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PATTERNS IN THE ACTIVITIES OF SWORDFISH, *XIPHIAS GLADIUS*

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ABSTRACT

The movements of swordfish were studied using acoustic telemetry to follow water temperature and depth of five swordfish in the Pacific near the tip of Baja California and one in the Atlantic near Cape Hatteras. Two of the Baja California fish showed a clear diel cycle of movement between an inshore bank during the day and deep water offshore at night. All the swordfish responded to light, swimming deep during the day and coming near the surface at night. In the Pacific, daylight depth appeared to be limited to about 100 meters by the oxygen minimum layer, but in the well-aerated waters of the Atlantic a mid-day depth of greater than 600 meters was recorded and the fish appeared to follow an isolume. Daytime depth of the fish 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 two hours. The implications of rapid vertical movements on buoyancy and swimbladder volume are discussed.

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INTRODUCTION

Information on the habits and behavior of swordfish comes from a limited number of scientific studies and from observations by fishermen which are generally limited to fish seen on the surface or captured by various types of fishing gear. Examination of their stomachs shows that swordfish feed on a wide variety of fish and cephalopods (Scott and Tibbo 1968; Ovchinnikoy 1971) and we have found them to contain odd food items including birds and edible shrimp. In feeding, the swordfish may strike its prey with a lateral motion of its bill and has been seen to go through schools of small fish stunning them to be swallowed later (Goode 1883). Fish taken from their stomachs may show signs of having been cut with the sword, damaging the muscle and vertebral column (Scott and Tibbo 1968). Swordfish are caught at night on longline fishing gear with hooks set at depths of 5 to 50 meters, but are rarely taken on such gear during daylight hours. They may slash at the bait and frequently get tangled in the line and foul-hooked on the outside of the body. Small phosphorescent lights are used successfully to attract them to the hooks in this fishery. In some regions the fish may commonly be found resting near the surface during the day, often with their dorsal and upper-caudal fins exposed. In this situation they can be approached and harpooned. This "basking" behavior may be part of a feeding pattern and spotter pilots for the harpoon fishery say that such fish often defecate before sounding or breaching.

Swordfish are aggressive and there are many accounts of their attacking ships, whales, and other objects into which they may ram their bills with remarkable force (Goode 1883; Gudger 1938; Smith 1956; and Jonsgard 1962). We have seen penetrating wounds in swordfish 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, they may be encountered in pairs with some regularity.

Swordfish occur generally throughout the temperate and tropical ocean, but aggregate seasonally along the edge of the continental shelf and on offshore banks in higher latitudes (Rich 1947; Wise and Davis 1973). An interesting suggestion of homing behavior comes from tagging experiments where swordfish were recovered near the point of release, even after a period of several years at large (Beckett 1974). Homing is suggested to explain this result, rather than just residence in the same spot, because it seems fairly certain that the fish migrate. The seasonal appearance of swordfish in the western North Atlantic and Hawaiian fisheries (Caddy 1976; Uchiyama and Shomura 1974) and the distribution of larvae and of swordfish with ripe gonads (Tåning 1955; Arata 1954; Markle 1974; Gorbunova 1969; Nishikawa and Ueyanagi 1974) indicate that a spawning migration takes place to waters warmer than 23-24°C and that there may be a movement between coastal and oceanic waters for nonspawning fish. Further evidence for long-distance movement comes from a 25-lb swordfish which was tagged near the Mississippi River delta on 17 March 1974 and recovered from Georges Bank on 20 August 1977 at a weight of 190 lb (personal communication, J. G. Casey, NOAA-NMFS, Narragansett, RI).

In this study we set out to learn what patterns might recur in the movements of swordfish and to determine the range of temperature and depth encountered by this species during its daily activities. We used acoustic telemetry to monitor temperature and vertical and horizontal movements of swordfish. The results presented here provide the first description of their activities based on direct observations of individuals over periods of days.

METHODS

Transmitters

Two types of sensors were used on the transmitters. Depth transmitters used a 500 or 1,000 psi Biotek strain gauge pressure transducer. Temperature transmitters had a 300K ohm 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 OD cylindrical ceramic transducer (Marine Research TCD 5) with 30-msec 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 amp-hr lithium cells (Mallory L0325) which give a useful life of about one week. Range was as great as 3 to 5 km at times, but very 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 1,000 meters depth. A miniature (6-cm-long) swordfish dart was tied to the end of the transmitter with a 13-cm loop of twisted 200-lb test monofilament nylon. An adapter 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. Changing battery voltage did not affect the pulse rate, 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 less than 1-meter depth when the fish was seen on the surface. A temperature transmitter recovered after 13 days 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 of the 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 some 100x 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 streamline 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 sec with a stopwatch and converting the pulse rate to temperature or depth with a pocket calculator using a linear regression for the calibration curve. A 0.1-sec counting error in a 30-sec count produced a depth error of approximately 2 meters. Data were taken routinely every 5 or 10 minutes 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 (Figure 8) 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 (Sippican 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 fish in those experiments where a temperature transmitter was not used.

Fishing

For the experiments near 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 AUDREY LYNN. Weights of the fish were estimated by the fishermen. Past experience has shown such estimates to be quite accurate.

RESULTS

We attempted to attach transmitters to some 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. The experiments will be described individually.

Swordfish #2, 19-24 April 1977

This 70-kg swordfish sounded when struck with the transmitter, but quickly came up and spent another 20 minutes on the surface. It appeared to be in good condition and unaffected by the depth transmitter. During a 5-day period it showed a clear cyclical pattern of movement between an inshore bank during the day and offshore waters at night (Figure 1). Each day it occupied the same area along the 100-meter depth contour on the bank. Several hours before sunset it would move offshore, going out as far as 26 km and remaining in deep water all night. At first light of dawn, 1 to 1.5 hours before sunrise, it would swim inshore again and return to the 100-meter contour on the bank.

The fish remained close to the bottom, coming to the surface in daylight only 3 times in 5 days (Figure 6). On 20 April it was usually 5 to 10 meters from the bottom, and on the following days usually 5 to 20 meters above it. For regions where the bottom was sloping, the relationship between the swordfish and the bottom is correct only for those instances where the vessel was moved directly over the fish before measuring bottom depth with the echo sounder. Each evening, an hour after sunset, Swordfish #2 rose to the surface and spent the night in the upper 10 meters. At first light, an hour before dawn, it descended and moved toward shore at depth with frequent vertical excursions.

Swordfish #3, 26-27 April 1977

This 70-kg fish was found close to where #2 had been tagged, and was harpooned with depth and temperature transmitters. It followed a very similar pattern to #2, moving offshore before sunset and turning inshore at first light (Figure 2). Several hours before sunset, both of these fish would leave their position on the 100-meter contour of the bank and swim offshore, the bottom dropping away from them as they moved into deep water. They swam twice as fast, perhaps 3 km per hr, 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 per hr again. 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 again was at a higher speed, about 3 km per hr.

From 1100 to 1800 on the second day, Swordfish #3 remained in one spot and appeared to be resting on the bottom during part of this time. This was determined by positioning the boat over the fish and noting that the echosounder depth was the same as that telemetered from the fish. At sunset it rose from the bottom and headed offshore. We lost it soon after this when our equipment was damaged in rough water.

Swordfish #4, 30 April 1977

This 80-kg fish was harpooned in 500 meters of water some 24 km off the coast. It moved slowly in a westerly direction (Figure 3) staying uncharacteristically near the surface, frequently with its fins showing, and did not descend below 10 meters. It was followed for only 2 hours, then abandoned because of technical problems.

Swordfish #5, 30 April 1977

This fish weighed about 100 kg and was harpooned close to where we left #4. It also moved slowly westward, covering less than 3 km in the first 5 hours (Figure 3). An hour before sunset it turned south and swam offshore over San Jose Canyon at a speed of 3.5 km per hr. During the day it surfaced five times, spending alternate periods on the surface and at 100 meters. Sunset marked a period of vertical activity and a gradual ascent to the upper 25-50 meters. We lost it in rough weather that night as it was swimming offshore on a southerly course.

Swordfish #6, 3-6 May 1977

Swordfish #6 weighed about 140 kg and was harpooned with depth and temperature transmitters in an area about 24 km offshore, near where #4 and #5 had been tagged (Figure 3). It also swam slowly west as those fish had done, moving 9 km in 5 hr, then turned south at sunset and moved down the axis of San Jose Canyon. It continued in a southwesterly direction when it reached deep water, and by dawn on 5 May, when we abandoned it, it had gone 88 km in 44 hr.

Swordfish #6 showed the now familiar pattern of vertical movements, staying near the surface at night and going deep during the day (Figure 7). Like

Swordfish #5, it made excursions to the surface during daylight hours, coming up five times to spend periods of 0.5 to 1.5 hours on the surface, then returning to depths of 75 to 100 meters.

While on the surface during the day, Swordfishes #5 and #6 swam about actively. No. 6 moved at an estimated 1.6-3.2 km per hr (1-2 knots) in a random 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 drive it down with the boat; but it settled 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 an hour.

Swordfish #7, 9-11 November 1977

This 70-kg swordfish was taken by longline about 100 km northeast of Cape Hatteras (36°00'N, 74°40'W) in 1,000 meters of water. The fishing gear was left in the water for only an hour 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, and its bluish color and movement gave the impression that #7 was in good condition. It was tagged with a depth transmitter and cut free within about 15 seconds after it had been brought alongside the boat.

The longline had been set in a patch of warm blue water (Figure 5). When released the fish swam in a general southeasterly 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 the northeast. At the end of the third day the flattening of the deep isotherms (Figure 8) suggested 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 hours.

During the first day, the vertical movements of #7 were complex. On the second and third day, however, it followed a clear pattern of coming near the surface at night and going deep during the day. An hour before dawn on 10 November it was in 27° water at a depth of 20 meters (Figure 8). It began to descend and was in 8°C water at 400 meters two hours after sunrise. An hour before sunset it had started back toward the surface and was at 20 meters at twilight. That night was spent at about 20 meters with four brief excursions to 100 meters. Some of these were caused by our tracking vessel, for swordfish would often dive when we drove the boat over them. This appeared to be a response to sound, as it happened even when the ship was darkened. The depth pattern on 11 November was similar to the previous day. Leaving the surface an hour before dawn, it dropped rapidly and was at 450 meters shortly after sunrise. It continued to sink, reaching 617 meters 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 to 80 meters, a pause for several minutes, then another rapid rise.

DISCUSSION

Horizontal Movements

Swordfishes #2 and #3 showed a clear cycle of movements between deep water and an inshore bank. During the day they occupied a rather narrow region, perhaps 8x1.5 km, along the 100-meter contour at the edge of the bank where the bottom fell off steeply to the south and east (Figure 2). They stayed close to the bottom, moving slowly, and may at times have been resting on it. Swordfish commonly feed on bottom fish and this location along the edge may have allowed them to prey on demersal fish moving on and off the bank.

In the evening Swordfishes #2 and #3 swam offshore rapidly and then spent the night moving slowly in positions about 20 km from the coast (Figures 1 and 2). 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 them. 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 wherever they were found over deep water at night.

In an area near Hawaii, Yuen (1970) used an acoustic transmitter to follow a skipjack (*Katsuwonus pelamis*) for an 8-day 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 Swordfishes #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 blue sharks (*Prionace glauca*) near Catalina Island was reported by Sciarrotta and Nelson (1977). This cycle was opposite in phase to that of the skipjack 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.

Swordfishes #4, #5, and #6, which were found offshore over 400-800 meters of water, moved slowly west after they had been harpooned (Figure 3). We abandoned #4, but #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 course of the canyon. The correspondence with the axis of the canyon is not exact, but the fact that both fish changed course and moved along the canyon suggests they were responding to the bottom topography. The connection between the swordfish and the canyon floor at 500-1,200 meters below is not apparent, but in other areas commercial longline fishermen feel that the submarine canyons and hummocky areas along the edge of the continental shelf are good places to find swordfish. Perhaps some effect of currents provides the link. It is also possible that there is a ladder of organisms reaching from the bottom where fish are attracted to areas of high relief, up through various species to the surface, providing an enriched environment which attracts swordfish.

Fishermen had suggested that swordfish in the area where #2 and #3 were followed were part of a resident population, while those in the area of #4, #5, and #6 were transient. Our results are consistent with this notion.

In the Atlantic, Swordfish #7 entered the Gulf Stream on the second day as indicated by the deepening of the isotherms in Figure 8. While in the stream it moved northeast at a speed of 5.5 km per hr, most of this velocity contributed by the current. There was a 1.5 or 2.0 km per hr southeasterly component to its swimming, however, for 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 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 prepared by the US Navy Oceanographic Office. Swordfish concentrate along the edge of the continental shelf, but are widely distributed over the ocean. The course that #7 followed may have been a normal one for swordfish in the Hatteras area, or it may have been influenced to swim offshore by the trauma of being caught on longline fishing gear.

Vertical Movements and Light

The swordfish showed a clear diel pattern of vertical movements, going deep during the daylight hours and coming to the surface at night. This is best illustrated by Swordfish #7 on 11 November (Figure 8). The fish spent the night at about 20 meters depth. About an hour before dawn, when light was just noticeable in the eastern sky, it swam down rapidly, reaching a depth of 400 meters by sunrise and working gradually deeper until it reached 617 meters at midday.¹ After noon the swordfish gradually rose again, increasing its rate of ascent sharply around sunset and reaching the surface about an hour later.

There is an obvious relationship between the vertical movements of swordfish and light. The most rapid changes in depth were during a 2-hour period at dawn and dusk when surface illumination changes by 6 or 7 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 #3. On these nights, which were starlit and calm, the swordfish were usually at depths less than 10 meters and often right on the surface. In the other experiments there was a full moon shining through clouds and it was windier. Nighttime depths for #5 and #6 were 10-50 meters (Figure 7), and for #7 about 25 meters (Figure 8). The fish were probably swimming at a greater depth in response to moonlight, although the wind might also have had an influence.

¹This was the greatest depth reached in our experiments, but it may be common for swordfish to swim to 600 meters or deeper. Church (1968) reported seeing a swordfish at 654 meters from the submarine DEEPSTAR, and the submarine ALVIN was attacked by a swordfish while on the bottom at 610 meters (Zarudski and Haedrich 1974).

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 meters while the moon was up, rose to 50 meters when the moon set. Our similar records for swordfish suggest that they 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 a clear, starry night when they came right to the surface, and somewhat less than in moonlight when they swam at 10-50 meters depth. We may use the values for irradiance of 3×10^{-1} uW/cm² under a clear night sky with full moon, 3×10^{-3} uW/cm² for a clear sky with no moon, and 3×10^{-4} uW/cm² for a dark night, from Clark and Kelly (1964). At noon, 11 November 1977, Swordfish #7 was at latitude 35°N and at a depth of 600 meters. Surface illumination, I_0 , for this time, recorded in Woods Hole and corrected for latitude, was 5×10^4 uW/cm² (supplied by Dr. R. E. Payne, Woods Hole Oceanographic Institution). 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 2.5×10^{-3} uW/cm², 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 small grapefruit 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 3×10^{-10} uW/cm² suggested as a threshold for vision in deep-sea fish (Clarke and Denton 1962; Denton and Warren 1957). 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 isolumes. 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 #7 is 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 will occur at greater depths. The gradual increase in depth during the fading daylight on this afternoon coincides with moving from slope to stream water and can be interpreted as maneuvering deeper to maintain a constant light intensity in the clearer water.

On 9 November, Swordfish #7, which had reached 400 meters by midmorning, came back up to 100 meters 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 which shows as a marked thermal inversion in Figure 8 and as a light-colored region in the satellite infrared image (Figure 5). 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 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 and 100 meter 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 clear vertical movement in response to sunrise and sunset was seen in all of the Baja California experiments. An interesting feature is apparent when these depth records are aligned vertically (Figure 6). The rapid descent which begins about an hour before dawn each morning is reversed at sunrise with the fish coming back up to about 100 meters. 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 (Figures 11 and 27 in Griffiths 1968). In its normal movement away from the surface with increasing light at dawn, the swordfish penetrated too deeply into this low-oxygen layer then came back up to spend the day at a depth with more suitable oxygen concentration. This acceptable oxygen concentration occurred at a shallower depth and higher light level than would normally have been occupied by the swordfish during the daytime.

In Baja California, swordfish frequently came to the surface during the day to lie with the tips of their dorsal and caudal fins out of the water for periods of 15-80 minutes at a time. This behavior at a time of day when in other circumstances we would expect them to be at their greatest depth, may be related to the low oxygen concentration at depth. The depth record for Swordfish #6 superimposed on an isotherm pattern in Figure 7 shows that it 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 #5 was below the thermocline in Figure 9 it was in an environment with an oxygen concentration only 10-20% that of air-saturated water. This is a much lower concentration than the 60% saturation suggested as the lower limit for skipjack, *Katsuwonus pelamis*, 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 this anoxic experience. There is a rough correlation between time spent on the surface and the duration of the preceding period below the thermocline.

$\text{Time}_{\text{surface}} = 0.2 \text{ Time}_{\text{depth}} + 16 \text{ min}$, correlation coefficient = 0.6, as would be expected if this were a recovery process.

In the Baja California area there was a marked difference in the frequency with which the inshore and the offshore swordfish came to the surface during the day. The inshore fish came up 6 times in 7 days and spent 2.8% of the daylight hours on the surface. The offshore fish were up 10 times in 2.5 days, spending 25.7% of the day 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 does not occur. They would probably encounter less anoxic conditions than the offshore fish which were well into the Pacific. 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 northeastern United States and Canada, where swordfish can be seen "finning" on the surface during the warm months, the water is well aerated from surface to bottom. However, temperatures on the bottom here can be quite cold and the swordfish which are feeding deep may be coming to the surface to warm their muscle or as an aid in digestion. Basking behavior by swordfish may be part of a recovery from a variety of stresses experienced at depth, but we obviously have more to learn about it.

Buoyancy

Swordfish have a conspicuous swimbladder with a large area of diffuse gas gland. The capillary *rete mirabile* of the gas gland are short, comparable to surface dwellers such as flying fish (N. B. Marshall 1960 and personal communication). Such a *rete* seems unsuitable for inflating the bladder to 60 atmospheres pressure at 600 meters. Our depth records show many examples of rapid vertical movements. On 11 November, Swordfish #7 rose from 300 to 40 meters in about 18 minutes and there are many times when the fish moved between 100 meters and the surface in less than 5 minutes. Such changes in depth could cause a tenfold expansion in a free bubble. The short capillaries in the *rete* and the frequent vertical excursions we observed make it unlikely that the swordfish can pump gas into and out of its bladder rapidly enough to maintain a constant gas bladder volume.

Swordfish swimming on the surface seem to have neutral buoyancy or enough positive lift to raise the dorsal and caudal fins out of the water. Swordfish taken by longline frequently float, bladders distended, when hauled to the surface and would have been at neutral buoyancy at some shallow depth. The swordfish probably inflates its bladder to give neutral density near the surface but allows it to collapse when going deep. If so, the rapid vertical maneuvering we observed could be done without the difficulties of pumping large amounts of gas in and out of the bladder. Even with the bladder collapsed at depth, the high lipid content of the flesh and porous fatty bone of the swordfish will lower its density and the flattened bill and fixed pectoral fins give it hydrodynamic lift. When not swimming, the excess density at depth 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 (personal communication, R. H. Backus, Woods Hole Oceanographic Institution). Frequent records of swordfish caught in bottom trawls indicate that resting on the bottom may be common behavior for them (Bigelow and Schroeder 1953; Eschmeyer 1963). Martin Bowen, a NOAA-NMFS observer on foreign squid-trawling vessels

working between Cape Hatteras and Cape Cod, reports 28 swordfish taken in bottom trawls during 72 days at sea in 1977 (personal communication). Observers in research submarines have seen swordfish on the bottom (Zarudski and Haedrich 1974), and in our records it appears that Swordfish #3 was on the bottom for several hours.

Temperature

Water temperatures encountered by swordfish in the Baja California area are illustrated in Figure 7. A 10°C gradient was present between the surface and the depth of the deepest dive, 300 meters. 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 are more influenced by the presence of anoxic water.

Our record for Swordfish #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 meters, a 19°C excursion in the space of 2.5 hours. This is a large change for any 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 4.5 hours included 1.5 hours at 27°C, 1.5 hours at 14°C, and 1.5 hours 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 Swordfish #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, and we look forward to experiments with swordfish in areas where water colder than 8°C is readily available.

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FOOTNOTES

1. This was the greatest depth reached in our experiments, but it may be common for swordfish to swim to 600 meters or deeper. Church (1968) reported seeing a swordfish at 654 meters from the submarine DEEPSTAR and the submarine ALVIN was attacked by a swordfish while on the bottom at 610 meters (Zarudski and Haedrich 1974).

FIGURE LEGENDS

- Figure 1. Track of swordfish #2, Baja California, separated into 4 panels for clarity. Each day this fish moved inshore to the 50-fathom curve on a bank then moved out over deep water at night. The turn inshore began about one hour before dawn, the offshore movement began several hours before sunset. Compare with the depth record in Figure 6. ● = sunset, O = sunrise. Tics at one-hour intervals. Bottom contour lines in fathoms.
- Figure 2. Track of swordfish #3 (solid line) superimposed on track of swordfish #2 (dotted line, Baja California). Number 3 was on the bottom during much of the indicated 8-hour period. The solid lines,, on the track of #2 indicate positions where this fish was moving slowly on the surface at night. ● = sunset, O = sunrise. One-hour tics on track of #3.
- Figure 3. Track of offshore swordfish, Baja California. These fish all moved west during the first afternoon, #4 and #5 then moved down axis of San Jose Canyon after sunset. Bottom contour lines at 200-meter intervals, ● = sunset, O = sunrise. One-hour tics.
- Figure 4. Track of swordfish #7 in the Atlantic near Cape Hatteras, 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 on 9 November. 3 It emerged from beneath the cold surface layer at 2000, 9 November. By 0500, 10 November, #7 was in the Gulf Stream. 5 At 1500, 11 November it had crossed the Gulf Stream and entered the Sargasso Sea. ● = sunset, O = sunrise. Tics at one-hour intervals, bottom depth in fathoms.

FIGURE LEGENDS (continued)

- Figure 5. Satellite infrared image with track of swordfish #7 superimposed. Light areas cold, dark areas warm. The Gulf Stream moving past Cape Hatteras pulls off a streamer of cold shelf water. Number 7 was tagged on the north side of this, swam under it (see Figure 8) and crossed the Gulf Stream into the Sargasso Sea.
- Figure 6. Depth record for swordfish #2 and #3 (Baja California) plotted from midnight to midnight. Depth to the bottom when on the bank is indicated by the crosshatched area. The fish swam near the surface at night and at a depth of about 100 meters during the day. The morning dive about an hour before sunrise carried the fish below its usual daytime depth.
- Figure 7. Depth record for swordfish #6 (Baja California) superimposed on an isotherm pattern drawn from bathythermograph lowerings. There was a full moon during this experiment and the usual nighttime depth was deeper than on the moonless nights during experiments 2 and 3. The fish swam below the thermocline during the day and was well into the oxygen minimum layer where oxygen concentration is estimated to be about 10% that on the surface. Isothermal interval 1°F (0.55°C).
- Figure 8. Depth record for swordfish #7 (Atlantic) superimposed on an isotherm plot drawn from expendable bathythermograph casts. On 9 November the swordfish passed under a cold streamer of shelf water (see Figure 5) 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 entering the Gulf Stream and it went deep during the day in this clear water. On 11 November the depth record suggests that the fish was following an isolume, descending an hour before dawn, reaching its greatest depth at midday and coming to the surface an hour after sunset. Continuous recording of depth 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 suggest that the fish had entered the Sargasso Sea.

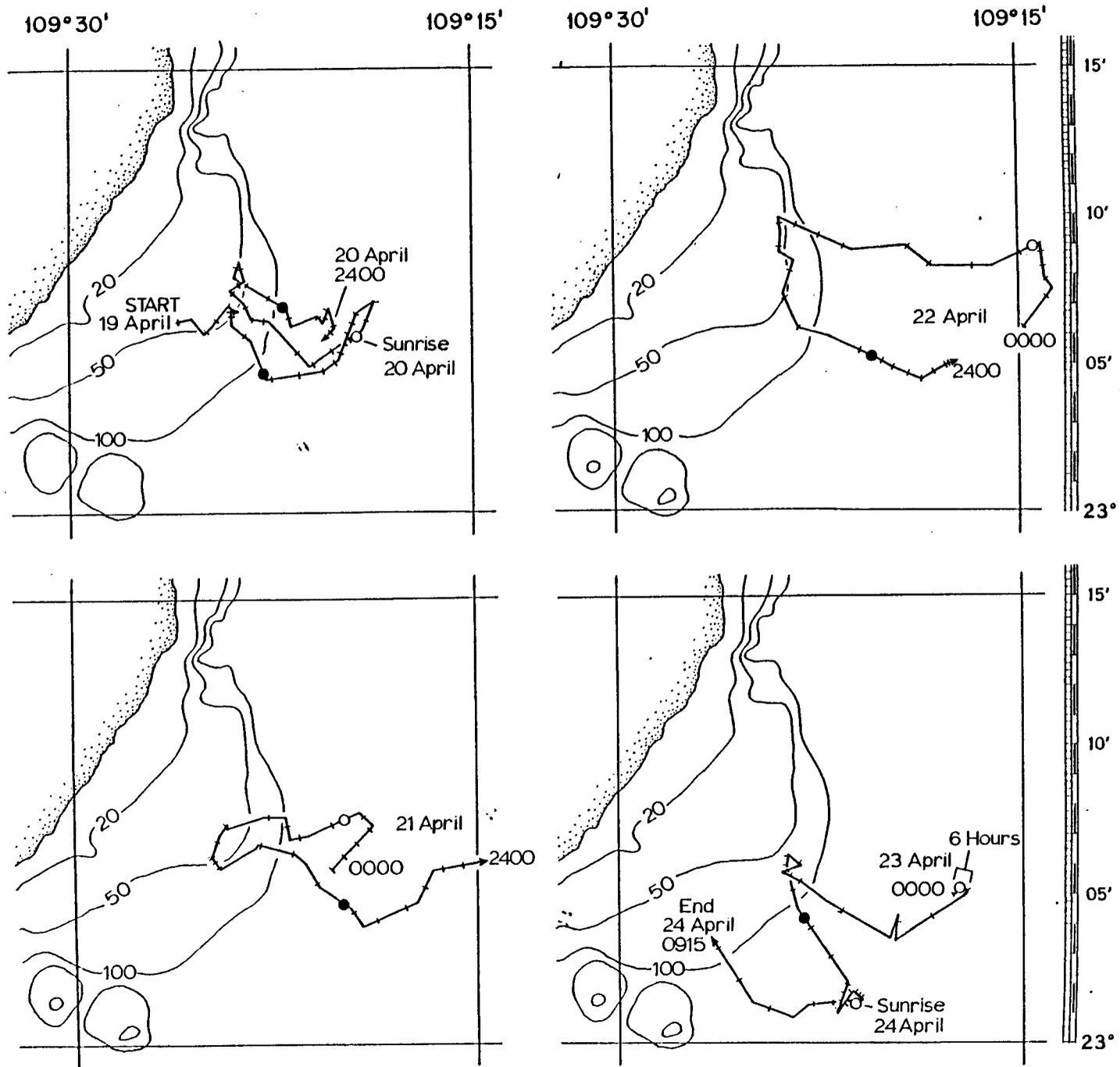


Figure 1

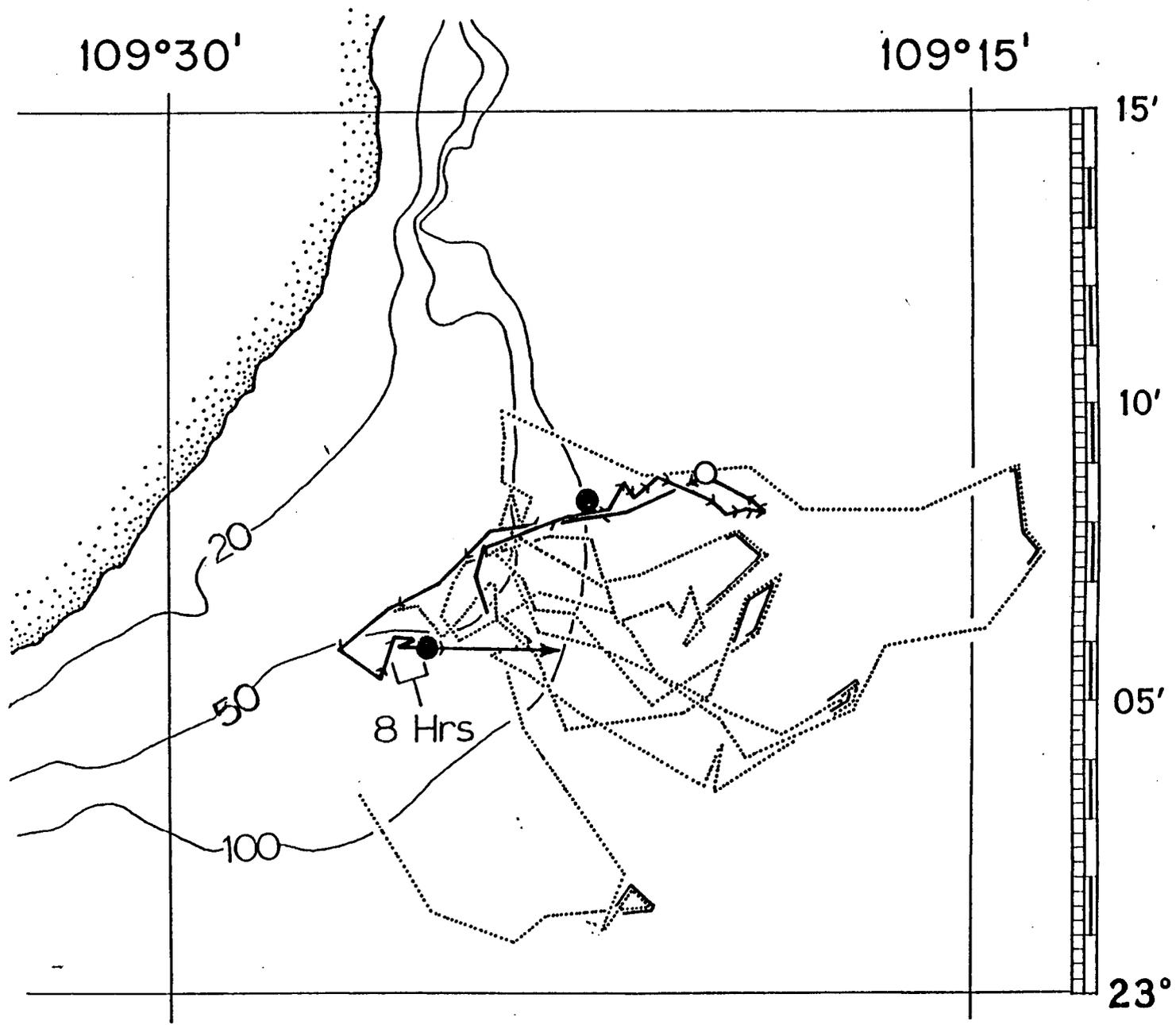


Figure 2

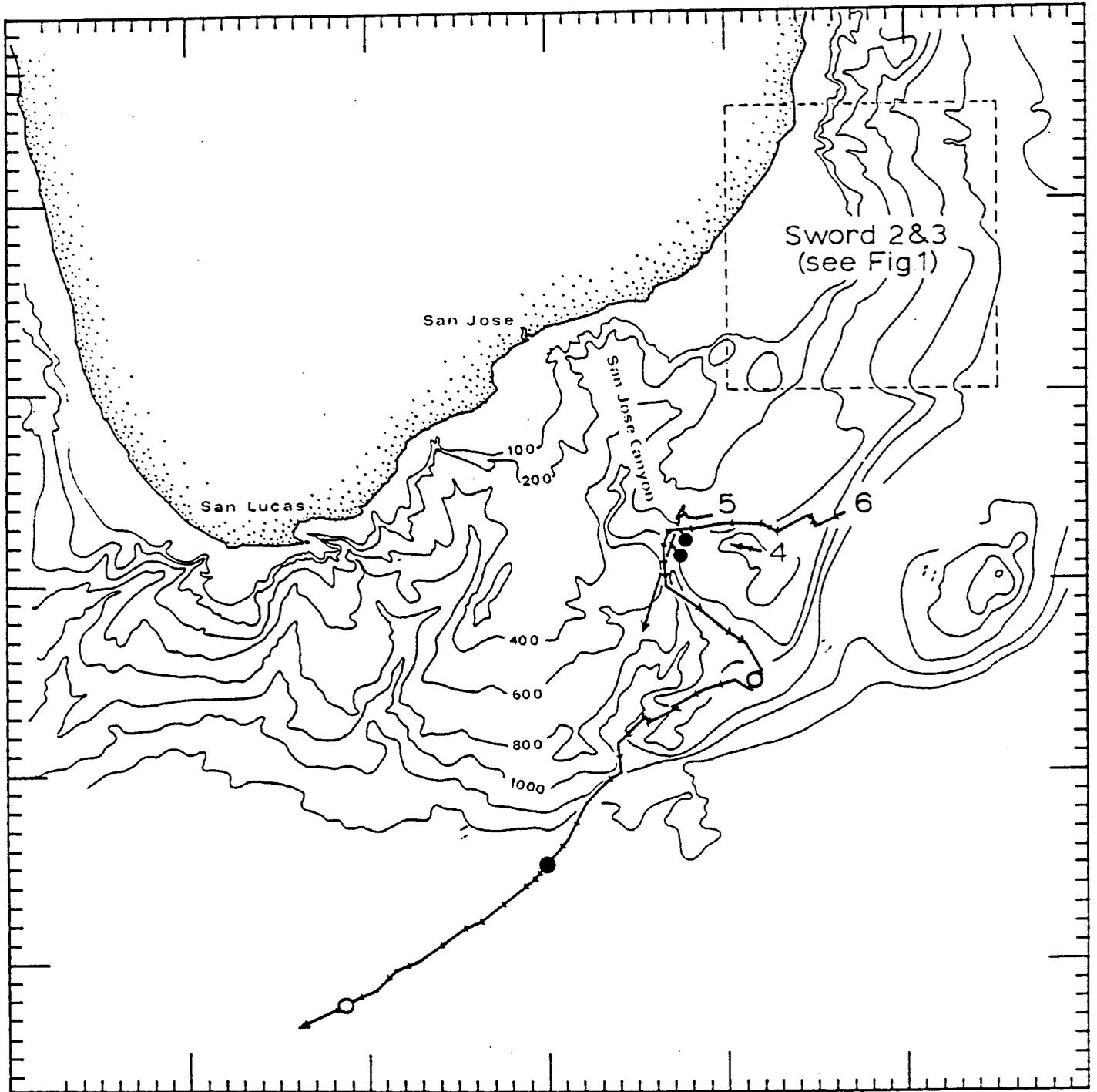


Figure 3

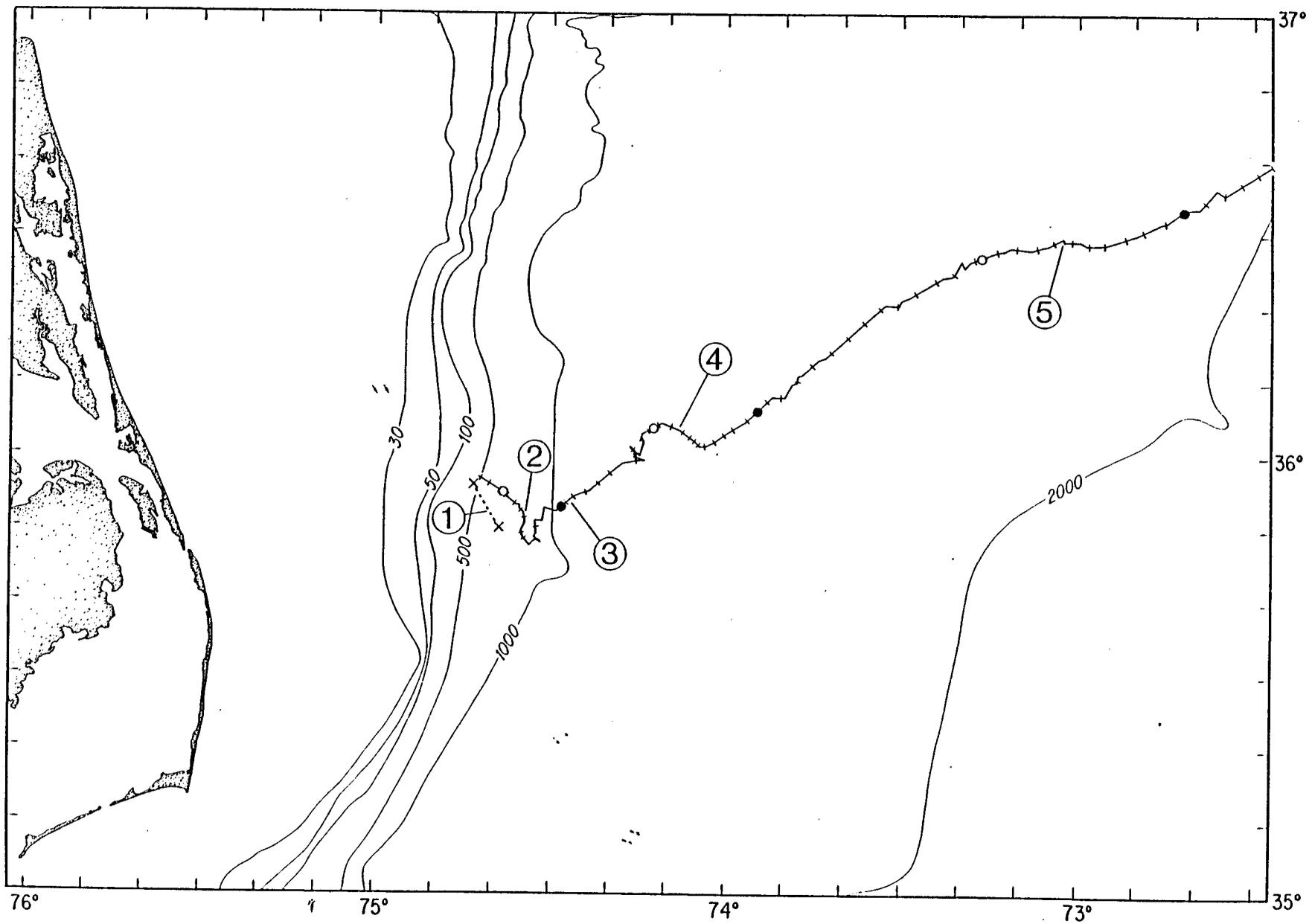


Figure 4



Figure 5

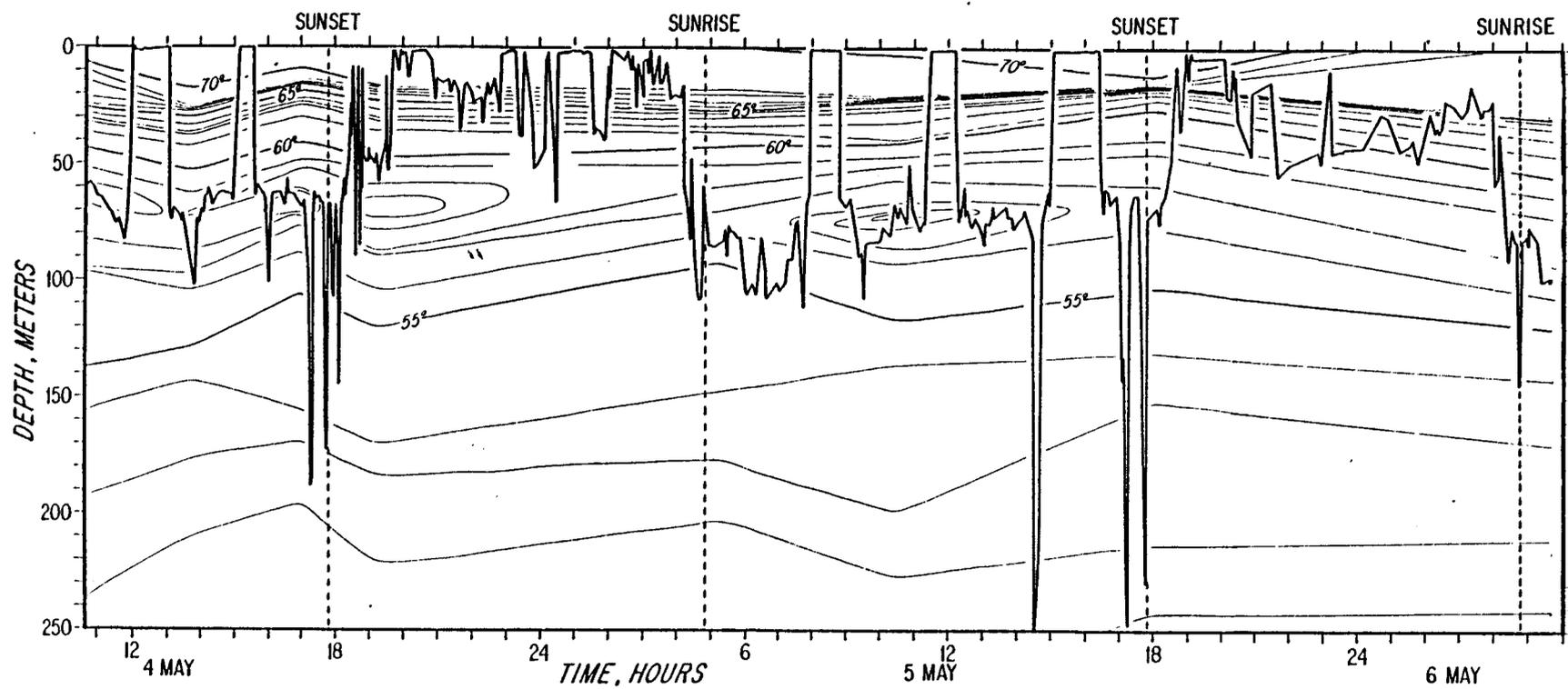


Figure 7

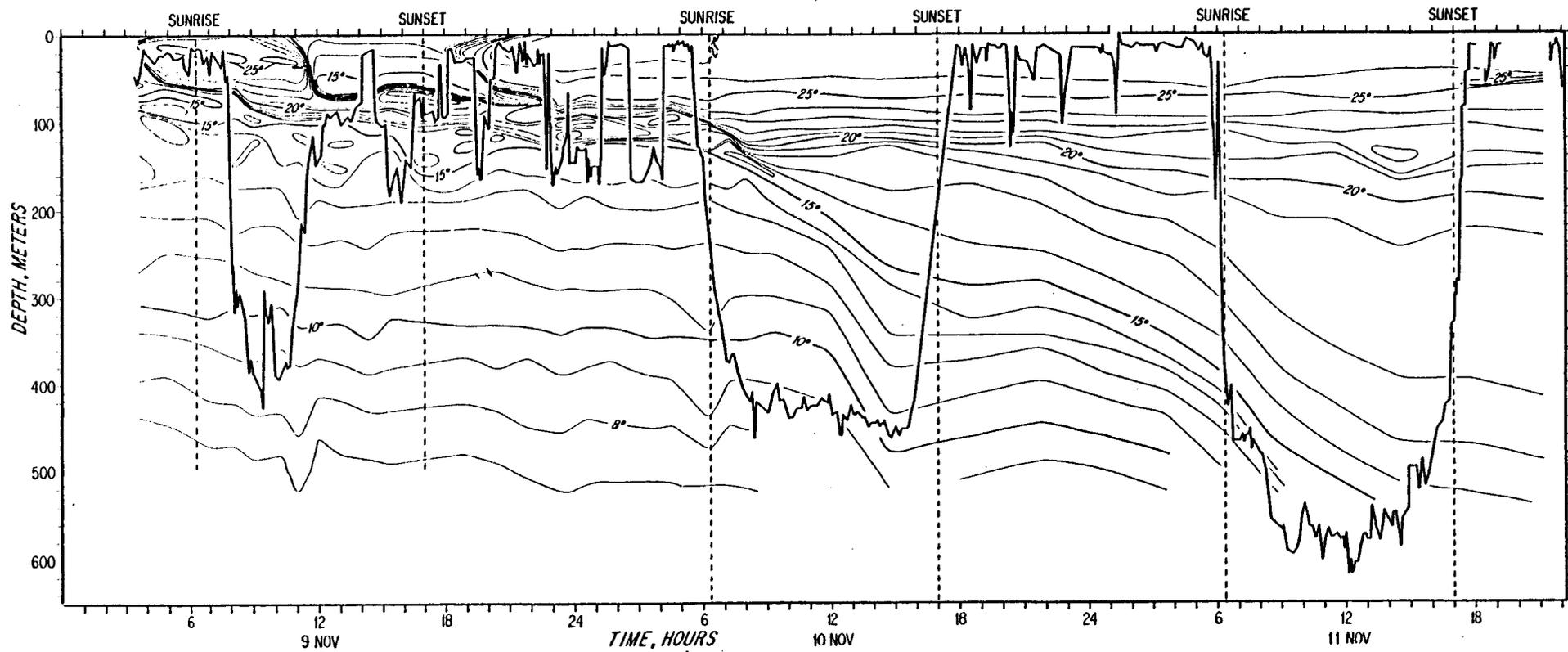


Figure 8