DIEL BEHAVIOR OF THE BLUE SHARK, *PRIONACE GLAUCA*, NEAR SANTA CATALINA ISLAND, CALIFORNIA[1]

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ABSTRACT

The diel activity levels and movements of the blue shark, *Prionace glauca*, were studied in the natural environment using ultrasonic telemetry. Two initial sharks were tagged with single-channel transmitters equipped with depth sensors. Twelve sharks were tagged with multichannel transmitters with various combinations of sensors to measure depth, swimming speed, swimming direction, and temperature. From March to early June, the sharks made an evening-twilight migration from their epipelagic daytime habitat to the shallower waters bordering the island. From late June to October, the sharks remained offshore throughout the day and night. This change in movement pattern is suggested to be in response to a seasonal shift in location of prey. The telemetry data indicated that the blue shark is basically nocturnal, showing highest activity in the early evening and lowest activity in the early daylight morning. Measured parameters increasing at night included 1) rate of horizontal movement, 2) swimming speed, 3) variability in depth, and 4) variability in swimming direction. The sharks usually remained within a relatively narrow range of water temperatures.

This paper describes a study in which the diel activities of an epipelagic shark were monitored remotely in the natural environment. Multichannel ultrasonic transmitters were used to telemeter certain behavioral and environmental parameters of free-ranging blue sharks, *Prionace glauca* (Linnaeus). The primary objective was to track the sharks continuously throughout the day-night cycle to determine diel patterns of activity and movement.

Prior to the initiation of this study, surprisingly little had been published on the behavior of the blue shark, one of the most abundant large predators in warm temperate seas. Bigelow and Schroeder (1948) summarized what was then known about the biology of the species. Suda (1953) studied embryonic development, size relationsips, and sex ratios as related to distribution in the north tropical and subtropical Pacific. Strasburg (1958) investigated the distribution, abundance, capture depths, reproduction, and food habits of pelagic sharks, including the blue shark, in the central Pacific. Miscellaneous data on blue sharks have been reported from the Atlantic (Aasen 1966), the Canadian Atlantic (Templeman 1963), and the Gulf of Alaska (LeBrasseur 1964). A study of the blue shark off southern California, still largely unpublished, was conducted by Bane (1968).

More recently, the blue sharks off southwest England have received investigation in regard to age determination, reproduction, diet, and migration (Stevens 1973, 1974, 1975, 1976; Clarke and Stevens 1974). Casey, Stillwell, and Pratt at Narragansett, R.I. have gathered considerable information on the biology of sharks of that area, including data on migrations, food habits, and reproduction of blue sharks (Weeks 1974; Casey 1976; Stevens 1976). Tag returns from these studies have documented some long-range, long-term movements by blue sharks in the Atlantic. Several similar movements have also occurred in the Pacific (Bane 1968; D. R. Nelson, unpubl. data—see Discussion). Short-term movements, however, such as related to the diel cycle, have not been described for the blue shark.

Observations relating to the diel patterns of sharks have been mentioned by several authors (Springer 1963; Limbaugh 1963; Randall 1967; Hobson 1968), but specific quantitative studies have been few. Nelson and Johnson (1970) found that the horn shark, *Heterodontus francisci*, and the swell shark, *Cephaloscyllium ventriosum*, exhibited distinctly nocturnal activity patterns

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under laboratory and field conditions. In subsequent work with the horn shark, Finstad and Nelson (1975) measured the effect of light intensity on releasing activity onset, both in the natural environment and in the laboratory under artificial twilight transitions. For a colony of captive bonnethead shark, *Sphyrna tiburo,* under seminatural conditions, Myrberg and Gruber (1974) reported a late-afternoon peak in patrolling speed, suggesting a diurnal activity rhythm.

Using ultrasonic telemetry, Standora (1972) established a basically nocturnal pattern of activity and a limited home range for the Pacific angel shark, *Squatina californica.* His multichannel transmitters were a similar, but earlier version of those used in the present study. Carey and Lawson (1973) tracked a free-ranging dusky shark, *Carcharhinus obscurus,* in order to study body temperature regulation. They used a two-channel, frequency-shifting transmitter that measured both surface and deep body temperatures. Thorson (1971) monitored long-term movements of the bull shark, *C. leucas,* with relatively long-life, sensorless pingers and automatic-recording receivers at several locations. Using this technique in conjunction with conventional tagging, he showed that bull sharks move via the San Juan River from the Caribbean Sea to Lake Nicaragua.

The present paucity of behavioral information on active, wide-ranging sharks, especially pelagic species, is undoubtedly due in part to the difficulty of studying them by direct observation. Ultrasonic telemetry now offers one promising avenue of approach to this problem. This paper reports on an initial study using this technique to investigate diel patterns of behavior in a wide-ranging pelagic shark.

METHODS

The present study is based on 14 individual telemetry trackings conducted between 3 March and 7 October 1972 (Table 1). Each tracking was initiated in the pelagic environment of the San Pedro Channel approximately 6 to 7 km north of the Isthmus, Santa Catalina Island, Calif. The blue shark was well suited for this telemetry study because of its moderately large size, high abundance for most of the year, and attractability to bait. The abundance and/or attractability of blue sharks in the offshore baiting area was low only during the months of January and February, the sharks being easily obtainable the rest of the year.

TABLE 1.—Summary of tracking data for 14 telemetered blue sharks.

Tracking no.	Date (1972)	Estimated TL (m)	Sex	Tracking duration (h)	Tracking period	Evening shoreward movement
1	3/3	1.8	M	7.0	1040–1740	?
2	3/11	2.3	F	8.5	0910–1740	?
3	3/17	2.3	?	6.4	1105–1730	beginning
4	3/30	2.0	M	11.6	1125–2300	yes
5	4/7	2.6	M	8.4	1145–2010	yes
6	4/15	2.0	F	16.1	1155–0400	yes
7	4/29	1.8	F	18.0	1200–0600	yes
8	5/6	2.0	M	21.9	1010–0805	yes
9	5/20	2.0	F	19.6	1155–0730	yes
10	6/3	2.2	M	16.3	1615–0830	yes
11	6/14	2.3	M	4.8	1145–1630	?
12	6/24	2.3	M	14.8	1445–0530	no
13	9/13	2.0	F	13.4	1305–0230	no
14	10/7	2.0	F	18.8	1215–0700	no

The estimated range in total lengths of blue sharks telemetered was 1.8 to 2.6 m; for those otherwise observed, 1.2 to 3.0 m.

Telemetry System

The ultrasonic telemetry system used in the present study has been described in detail by Standora (1972), Ferrel et al. (1974), and Nelson (1974). The transmitters were of the oil-filled type, about 15 to 18 cm long, 3.5 cm in diameter, and emitted 10-ms pulses (tone bursts) at 40 kHz. The units were set for a life of several days, and a maximum range of 3 km (average conditions) to 5 km (ideal conditions). Data were encoded as pulse rate (pulse interval) which varied with the value of resistive sensors. The first two trackings utilized single-channel transmitters incorporating depth sensors. The remaining 12 trackings were performed with multichannel units (rapid-multiplexing type) with various combinations of sensors to measure depth, swimming speed, swimming direction, and temperature.

Two commercial tunable ultrasonic receivers were used. For continuous monitoring of relatively clear, nearby signals, the Smith–Root Ta-25[4] receiver (25–80 kHz) was employed using an omnidirectional hydrophone on a 25-m cable. The more sensitive, narrow-band DuKane model N15A235 receiver (30–45 kHz) with its staff-mounted directional hydrophone was used for directional tracking and for reception of weaker signals.

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

Application, Tracking, and Recovery

The sharks to be tagged were attracted with bait to the 7-m tracking boat. Cut Pacific mackerel, *Scomber japonicus,* in two bait cannisters, was suspended at depths of about 5 and 15 m. Since drifting of the boat established the odor corridor necessary for shark attraction, the time needed for attraction decreased as the wind (and drift rate) increased. The time necessary to attract the first blue shark ranged from 10 min to 4 h and the mean was 1.5 h.

Whenever a choice was possible, a larger individual shark was selected for tagging in order to lessen the possible effect of the transmitter on its behavior. The shark to be tagged was enticed to the surface next to the boat using a short baited line, then harpoon tagged in the middorsal region anterior to the first dorsal fin. The sex of the shark was noted and its total length estimated (Table 1). An attempt was made to prevent the shark from actually taking the bait, as this might have influenced subsequent feeding motivation.

The transmitter was attached to the shark by a stainless steel dart (Floy FH 69) thrust beneath the skin with a hand-held applicator pole. The transmitter package included a syntactic foam float and a magnesium breakaway link which corroded through in a roughly predictable time, allowing the unit to float to the surface for recovery.

The tracking procedure involved continuous monitoring of the signal from the drifting boat using the omnidirectional hydrophone. As the signal became weak, its direction was determined with the directional hydrophone, and the boat was then moved closer to the shark. Distance to the shark was estimated primarily from approximate signal strength and by triangulation from successive positions of the moving boat. To minimize the effect of the boat on the shark's behavior, an effort was made to maintain a distance of at least 200 m between the boat and the shark.

Ultrasonic tracking in the study area at times presented certain problems. Noise from crustaceans, echo-locating cetaceans, ship traffic, wave action, hydrophone turbulence, and bottom echoes could be picked up by the receivers, and if of high enough level, would mask the data pulses. Signal reception was also affected when the shark went below the thermocline (reflection) or was swimming very near the surface (wave shielding, bubble attenuation, downward ray refraction). These factors at times caused signal losses that could be counteracted only by lowering the hydrophone to a depth of about 10 or 15 m.

Data Recording and Reduction

Approximately once per half-hour, a 30-s data sequence was recorded on magnetic tape and the estimated position of the shark plotted. The omnidirectional hydrophone was preferred for recording purposes whenever the signal was sufficiently strong. It was less convenient to use the directional hydrophone for recording long data sequences because of the difficulty of maintaining continuous accurate aim, thus resulting in greater signal-strength variability.

Decoding of the single-channel depth data required only a stopwatch and calibration graph. Ten pulse intervals were timed and converted to a depth value. For the multichannel data, the tape recordings were converted into paper oscillograms on which the pulse intervals were measured manually. For analysis, the mean value for three clear 8-channel sequences were graphed for each half-hour recording period.

RESULTS

The telemetered blue sharks were generally most active at night, with highest activity in the early evening and lowest activity in the early daylight morning. While some activity occurred throughout the diel cycle, the mean recorded values for all trackings were greater at night for 1) rate of horizontal movement, 2) swimming speed, 3) variability in depth, and 4) variability in swimming direction. Experienced tracking personnel were also able to detect by ear subtle changes in the multiplexed pulse intervals. Although not quantified, the trackers received the distinct impression that these changes occurred more often at night—thus further supporting a nocturnal activity maximum.

Horizontal Movement—Island-Oriented Migration

The most striking behavior demonstrated by the present study was a seasonal, evening-twilight migration from the epipelagic offshore habitat to the shallower waters bordering the island. Between late March and early June, each of the seven sharks tracked made this movement to-

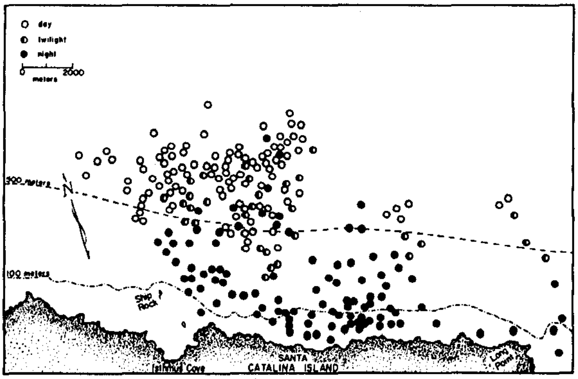

FIGURE 1.—Positions of seven blue sharks tracked from late March through early June 1972. Note that all day positions are offshore from the island, while the majority of night positions are nearshore, often in relatively shallow water.

wards the island shoreline. Examples of trackings of this type are shown in Figures 1 and 2.

These sharks remained offshore in the general vicinity of the tagging during the daylight hours. Approximately at dusk, the sharks initiated a relatively straight-line course towards the island. It is difficult to place precise times on when the sharks began this move, but it appeared to be from about 1.6 h before to 1.3 h after sunset, with a mean slightly after sunset. During the shoreward movement, the sharks swam at depths varying from near the surface to over 90 m. Once near the island, the sharks usually moved in an easterly direction parallel to the shoreline. Several hours before sunrise, there was a directed movement away from the island back to the offshore environment. The closest estimated nighttime approaches to the island for these individuals averaged 1,100 m (range, 200–4,000), corresponding to water depth averaging 115 m (range, 80–380).

Although three preliminary trackings in early and mid-March ended prior to nightfall, the last of these appeared to show the beginnings of a shoreward movement prior to transmitter release. One tracking in mid-June ended prematurely prior to dusk. From late June until early October, the three sharks successfully tracked remained offshore throughout the day and night over bottom depths of 500 m or more (Figures 3, 4).

Rate of Horizontal Movement

Rate of movement was calculated for each shark from its half-hourly estimated positions such as shown in Figures 2 and 4. The mean values for all sharks tracked (Figure 5) showed an increase in rate of movement at sunset which continued through most of the night. The mean rate of movement for the daytime was 1.2 km/h (range, 0.3–7.0); for the nighttime, 1.8 km/h (range, 0.4–4.0).

Swimming Speed

There was a definite increase in telemetered instantaneous swimming speed at night (Figure 5). However, no abrupt increase in speed occurred at the dusk transition, as might be expected in view of the rate of movement increase at that time. Swimming speed peaked a few hours after sunset and remained comparatively high until a few hours before sunrise. The artifactual burst of speed immediately after tag application was short lived, even in those sharks that did not promptly return to the bait cannister.

Although the maximum speed capability of the sensor was 5 km/h, this speed was not often reached during the half-hourly data recording periods, which suggests speeds in excess of 5 km/h seldom occurred. The mean swimming speed for the daytime was 1.3 km/h, for the nighttime 2.8 km/h, while the range for both covered the entire sensor range.

Increases in swimming speed were often associated with brief dives during the same recording session (Figures 2, 4). In seven of the eight trackings in which both speed and depth were telemetered, and where tracking extended at least into dusk, the highest mean speeds occurred at relatively great depths (means: 4.8 km/h, 69 m) while the lowest speeds occurred at much shallower depths (means: 0.5 km/h, 20 m). This suggests that some factor in deeper water stimulated this speed increase, possibly presence of food.

Swimming Direction

Figure 5 shows clearly the relationship between swimming speed and rate of movement throughout the diel cycle. As expected, swimming speeds had the higher values, as the two measures would have been equal only in cases where the shark swam in a straight line for the entire 30-min interval between position determinations. During daylight hours both rates were moderately close, suggesting that the sharks made gradual changes in swimming direction rather than abrupt

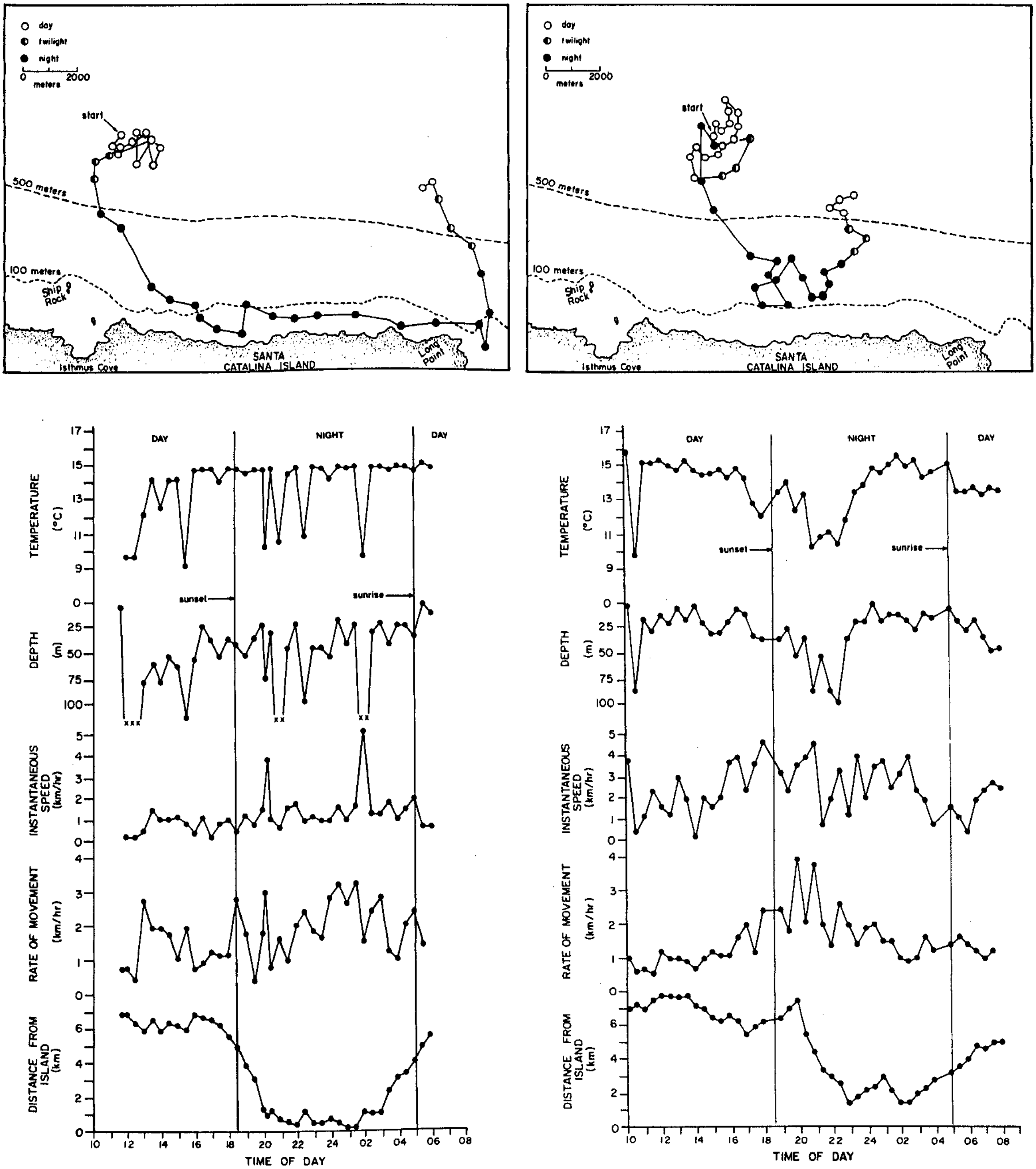

FIGURE 2.—Data from two individual trackings of blue sharks typical of the late March to early June period. Top, shark positions at approximately 0.5-h intervals. Bottom, telemetered sensor data. Note the characteristic evening-twilight migration towards the island, the initial plunge occurring immediately after transmitter application, and the close correlation between temperature and depth. Depths in excess of 110 m (the sensor limit) are indicated by ××.

changes. During the dusk transition, rate of movement most closely matched swimming speed, indicating the greatest consistency in swimming direction. In timing, this coincides with the relatively oriented shoreward migrations of from late March to early June. The greatest disparity be-

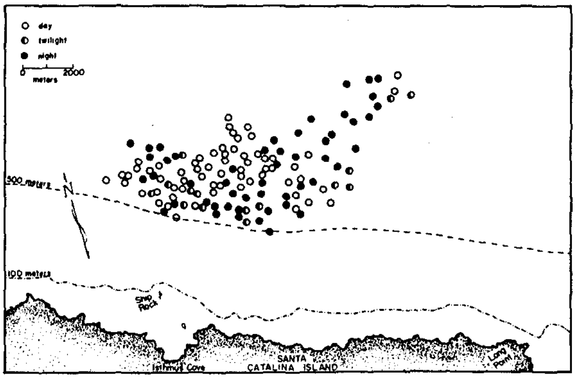

FIGURE 3.—Positions of three blue sharks tracked from late June to early October 1972. Note that both day and night positions are well offshore over relatively great depths.

tween rate of movement and swimming speed was during the early evening, evidence that much of the swimming then was variable in direction—a possible indication of searching for and/or pursuing prey. Beginning in the early morning and continuing through dawn, the differences between the two rates lessened.

A compass sensor for direct measurement of instantaneous swimming direction (azimuth) was incorporated during only one successful tracking. The compass data from this tracking (Figure 4) show that the greatest number of multiple-direction recordings (i.e., during single-recording periods) occurred at night, suggesting that variability of swimming direction is generally greater at night. During one nighttime recording, a change of at least 360° coupled with a speed change of 1 to 5 km/h was noted during one 15-s period.

Vertical Movement

Figure 6 illustrates the mean depths telemetered from all sharks with transmitters equipped with depth sensors. The sharks were within a depth range of 18 to 42 m for 92% of the time; they appeared to equal or exceed 100 m only during 3.9% of the readings (excluding initial plunges). The apparent tendency was a slight increase in mean depth at night. The mean daytime depth was 30 m; at night 40 m. Individual tracking graphs show that the sharks covered the entire depth range of the sensors (0–110 m) during both day and night, but that at night there were more vertical excursions from shallow to deep, i.e., greater variability in depth. During four trackings, the sharks may have been close to the bottom when in the relatively shallow water near the island.

The first hour of depth data were excluded from Figure 6 because of what appears to be an initial plunge induced by tagging trauma. As shown in Figure 7, the data also suggest that this initial effect decreased or disappeared within 1.5 h after tagging. About half of the sharks tagged exhibited this "abnormal" plunge (to a mean depth of at least 95 m) within 0.5 h of being tagged. The others apparently did not—possibly a result of the tag dart penetrating in a less sensitive spot. Of the first nine sharks tagged, six were seen to return to the bait cannister within seconds after transmitter application—suggesting little, if any, tagging trauma. Two of these six sharks, however, still made a deep dive by the next recording session.

Temperature

Blue sharks in the study area appeared to prefer a relatively narrow range of water temperatures. Overall, the telemetered sharks were found in a temperature range of 8.5° to 17.5°C, but occurred in the much narrower range of 14.0° to 16.0°C for 73% of the time. Seasonality of diel depth/temperature selectivity was not apparent from either the temperature or depth data. As expected, the telemetered depth and temperature data usually corresponded quite well, i.e., an increase in depth accompanied by a decrease in temperature (Figures 2, 4). Individuals were most often seen swimming at the surface during the cooler months, but rarely during either the coldest or warmest months, a behavior that may have been influenced by surface temperatures.

DISCUSSION

It is not surprising that the blue shark appears more active at night than during the day. Carcharhinids in general are considered by Randall (1967) to be nocturnal. In addition, most sharks studied quantitatively in this regard have proven to be basically nocturnal, the bonnethead shark studied by Myrberg and Gruber (1974) being a possible exception. Like other nocturnal sharks, however, blue sharks certainly feed diurnally at times, and it is common knowledge that they readily respond to opportunistic feeding stimuli (e.g., bait) during the day. There have also been observations of blue sharks feeding naturally during

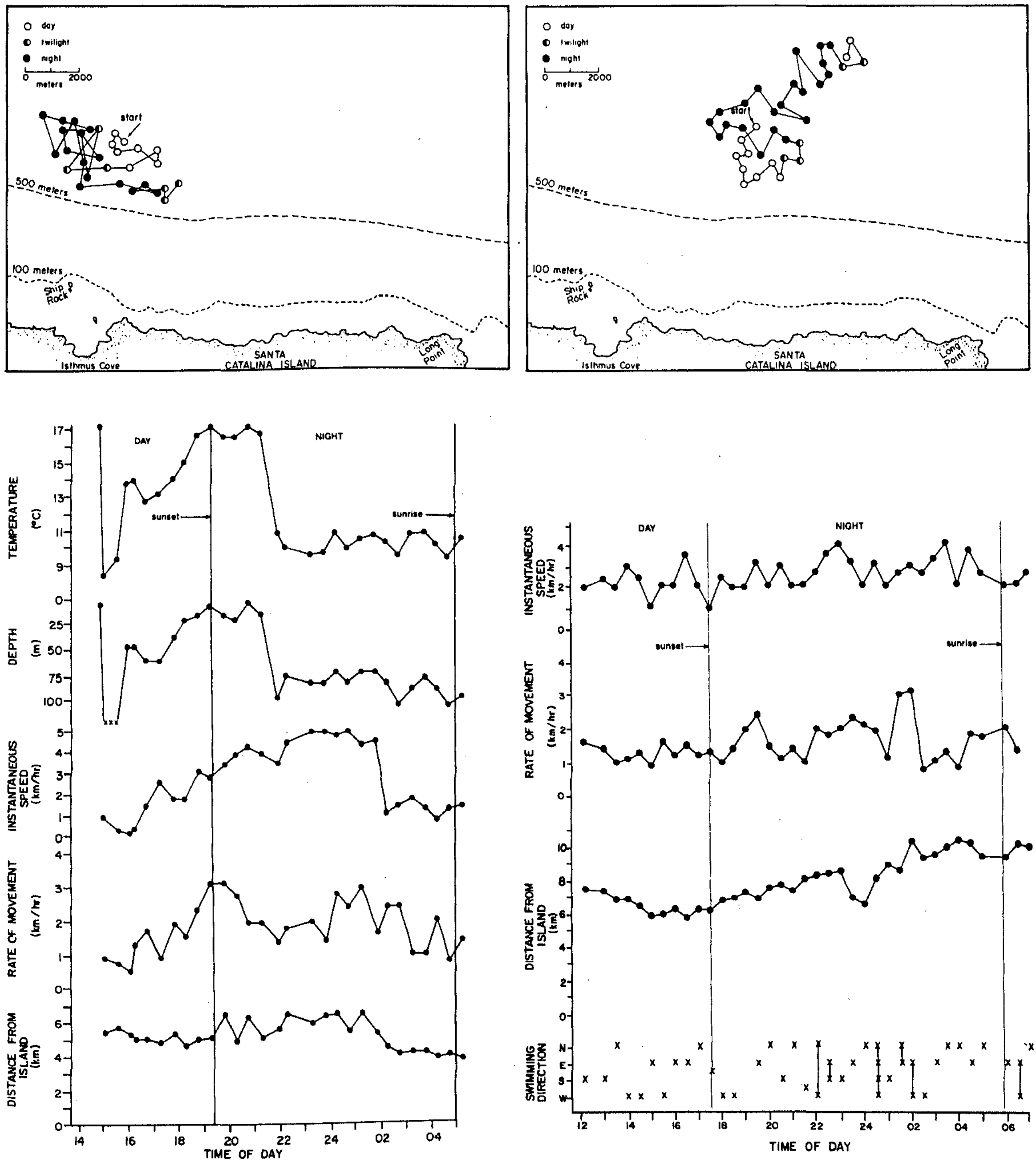

FIGURE 4.—Data from two individual trackings of blue sharks typical of the late June to early October period. Top, shark positions at approximately 0.5-h intervals. Bottom, telemetered sensor data. Note the absence of shoreward movement, the increased swimming speed and depth at night (left), and the greater frequency of sudden direction change, i.e., multiple-direction recordings, at night (right).

the day, e.g., on blacksmith, *Chromis punctipinnis* (R. R. Given pers. commun.; D. R. Nelson unpubl. data) and on northern anchovy, *Engraulis mordax* (T. C. Sciarrotta unpubl. data).

The large size of the blue shark's eye suggests adaptation to low light, as in general, nocturnal fishes have relatively large eyes. However, large eyes are also associated with moderately deep

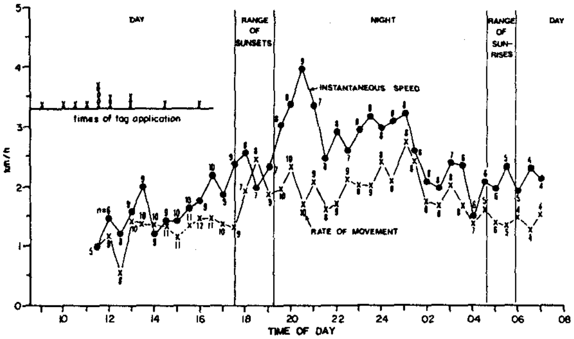

FIGURE 5.—Comparison of mean rate of movement (all sharks) and telemetered swimming speed (sharks with speed sensors) for blue sharks. Note the increase in both parameters at night, the greater values for swimming speeds (as expected), the close similarity during times corresponding to shoreward movements (relatively straight swimming), and the large disparity in early evening (relatively nonstraight swimming).

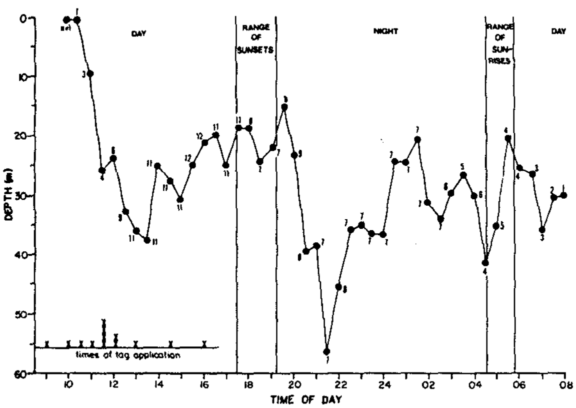

FIGURE 6.—Mean depths of all blue sharks tracked with transmitters having depth sensors. The first hour of each tracking is deleted because of the initial plunge in response to tag application. Note the generally greater depths at night.

habitat (mesopelagic), but since the blue shark's habitat appears relatively shallow (epipelagic), the large eye would seem best suited to visual hunting at night.

It is known that cephalopods and small pelagic fishes form a major part of the diet of blue sharks (Strasburg 1958; Stevens 1973; Tricas 1977). The observed seasonal differences in diel movement patterns (Figures 1, 3) may reflect differences in type or location of prey. Fishery landings of market squid, *Loligo opalescens*, were high during February to June 1972, but low from July to December (Pinkas 1974), thereby indicating the inshore presence of spawning congregations (Frey

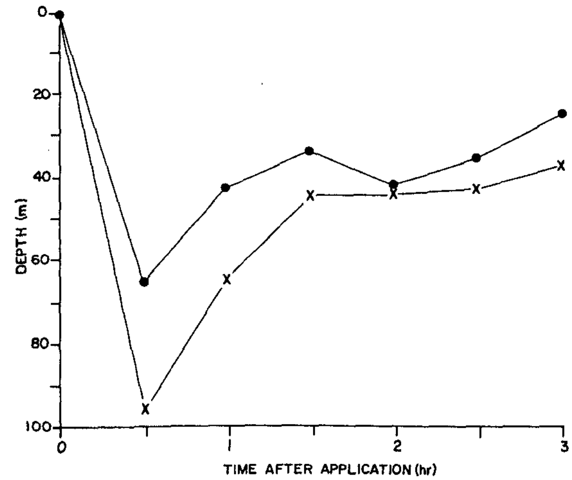

FIGURE 7.—Mean depths of blue sharks for the first 3 h of each tracking. Upper curve, all 12 sharks carrying transmitters with depth sensors. Lower curve, seven sharks judged to have made an "abnormal" plunge in response to the trauma of tag application. Note that the initial depth response appears to have subsided by the recording session 1.5 h after application.

1971), which are susceptible to commercial fishermen using night-lighting techniques. Cousteau and Cousteau (1970) described blue sharks gorging themselves on spawning squid that were light-attracted to the surface near their vessel.

The evening-twilight onshore movements which occurred during March to early June may be due to the nearshore abundance of squid and a possibly reduced availability of prey offshore. Conversely, the offshore pattern from late June to October may be a result of reduced squid population nearshore, but increased populations of jack mackerel, *Trachurus symmetricus*, and anchovy offshore. The limited stomach-content data collected during this study support this hypothesis.

In regard to depth/temperature preferences, the results of Strasburg (1958) are somewhat different from those of the present study. His longline catches of blue sharks at equivalent latitudes were from depths of 53 to 93 m (45%), 93 to 143 m (30%), and 123 to 166 m (25%). The blue sharks tracked in the present study appeared to exceed 93 m only about 5.1% of the time (excluding initial plunges). It is conceivable, however, that Strasburg's percentages may have been influenced by the sharks being attracted deeper than normal by the sloping odor corridors from baits on the gradually sinking longlines. That blue sharks on occasion go even deeper than Strasburg's deepest hooks was noted by Pethon (1970) who reported captures in Norwegian waters from depths as great as 370 m. Davies and Bradley (1972) observed individuals at depths between 100 and 275 m during a descent in the submersible *Deepstar 4000*. A large school of northern anchovy was also observed in this depth range and a predator-prey relationship was suggested, although the possibility of the sharks following the descending submersible could not be eliminated.

In regard to temperature, Strasburg (1958) recorded 99% of his catches over the range of 7° to 20°C, with 67% between 10° and 15°C. Thus, temperature alone may not be reason for the apparent absence of blue sharks from the offshore study area during January and February 1972 when the surface temperature was about 13°C.

The navigational mechanism employed by the sharks during their island-oriented migration is unknown. Traditional explanations for such fish movements include sun-compass orientation, visual landmark recognition, and orientations to chemical or thermal gradients. None of these mechanisms seem plausible in view of the constancy of the pelagic environment, depths usually occupied during the movement, and the relative darkness in which the movements often occurred. Orientation to magnetic or electric fields is one possibility that must be considered in view of the recent findings of Kalmijn (1971, 1973) demonstrating magnetic/electric responses in sharks of adequate sensitivity for such a mechanism. Another possibility is orientation by passive acoustic means to the sounds of the island shoreline, in a manner similar to that suggested by Evans (1971) for dolphins.

The diel inshore-offshore migration shown by this study must also be considered in view of the much longer range movements exhibited by blue sharks. Individuals off California are known to segregate by sex, and seasonal changes in sex ratios imply seasonal north-south migration, perhaps in response to water temperature (Johnson 1974; Bane 1968; Tricas 1977). Tagged individuals have exhibited some very long-range movements. One blue shark tagged by Bane off Newport Beach, Calif. in July 1967 was recovered in December of the same year about 1,300 km west of Nicaragua. Another tagged by D. R. Nelson (unpubl. data) off San Diego, Calif. in October 1966 was recovered in October 1969 about 1,800 km west of the Galapagos Islands, a distance of 4,000 km from its tagging site. This shark was captured only 8 days short of a full 3 yr at liberty and, therefore, did not appear to be participating in any seasonal north-south migration. Both of the above sharks were recovered by Japanese fishing vessels, presumably longlining in relatively deep, cool water.

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