolute maximum range of the transmitter-hydrophone system under ideal conditions was approximately 4,000 m although transmission loss greatly reduced the audible signal at ranges greater than 2,000 m.

Transmitter signals were monitored from a 7-m tracking boat in which bearing and range estimates of the shark were recorded every 15 min. Bearings were taken with an oil-filled navigation compass based on the direction of the strongest audible signal. Accuracy of the bearing estimates was tested and found to be within $\pm 7^\circ$. Range estimates were based on the relative

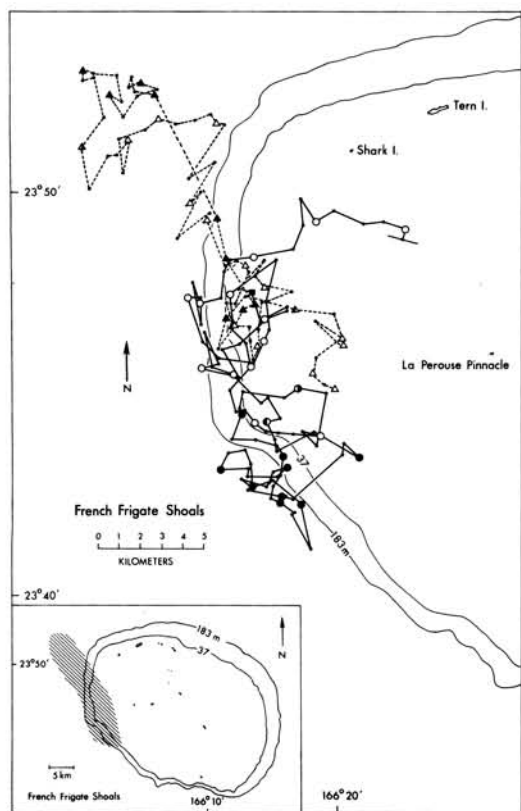


Fig. 1. Movements of tagged shark during first 24-h tracking period beginning 1000 h, 25 June 1977 (dots), and second 24-h period beginning 1000 h, 26 June (triangles). Small dots indicate 15-min location plots. Large dots and triangles indicate hourly plot taken during daylight (hollow), dusk (hollow-solid), night (solid), and dawn (solid-hollow). Inset shows entire shoal with area of shark movements indicated by hatching.

strength of the audio signal. Transmitter tone bursts had a proportional range/attenuation characteristic that could be estimated to an accuracy better than 500 m when receiver-to-transmitter distance was under 2,000 m. For this reason, tracking boat-to-shark distance was kept under 1,500 m. Radar fixes of the tracking boat were also taken at 15-min intervals by the crew of the nearby 24-m support vessel, Easy Rider. Location was determined using La Perouse Pinnacle and Tern Island as radar landmarks, and was accurate within 15 m.

Results.—Careful consideration was given to techniques used in capture of the shark, tag

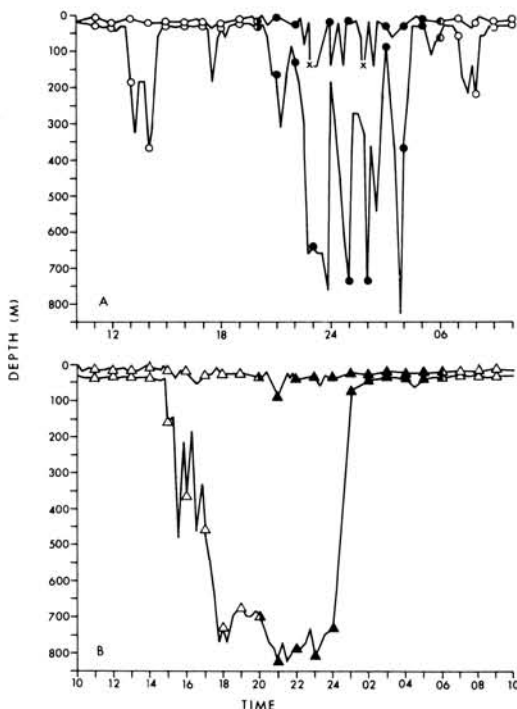


Fig. 2. Depth of tagged tiger shark and underlying bottom during first 24-hour tracking period (circles), and second 24-hour tracking period (triangles). Other points indicate depths recorded at 15-min intervals. "X" 's and adjacent points represent limit of depth sensor (140 m), thus shark may have been deeper.

application and tracking procedure in order to minimize stress and extraneous influences to the animal during the tracking session. On the morning of 25 June, a 4-m female tiger shark was taken by longline (baited with shark flesh) set at dusk the night before. The active swimming of the shark on the line indicated that it was in relatively good health. The shark was brought alongside the small tracking boat, and the transmitter was applied adjacent to the first dorsal fin via a stainless-steel dart and applicator pole. Application of the tag caused no overt response from the shark (e.g., thrashing, rolling, etc.). The wire leader was then cut at the eye of the hook (which was snagged in the corner of the mouth), and the shark was released.

Horizontal movements of the shark over a 48-h period are summarized in Fig. 1. After release, the shark moved towards the deeper waters of the leeward drop-off where it swam near the bottom for the remainder of the day-

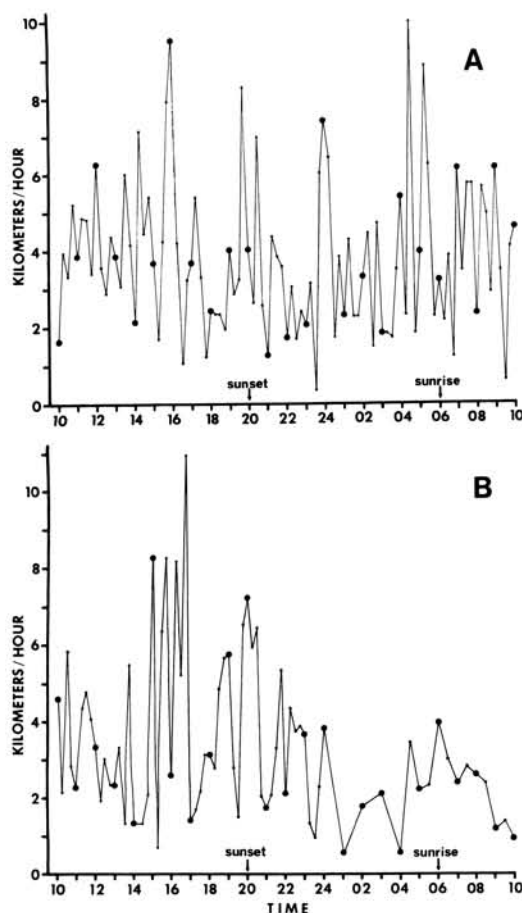


Fig. 3. Rate of horizontal movement of tagged tiger shark during A) first 24-h tracking period (\bar{x} = 3.74 km/h; SD = 1.97), and B) second 24-h period (\bar{x} = 3.37 km/h; SD = 2.12). Points calculated from distance moved divided by corresponding elapsed time interval. Dots represent instantaneous speed of shark at hourly (large) and 15-min (small) plots.

light hours. Near sunset, the animal moved beyond the drop-off into more oceanic waters and began a series of rapid vertical excursions to depths greater than 140 m (Fig. 2). Approximately 1.5 h before dawn, the shark moved back into shallower waters over the reef and remained there until mid afternoon when it again swam out beyond the edge of the reef. There it swam in the epipelagic habitat at depths of 20–40 m until dark, when it began more vertical excursions. Near midnight, the shark returned to shallower reef waters (40 m)

and swam close to the bottom for the remainder of the tracking session.

Rate of horizontal movement for the shark is shown in Fig. 3. The shark ranged over an elongate area of approximately 100 km² centered near the reef drop-off. Cumulative linear horizontal distance of the shark's path was approximately 82 km/day. More horizontal area was covered by the shark during daylight hours (53.5 km²) than at night (33.8 km²). Rate of horizontal movement (Fig. 3) ranged from 0.4 to 11.0 km/h, with an overall mean of 3.6 km/h. Nighttime rates averaged slightly lower (3.3 km/h; SD = 1.97) than daytime (3.77 km/h; SD = 2.1).

Discussion.—We are reluctant to make generalizations on the habits of all tiger sharks from the data of only one shark tracking. This study is significant, however, because it provides the first high-resolution information on space-related behavior of this predator over a substantial period of time.

It is unlikely that the trauma of tag application significantly affected the shark's behavior after release. No sign of post-release disorientation was observed as the shark moved towards the reef drop-off, and the animal showed similar movement patterns over the next two days. Blue sharks, *Prionace glauca*, tagged by Sciarrotta and Nelson (1977) and Tricas (1977) often showed an 'initial plunge' response after transmitter application but also returned to an apparent normal swimming pattern within two hours.

A general diurnal activity pattern is evident for the tiger shark over the 48-h period. The shark spent 68% of its daytime activity on the outer leeward reef where it swam close to the bottom and occasionally ascended into the water column. Tiger sharks were observed near the bottom in waters near reef drop offs during the day (McNair, 1975) and often swam up into the water column to investigate objects near the surface (McNair, 1975; J. McKibben, pers. comm.). Our data and observations also indicate such daytime behavior.

Eighty-three percent of the shark's nocturnal activity was centered above or beyond the leeward drop-off. Depth data (Fig. 2A, approximately 2230–0400 h) show that the shark did not swim close to the bottom as it had during the day, yet similarities between the slopes of many dives and the underlying drop-off con-

tours indicate some orientation relative to the reef topography.

Even though total horizontal area and horizontal rates of movement were higher during daylight than night hours, this shark showed most vertical activity at night. Standora and Nelson (1977) found an increase at night in both rate of horizontal movement and instantaneous swimming speed for the demersal Pacific angel shark, *Squatina californica*. Telemetered blue sharks, *Prionace glauca*, near Santa Catalina Island, California showed increased rates of horizontal movement, a higher average swimming speed and slightly deeper excursions at night (Sciarrotta and Nelson, 1977). Blue sharks near Catalina were found to feed primarily at night (Tricas, 1979) and such increases in activity of tiger sharks may likewise be related to search, chase, and capture of prey. Rancurel (1973), for example, found that tiger sharks sampled near the Loyalty Islands fed on the pelagic squid, *Histioteuthis* sp., and suggested that the sharks disrupted squid schools before prey capture. Perhaps the diving behavior of the shark in the present study was related to feeding on cephalopod and fish assemblages that occur at the seaward edge of the reef at French Frigate Shoals.

The shark concentrated its movements within the western sector of the shoal and frequented certain areas more than others. Geographic home ranges are well documented for terrestrial vertebrate predators and vary considerably in relation to body size, sex, feeding strategy, time of day, breeding cycle, etc. (Brown, 1975). Studies on marine teleost fishes established that many species associate with a general region of a reef (Bardach, 1958; Randall, 1961; Ogden and Buckman, 1973; Reese, 1973; Ogden and Ehrlich, 1977) for periods up to years in duration. Some inshore sharks also associate with a specific geographic area. Standora and Nelson (1977) demonstrated that the nocturnally active Pacific angel shark, *Squatina californica*, moved within a limited inshore area. Movements of telemetered gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak Atoll, Marshall Islands showed daily movement patterns, geographic home ranges, and specific sites used by individuals on a daily basis (D. Nelson, pers. comm.). Although our data may be interpreted to support the hypothesis of structured activity patterns for tiger sharks, further long-term trackings (e.g., on the order of months

or years) are needed to adequately characterize the determinants of home range size and flexibility of their activity patterns.

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