

# DAILY PATTERNS IN THE ACTIVITIES OF SWORDFISH, *XIPHIAS GLADIUS*, OBSERVED BY ACOUSTIC TELEMETRY

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## ABSTRACT

Horizontal and vertical movements of swordfish were studied using acoustic telemetry. Five swordfish in the Pacific and one in the Atlantic were tagged with transmitters which provided information on location, depth, and surrounding water temperature. Two of the Pacific fish showed a clear daily cycle of movement between an inshore bank during the day and deep water offshore at night. All of the swordfish responded to light, swimming deep during the day and coming near the surface at night. In the Pacific depth during daylight appeared to be limited to about 100 m by the oxygen-minimum layer, but in well-oxygenated waters of the Atlantic, a midday depth of greater than 600 m was recorded and the fish appeared to follow an isolume. Depth of the Atlantic fish in daylight was related to changes in light caused by variation in water transparency. The vertical movements were associated with temperature changes of as much as 19° C within 2 hours. The implications of rapid vertical movements on buoyancy and swim bladder volume are discussed.

Despite their high commercial value and their significance as one of the large predators of the open ocean, relatively little is known about the habits and behavior of the swordfish, *Xiphias gladius*. The information which is available comes chiefly from observations made at the sea surface by commercial fishermen and from a few scientific studies based on commercial captures. Swordfish are large, fast-swimming fish that offer little opportunity for direct observation; however, some aspects of their behavior can be readily examined by telemetry from attached sensors.

*Xiphias gladius* is found throughout tropical and temperate waters. Its appearance in higher latitudes usually occurs in warm-season aggregations along the edge of the continental shelf and on offshore banks (Rich 1947; Wise and Davis 1973). The seasonal appearance of swordfish in both the western North Atlantic and Hawaiian fisheries (Uchiyama and Shomura 1974; Caddy<sup>3</sup>) coupled with the known distribution of their larvae and of adults with ripe gonads indicate a spawning migration to waters warmer than 23°-24° C (Arata 1954; Taning 1955; Gorbunova 1969; Markle 1974; Nishikawa and Ueyanagi 1974),

while nonspawning fish appear to move between coastal and oceanic waters. Tagging studies show that some swordfish undertake long-distance movements. For example, a 12 kg swordfish tagged near the Mississippi Delta in March 1974 was recovered from Georges Bank at a weight of 86 kg in August 1977 (Casey<sup>4</sup>). The recovery of tagged swordfish near the point of release, even after several years at large (Beckett 1974), implies homing behavior if we assume that these fishes are regular migrators.

Longline fishery captures of swordfish occur primarily at night on hooks set at depths of 5-50 m. Deeper vertical excursions have been documented by DSV *Alvin* when the submersible was attacked by a swordfish at 610 m (Zarudski and Haedrich 1974) and by observation from *Deepstar* at 654 m (Church 1968). The harpoon fishery relies on the occurrence of swordfish near the surface during the day where they are commonly found resting in the warmer surface waters, often with their dorsal and upper caudal fins exposed. In this situation they can be approached and harpooned. This "basking" behavior may warm the fish and aid in the digestion of prey caught while foraging at greater depths. Spotter pilots for the harpoon fishery report that basking swordfish often defecate before sounding or breaching.

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<sup>3</sup>Caddy, J. F. 1976. A review of some factors relevant to management of swordfish fisheries in the northwest Atlantic. Environ. Can., Fish. Mar. Serv., Tech. Rep. 633, 42 p.

<sup>4</sup>John G. Casey, Apex Predator Program, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882, pers. commun. 1978.

Examination of swordfish stomach contents (Scott and Tibbo 1968; Ovchinnikov 1970) showed that they feed on cephalopods and a wide variety of nektonic fishes (e.g., anchovies, hake, mackerel) and micronektonic fishes (e.g., myctophids, paralepidids) and that a significant portion of their diet consisted of vertically migratory mesopelagic species. We have also found unusual items in their stomachs including birds and shrimp. Swordfish have been observed swimming through schools of fish, stunning them with their swords before eating them (Goode 1883). Fish removed from swordfish stomachs often show damage to the muscle and vertebral column from having been hit by the sword (Scott and Tibbo 1968). Swordfish have large eyes and are efficient visual predators even in dim light. Small phosphorescent lights are occasionally used to attract them to longline hooks, which indicates that they may also respond to bioluminescence.

Swordfish are aggressive and there are many accounts of their attacking and ramming their bills into ships, whales, and other objects (Goode 1883; Gudger 1938; Smith 1956; Jonsgard 1962). We have seen penetrating wounds in swordfish and Edlin<sup>5</sup> found a 15 cm fragment of a swordfish bill that entered near the heart of a 70 kg swordfish and was driven back into the body cavity, which may indicate that they strike each other. While they are generally solitary, longline fishermen say that in the Straits of Florida, a spawning area, swordfish may be encountered in twos with some regularity.

In the present study we investigate the horizontal and vertical movements of swordfish during their daily activities and attempt to determine the range of temperatures they encounter. We used acoustic telemetry to monitor data from depth and temperature sensors attached to the fish for periods of up to 5 d. The results presented here provide the first description of their activities based on continuous direct observations of individuals.

## METHODS

We attempted to attach transmitters to seven swordfish and were successful with five in the Pacific, near Cabo San Lucas at the tip of Baja California, and one in the Atlantic, east of Cape Hatteras, N.C.

For the experiments off Baja California, the swordfish were located on the surface by aircraft and the transmitters harpooned into the free-swimming fish from the tracking vessel *Sea World*. In the Atlantic, the swordfish were taken on commercial longline fishing gear set by the tracking vessel *FV Diane Marie*. Weights of the fish were estimated by the fishermen.

## Transmitters

Two types of sensors were used in the transmitters. Depth transmitters had a 500 or 1,000 lb/in<sup>2</sup>g Biotek<sup>6</sup> strain gage pressure transducer. Temperature transmitters had a 300 kΩ Fenwall GA53M2 thermistor linearized with a series resistor. An up-down integrating circuit converted resistance changes in the sensor to a varying pulse rate. The pulses keyed an oscillator and output stage which drove a 1.27 cm long, 2.79 cm (outer diameter) cylindrical ceramic transducer (Marine Research TCD 5) with 30 ms pulses of ultrasound at an electrical power level of one to several watts. The transducers, which were mechanically resonant at 33 kHz, were operated at 32 kHz for temperature and 34 kHz for depth so that signals could be separated in experiments where both were used simultaneously.

Power was supplied by a battery of five 1.2-Ah lithium cells (Mallory L0325) which give a useful life of about 1 wk. Range was as great as 3-5 km at times, but much shorter when propagation conditions were poor.

The transmitters were 14 cm long, 4.5 cm wide by 3 cm thick and weighed 250 g in air and 90 g in water. They were cast in a strong epoxy plastic (Hysol 2039 resin, 3561 hardener) and tested to withstand hydrostatic pressures equivalent to a depth of 1,000 m. A miniature (6.5 cm long) swordfish dart was tied to the end of the transmitter with a 13 cm loop of twisted 200-lb (91 kg) test monofilament nylon (Figure 1). An adapter which fitted on a standard swordfish harpoon had a crosspiece which limited penetration of the dart to about 10 cm. In some experiments depth and temperature transmitters were tied in tandem and attached to the fish with a single dart. The swordfish showed no obvious reaction to the tags once they were attached.

The instruments were stable and accurate.

<sup>5</sup>Robert Edlin, P.O. Box 341303, Coral Gables, FL 33134, pers. commun. 1980.

<sup>6</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

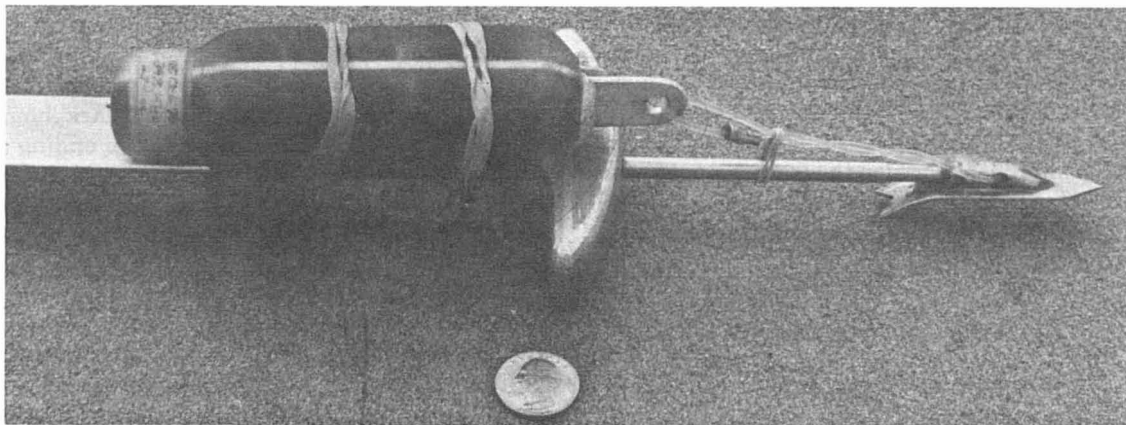


FIGURE 1.—Depth transmitter for swordfish. Rubber bands hold the transmitter to an adapter which fits on a standard swordfish harpoon. The crossbar on the adapter serves to limit penetration of the harpoon dart. A conductive path between two elements of a seawater switch turns the transmitter on when it enters the water. The coin is 24 mm in diameter.

Changing battery voltage did not affect the pulse rate of either type of transmitter, and the pulse rate of depth transmitters was not affected by temperature changes in the range 5°-30° C. In use we found that several days into an experiment the depth transmitters would still indicate <1 m when the fish was seen on the surface. A temperature transmitter recovered after 13 d on a fish was recalibrated and found to be within 0.1° C of the original calibration.

### Receiving

We listened to the transmitters with a directional hydrophone constructed of seven ceramic transducer rings wired in parallel in a cylindrical array 10.5 cm long. The rings were backed with a layer of closed-cell polyethylene foam and cast in epoxy. A preamplifier in the hydrophone amplified the signal 100× and reduced problems from electrical noise picked up on the cables. The upper and rear surfaces of the horizontally mounted hydrophone cylinder were acoustically shielded with four alternating layers of 3 mm thick foam rubber and steel, leaving an approximately 140° sector uncovered and facing forward and down. The hydrophone was mounted at the bow of the vessel on a streamlined fin arranged so that it could pivot and follow the flow of water as the boat yawed. A shaft through the fin allowed the hydrophone to be rotated by a rope and pulley system from the bridge of the vessel.

The receivers (Lawson Instrument Company and CAI CR-40) were mounted on the bridge so

that one person could follow the fish by rotating the hydrophone to find the strongest signal, then steering the boat in that direction. Data were recorded by timing a fixed number of pulses to the nearest 0.1 s with a stopwatch and converting the pulse rate to temperature or depth using a linear regression for the calibration curve. A 0.1 s counting error in a 30 s count produced a depth error of approximately 2 m. Data were taken routinely every 5 or 10 min and more frequently when the fish was changing depth. An automatic data recording system, based on a phase lock receiver, was used on 11 November 1977 and gave a continuous, detailed record of a swordfish rising to the surface in a series of steps.

### Navigation

In the Baja California area we used radar to determine range and bearing to various peaks and headlands. The relative accuracy of this technique was good as checked by comparison of echo sounder depth with depth given on the chart at the plotted position. In the experiment near Cape Hatteras we used loran C with an accuracy better than 1 km. The position of the vessel was recorded when it was brought close to the fish and the plot of these positions used to approximate the fish's course.

### Temperature

Temperature of the water was measured with expendable bathythermograph probes (XBT) (Sip-

pican T-6 and T-10) which were dropped routinely every several hours and more frequently when passing through boundaries between water masses. The XBT records were used to construct plots of isotherm depth. By superimposing the plot of swordfish depth on the isotherms, we could tell water temperature at the location of the fish in those experiments where a temperature transmitter was not used.

## RESULTS

### Swordfish No. 2, 19-24 April 1977, Baja California, Mexico

This 70 kg swordfish sounded when struck with the transmitter, but quickly came up and spent 20 min on the surface. It appeared to be in good condition and unaffected by the depth transmitter. During a 5-d period it showed a clear cyclical pattern of movement between an inshore bank during the day and offshore waters at night (Figure 2). Each day it occupied the same area along the 50-fathom (91 m) depth contour on the bank. Several hours before sunset it would move offshore, going out as far as 26 km from land, and remain in deep water all night. At first light of dawn, 1.0-1.5 h before sunrise, it would swim inshore again and return to the 50-fathom contour on the bank.

The fish remained close to the bottom while on the bank, coming to the surface during daylight only three times in 5 d. On 20 April it was usually 5-10 m up from the bottom and on the following days, usually 5-20 m above it. Each evening, an hour after sunset, swordfish no. 2 rose to the surface and spent the night in the upper 10 m. At first light, an hour before dawn, it descended and moved toward shore at depth with frequent vertical excursions.

### Swordfish No. 3, 26-27 April 1977, Baja California, Mexico

This 70 kg fish was found close to where no. 2 had been tagged and was harpooned with both depth and temperature transmitters. It followed a similar pattern to no. 2, moving offshore before sunset and turning inshore at first light (Figure 3). Several hours before sunset both of these fish would leave their position on the 50-fathom contour of the bank and swim offshore into deeper water. They swam twice as fast, perhaps 3 km/h,

when moving offshore as they had while on the bank. When on the surface several hours after dark, swimming speed usually slowed to 1 or 2 km/h. The movements during the dark hours showed a distinct offshore progression ending at an average distance of about 19 km offshore where the fish moved about slowly until first light. The journey back to the bank was again at a higher speed, about 3 km/h.

From 1100 to 1800 h on the second day, no. 3 remained in one spot and appeared to be resting on the bottom during part of this time (determined by positioning the boat over the fish and noting that the echo sounder depth was the same as that telemetered from the fish). At sunset it rose from the bottom and headed offshore. We lost it soon afterward when our equipment was damaged in rough water.

### Swordfish No. 4, 30 April 1977, Baja California, Mexico

This 80 kg fish was harpooned in midmorning in 500 m of water some 24 km off the coast. It moved slowly in a westerly direction (Figure 4) staying uncharacteristically near the surface, frequently with its fins showing, and did not descend below 10 m. It was followed for only 2 h, then abandoned because of technical problems.

### Swordfish No. 5, 30 April 1977, Baja California, Mexico

This fish weighed about 100 kg and was harpooned close to where we left no. 4. It also moved slowly westward, covering < 3 km in the first 5 h (Figure 4). An hour before sunset it turned south and swam offshore over San Jose Canyon at a speed of 3.5 km/h. During the day it surfaced five times, spending alternate periods on the surface and at 100 m. Sunset marked a period of vertical activity and a gradual ascent to the upper 25-50 m. We lost the fish in rough weather that night as it was swimming offshore on a southerly course.

### Swordfish No. 6, 3-6 May 1977, Baja California, Mexico

Swordfish no. 6 weighed about 140 kg and was harpooned with depth and temperature transmitters in an area about 24 km offshore, near where no. 4 and 5 had been tagged (Figure 4). It swam slowly westward as those fish had done,

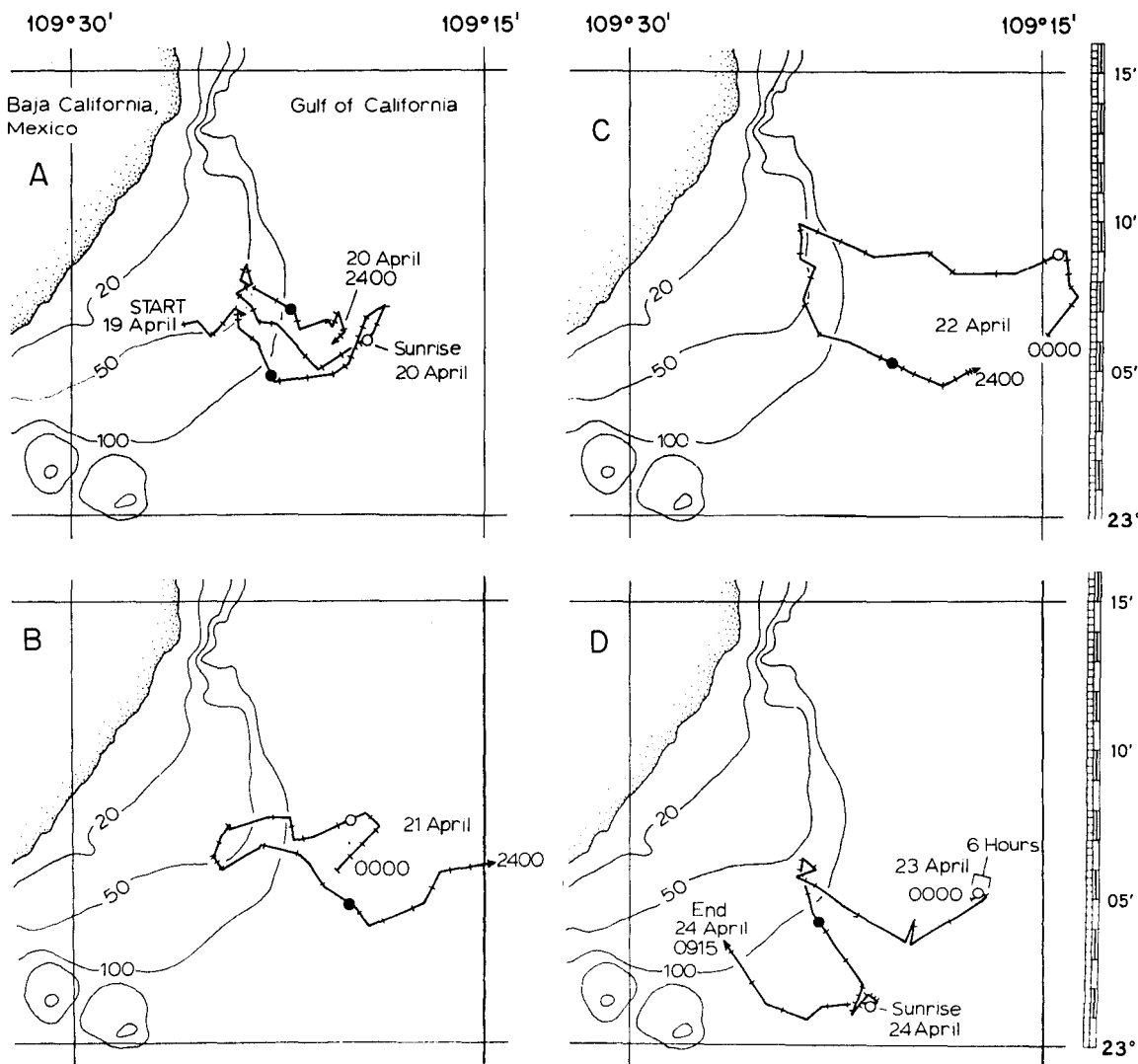


FIGURE 2.—Track of swordfish no. 2, Baja California, separated into four panels for clarity. Each day this fish moved inshore to the 50-fathom (91 m) curve on a bank then moved out over deep water at night. The turn inshore began about 1 h before dawn; the offshore movement began several hours before sunset. Compare with the depth record in Figure 9. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in fathoms.

moving 9 km in 5 h, then turned to the south at sunset and moved down the axis of San Jose Canyon. It continued in a southwest direction when it reached deep (2,000 m) water, and by dawn on 6 May when we abandoned it, it had gone 88 km in 44 h.

No. 6 showed the now-familiar pattern of vertical movements, staying near the surface at night and going deep during the day (Figure 5). Like no. 5 it made excursions to the surface during daylight hours, coming up five times to spend periods

of 0.5-1.5 h on the surface, then returning to depths which averaged 75-100 m, but included much deeper excursions.

While on the surface during the day, no. 5 and 6 swam about actively. No. 6 moved at an estimated 1.6-3.2 km/h (1-2 kn) in a haphazard pattern with much turning, so that progression along its course was considerably slower than its swimming speed. It appeared to be responsive and moved after a live Pacific mackerel, *Scomber japonicus*, which was thrown to it. On one occasion we attempted to

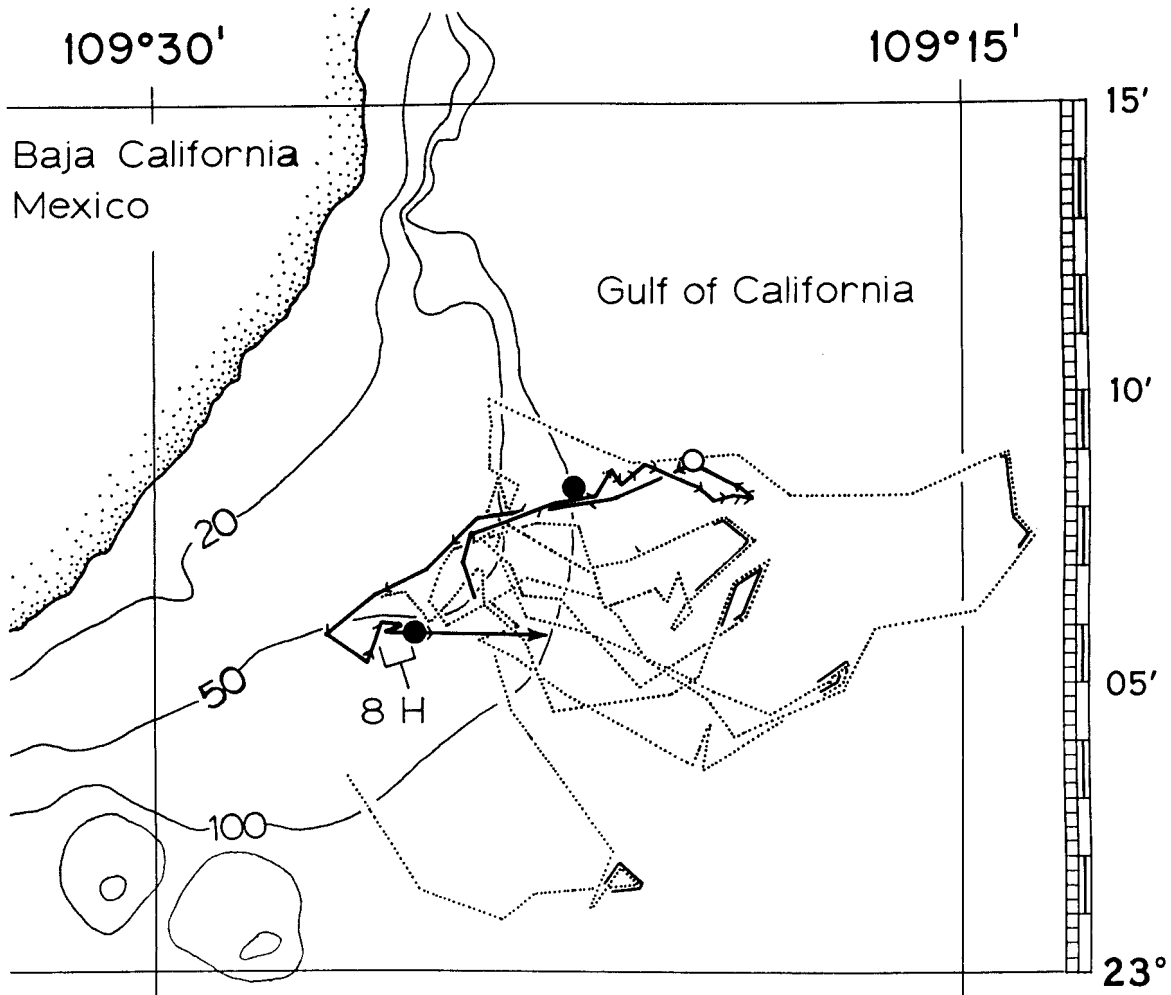


FIGURE 3.—Track of swordfish no. 3 (solid line) superimposed on track of swordfish no. 2 (dotted line), Baja California. No. 3 was on the bottom during much of the indicated 8-h period. The narrow solid lines near the track (dotted line) of no. 2 indicate positions where it was moving slowly on the surface at night. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in fathoms.

drive it down with the boat, but it sank just a few meters and avoided us. When hard pressed, it easily escaped in a series of long horizontal leaps, but did not go below a few meters depth until it had been on the surface for about 1 h.

#### Swordfish No. 7, 9-11 November 1977, Atlantic Ocean

This 70 kg swordfish was taken by longline about 100 km northeast of Cape Hatteras (lat.  $36^{\circ}00' N$ , long.  $74^{\circ}40' W$ ) in a depth of 1,000 m (Figure 6). The fishing gear was left in the water for only 1 h to reduce the time that the fish would

be struggling on the line. The fish was hooked in the tip of the lower jaw, a place where little damage would be expected; its bluish color and active movement gave the impression that it was in good condition. It was tagged with a depth transmitter and cut free within about 15 s after it had been brought alongside the boat.

The longline had been set in a patch of warm blue water (Figures 6, 7). When released the fish swam in a general southeast direction, a course which took it under a tongue of cold, grey-green shelf water. After several course changes, it came out from under this cold water on the second day and entered the Gulf Stream which swept it to

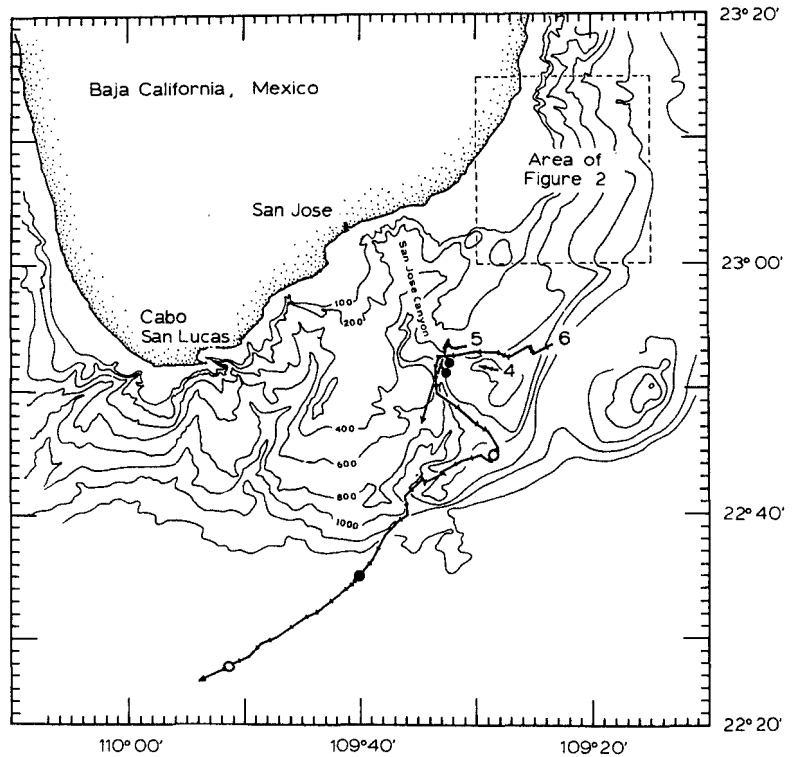


FIGURE 4.—Track of swordfish no. 4, 5, and 6, Baja California. These fish all moved west during the first afternoon; no. 5 and 6 then moved down the axis of San Jose Canyon after sunset. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in meters.

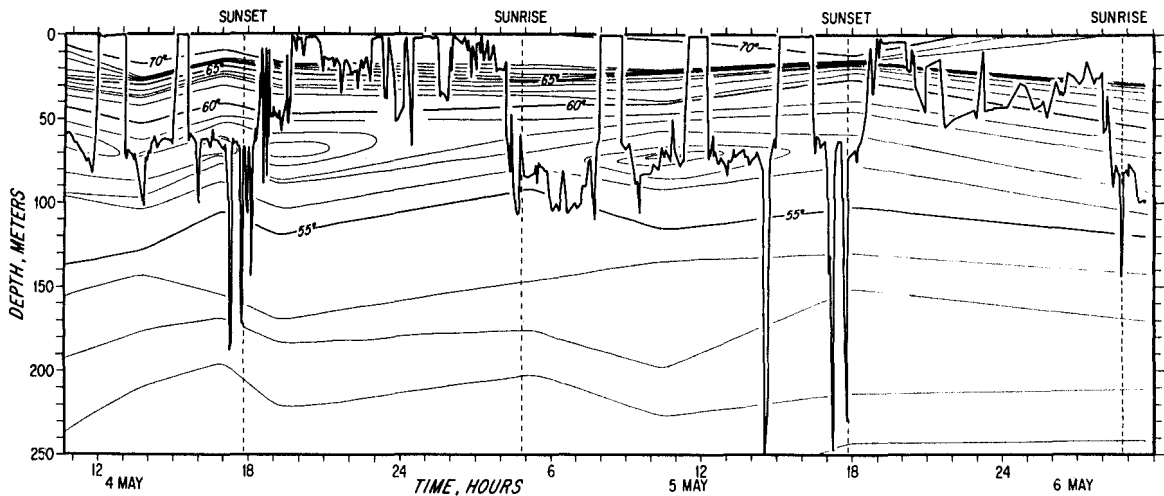


FIGURE 5.—Depth record for swordfish no. 6 off the tip of Baja California superimposed on an isotherm pattern drawn from bathythermograph lowerings. There was a full moon during this experiment and the usual nighttime depths were deeper than those on the moonless nights during experiments with swordfish no. 2 and 3. The fish generally swam below the thermocline during the day and was well into the oxygen-minimum layer, where oxygen concentration was estimated to be about 10% that on the surface. Isotherm interval 1° F.

the northeast. At the end of the third day the flattening of the deep isotherms (Figure 8) indicated that it had crossed the center of the Gulf Stream

and entered the Sargasso Sea. When we abandoned the fish it had gone a distance of 240 km in 67 h.

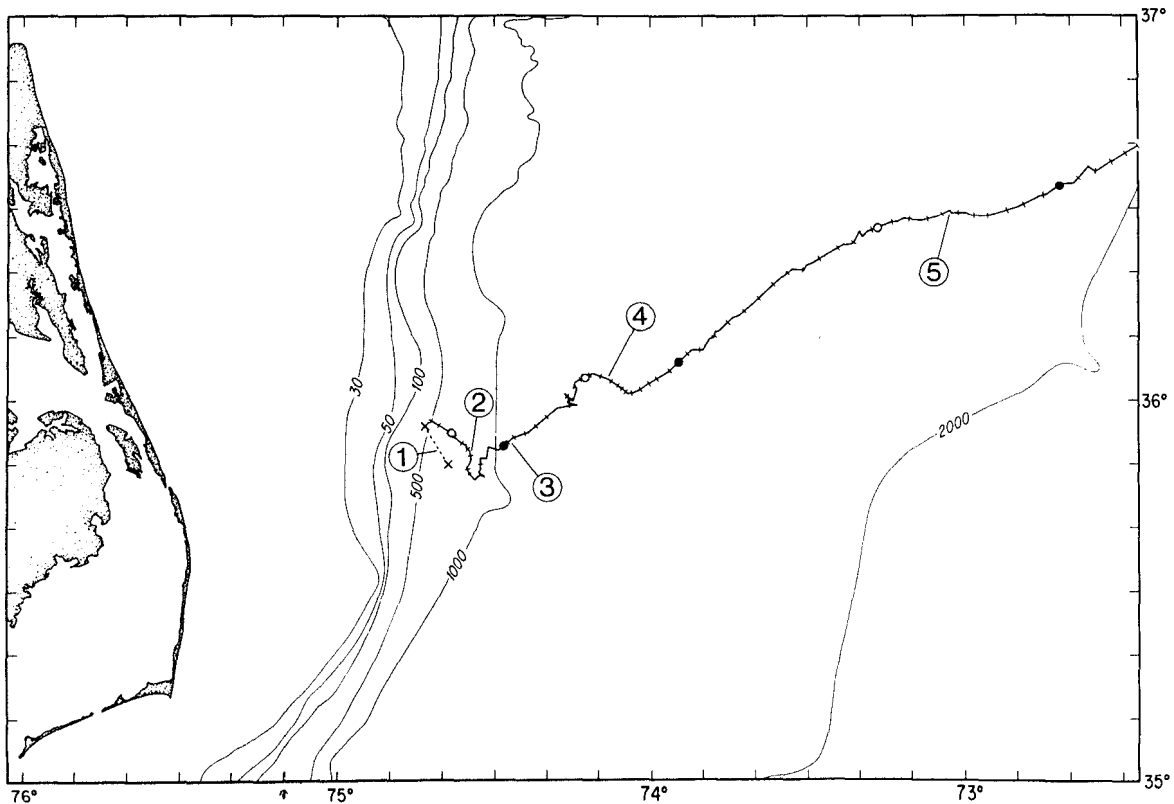


FIGURE 6.—Track of swordfish no. 7 in the Atlantic near Cape Hatteras, N.C. 1) Dotted line indicates position of longline gear where this fish was caught. 2) The swordfish moved beneath a layer of cold surface water at 1000 h on 9 November. 3) It emerged from beneath the cold surface layer at 2000 h on 9 November. 4) By 0500 h 10 November, it was in the Gulf Stream. 5) At 1500 h 11 November, it had crossed the Gulf Stream and entered the Sargasso Sea. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contour lines in fathoms.

During the first day, the vertical movements of no. 7 were complex. On the second and third day however, it followed a clear pattern of moving near the surface at night and going deep during the day. An hour before dawn on 10 November it was in 27° C water at a depth of 20 m (Figure 8). It began to descend and was in 8° C water at 400 m 2 h after sunrise. An hour before sunset it started back toward the surface and was at 20 m at twilight. No. 7 spent the night at about 20 m with four brief excursions to 100 m. Some of these were caused by our tracking vessel, for swordfish would often dive when we drove the boat over them and would do this even at night when the ship was darkened. The depth pattern on 11 November was similar to the previous day. Leaving the surface 1 h before dawn, it descended rapidly and was at 450 m shortly after sunrise. It continued to descend, reaching 617 m at noon,

then starting back up, slowly at first, then more rapidly around sunset.

A continuous recording of the final ascent, made with the phase lock receiver, shows that it was done in steps with a rapid rise of 20-80 m, a pause for several minutes, then another rapid rise (Figure 8).

## DISCUSSION

### Horizontal Movements

Swordfish no. 2 and 3 showed clear cycles of movement between deep water and an inshore bank. During the day they occupied a rather narrow region, perhaps 8 by 1.5 km, along the 50-fathom (91 m) contour on the bank where the bottom fell off to the south and east (Figure 3). They stayed close to the bottom, moving slowly,



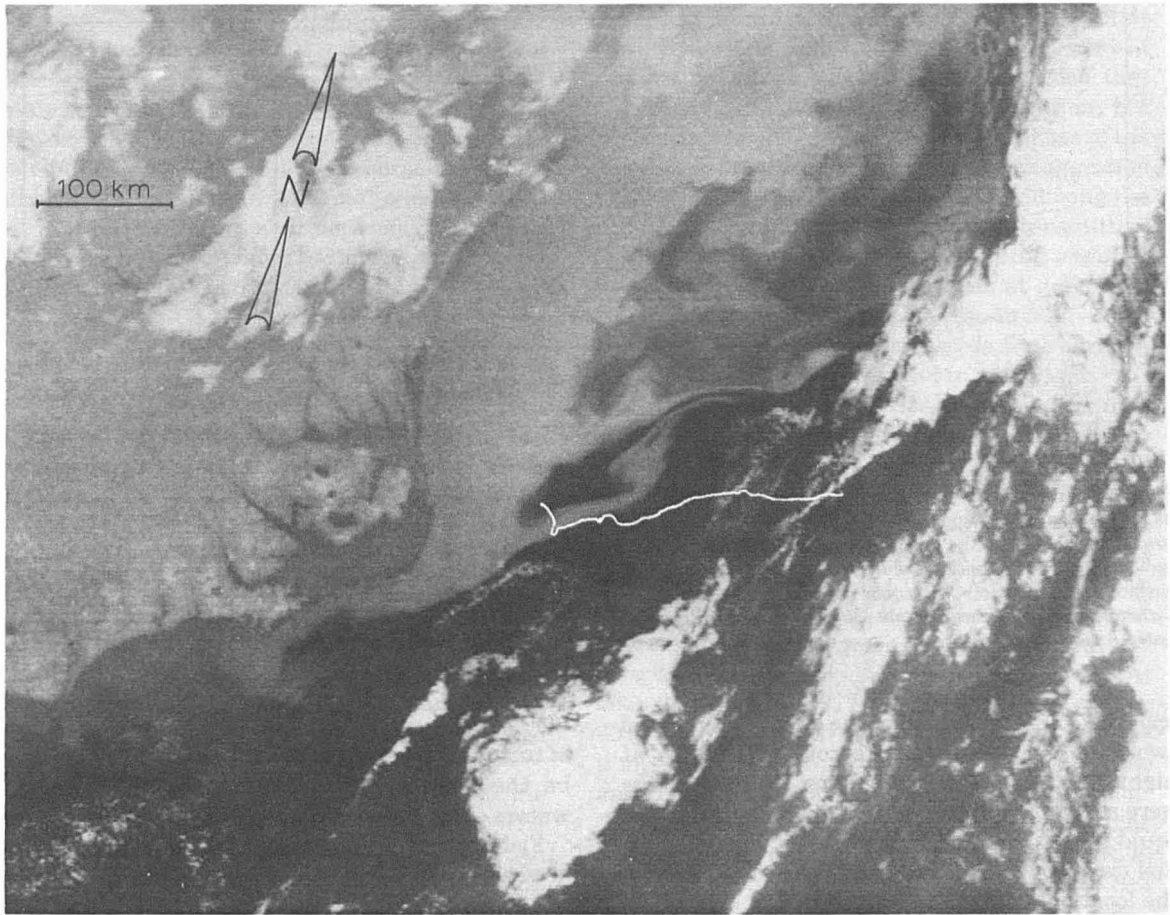


FIGURE 7.—Satellite infrared image of the Atlantic east of Cape Hatteras, N.C. (left center), with track of swordfish no. 7 superimposed. Light areas indicate cold water and dark areas warm water. The Gulf Stream moving past Cape Hatteras pulls off a streamer of cold shelf water. Swordfish no. 7 was tagged on the north side of this streamer, swam under it (see Figure 8), and crossed the Gulf Stream into the Sargasso Sea.

and may at times have been resting on it. Swordfish commonly feed on bottomfish (Scott and Tibbo 1968), and this location may have allowed them to prey on demersal fish moving on and off the bank.

In the evening no. 2 and 3 swam rapidly offshore and spent the night moving slowly in positions about 20 km from the coast (Figures 2, 3). A different area was visited each night, but they returned to the same spot on the bank every day. Squid, which were abundant on the surface at night, came to our lights in large numbers when we stopped. It is likely that the swordfish moved offshore to feed on the squid and other vertically migrating fauna which concentrate near the surface at night. The onshore-offshore movements which we observed may have been a feeding routine which allowed the swordfish to prey on

demersal fish available in a prescribed spot on the bank during the day and to feed on squid and other prey wherever they were found over deep water at night.

In an area near Hawaii, Yuen (1970) used an acoustic transmitter to follow a skipjack tuna, *Katsuwonus pelamis*, for an 8-d period. He found that the fish remained with its school which spent the day on a bank and moved out over deep water at night. The nighttime positions were 20-100 km away from the bank, and like swordfish no. 2 and 3, a different area was visited each night. The behavior of the school during the day suggested to Yuen that the fish were foraging. A diel inshore-offshore movement cycle in the blue shark, *Prionace glauca*, near Catalina Island was reported by Sciarrotta and Nelson (1977). This cycle was

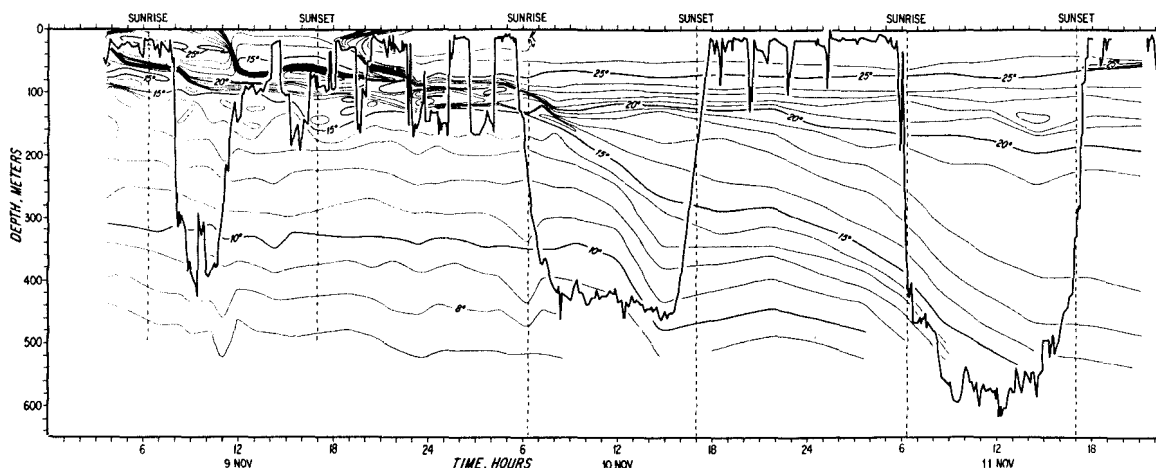


FIGURE 8.—Depth record for swordfish no. 7 off Cape Hatteras in the Atlantic superimposed on a  $1^{\circ}$  C isotherm plot drawn from expendable bathythermograph casts. On 9 November the fish passed under a cold streamer of shelf water (see Figure 7) and rose toward the surface in the middle of the day, probably in response to the decreased light. On 10 November the deepening isotherms indicate that the fish was following an isolume, descending 1 h before dawn, reaching its greatest depth at midday and coming to the surface 1 h after sunset. Continuous recording of depth on 11 November shows that the rise toward the surface at sunset was made as a series of steps with several minute pauses at each level. The flattening isotherms toward the end of the record indicate that the fish had entered the Sargasso Sea.

opposite in phase to that of the skipjack tuna and swordfish, with the sharks coming inshore at night. The authors suggested that the movements were associated with the nighttime availability of squid near the beach. It is likely that all of these diel cycles of movement are linked to changes in the location and availability of food.

Swordfish no. 4, 5, and 6, which were offshore in water 400-800 m deep, moved slowly west after they had been harpooned (Figure 4). We abandoned no. 4, but no. 5 and 6 continued until they were over San Jose Canyon, the most prominent submarine canyon in the area. Near nightfall, both of these swordfish changed course and moved south along the length of the canyon. The correspondence with the axis of the canyon is not exact, but the course change and the movement of both fish along the canyon suggests they were responding to the bottom topography. Commercial longline fishermen feel that the submarine canyons and hummocky areas along the edge of the continental shelf are good places to find swordfish.

Currents flowing over rough bottom produce eddies and flow separation features which may extend to the surface. The patterns of such turbulent flow affect the distribution of biological sound scattering particles and produce concentrations of organisms which can be seen in 200 kHz echograms made over Hudson Canyon in the Atlantic

(Orr<sup>7</sup>). The concentration of organisms as a result of turbulence generated by the rough bottom may be the feature that attracts swordfish to the waters over submarine canyons.

Fishermen had suggested that swordfish in the area where no. 2 and 3 were followed were part of a resident population, while those in the area of no. 4, 5, and 6 were transient. Our results are consistent with this notion.

In the Atlantic, swordfish no. 7 swam in a southeasterly direction at a speed of 1.5-2.0 km/h during the first day. On the second day it entered the Gulf Stream as indicated by the deepening of the isotherms in Figure 8. While in the Gulf Stream it moved on a course a little north of east at a speed of 5.5 km/h, with most of this velocity contributed by the current which was flowing northeast. The course of the fish was to the south of the direction of the current, indicating that there was a southerly component to its swimming. It probably continued to swim on its original course and speed after entering the Gulf Stream. By the time we abandoned it on the third day, it had crossed the Gulf Stream, which is about 75 km wide at this point, and entered the Sargasso Sea. This can be seen from the flattening of the deep

<sup>7</sup>Marshall Orr, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1980, manuscript in prep.

isotherms at the end of the track in Figure 8 and from the position of the Gulf Stream indicated on the 9 November 1977 Experimental Ocean Frontal Analysis Chart.<sup>8</sup> Swordfish concentrate along the edge of the continental shelf, but are widely distributed over the ocean. The course that no. 7 followed may have been a normal one for swordfish in the Hatteras area, or no. 7 may have been influenced to swim offshore by the trauma of being caught on longline fishing gear.

### Vertical Movements and Light

The tagged swordfish showed a clear diel pattern of vertical movements, going deep during the daylight hours and coming to the surface at night (Figures 5, 8, 9). This is best illustrated by swordfish no. 7 on 11 November (Figure 8). The fish spent the night at about 20 m. About 1 h before dawn, when light was just noticeable in the east, it swam down rapidly, reaching a depth of 400 m by sunrise, and worked gradually deeper until it reached 617 m at midday. After noon the swordfish gradually rose again, increasing its rate of ascent sharply around sunset and reaching the surface about 1 h later.

There is an obvious relationship between the vertical movements of swordfish and light. The most rapid changes in depth were during a 2-h period at dawn and dusk when surface illumination changes by six or seven orders of magnitude (Brown 1952), and the greatest depth was reached at noon when light at the surface was at a maximum. The U-shaped pattern of the depth curve would be expected for an animal following an isolume (Blaxter and Parrish 1965; Boden and Kampa 1967).

The swordfish also appeared to respond to moonlight. There was no moon during experiment 2 (new moon, 21 April) and only a thin crescent for swordfish no. 3. On these nights, which were starlit and calm, the swordfish were usually at depths <10 m and often right on the surface (Figure 9). In the other experiments there was a full moon shining through clouds and it was windier. Nighttime depths for no. 5 and 6 were 10-50 m (Figure 5) and for no. 7 about 25 m (Figure 8). The fish were probably swimming at a greater depth in response to moonlight, although the wind might also have had an influence.

Guitart Manday (1964) analyzed the depth at which swordfish were taken in a Cuban fishery at various phases of the moon. He concluded that moonlight did not affect vertical migration, but noted that the fishermen felt that the phase of the moon was important and there is some suggestion in his data that fish were taken deeper during the full moon. Tesch (1978) used acoustic transmitters to follow the silver eel stage of *Anguilla anguilla* and reported that one which swam at a depth of 100 m while the moon was up rose to 50 m when the moon set. Our similar records for swordfish suggest that they also respond to moonlight.

If swordfish move vertically to maintain a constant level of illumination, the light level they follow should be somewhat greater than that on the clear, starry nights when they came to the surface and somewhat less than in moonlight when they swam at 10-50 m depth. We may use the values for irradiance of  $3 \times 10^{-1} \mu\text{W}/\text{cm}^2$  under a clear night sky with full moon,  $3 \times 10^{-3} \mu\text{W}/\text{cm}^2$  for a clear sky with no moon, and  $3 \times 10^{-4} \mu\text{W}/\text{cm}^2$  for a dark night from Clarke and Kelly (1964). At noon, 11 November 1977, swordfish no. 7 was at lat.  $35^\circ$  N and at a depth of 600 m. Surface illumination,  $I_0$ , for this time, recorded in Woods Hole and corrected for latitude, was  $5 \times 10^4 \mu\text{W}/\text{cm}^2$  (Payne<sup>9</sup>). Light,  $I$ , at depth,  $L$ , of the fish can be calculated assuming an attenuation coefficient,  $k$ , of 0.028 for the clear Gulf Stream-Sargasso Sea water in this area, (Clarke and Backus 1964). The relationship

$$I = I_0 e^{-kL}$$

gives  $2.5 \times 10^{-3} \mu\text{W}/\text{cm}^2$ , a value similar to that on a clear, moonless night when the fish might be expected to come to the surface. The fact that swordfish may also come to the surface during the day indicates that they are not locked to an isolume, but under some conditions they do appear to adjust their vertical position in a manner which would maintain a constant, dim illumination throughout the day.

Vision is obviously important to swordfish. The eyes of a 150 kg fish are as large as an orange and almost touch in the midplane of the skull. The amount of light we calculate for the isolume followed by swordfish is many orders of magnitude greater than the  $3 \times 10^{-10} \mu\text{W}/\text{cm}^2$  suggested as a

<sup>8</sup>U.S. Navy Oceanographic Office NSTL Station, Bay St. Louis, MS 39522.

<sup>9</sup>R. E. Payne, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1977.

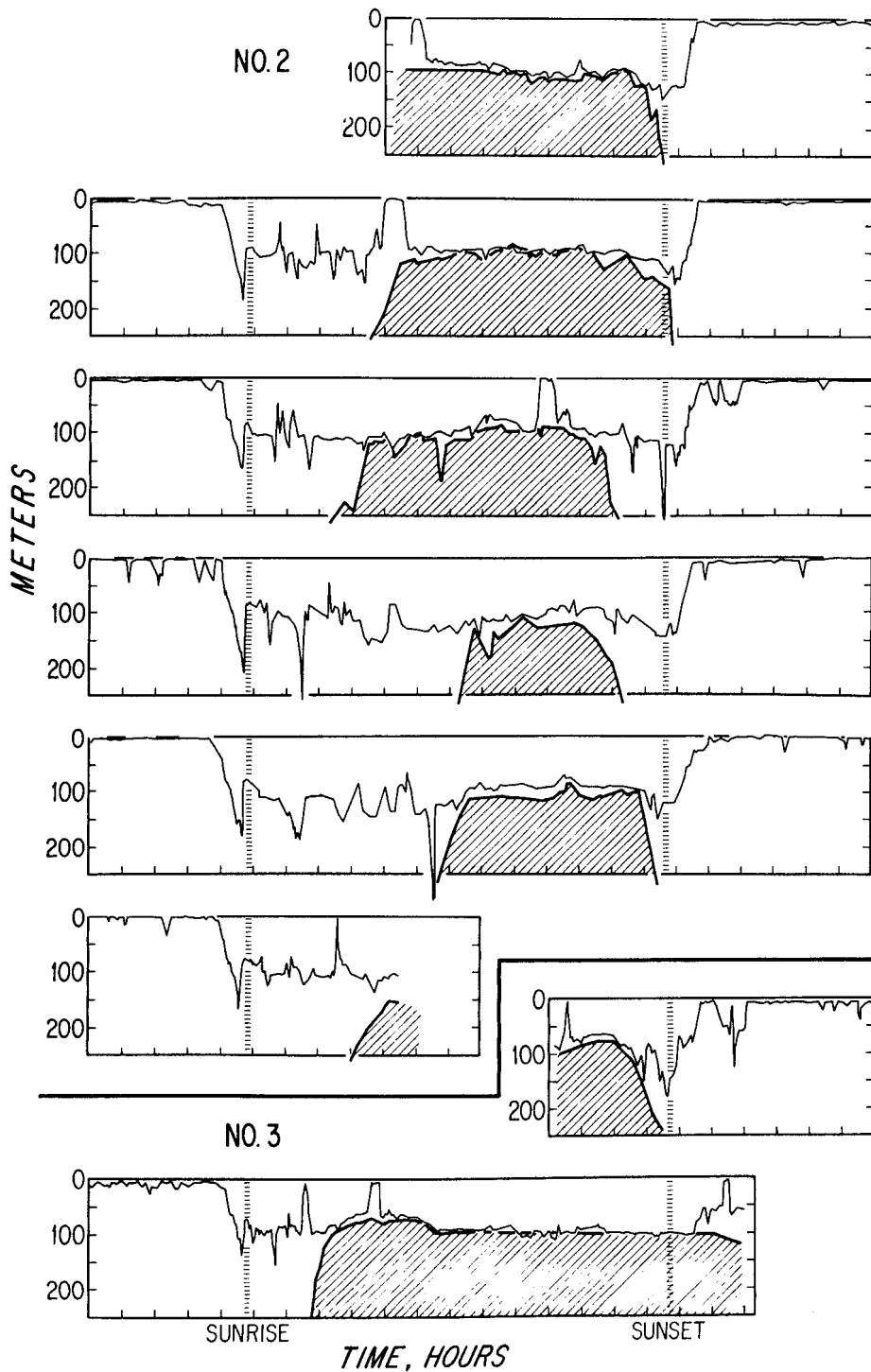


FIGURE 9.—Depth records for swordfish no. 2 and 3, Baja California, plotted from midnight to midnight. The crosshatched area indicates a bank. The fish swam near the surface at night and at a depth of about 100 m during the day. The morning dive about 1 h before sunrise carried the fish below its usual daytime depth.

threshold for vision in deep-sea fish (Denton and Warren 1957; Clarke and Denton 1962). The swordfish should be able to locate its prey visually in its dimly lit environment both day and night.

Our depth records for swordfish show many variations from the U-shaped pattern expected if they are following isolumens. Much of this variation can be explained as modification of a response to light by other environmental factors. On 10 November the depth record for no. 7 was skewed, with the greatest depth reached late in the afternoon (Figure 8). The deepening isotherms during this day indicate that the fish was moving from shelf and slope water into the warm, clear water of the Gulf Stream. Light attenuation is much greater inshore than in the Gulf Stream (Jerlov 1968) where the same level of illumination occurs at greater depths. The gradual increase in depth during the fading daylight on this afternoon coincided with the movement from slope to Gulf Stream water and can be interpreted as the fish maneuvering deeper to maintain a constant light intensity in the clearer water.

On 9 November, no. 7, which had reached 400 m by midmorning, returned to 100 m at noon. This unexpected midday rise from depth occurred when the fish left a region of clear blue slope water and passed under a streamer of dark grey-green shelf water (indicated as a marked thermal inversion in Figure 8 and as a light-colored region in the satellite infrared image, Figure 7). Swimming under this dark shelf water, the swordfish entered a shadowed area. By rising toward the surface it would have returned to a light level which prevailed at greater depth in the blue water. A change of attenuation coefficient from 0.035 in blue water to 0.140 in shelf water would result in the same light intensity at 400 m as at 100 m depths, respectively. These are reasonable attenuation values and it is possible that the swordfish was maintaining a constant light level during this vertical movement.

### Oxygen

A vertical movement in response to sunrise and sunset occurred in all of the Baja California experiments. An interesting feature is apparent when these depth records are aligned vertically (Figure 9). The rapid descent which began about an hour before dawn each morning reversed at sunrise when the fish came back up to about 100 m. A well-developed oxygen-minimum layer

exists in this area of the eastern tropical Pacific and the oxycline at the top of the low oxygen region is parallel to the thermocline, but at somewhat greater depth (Griffiths 1968, fig. 11 and 27). In its normal movement away from the surface with increasing light at dawn, the swordfish penetrated deeply into this low oxygen layer, then returned to spend most of the day at shallower depths with higher oxygen concentration. The presence of the oxygen-minimum layer caused the swordfish to spend the day at a shallower depth and higher light level than normal.

In Baja California swordfish frequently came up during the day to bask on the surface with the tips of their dorsal and caudal fins out of the water for periods of 15-80 min. This basking behavior, at a time of day when we would expect them to be at their greatest depth, may be related to the low oxygen concentration at depth. The depth record for no. 6 superimposed on an isotherm pattern in Figure 5 shows that the fish was well below the thermocline during much of the day. We did not measure oxygen, but using the data in Griffiths (1968) we can infer concentrations from water temperature and depth. When swordfish no. 5 and 6 were below the thermocline, they were in an environment with an oxygen concentration only 10 to 20% that of air-saturated water. This is a much lower concentration than the 60% saturation suggested as the lower limit for skipjack tuna in the vicinity of an oxygen-minimum layer (Ingham et al. 1977). The less active swordfish, with its large mass of white muscle, might be more resistant to anoxia and able to accumulate an oxygen debt. If so, the periodic excursions to well-aerated surface waters would allow it to recover from anoxia. There appears to be a rough correlation between time spent on the surface and the length of the preceding period below the thermocline, as would be expected if this were a recovery process:  $T_s = 0.2 T_L + 16$  ( $r = 0.6$ ;  $n = 10$ ) where  $T_s$  is time on surface in minutes and  $T_L$  is time at depth in minutes.

In the Baja California area, there was a marked difference between frequencies at which the inshore and offshore swordfish came to the surface during the day. The inshore fish surfaced six times in 7 d and spent 2.8% of the daylight hours on the surface. The offshore fish surfaced 10 times in 2.5 d, spending 25.7% of the daylight hours on the surface. This difference may be related to oxygen concentrations, for the inshore fish were near the mouth of the Gulf of California where the oxygen-

minimum layer is not well developed. They would probably encounter less anoxic conditions than the offshore fish which were well into the Pacific. Because of this, an attempt to compare abundance of swordfish in these two areas from the numbers seen on the surface could be grossly misleading.

On the continental shelf off the northeastern United States and Canada where swordfish can be seen "finning" on the surface during the warm months, the water is well oxygenated from surface to bottom. However, temperatures on the bottom can be quite cold, and the swordfish which are feeding deep may be coming to the surface to warm their muscles or as an aid in digestion. Basking behavior by swordfish may be part of a recovery from a variety of stresses experienced at depth.

### Buoyancy

Swordfish swimming on the surface seem to have neutral or sufficient positive buoyancy to raise the dorsal and caudal fins out of the water. Swordfish taken on longline frequently float, swim bladders distended, when hauled to the surface, and would have been at neutral buoyancy at a pressure of a few atmospheres. The swordfish are clearly able to inflate their bladder to a volume which will give them neutral density at some near-surface depth. The capillary retia mirabilia of the gas gland are short, about 1 mm long, and similar to those of surface dwellers such as the flying fish (Marshall 1960, see footnote 10). Thus the structure of the gas gland does not seem suitable for rapid pumping of large volumes of oxygen under pressures up to 60 atm at 600 m. Our depth records (Figures 5, 8) show many examples of rapid vertical movements with the fish sometimes moving from 100 m to the surface in <5 min. Such changes in depth could cause a 10-fold expansion in the volume of a free bubble. It seems unlikely that the swordfish could pump gas into and out of its swim bladder rapidly enough to maintain constant volume during these excursions. The necessity for doing this could be avoided if the bladder were allowed to compress with hydrostatic pressure as the depth increased. This would increase the density of the fish, but even with the bladder partially collapsed at depth, the high lipid content and porous fatty bone of the swordfish would lower its density and the

flattened bill and fixed pectoral fins would give it hydrodynamic lift while swimming.

When at rest at depth, excess density would prevent the swordfish from hovering easily and it might find resting on the bottom to be a convenient position. While on the bottom the fixed pectoral fins would form an effective tripod with the tail (R. H. Backus<sup>11</sup>). Frequent records of swordfish caught in bottom trawls indicate that resting on the bottom may be common in this species (Bigelow and Schroeder 1953; Eschmeyer 1963). Martin Bowen,<sup>12</sup> a National Marine Fisheries Service (NMFS) observer on foreign squid trawling vessels working between Cape Hatteras and Cape Cod, Mass., reported 28 swordfish taken in bottom trawls during 72 d at sea in 1977. Observers in research submarines have seen swordfish lying on the bottom (Zarudski and Haedrich 1974), and in our records it appears that swordfish no. 3 was on the bottom for several hours.

### Temperature

Water temperatures encountered by swordfish in the Baja California area are illustrated in Figure 5. A 10° C (18° F) gradient was present between the surface and the depth of the deepest dive, 300 m. The gradient between surface and the usual daytime depth was 5°-7° C. The fish made frequent excursions through the thermocline, passing such gradients in a few minutes. While these are significant temperature changes, they did not seem to affect the activities of the fish, which in this area appear to be more influenced by the presence of anoxic water.

Our record for swordfish no. 7 in the North Atlantic shows the impressive ability of this species to penetrate marked thermal boundaries (Figure 8). The greatest temperature change occurred on the morning of 10 November when this fish moved from 27° C water on the surface to 8° C water at 420 m, a 19° C excursion in 2.5 h. This is a large change for any heterothermal organism to undergo and remain active. It was not just a brief excursion, for it remained in the cold water all day. The thermal history of the fish before this dive was complex, but the preceding

<sup>11</sup>R. H. Backus, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1972.

<sup>12</sup>M. Bowen, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. 1978.

<sup>10</sup>N. B. Marshall, Park Lane, Saffron Walden, Essex, Engl., pers. commun. 1975.

4.5 h included 1.5 h at 27° C, 1.5 h at 14° C, and 1.5 h at 27° C for an average water temperature of 22°-23° C before the descent. The swordfish is clearly able to function over a wide range of ambient temperatures.

The coldest water which no. 7 entered was 8° C. This may represent a lower preferred limit for swordfish, as it agrees with the 8° C temperatures reported for deeper sightings from research submarines (Zarudski and Haedrich 1974). The 8° C temperature may only be coincident with a light or depth limit or the location of prey; we look forward to experiments with swordfish in areas where water <8° C is readily available.

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