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Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system

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Summary. Movement patterns of scalloped hammerhead sharks in the vicinity of El Bajo Espiritu Santo, a seamount in the Gulf of California, were determined by tracking by ultrasonic telemetry 13 sharks and marking 100 sharks. The 13 tracked sharks swam back and forth along the seamount ridge throughout the day. They did not swim in different directions to reduce swimming effort when currents changed from a parallel to a perpendicular orientation to the ridge. Sharks tracked up to 8 km away into the pelagic environment soon returned to the seamount. From such trackings and repeated observations of marked sharks over periods of several weeks, it is believed that most sharks disperse and return to the seamount in a rhythmical fashion. The separate departures of individual hammerheads in five paired trackings indicated that the sharks left the seamount either in small groups or singly. For these reasons, we argue that the social system of the scalloped hammerhead shark can be described as a refuging system.

Introduction

Individuals of some shark species swim slowly or remain on the bottom at a single location during the day. These sharks often form groups. Such species are *Heterodontus portusjacksoni* (McLaughlin and O'Gower 1971), *Triaenodon obesus* (Randall 1977), and *Carcharhinus amblyrhynchos* (Johnson 1978; Nelson and Johnson 1980). This behavior may reflect a common strategy of these predators to minimize activity when not foraging by remaining at a single central location in their home range and is termed refuging by Hamilton and Watt (1970).

Adult scalloped hammerheads (*Sphyrna lewini*) remain during the day in large polarized schools along dropoffs into deep water in the Gulf of California. In this paper, we will describe the orientation of hammerhead sharks to a seamount, El Bajo Espiritu Santo (24 deg 41 min N., 110 deg 16 min W.) in the Gulf of California, show that the pattern to these orientations closely fits the refuging model of Hamilton and Watt, and examine two reasons why such groups might form at the seamount.

Materials and methods

Bathymetry of study site. It was our intent to examine hammerhead movements in relation to the bathymetry of El Bajo Espiritu Santo. For this reason, the bottom topography of the seamount was charted (Fig. 1). The research vessel was positioned above the highest point of the seamount, and radial transects were made in a small skiff equipped with a fathometer/odometer. This was done by moving outward until reaching the maximum depth resolved by the recorder, then moving circularly until a prechosen return bearing was reached, and moving inward to the research vessel before starting outward again. Bottom topography was recorded as an irregular trace on the recorder paper together with concentric traces at distances through the water of 18 m. Depths and distances were then transcribed from the map paper to produce a chart with depth contours. The contour lines were drawn as curves rather than straight lines to better reflect the intervening topographical changes. A few contours were drawn where measurements were lacking, but these are indicated by dashed lines. Bottom resolution was greatest at the center of the transect pattern close to the highest point on the ridge.

Ultrasonic telemetry. Movements of sharks were most often determined by means of ultrasonic telemetry. Transmitters were designed and fabricated in the laboratory of the second author, and are described in detail in Nelson and McKibben (1981). They were attached underwater with a pole spear to the shark's dorsum between the first and second dorsal fins with a subcuta-

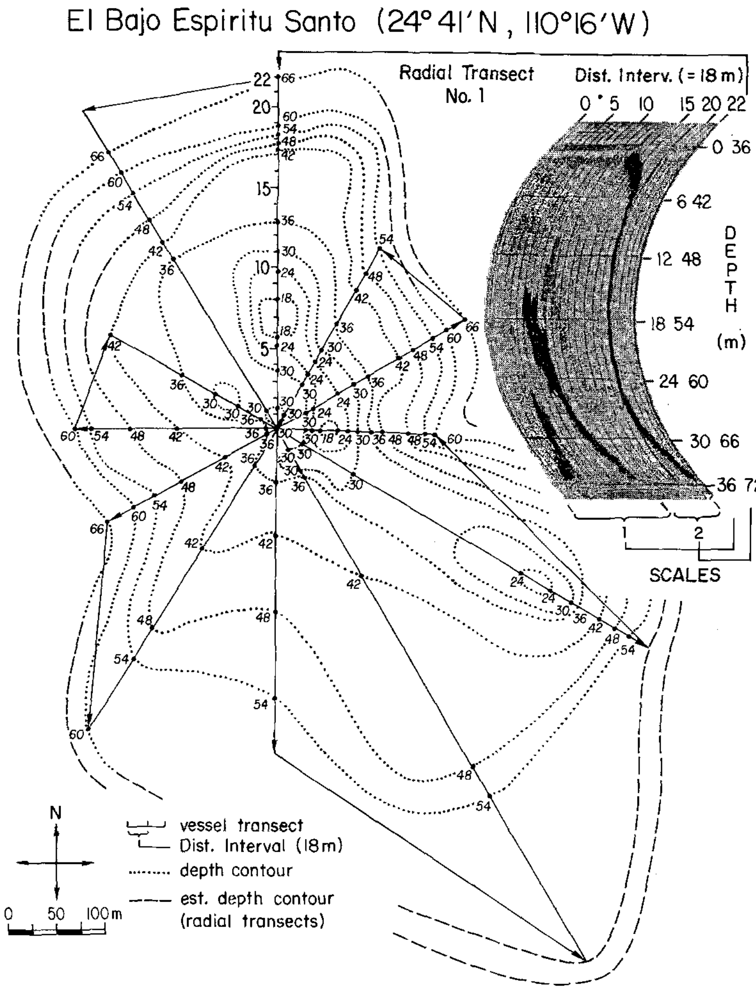

Fig. 1. Illustration of method of charting bottom topography at El Bajo Espiritu Santo. Chart paper (*upper righthand corner*) from fathometer/odometer with irregular depth trace and concentric marks indicating 18 m distances moved through the water. The end of the fathometer record of the first transect is connected by an *arrow* to the end of the first transect on the chart. Depth contours (*dotted lines*) indicate 6 m differences in depth. They are formed by connecting points on the radial transects (*solid lines*) at those depths by using the 18 m distance intervals (*ticks*) as a reference

neous dart with the transmitter attached to it by monofilament line. Due to the neutral buoyancy of the transmitters, they floated just above the dorsum of the shark except when the shark accelerated rapidly. In five paired trackings an attempt was made to relocate the tagged shark within a school and to tag a second member of the school. Either a single or two receivers (Dukane, N30A5 and Burnett, 522) were used to localize the source of the telemetry signals.

Due to the 17 km distance of the seamount from the coast of Isla Espiritu Santo and the even greater distance from the mainland, bearings could not be used to position the sharks accurately as they moved within the small area of the seamount. However, once the hammerheads left this area to move over larger distances in the pelagic environment, it was possible to position the sharks from bearings to landmarks and the anchored research vessel.

Positions on the seamount were determined in three manners. For the first four hammerhead sharks tagged, a single tracking team anchored its boat on the highest pinnacle of the seamount and obtained directional bearings to the tagged sharks (at 5-min intervals for the former two sharks and at 15-min intervals for the latter two sharks). For the next three and last two sharks the tracking team stationed its boat over the shark and then positioned itself (and the hammerhead) from bearings to two spar buoys or vessels anchored at either end of the seamount ridge. The distance between these markers was determined with a rangefinder and corroborated by averaging distance measurements made by the fathometer/odometer between the markers in opposite directions to eliminate the confounding effect of the current. With the next four telemetered sharks two tracking teams remained stationary in skiffs anchored at either end of the seamount ridge and simultaneously took bearings to the sharks. These bearings were then transmitted by CB transceivers to the research vessel where the positions of the shark were immediately plotted. This technique was superior to the former because the position of the shark was directly triangulated and the shark was not frightened by a constantly moving small boat.

Lines of position were drawn on acetate sheets superimposed upon a large clipboard with a chart laminated to its surface. Positions separated by 15 min were connected with straight lines to become track segments. Both the longest tracking and some of the paired trackings are presented in this manner. It must be remembered that the track segments represent the result of swimming movements over a 15-min period with the hammerhead shark at any time during that period not necessarily along the track segment. Successive positions were in some cases represented by unconnected points, each of which represented a positional estimate over a 15-min period. The center of activity for such positions was determined using the technique of Hayne (1949). The surrounding positions were ranked in relation to their distances from this central point.

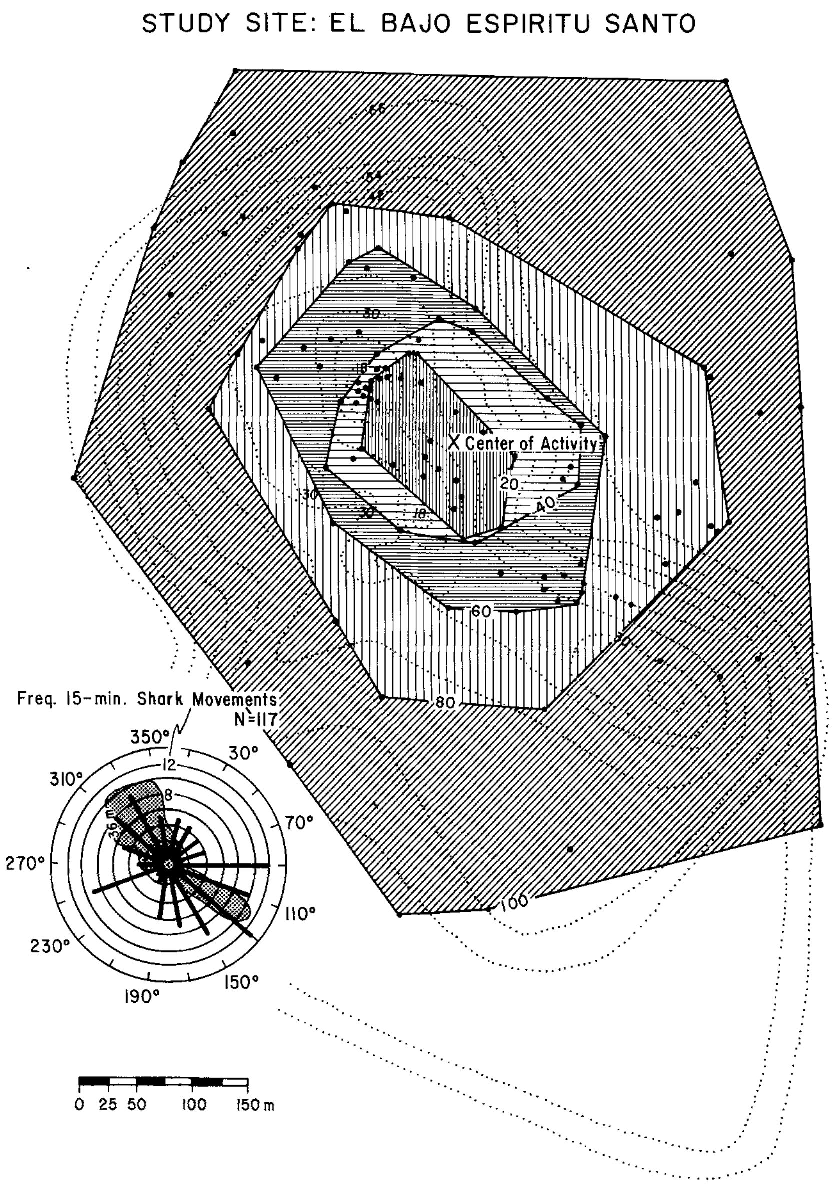

Fig. 2. Positions determined every 15 min for 13 sharks in the vicinity of El Bajo Espiritu Santo. Center of activity and cumulatively increasing 20% activity contours (*solid lines*) are superimposed upon bathymetric contours (*dotted lines*). Areas within contours indicated by *cross-hatching* of different coarsenesses and directions. Frequency distribution of directions of movements between successive 15 min positions is on polar plot in *lower lefthand corner*. Area of seamount above the 36 m depth contour indicated by *stippling*

Twenty-percent contours were formed by connecting the outermost points with straight lines in a manner producing a convex polygon such as recommended by Southwood (1978).

In order to compare directional movements in relation to the axis of the seamount ridge when currents were flowing in different directions and velocities, bearings from each position to its following position were totaled in 20 deg classes on polar plots. A depth contour of the seamount was superimposed on each polar plot.

Hourly measurements of surface current direction and velocity were made with a current meter and handheld compass.

Marking. In order to determine the degree of attachment of the hammerheads to the seamount, 100 sharks were marked between the first and second dorsal fins with color-coded, plastic streamers. These marks were applied underwater in the same manner as the transmitters. Forty tags were deployed during each of the summers of 1979 and 1980; twenty during the summer of 1981. During the summers of 1980 and 1981 the site was visited repeatedly over periods of a month and a month and a half, respectively. At the time of these visits reobservations of tagged sharks were recorded. Conclusions drawn from the reobservations must be considered tentative since the rate of tag shedding was not determined. Wounds or scars left from shedded tags, however, were not observed on hammerheads at the seamount.

Results

Ultrasonic telemetry

Thirteen trackings of scalloped hammerhead sharks were carried out from July through September 1981 and 1982 at El Bajo Espiritu Santo. Transmitters were applied at times ranging from 930–1,510 hours. Durations of the trackings

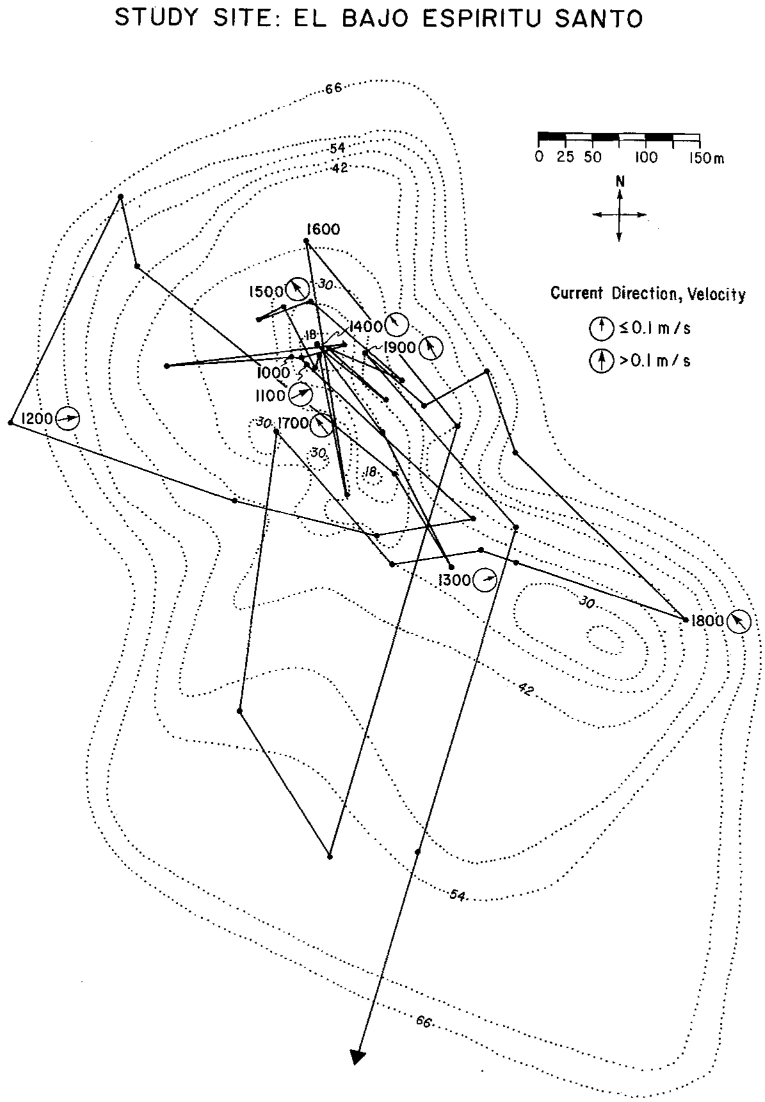

Fig. 3. Movements between positions determined for every 15-min for hammerhead no. 9 at El Bajo Espiritu Santo. Hourly measurements of current direction and velocity indicated by *arrows within circles*. The *direction of the inscribed arrow* indicates the direction of the currents, and the *length of the arrow* whether currents were slow ($\leqq 0.1$ m/s, *small arrow*) or fast (> 0.1 m/s, *large arrow*)

ranged from 15 min to 14 h. Some durations of trackings were short because we were interested primarily in orientations of the hammerheads to the seamount, and for this reason, we did not follow the sharks once they left the seamount.

During the day the scalloped hammerheads generally remained close to the seamount ridge. The center of activity determined from the tracking positions was just 25 m east of the 30 m depth contour of the ridge and was rather equally spaced between two of the pinnacles rising to less than 18 m from the surface (Fig. 2). The activity contours (solid lines) roughly paralleled the depth contours (dotted lines), indicating a preference for the ridge. The circular distribution of the directions of the movements was nonuniform (χ^2 Test, $P <$ 0.02). The directional bearings were bimodally distributed with maxima corresponding to the seamount ridge's axis (see lower lefthand corner, Fig. 2). The longest tracking in the vicinity of the seamount (No. 9) further illustrates this daytime attachment to the seamount ridge (Fig. 3). Although the shark occasionally moved outside the 48 m depth contour, it repeatedly returned to the larger of the two pinnacles. Most of the movements were parallel to the direction of ridge.

A reason for the schooling hammerhead sharks to remain at the seamount might be to take advantage of reduced current velocities inside eddies downcurrent from the seamount ridge. If the sharks remained in such eddies, they would not have to swim as fast during the resting phase of their diel cycle. Due to the presence of currents flowing roughly perpendicular to the axis of the seamount ridge at some times and parallel to the axis at other times, it was possible to test whether

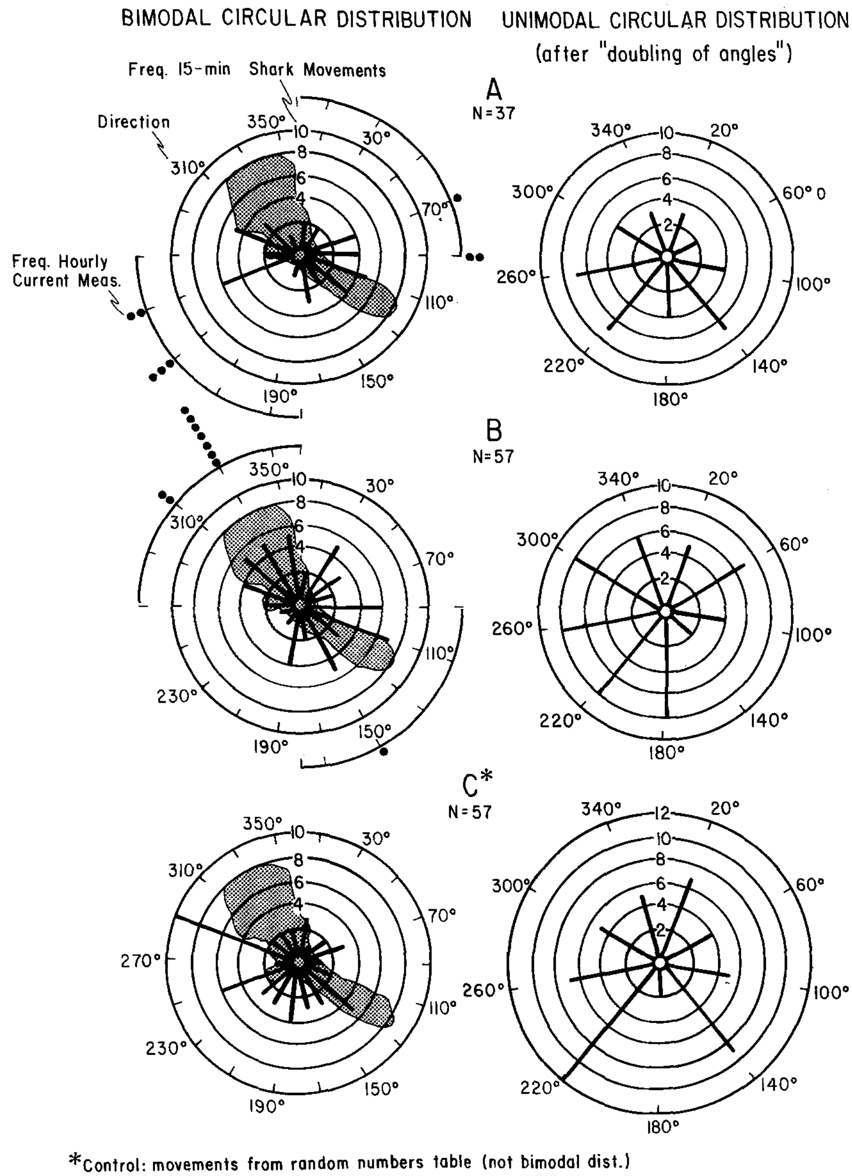

Fig. 4. Polar plots with bimodal (*lefthand*) and unimodal (*righthand*) frequency distributions of directions between 15-min positions and directions of hourly current measurements for currents flowing perpendicularly (**A**) and parallel (**B**) to the axis of the seamount. Also shown is a distribution of directional movements (**C**) created with a random numbers table. Bimodal converted to unimodal distributions by "doubling the angles" technique of Batschelet

a change in the direction of the current affected the directions moved by the tagged sharks. Tracking positions, their centers of activity, and activity contours differed little for currents flowing perpendicular to the seamount ridge and in its direction. Although the longitudinal axes of the 20, 30, and 60% activity contours under both current regimes paralleled the seamount ridge, the 80 and 100% contours were elongated in a westerly direction away from the seamount ridge when perpendicular (southwesternly) currents were present and were elongated in a southernly direction away from the ridge when parallel (northwesternly) currents were present.

Were the tagged scalloped hammerheads, presumably within the schools, changing their positions in response to changes in currents in a statistically significant manner? In order to test this, frequencies of directions moved were plotted on polar coordinates for both current regimes (Fig. 4). The frequency distributions were roughly centrally symmetrical with frequency modes of 70 and 250 deg for currents perpendicular to the seamount ridge (see Fig. 4A), and 110 and 330 deg for currents parallel to the ridge (Fig. 4B). In order to compare the two distributions, they were converted from bimodal to unimodal distributions by the "doubling the angles" method of Batschelet (1965). The two distributions did not differ statistically (F-Test, $P > 0.05$). Furthermore, the distributions under different current regimes did not differ significantly from a control distribution (Fig. 4C)

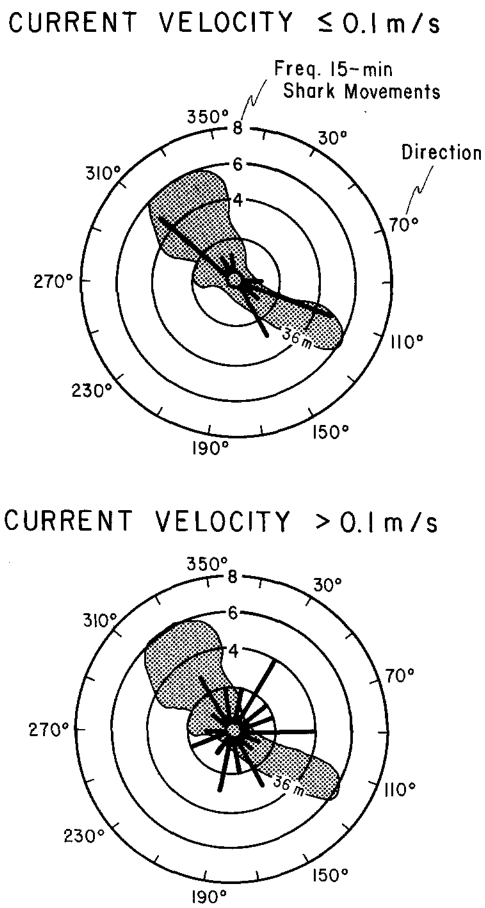

Fig. 5. Polar plots of frequency distributions of movement directions between successive 15-min positions for current velocities ≦0.1 m/s and >0.1 m/s

formed with the use of a random numbers table (F-Test, $P>0.05$). Thus, the hammerheads did not appear to change their positions in response to changes in current direction. Supporting this conclusion was the lack of correlation between the movements of hammerhead no. 9 in the vicinity of the seamount with current directions (see Fig. 3). Although some of the movements preceeding or following the hourly current measurements were either in the same or opposite directions (see 1,400, 1,700–1,900 hours), others were in perpendicular directions (see 1,100 and 1,300 hours).

The scalloped hammerheads did not appear to remain at the seamount by using a rheotaxis. Directional movements with currents flowing from the northwest in a direction parallel to the ridge were separated into those occurring in currents of slow (≦0.1 m/s) and fast velocities (>0.1 m/s) (Fig. 5). With the currents slow the directions of shark movements were almost all with or against the current. However, when currents were fast, the directions of shark movements were in many directions. If the sharks were using current direction as a cue to remain at the seamount, the movements should have been less directional when the currents were weak than when they were strong.

It appeared that the tagged hammerheads swam faster later in the day. Distances between subsequent positions were combined into five 2 h classes from 1,000–1,145 hours to 1,800–1,945 hours. The medians differed significantly (Kruskal-Wallis Test, $P<0.05$), and they increased successively for the first four time periods from 87.5 to 171.0 m. All tagged sharks departed from the vicinity of the seamount by night.

After leaving El Bajo Espiritu Santo, the tagged scalloped hammerheads swam in a nondirectional (Tracking no. 6) or directional manner (no. 7 and 9). Trackings of these three sharks are plotted together with hourly current directions and velocities on a bathymetric chart (Fig. 6). Distributions of directions of the movements between 15-min positions for the three sharks were tested against uniform distributions with the Rayleigh Test. Although the directional movements in tracking no. 6 did not differ significantly from a uniform distribution ($P>0.05$), the directional movements in trackings nos. 7 and 9 differed significantly ($P<0.02$ and $P<0.01$, respectively). The relatively straight-line movements of nos. 7 and 9 did not result from their being carried with the prevailing currents since these currents, usually greater than 0.1 m/s, were flowing in directions opposite to those of the sharks' movements. It is possible that the sharks were deriving orientational information from the oppositely flowing currents to move over large distances in a straight-line manner. Further indicating an ability for the hammerhead sharks to utilize directional cues in the open ocean was the prompt return of four sharks to the seamount after extensive movements away from the seamount.

Both the depths at which hammerhead shark no. 13 swam and the bottom depths beneath it at the time of its positioning are shown in Fig. 7. During the first day the shark remained over the seamount at a relatively constant depth of ca. 12 m; and at 1,828, soon after sunset, the shark moved away from the seamount. The shark moved in a northeasterly direction while making brief dives. The shark returned to the seamount on the following day and spent most of the day at a depth of 30 m, possibly along the edge of the seamount as indicated by the greater bottom depths underneath the shark. After sunset the shark again left the vicinity of the seamount in a northeasterly direction and made brief dives.

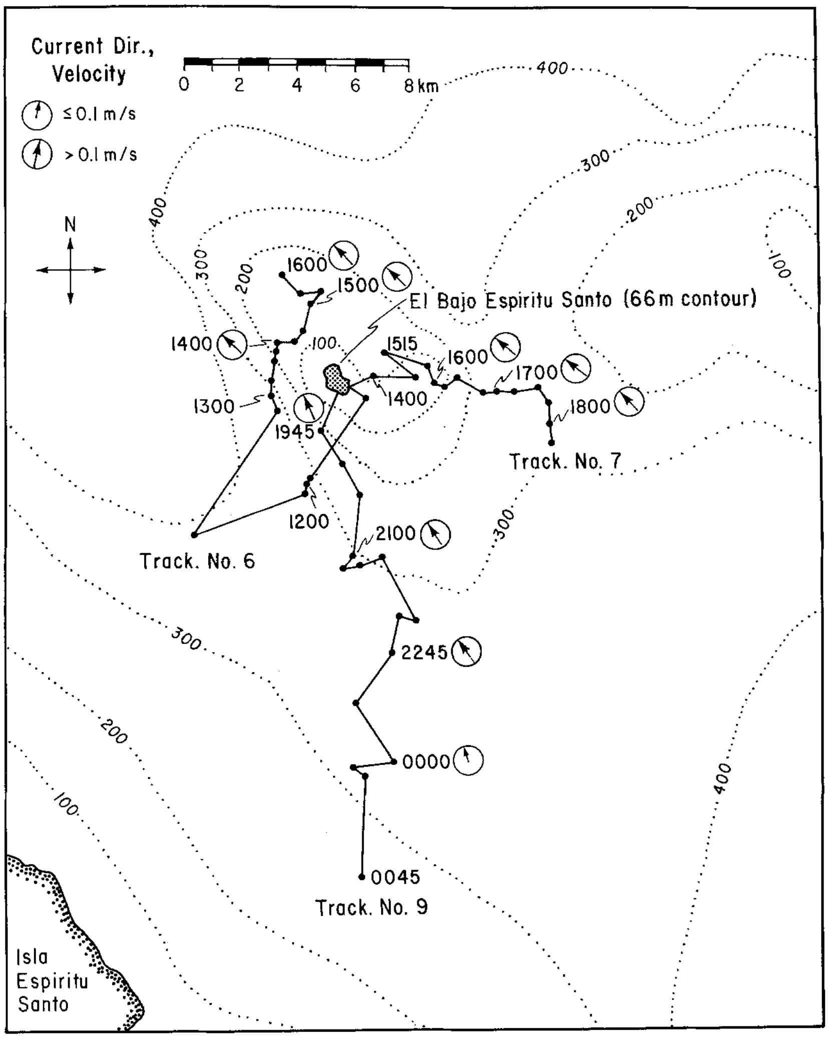

Fig. 6. Movements between 15-min positions for three scalloped hammerheads (nos. 6, 7, and 9) after they left El Bajo Espiritu Santo

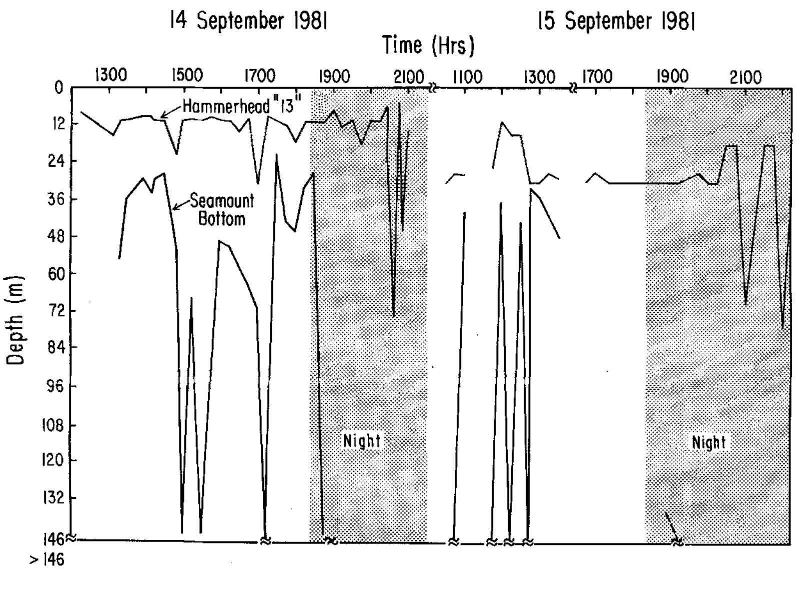

Fig. 7. Swimming depths of hammerhead no. 13 tracked on 14 and 15 September 1981 and bottom depths beneath the shark at 15-min intervals. Note that the tracking was intermittent, and the time abcissa is broken at points to indicate when positions were not taken. The limit of the fathometer's depth scales was 146 m

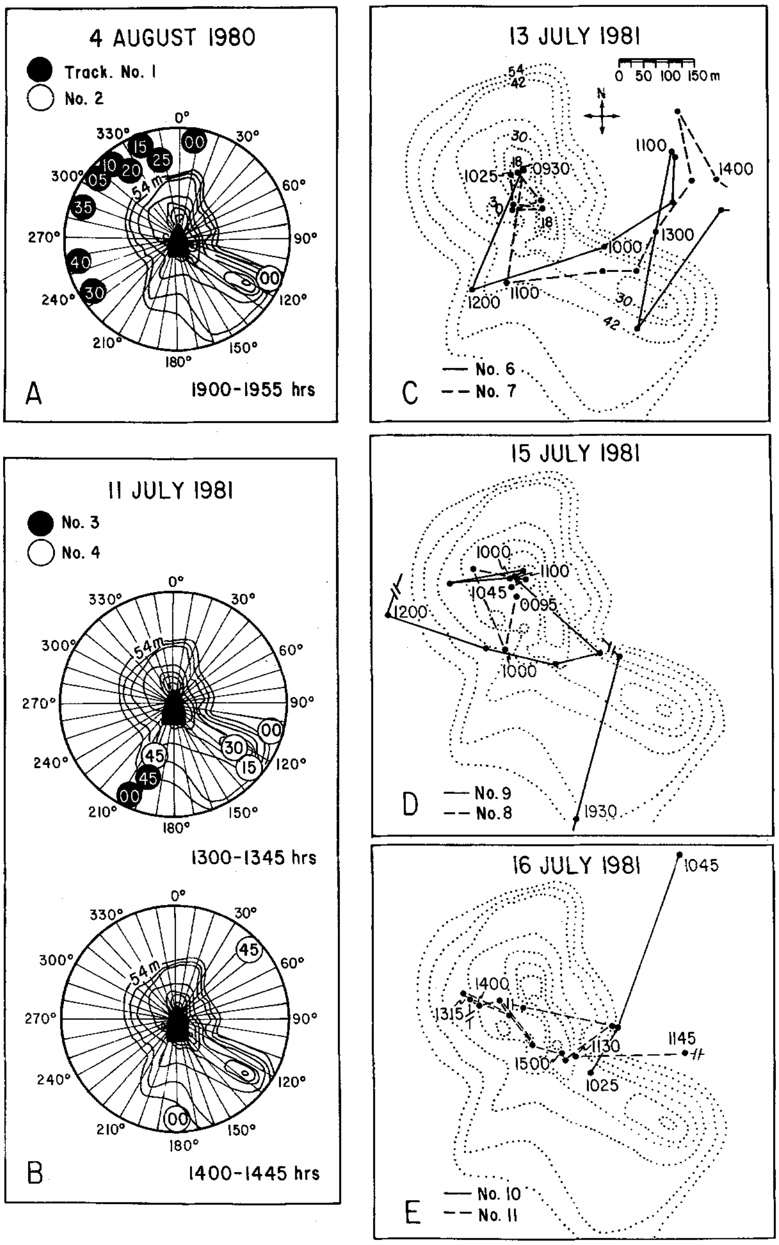

Fig. 8. Five attempted paired telemetry trackings at El Bajo Espiritu Santo during 1980 and 1981. The former two trackings with the bearings of the two sharks indicated as *shaded and clear circles* with the time (min) enclosed within the circles. The position of the boat and bathymetric contours are superimposed upon the plots. The latter three trackings consist of the positions of the two sharks (connected by *solid or dashed lines*) plotted on bathymetric charts

An attempt was made to determine whether the sharks left the seamount in schools to forage socially by tagging two sharks with transmitters and simultaneously tracking them. The sharks might remain together during the day so that they could easily form groups at night. Five paired trackings were attempted during the summers of 1980 and 1981 (Fig. 8).

In paired trackings A and B it was possible only to determine bearings to the two sharks simultaneously from the tracking vessel anchored over the seamount. In these trackings one hammerhead left the vicinity of the seamount before the other and in a different direction than that of the other. While near the seamount the bearings of the two sharks were very similar (not shown Fig. 8A, but see Fig. 6 in Klimley 1982a) suggesting that they might be swimming within a single school. Positions of the two sharks were determined in the next three paired trackings. In Fig. 8C the two sharks did not remain together prior to their departure. In Fig. 8D no. 8 remained momentarily near no. 9 above the seamount ridge before leaving early during the day. No. 9 swam back and forth along the seamount ridge throughout the day until it left in a southernly direction in the evening. And finally, in Fig. 8E no. 10 left the seamount before no. 11 was tagged. The departure of pair members at different times and in different directions, of course, did not prove that the hammerheads were leaving by themselves. If the size of the population of hammerheads at El Bajo Espiritu Santo was large, group composition dynamic, and the departing groups small, the probability of members of five shark pairs separating, yet leaving with other sharks would be high.

Marking

Some marked sharks were seen again repeatedly while others were never again observed, indicating a steady rate of emigration from the seamount. During ten visits to the seamount, a continuously decreasing number of tagged sharks was seen. This indicated that sharks were emigrating from the site, and not just mixing into local population. If one considers only the reobservations of the first 30 sharks tagged during 1980, one finds a steady decrease in observations of 7 on 4 Aug., 5 on 5 Aug., 1 on 6 Aug., 6 on 16 Aug., 3 on 21 Aug., 3 on 22 Aug., 2 on 29 Aug., and only 1 on 26 August. After returning to the seamount for several days, marked sharks might be moving to other locations where grouping occurred. Although five other locations in the middle and lower Gulf of California (see Klimley 1982b) were visited on a seasonal basis from 1979 to 1981, none of the sharks marked at El Bajo Espiritu Santo were observed at these locations.

Despite the steady rate of emigration, a shark tagged on 30 July 1980 was observed five times over a 28-day period, and a shark tagged on 30 July 1981 was observed five times over a 6 week period ending on 26 September. Sharks that were repeatedly seen at the seamount probably moved away to forage during the night and returned during the following day to swim among the schools at the seamount as did telemetered shark no. 13. Few identifications of the sex of marked sharks were made; and for this reason, it was impossible to determine whether females remained for longer periods at the seamount than males. A greater site attachment by females might explain their greater numbers in the groups (Klimley 1982b).

One shark marked in August 1979 was observed on the seamount during the same month a year later; another was observed during the same month two years later. Few hammerhead groups were seen at the seamount during the fall, winter, and spring of 1980 and 1981, and those seen did not include the tagged sharks. It is probable that these marked sharks observed on successive years did not remain at the seamount throughout the year, but returned to it after making migratory movements.

Discussion

Hamilton and Watt (1970) divided central place social systems into three overlapping categories. The most socially complex system, characterized by large numbers of individuals with complex communication systems and cooperative behavior patterns was termed a refuging system. Characteristic of such a system are large groups of animals which remain in a small core area during the inactive phase of their diel cycle, and disperse large distances into a large feeding arena to forage either in small groups or as solitary individuals. The composition of such groups is dynamic, and aggressive encounters frequently occur among school members. The social system of the scalloped hammerhead closely resembles that of other refuging species. During the day the telemetered sharks swam slowly back and forth along the seamount ridge. This core areas was small compared to the extensive area of the pelagic environment in which the tagged sharks swam at night. When at the seamount the hammerheads did not forage. Feeding responses were never observed there although the hammerheads were often seen swimming through diffuse schools of potential prey. No feeding responses were shown to bait or to sounds resembling those of prey (Klimley and Nelson 1981). Trackings together with the continued observation of many marked sharks indicated that a rhythmical dispersion of sharks was occurring from the seamount into the pelagic environment late in the day and back again early in the morning. The separate departures of members of the pairs of tagged sharks suggested that the hammerheads might be leaving either in small groups or as solitary individuals.

Other species of sharks also form refuging groups. The gray reef shark (*Carcharhinus amblyrhynchos*) was found by Johnson (1978) and Nelson and Johnson (1980) to mill slowly in groups in a small core area of its home range. The feeding motivation of school members was never examined, but the sharks appeared uninterested in local fishes which were potential prey. At dusk the gray reef sharks moved away from this core area. Nelson and Johnson (1980) and Randall (1977) observed that the reef whitetip (*Triaenodon obesus*) remained inactive at times in small groups during the day in caves, and the same individuals repeatedly returned to the same caves over several successive days. Another possible refuging species is the bullhead shark (*Heterodontus portusjacksoni*). McLaughlin and O'Gower (1971) found groups of up to 16 bullhead sharks during the day in caves on a rocky reef. The authors concluded from their diet of benthic invertebrates that the sharks foraged extensively during the night over both the reef and the surrounding soft bottom.

The refuging of these species of sharks may function to optimize energetic output. Energy could be conserved during the day by the scalloped hammerheads as they slowly swam back and forth along the small seamount ridge. Yet they could also remain at a point central in their feeding area. This landmark might also be used as a reference for their daily movements. Additional benefits accured from remaining at the seamount in groups might be the ease with which social activies leading to mating could occur.

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