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Movements and swimming behavior of three species of sharks in La Jolla Canyon, California

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Synopsis

We tracked six individuals of three shark species, the shortfin mako, *Isurus oxyrinchus*, great white, *Carcharodon carcharias*, and blue, *Prionace glauca*, near the submarine canyon off La Jolla, southern California during the summers of 1995 and 1997. The duration of tracking ranged from 2 to 38 h per shark. The mode of travel differed in one respect among species. The rate of movement of the endothermic species, the mako and white shark, exceeded that of the ectothermic species, the blue shark. Similarities among species were more common. Firstly, individuals of all three species swam in a directional manner. Secondly, individuals constantly moved up and down in the water column, exhibiting oscillatory or yo-yo swimming. Thirdly, members of the three species swam at the surface for prolonged periods. Finally, the movements of the mako and white sharks were at times loosely associated with bottom topography. We discuss the various adaptive advantages that have been proposed for these behavioral patterns. Oscillatory swimming has been attributed to the following: (1) heating the body in the warm surface waters after swimming in cold, deep water, (2) alternating between two strata of water, one carrying chemical information as to its source, and deriving a direction to that stratum's origin, (3) conserving energy by quickly propelling oneself upward with many tail beats and slowly gliding downward with few beats, and (4) descending to where magnetic gradients are steeper, more perceptible, and useful to guide migratory movements. At the surface, an individual would be able to swim in a straight line by using following features as a reference: (1) celestial bodies, (2) polarized light, or (3) the earth's main dipole field. Furthermore, an individual would conserve energy because of the greater ease to maintaining a warm body in the heated surface waters.

Introduction

The swimming behavior and movements of pelagic fishes have often been described in single-species studies. Each individual is followed by boat to acquire a description of its behavior (depth, speed, and heading) and environment (water temperature). Measurements of these properties are recorded by sensors on an ultrasonic transmitter, which is attached to the subject. This method has been used to provide descriptions of the behavior of a variety of species such as tunas (Hunter et al. 1986) and sharks (Nelson 1990) in different physical environments at widely separated geographical locations. Recently, individuals in different age classes have been tracked under similar physical conditions in the same geographic locality (Brill et al. 1999) or individuals of one age class toward a limit of its range (Block et al. 1999). However, an equally important, but less common perspective, is to compare the responses of multiple species to the same environment. Similarities between the behavior of these species likely result from mechanisms of migration common among the species.

We present a description of the movements and behavior of three species of sharks, the blue, *Prionace glauca*, shortfin mako, *Isurus oxyrhinchus*, and white, *Carcharodon carcharias*, in La Jolla Canyon, southern California. We draw attention to common properties in their diving records and discuss theories explaining their adaptive significance. Finally, we make recommendations for future studies of the mechanism(s) of open-ocean migration.

Methods

Three shortfin mako, one juvenile great white, and two blue sharks were tracked in the vicinity of La Jolla submarine canyon (Table 1, Figure 1). Each shark was captured by hook and line. It was kept temporarily (<5 min) in a life-support container with circulating oxygenated water, while tagged with an ultrasonic transmitter, some of which were equipped with depth and temperature sensors (Vemco Ltd., V32TP-4H). The transmitter was mounted on the end of a pole spear with a tether leading to a stainless steel dart held in a slot on the tip of the spear. The dart was inserted into the muscle of the shark's dorsum between the first and second dorsal fins.

The sharks were tracked in a small vessel using a directional hydrophone and ultrasonic receiver (Vemco Ltd., VR-60). This provided a directional heading from the tracking vessel to the shark. We kept the boat over the tagged fish unless swimming on the surface in order to approximate its position. The range of signal reception was approximately 750 m, depending on sea surface conditions and ambient noise. If the shark swam out of range, a second hydrophone and ultrasonic receiver (Dukane Corp., N30ASB) with greater range was used to get a bearing to the shark. The former receiver was linked to a laptop computer, which converted the intervals between pulses to swimming depths and water temperatures. Also linked to the system was a differential-corrected global positioning system (GPS) [Magellan, NAV DLX-10] providing latitude and longitude positions (+/−5 m) of the tracking vessel. Depth and temperature were recorded every three seconds, latitude and longitude every one minute. We collected profiles of temperature with a bathythermograph (Vemco Ltd., SeaLog 291) every one or two hours while tracking. The blue sharks were tracked for shorter periods because their purpose was to train the staff of the Aquarium Department at Sea World-San Diego.

We chose an interval of 5 min between positions for calculating rates of movement and headings. The basis for this decision was that the standard deviations (SD) of the distances traveled between consecutive positions determined at 1- and 2-min intervals were significantly higher than those obtained at 5-, 10-, and 15-min intervals and the latter three SDs differed little among each other. We reasoned that the high SDs were due to our inability to position the boat over the shark during the shorter time scales. All measurements of depth and temperature were included in our analyses.

Results

We will initially describe the tracks of the three species of sharks on an individual basis. After that, we will draw attention to the similarities in the behavior and movements within and among species.

Tracked sharks

Mako shark 1 (M1). This female with a total length (TL) of 119 cm was tagged and released at 13:18 h on 25 June 1997 on the northern slope of La Jolla Canyon (Table 1, Figure 1). During the shark's 12-h track, she traveled continuously in an offshore direction over the canyon. Initially swimming northwest, parallel to the northern edge of La Jolla Canyon, the shark turned

Table 1. Sharks tracked in La Jolla submarine canyon (TL = total length (* = estimated); M = Male; F = Female; D = Depth; T = Temperature).

Shark no.	Species	Common Name	TL (cm)	Sex (M/F)	Transmitter sensor (D/T)	Tracking		
						Date	Start (h)	Duration (h)
B1	*Prionace glauca*	Blue*	150			8 July 1995	14:00	1:55
B2	*Prionace glauca*	Blue*	150		D	14 July 1995	14:00	2:05
W1	*Carcharodon carcharias*	White	152	M	D,T	18 July 1995	14:55	3:40
M1	*Isurus oxyrinchus*	Shortfin mako	119	F	D,T	25–26 June 1997	13:18	12:30
M2	*Isurus oxyrinchus*	Shortfin mako	142	M	D,T	9–10 July 1997	15:15	21:55
M3	*Isurus oxyrinchus*	Shortfin mako	135	M	D,T	11–13 Sept 1997	10:26	38:10

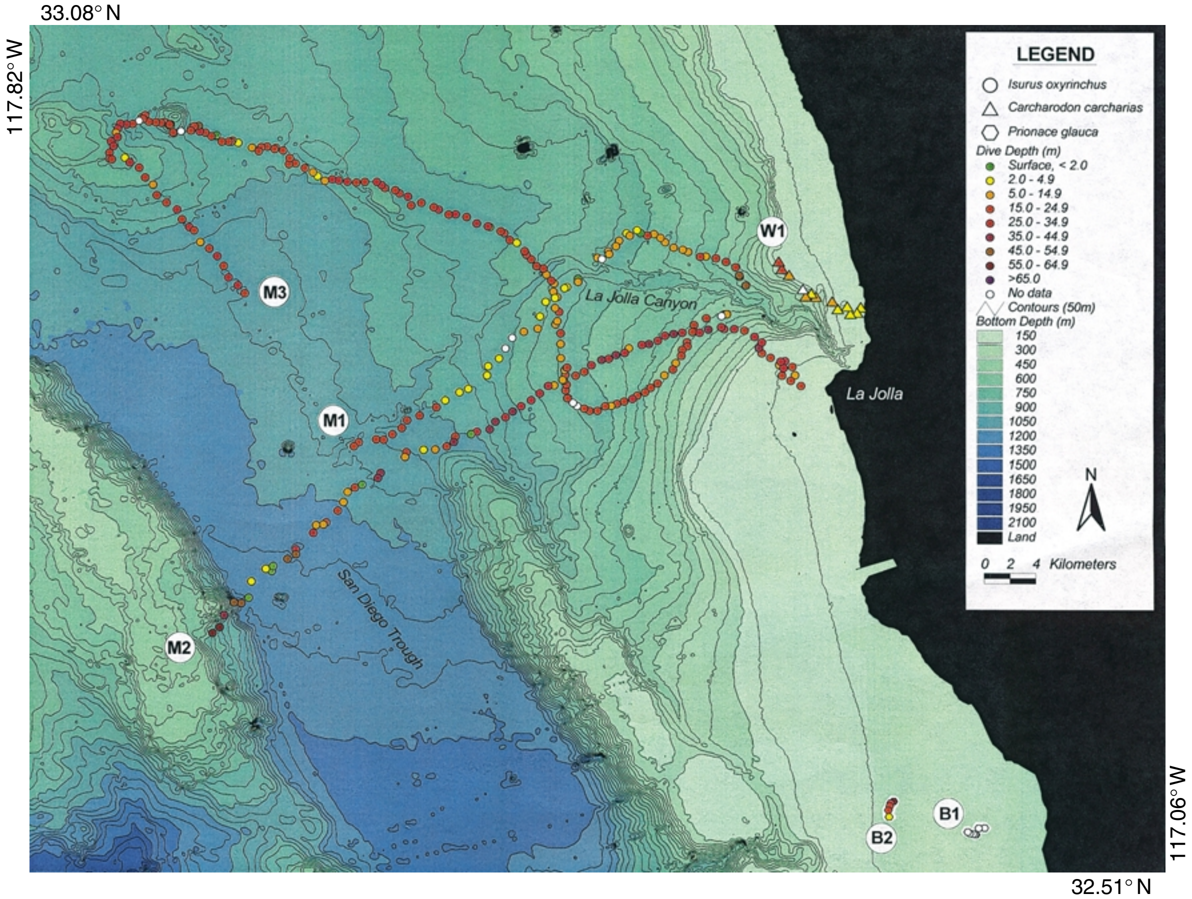

Figure 1. Tracks of three mako sharks (M1–3), two blue sharks (B1–2), and one white shark (W1) off La Jolla, Southern California. Positions plotted at 15-min intervals with symbols color-coded for depth. Each contour line indicates a 50-m change in depth. Note that individuals of all three species swam at times near the surface (see green and yellow symbols).

to the southwest after approximately 2 h, and followed this general heading until contact was lost at 1:18 h on 26 June. Through the entire track, the shark covered a total distance of 40.0 km, and its median point-to-point rate of movement was 0.9 m s^{-1} (0.8 body lengths [BL] s^{-1}). She showed a few spurts of activity during the night hours with swim speeds peaking at 7.8 m s^{-1} (6.6 BL s^{-1}) (see peaks in Figure 2a). Mako M1 maintained higher rates of movement at night with a mean of 1.1 m s^{-1} (0.9 BL s^{-1}) versus day with a mean of 0.8 m s^{-1} (0.7 BL s^{-1}) (Figure 3a).

Upon release M1 dived to a depth of 55 m to a temperature of 12°C (Figure 4a). After 30 min the shark rose to 25 m and remained there for another 35 min. At 14:40 h M1 ascended again to above 10 m, and for the next 2 h made regular dive oscillations between 5 and 20 m, presumably passing through the thermocline. At 17:00 h the shark rose into the mixed layer and then surfaced at 18:16 h. M1 dived below the thermocline again at 18:40 h to 17.3 m, then returned to the mixed layer in less than 10-m depth, and remained there for 3 h. At 21:45 h the shark dived to 15 m, within the thermocline, and swam there for 10 min. The shark then surfaced again and stayed between the surface and 10 m for the next 1.5 h. At 23:40 h M1 began a descent to 20 m where she stayed until contact was lost at 1:18 h on 26 June.

Mako shark 2 (M2). This 142-cm TL male was tagged and released at 15:15 h on 9 July 1997 at the southern slope of La Jolla Canyon (Table 1, Figure 1). For the first hour following release, this shark swam shoreward and seemed to direct its activity at and around a large sportfishing vessel. After he left the vicinity of the

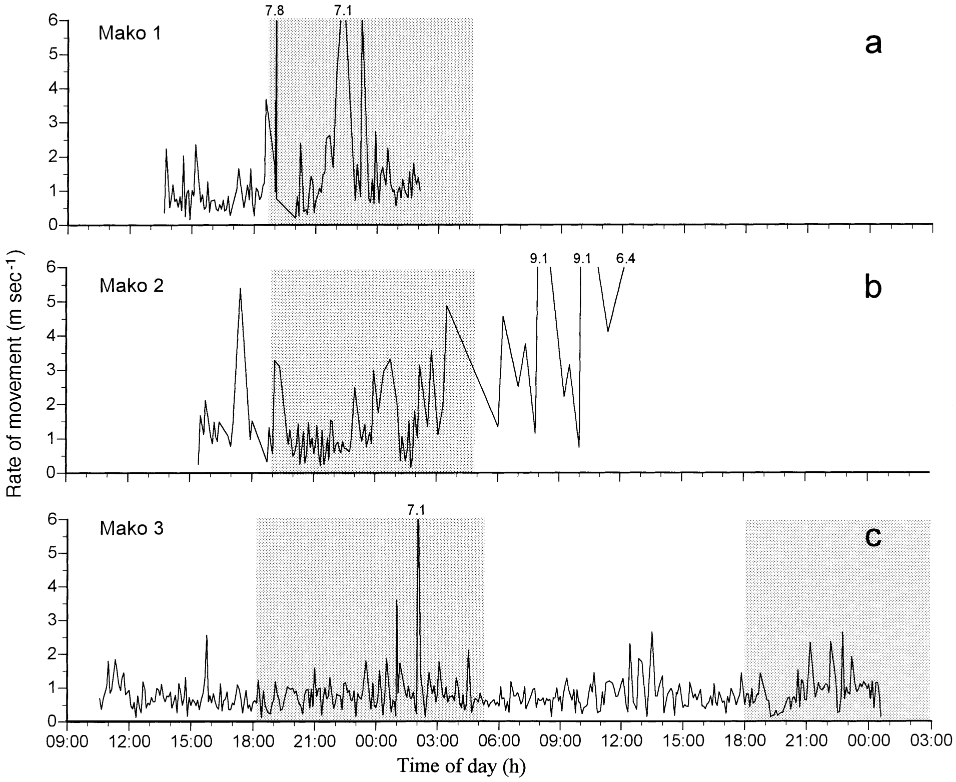

Figure 2. Rates of movements over period of tracks for three mako sharks: a – Mako M1 tracked on 25 June 1997, b – M2 tracked on 9 July 1997, and c – M3 tracked on 11 September 1997. The rates are calculated between consecutive positions separated by 5-min intervals. Stippling indicates nighttime. Values are given above truncated peaks in the curves for the infrequent high swimming speeds in order to distinguish the variability at lower speeds.

sportfishing vessel, he spent the remainder of his 22-h track moving offshore. M2 spent his first two hours traveling parallel to the canyon edge in a northwest direction and then turned southwestward as did M1. The shark then traveled out across the San Diego Trough and headed directly toward a 364-m deep pinnacle on the edge of the 30-Mile Bank. Contact with M2 was lost at 13:16 h on 10 July shortly after the shark had reached the shallower depths of this bank. The shark's median point-to-point rate of movement over the 53.0-km track was 1.2 m s^{-1} (0.8 BL s^{-1}). This shark showed many spurts of heightened activity during both day and night, the highest calculated rate being 9.1 m s^{-1} (6.4 BL s^{-1}) (Figure 2b).

After his release at 15:15 h, M2 immediately dived to 28 m and over the following hour slowly ascended to 18 m (Figure 4b). The shark then began a series of regular diving oscillations below the thermocline between 18 and 44 m. After 22:00 h the thermocline in the area where the shark was swimming became less distinct, and he began larger diving oscillations, at times from the surface to >40 m. M2 continued swimming in this fashion until the end of his track. When contact with M2 was lost at 13:16 h, he made the deepest dive of the track to 65 m. Just over 300 m below the shark was the only seamount in the immediate area (Figure 1). M2 showed a preference for slightly deeper waters at night, spending 66% of the night below a depth of 26 m (Figure 5b). During the day most of his diving oscillations were between 10 and 26 m. This shark experienced a temperature range of 10°C throughout the track, appearing to favor cooler waters than M1, spending 31% of the track in the 13.0–13.9°C range (Figure 6).

Mako shark 3 (M3). This 135-cm TL male was tagged and released at 10:26 h on 11 September 1997 on the southern edge of La Jolla Canyon (Figure 1). His 38-h

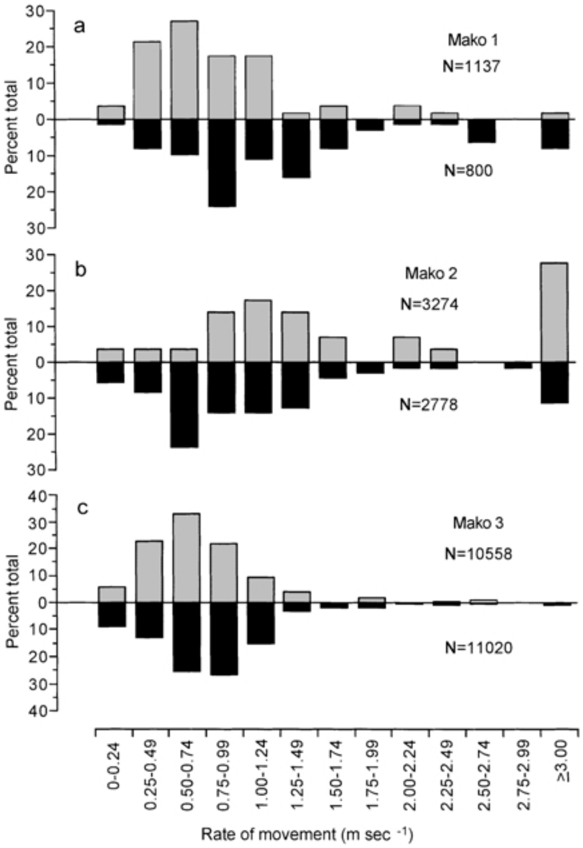

Figure 3. Percentages of the total number of movements of different rates recorded for mako sharks: a – M1, b – M2, and c – M3. Stippled bars above abscissa indicate daytime rates of movement; solid bars below denote nighttime rates.

track differed noticeably from the tracks of M1 and M2. From the release site, M3 headed southwest, tracing the 400-m depth contour on the south slope of the canyon, until 16:00 h when the shark turned almost due north. At 21:00 h he turned again, and traveled west-northwest directly toward a 640-m pinnacle, which was passed at 12:45 h on 12 September. Then at 16:15 h the shark turned to the southeast and swam out into the San Diego Trough and parallel to shore. M3 maintained this heading until contact was lost at 00:40 h on 13 September. This shark traveled 93.9 km at a median point-to-point rate of movement of 0.7 m s^{-1} (0.5 BL s^{-1}). M3 was comparatively less active than the other two makos with only a few bursts of swim speeds greater than 2.0 m s^{-1} (1.5 BL s^{-1}) (Figure 2c). He maintained a fairly consistent rate of movement both day and night throughout the entire track (Figure 3c).

As the other two individuals, M3 dived immediately after release. This shark descended to a depth of 52 m initially, but within 10 min he rose to 8 m, and then descended again to 34 m. M3 then began frequent diving oscillations below and within the thermocline, which continued with little change through the entirety of the track (Figure 4c). Occasionally he ascended into the mixed layer ($>$23°C), but each time quickly returned to cooler waters below the thermocline ($<$19°C). No change in diving behavior was observed between day and night (Figure 5c). At 12:12 h on 12 September, M3 made a noticeably deeper dive to 52 m. The shark was very near the 640-m pinnacle when this dive occurred (Figure 1). M3 showed a more distinct distribution of depth and temperature preferences. As M2, M3 spent more time in deeper waters at night, with a peak at 22.0–23.9 m (Figure 5c). His daytime preference was 18.0–19.9 m. M3 experienced a temperature range of 11°C, but showed a clear preference for the 17.0–17.9°C waters (Figure 6c).

White shark 1 (W1). This 152-cm TL male was released at 14:55 h on 18 July 1995 near the shore north of La Jolla Point (Table 1, Figure 1). W1 traveled continuously away from shore in a northwesterly direction during the 3.6-h track. The shark swam parallel to the northern edge of La Jolla Canyon over the 100 and 150 m contours. Tracking was discontinued at 18:35 h as W1 approached the mouth of the submarine canyon. This shark swam a distance of 10.1 km with a median point-to-point rate of 0.8 m s^{-1} (0.5 BL s^{-1}). W1 displayed no rates of movement greater than 1.3 m s^{-1} (0.9 BL s^{-1}). No tracking occurred during night hours for this shark.

W1 was released near shore over shallow water ($<$5 m), and dived to the bottom upon his release. While W1 moved offshore toward deeper water, he made numerous excursions between the bottom and the surface (Figure 7). The shark seemed to orient to the bottom until 15:20 h when the bottom dropped off to 18 m. At this time he rose to the surface and oscillated between 8 m and the surface. At 15:40 h the shark made his first excursion below the thermocline, and then began a series of dive oscillations between the surface and 25 m that continued until the end of the track. The shark spent little time swimming within the thermocline, but passed through it several times during the track. W1 usually swam $<$20 m from the surface, and never went deeper than 26 m, even though it swam over depths exceeding 100 m for much of the track. The

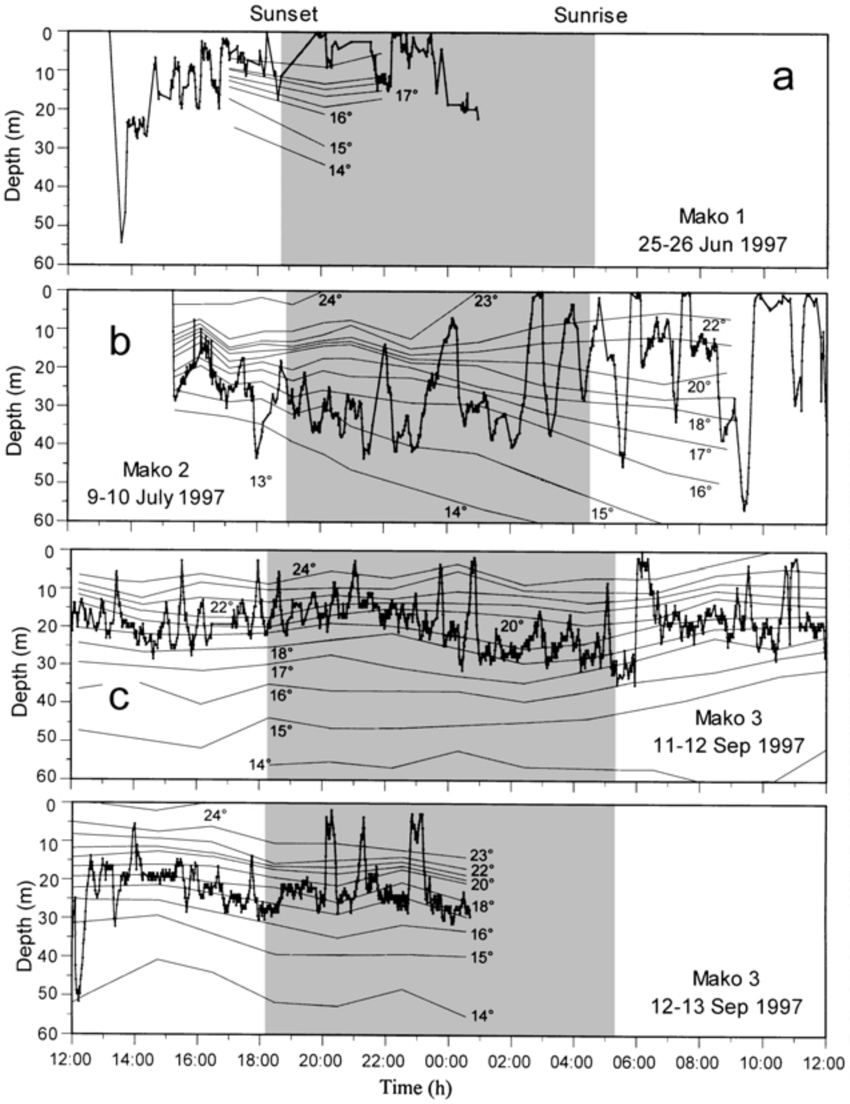

Figure 4. Diving records of three mako sharks: a – M1, b – M2, and c – M3. Nighttime indicated by stippling.

shark spent nearly even amounts of time at 0.0–1.9 m (with temperatures of 20.0–20.9°C) and at 16.0–17.9 m (15.0–15.9°C).

Blue shark (B1). This shark was released at 13:17 h on 8 July 1995 in near shore waters (Figure 1). It swam due west from the release site for the entirety of the 2-h track. B1 traveled a total of 4.3 km in waters <50 m deep at a median point-to-point rate of 0.6 m s^{-1} (0.4 BL s^{-1}). The fastest rate recorded for B1 was 2.5 m s^{-1} (1.7 BL s^{-1}).

Blue shark (B2). This individual was released at 13:00 h on 14 July 1995 west of where the track of B1 was concluded (Figure 1). This shark swam due south, parallel to the 50-m depth contour throughout the 2-h track. B2 swam a total of 2.0 km at a median point-to-point rate of 0.3 m s^{-1} (0.2 BL s^{-1}), the slowest of the sharks tracked in this study. Its fastest recorded rate was 0.6 m s^{-1} (0.4 BL s^{-1}), only slightly faster than the median rate of movement of B1. This blue shark made the deepest post-release dive of the sharks presented here, sounding to 65 m upon release. The

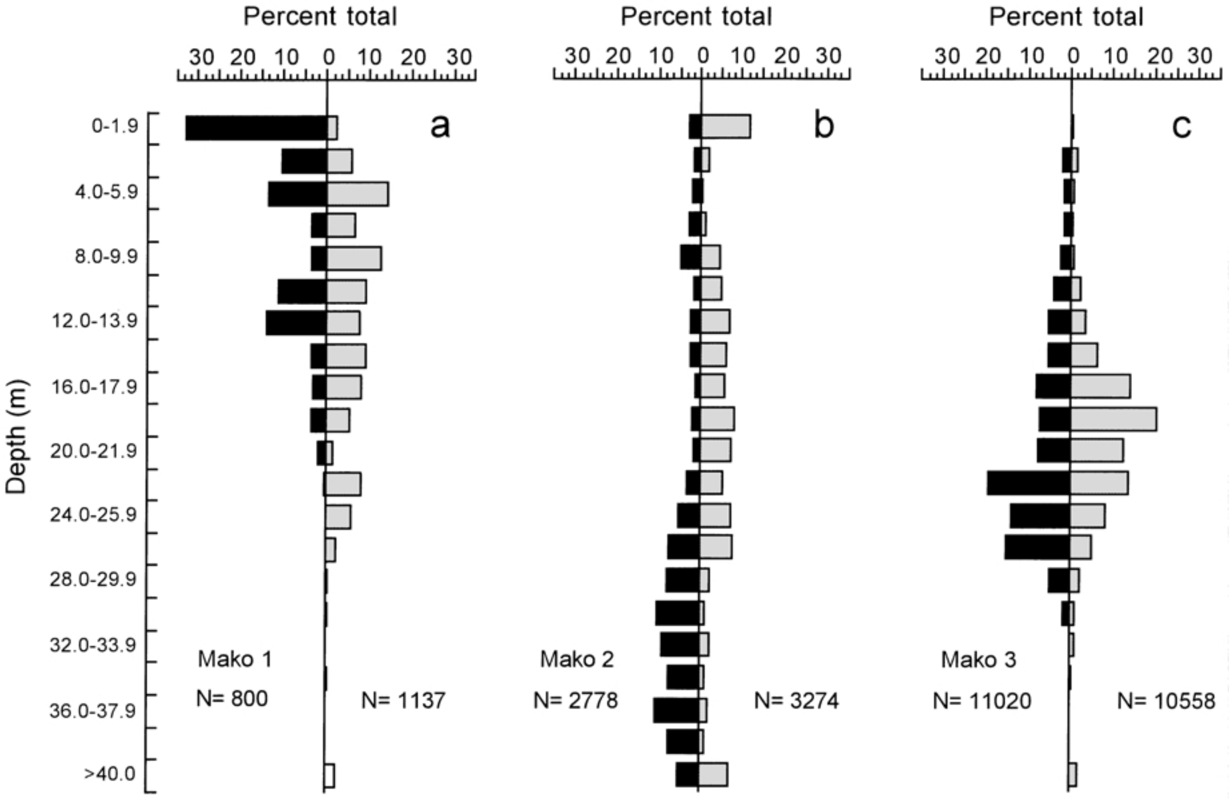

Figure 5. Percentages of the total number of depths recorded for three mako sharks: a – M1, b – M2, and c – M3. Stippled bars to right of ordinate indicate daytime depths; solid bars to left denote the nighttime swimming depths.

temperature at this depth was <10°C. Within 5 min of reaching these depths B2 began ascending, and within 20 min was swimming steadily below the thermocline at 20 m, where it remained for approximately 50 min. At 14:20 h the shark ascended into the thermocline, and oscillated between 5–10 m until the end of the track at 15:00 h. B2 spent 45% of the track time between 20.0–25.9 m, making frequent but small oscillations within this depth range.

Inter-species comparisons

The median rates of movement for the mako sharks (daytime: 0.7 m s^{-1} [0.5 BL s^{-1}] nighttime: 0.8 m s^{-1} [0.5 BL s^{-1}]) were similar to the daytime rate of the white shark (0.8 m s^{-1} [0.5 BL s^{-1}]), but greater than the median rate for the blue shark (0.3 m s^{-1} [0.2 BL s^{-1}]). The mako and white sharks most often swam at rates ranging from 0.50 to 0.99 m s^{-1} (0.4 and 0.3–0.8 and 0.7 BL s^{-1}, respectively) during daytime (see histograms, Figure 9a,b), but the blue shark swam at a slower rate of 0–0.74 m s^{-1} (0–0.5 BL s^{-1}) (Figure 8c). Thus the spaces between the symbols denoting 15-min positions of the mako and white sharks are similar and are separated farther apart than the symbols indicating the positions of the blue sharks (Figure 1). These faster rates were sustained over long periods of each track. However, periodically the mako and blue sharks made short bursts of movement >3 m s^{-1} (2.3 and 2.0 BL s^{-1}, respectively) (Figure 8).

By looking at the tracks shown in Figure 1, it is immediately noticeable that all five of the sharks were very directional in their courses. The mako sharks traveled over great distances with little alteration in heading. Only M3 altered its northwesterly course once after it passed a seamount to a southeasterly heading. The single white shark swam in a sustained manner in the northwesterly direction. One of the two blue sharks swam in a sustained direction; the second was tracked

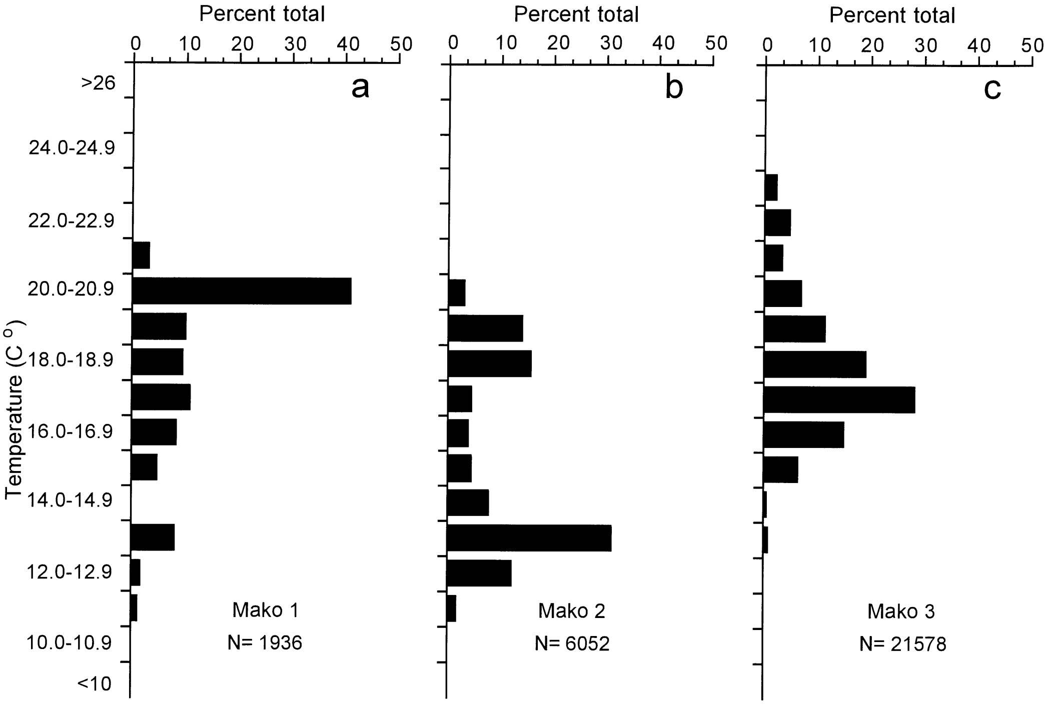

Figure 6. Percentages of total number of measurements of different temperatures recorded at three mako sharks: a – M1, b – M2, and c – M3.

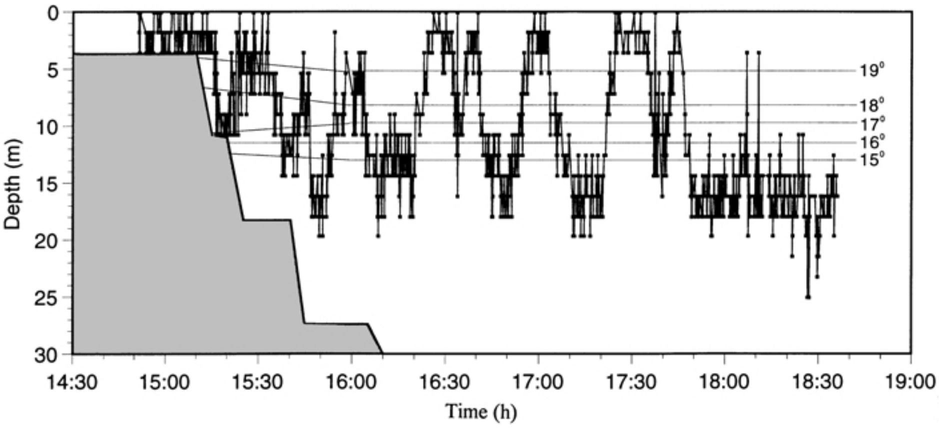

Figure 7. Diving record of juvenile white shark tracked along the edge of the La Jolla Canyon. Stippling indicates seafloor. Note the amount of time spent swimming at or near the surface.

too briefly to ascertain its directionality. We present circular plots showing the change in the direction of consecutive vectors between positions separated by 5-min intervals (Figure 9). High frequencies of headings in the initial angular classes to either side of zero (where both headings were identical) were indicative of heading persistence, i.e., the ability of the shark to swim in a straight line over time. The mako sharks exhibited high heading persistence with most of their vectors occurring in the two angular classes, <0–19° (Figure 9a). The white shark also showed considerable directionality to its headings. Two of the four peaks in

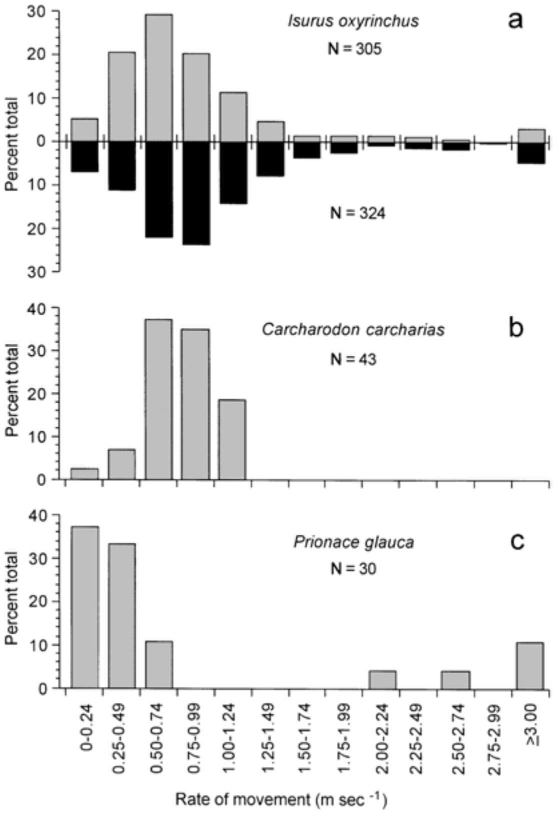

Figure 8. Percentages of the total number of movements of different rates recorded for: a – three mako sharks, b – one white shark, and c – two blue sharks. Stippled bars above abscissa indicate daytime rates; solid bars below denote nighttime rates of movement.

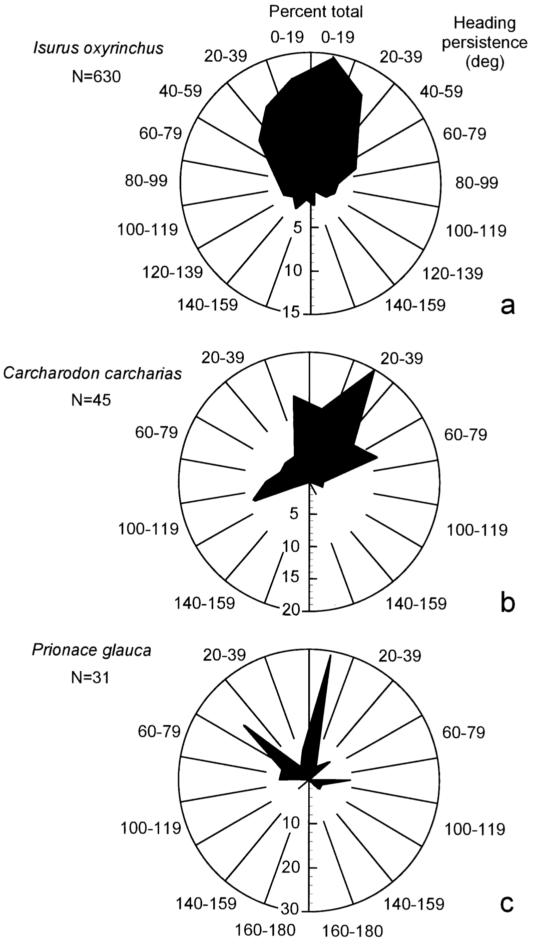

Figure 9. Heading persistence of: a – three mako, b – one white, and c – two blue sharks. The percentage of the total number of alterations in course recorded between consecutive pairs of positions in 20-deg divisions either to the right or left of the direction of the vector determined between the prior pair of positions.

the plot of heading persistence occurred in the 0–19° and 20–39° angular classes (Figure 9b). Finally, the blue sharks also showed high directionality to their movements with one of two peaks in the 0–19° class (Figure 9c).

Both the mako and white sharks exhibited an oscillatory pattern to their diving records, which has been termed 'yo-yo' diving (Carey & Scharold 1990). The time periods between successive peaks in the diving excursions of the mako sharks ranged from 0.5 to 1.5 h covering depths ranging from 10 to 30 m (Figure 4). The time periods between successive peaks to the diving excursions of the white shark varied around 0.5 h and the excursions covered a depth range of 30 m (Figure 7). The frequency distribution of depths, at which mako sharks swam during daytime, had a single peak at 18.0–19.9 m (Figure 10a), and this differed little from the peak frequency of blue sharks dives at 20.0–21.9 m (Figure 10c). The frequency distribution of the white shark had two peaks, one at 0–1.9 m and the other at 16.0–17.9 m (Figure 10b). While the white shark often swam at the surface (36% of time), the mako sharks spent only a small amount of time on the surface (2.5%). The periods of surface swimming are evident from the presence of green symbols (indicating dive depth <2 m) in the plots of the tracks of individuals of both species (Figure 1).

The mako and white sharks swam in slightly warmer water than the blue sharks. The most common temperature experienced by mako sharks was 19.0–19.9°C (Figure 11a). The frequency distribution of the blue shark possessed two barely separated peaks, possibly

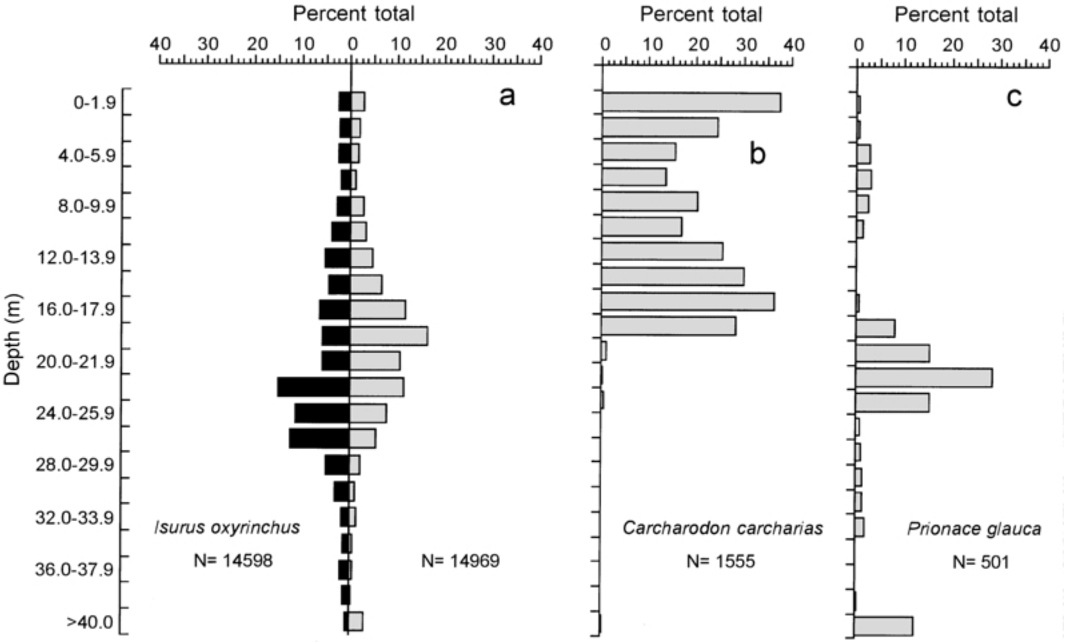

Figure 10. Percentages of the total number of depths recorded from: a – three mako sharks, b – juvenile white shark, and c – two blue sharks. Stippled bars to right of the ordinates indicate the daytime depths; solid bars to left of ordinates denote the nighttime swimming depths.

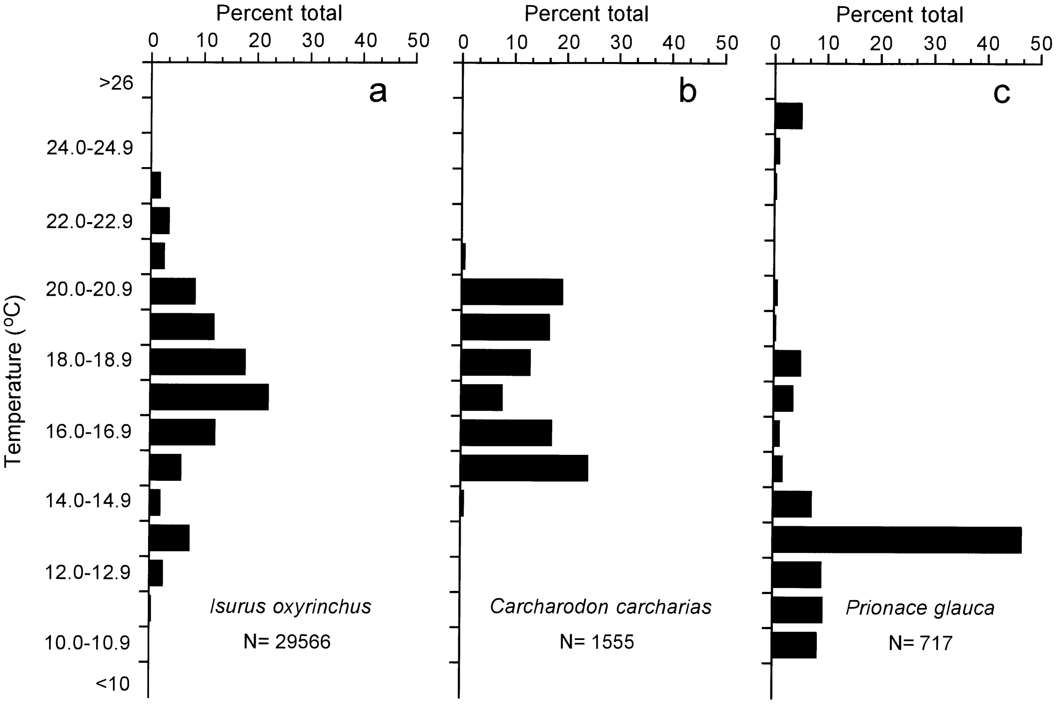

Figure 11. Percentages of total number of water temperatures recorded from: a – three mako sharks, b – one white shark, and c – two blue sharks.

due simply to the small sample size, one at 10.0–22.9°C and at 15.0–15.9°C (Figure 11b). The single peak for the temperature experienced by the single blue shark carrying a transmitter with a temperature sensor was at 13.0–13.9°C (Figure 11c). We did not record surface-swimming by the two blue sharks that we tracked during the study.

Discussion

Variation existed in the travel styles of these six sharks, even among the same species. It is difficult to draw conclusions from the shorter tracks of the white and blue sharks. Nonetheless, there are some differences and similarities that are worth noting and which may offer a better understanding of the behaviors of these shark species. With regard to differences, the endothermic species, the mako and white sharks, moved over ground faster than the ectothermic blue sharks. With regard to similarities, the blue, mako, and white sharks swam in a highly directional manner. The mako and white sharks constantly moved up and down in an oscillatory fashion and often swam for prolonged periods at the surface. All sharks performed deep dives immediately after being tagged and released.

Rates of movement

The rates of movement of these sharks are consistent with a distinct difference between endothermic lamnid and the ectothermic carcharhinid species. The mako and white sharks maintained faster rates than the blue sharks. The blue sharks spent 70% of their tracks swimming $<0.5\ \mathrm{m\,s^{-1}}$ ($<0.3\ \mathrm{BL\,s^{-1}}$), whereas the makos and white swam at faster rates of 0.5–$1.2\ \mathrm{m\,s^{-1}}$ during 60% (0.4–$0.8\ \mathrm{BL\,s^{-1}}$) and 90% (0.3–$0.8\ \mathrm{BL\,s^{-1}}$) of the time tracked, respectively.

Similar slow rates of movement, $0.1\ \mathrm{m\,s^{-1}}$ ($0.04\ \mathrm{BL\,s^{-1}}$), $0.4\ \mathrm{m\,s^{-1}}$ ($0.2\ \mathrm{BL\,s^{-1}}$) during daytime, and $0.8\ \mathrm{m\,s^{-1}}$ ($0.4\ \mathrm{BL\,s^{-1}}$) during nightime, were recorded for the blue shark by Carey & Scharold (1990) and by Sciarrotta & Nelson (1977), respectively. Nelson et al. (1997) noted the sluggishness of the blue shark, even when compared to other large carcharhinids. A tiger shark, *Galeocerdo cuvier*, tracked at French Frigate Shoals, Hawaii, averaged $1.0\ \mathrm{m\,s^{-1}}$ ($0.3\ \mathrm{BL\,s^{-1}}$) (Tricas et al. 1981). A bull shark, *Carcharhinus leucas*, and sandbar shark, *Carcharhinus plumbeus*, that were tracked in a large aquarium averaged $0.7\ \mathrm{m\,s^{-1}}$ ($0.3\ \mathrm{BL\,s^{-1}}$) and $0.6\ \mathrm{m\,s^{-1}}$ ($0.3\ \mathrm{BL\,s^{-1}}$) (Weihs et al. 1981). It seems unlikely, however, that these ectothermic species would be able to sustain these faster rates in the temperate waters where these blue sharks were tracked.

Directional swimming

The tracks of the three species of sharks in La Jolla Canyon were highly directional (see Figure 1). The mako sharks traveled over great distances for many hours with little alteration in their headings. The individuals of all three species showed very little deviation in their course between successive point-to-point movements (see Figure 9a–c). The majority of consecutive headings differed by <20° to the left or right of their prior heading. If the sharks were to change their direction in a uniform manner, the plots would show a uniform radial pattern to the distributions of angular changes shown in the circular plots. Directional swimming has also been observed in the Atlantic salmon, *Salmo salar* (Westerberg 1982a), and the marlin, *Makaira nigricans* (Holland et al. 1990). It seems unlikely that such steady courses could be held without some form of guiding sensory reference in the surroundings. Individuals could use the following environmental properties to guide their movements: (1) irradiance, (2) chemical gradients, and/or (3) geomagnetic fields.

For fishes to maintain a constant course using a celestial body as a visual reference, they would have to swim close to the surface following the blurry image of the sun (Klimley 1993). Visual cues from celestial bodies might be used at times, but not all of the time due to the rapid absorption and scattering of light in sea water, even at relatively shallow depths and in temperate waters with higher amounts of primary productivity. Nighttime would be especially difficult for navigation by this means. Yet evidence exists that aquatic species can utilize the sun as a reference (Hasler et al. 1958, Winn et al. 1964, Groot 1965, Loyacano et al. 1977). Gruber et al. (1988) argued that lemon sharks, *Negaprion brevirostris*, used the sun as an orientational cue during daytime in shallow lagoons in the Bahamas. Orientation at greater depths during daytime could be indirectly related to the sun, and based on the perception of polarized irradiance in the ultraviolet region. Hawryshyn et al. (1990) trained small rainbow trout, *Oncorhynchus mykiss*, to orient to UV polarized light. This irradiance was detected at intensities that would stimulate photoreceptors at depths reaching 15 m.

Sharks tracked during this study swam in an oriented manner during daytime and nighttime. Furthermore, the sharks swam in a straight-line manner while at considerable distances from the surface. It is doubtful that they could always clearly see the disk of the sun or moon or detect polarized light. Scalloped hammerhead sharks also swam with great directionality during nighttime while in deep water where irradiance levels were below the visual threshold of the species (Klimley 1993).

Alternatively, the sharks might use chemical cues to swim in a directional manner. It is doubtful that a chemical gradient would exist in the westerly direction in La Jolla Canyon, in which the sharks swam, but more likely one would exist parallel to the coast due to the flow of the California current. Klimley (1993) argued that it was doubtful that hammerhead sharks swam repeatedly along the same convoluted paths between a seamount and the surrounding waters simply by orienting to chemicals born by moving masses of water. The flows along the paths of the sharks varied too greatly in direction and speed when migrating to and from the seamount. Carey & Scharold (1990) noted the importance of chemoreception in blue sharks, but were doubtful that it could guide the sharks over such great distances, across complex currents, and radically shifting thermal gradients.

Unidirectional current flow could also explain the directional movement of individuals over ground. However, the westward coastal movements of mako sharks observed during this study were not likely caused by the north–south flow of the California Current, as Holts & Bedford (1993) suggested for the mako sharks that they tracked in the Southern California Bight. Satellite images of sea surface temperatures were obtained for each of our tracks. The images indicated some warm eddies, and areas of upwelling, but the movements of the individual sharks did not appear to be altered in any way as they swam through these areas. It would seem that there is another force at work guiding the sharks' movements.

Makos M1 and M2 and white shark W1 did move offshore along the axis of the La Jolla Canyon as if guided by topography (see Figure 1). Furthermore, mako M1 turned from a northwesterly to a southwesterly direction near where the La Jolla Canyon similarly changes direction. It was impossible for these sharks to see the bottom, as they were swimming in the upper 70 m of the water column, well out of view of the bottom 100–1500 m below. It is possible that the sharks might have been following patterns in the magnetization of the seafloor, which is to some extent linked to bottom topography. Klimley (1993) related the paths taken by scalloped hammerheads, *Sphyrna lewini*, to and from a seamount in the Gulf of California to magnetic ridges (maxima) and valleys (minima) leading away from the seamount. Sharks could swim for great distances in a roughly north–south direction, if they were to use the earth's dipolar main field as a reference. Carey & Scharold (1990) also observed that the straight-line movements of blue sharks coincided with ridges and valleys in the magnetic field (magnetic lineations), but felt that the sharks were more likely orienting to the earth's dipole field.

Oscillatory or yo-yo swimming

One of the most common behaviors of marine vertebrates in the open ocean is oscillatory swimming. We observed this dive pattern in both the mako and white sharks (see Figures 4, 7). The onset of this oscillating pattern occurred soon after a deep post-release dive that may be due to discomfort caused by tag application. This trauma appeared to diminish 20–60 min after release. This fast dive in to deeper waters may either be an attempt to repay the oxygen debt incurred during the strenuous capture of these obligate ram ventilators by entering cooler, more oxygen-rich waters (Holland et al. 1990) or an attempt to cool their internal temperature by dissipating excess heat in the cool waters below the thermocline (Holts & Bedford 1993).

Although only small oscillations were observed in our track of a blue shark, the absence of larger excursions may have been due to the shortness of the track. Carey & Scharold (1990) observed oscillatory swimming in the blue sharks that were tracked off the eastern coast of the United States; Landesman (1984) found similar diving behavior off the western coast. Why do so many oceanic species constantly move up and down in the water column? One would expect pinnipeds such as the elephant seal to move up and down in the water column (see many dive profiles in Le Boeuf & Laws 1994) because they need to surface periodically to breathe after feeding upon mid- and deep-water squids (Antonelis et al. 1994). However, why would fishes swim in a yo-yo pattern, continuously alternating ascents with descents, when they need not breathe at the surface?

Many functions have been proposed for this common behavioral pattern. The most widely proposed has been to warm the body after heat loss during descent into cooler water. Tunas maintain an internal body temperature above that of the surrounding water (Carey 1973), and, in this way, improve their muscular efficiency and enable themselves to swim at burst speeds in cold water (Graham & Diener 1978). In all fishes, oxygenated arterial blood leaves the gills with a temperature equal to the ambient water temperature. However, in the tunas warm blood leaving the muscles passes through retes with arteries interlaced with veins resulting in the flow of heat to the latter before the blood reaches the peripheral tissues of the fish (Carey 1973). Tunas searching for prey in cold water below the thermocline would need to surface periodically in order to reheat their bodies before returning again to colder water to capture prey with rapid accelerations.

Consistent with the importance of thermoregulation during diving is the reduction of thermal conductivity during descent by two orders of magnitude greater than during ascent (Holland et al. 1992). This is evident from the increase in separation between curves of body temperature (B) and ambient water temperature (A) when an individual descends into cooler water versus a decreasing separation when the tuna rises to warmer water near the surface (Figure 12). The physiological explanation for this thermal response is that heat loss is prevented during diving by the engagement of an internal heat exchanger (rete) when the difference between internal and external temperatures rises above a critical value and the rete's deactivation when below that value. Using this model, Holland et al. (1992) were able to mathematically predict internal temperatures (C) similar to those measured on the body of the tuna (B) in response to external water temperatures recorded near the tuna (A).

The change in the extent of oscillations in different thermal environments at different geographical locations may provide insight into what limits the depth to which the sharks dive. In this study, the vertical excursions of the three sharks ranged between the surface and 50 m and water temperatures of 24°C and 14°C. Other mako sharks, which were tracked in the Southern California Bight, demonstrated similar depth and temperature distributions (Holts & Bedford 1993). However, a mako shark tracked off Florida, where the same temperature gradient was distributed over 400 m, descended into much deeper water of 400 m (Carey & Scharold 1990). These observations suggest that mako sharks avoid diving into a water stratum with a temperature <14°C. Thermoregulation is probably not the only function of oscillatory swimming because the behavioral pattern is also observed in ectothermic fishes such

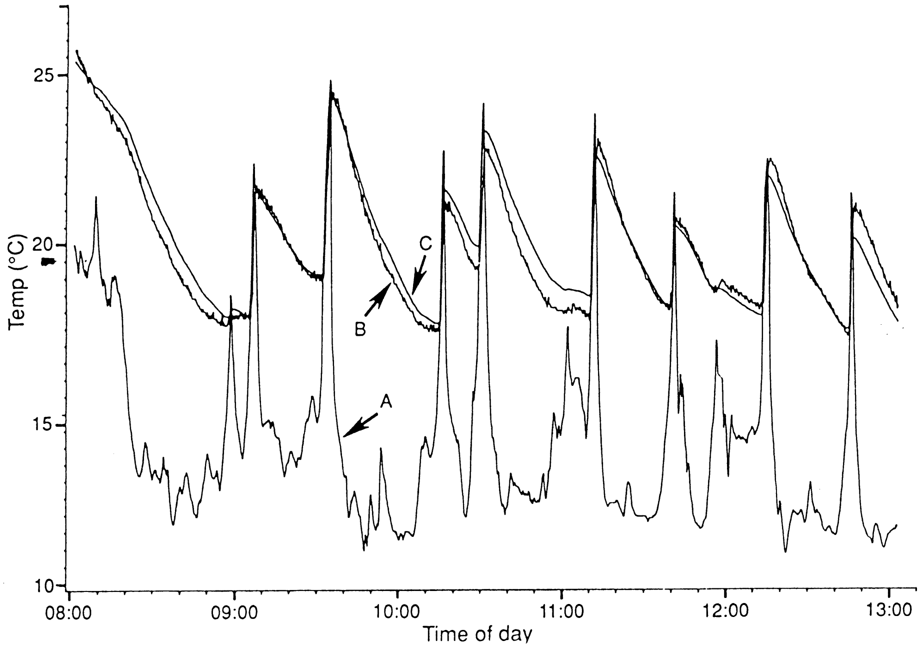

Figure 12. Relationship between ambient temperature (A), observed body temperature (B), and estimated body temperature (C) in a bigeye tuna (*Thunnus obesus*). Taken from Holland et al. (1992).

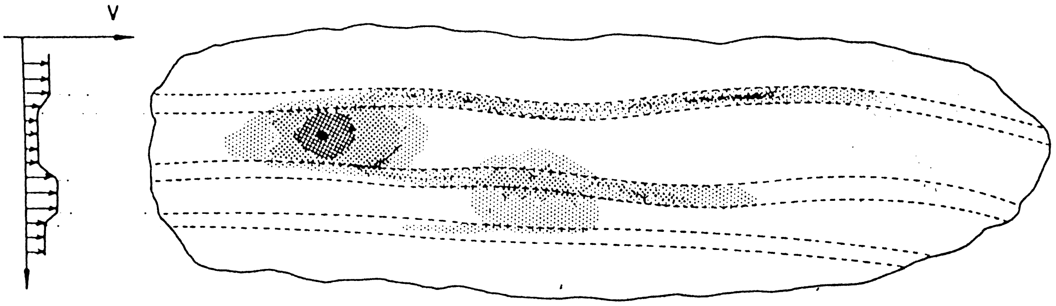

Figure 13. Illustration of odor cloud spreading from a source through the water column. Water column shown on the right; velocity of water flow plotted on left. Thick layers of water with homogenous flow are separated by narrow layers with strong flow gradient. Lines with dashes indicate the boundaries between these layers. Taken from Westerberg (1984).

as the blue shark (Carey & Scharold 1990) and scalloped hammerhead shark (Klimley 1993), which do not have extensive retes to keep heat within the body.

Another function proposed for yo-yo swimming is to explore the water column to gain directional information used to guide homeward migrations (Westerberg 1982b). The direction of movement to a stratum of oceanic water can be derived from the composition of its water. The water column contains thick layers of homogenous water with weak vertical gradients in physical properties that alternate with thin layers with strong vertical gradients (Figure 13). Each of these thicker layers originates from a specific source and may carry a unique chemical composition. Odor originating within a specific layer of water would spread along the boundary between the layers above and below it (see stippling, Figure 13). Westerberg (1984) argued that salmon could find their home direction by moving back and forth between the source stratum, identified by a unique odorant, and an adjacent one.

An orienting individual would need to use one of its sensory systems to ascertain the flow direction of the home water mass. The magnetic sense might perceive the difference in the magnitude of electrical fields induced by two masses moving in different directions, the visual sense to detect the differential movement of particles above and below the boundary between the layers, or the tactile sense to detect the difference in pressure from water flowing in different directions. Supporting this mechanism of orientation were two observations of Westerberg et al. (1985). Firstly, they observed salmon to make greater excursions through the water column when their olfactory sense was blocked than unblocked, presumably searching vainly for the boundary between source and adjacent strata. Secondly, they found single olfactory bulb neurons to respond differently to water from different depths along the migratory track of migrating salmonids.

A fourth reason for yo-yo swimming could be to minimize the expenditure of energy during swimming. Weihs (1973) suggested that the most efficient mode of travel for fishes was to alternatively swim upward with a given number of tail beats and slowly glide downward with fewer tail beats. Holland et al. (1990) illustrated this fly-glide style by presenting a dive record of a yellowfin tuna near a Hawaiian fish-aggregating device: each positive slope (ascent) in the track of the animal was steeper than the subsequent negative slope (descent). Consistent with this, are the greater rates of change of depth calculated by Block et al. (1997) for ascents than the rates of descent of yellowfin tuna tracked off Southern California (Figure 14). Additional evidence for this behavior is in video records of marine mammals showing fewer tail beats during descent than ascent (Williams et al. 2000).

A fifth and final function given here for oscillatory diving may be to more easily detect the patterns of magnetization in the sea floor. The pattern of total fields at the earth's surface is the sum of two magnetic sources, the earth's inner core and outer crust. Circulation of electrically conductive liquid in the earth's core creates a dipolar moment in the earth's field (Elsasser 1946). Magnetic minerals (i.e., oxides of iron and titanium) in the earth's crust produce minute distortions in the dipole or main field. They form patterns such as the dipole moments associated with seamounts and bands of strong and weak magnetization of the sea floor.

The dipoles are caused by extrusion of basalt laden with magnetic particles (magnetite) during volcanic eruptions occurring during the long geological history of the earth. The particles are both parallel and

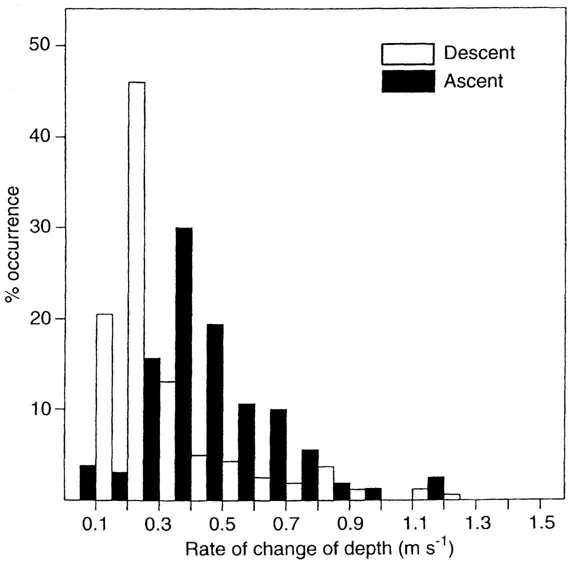

Figure 14. Rates of ascent and descent of three yellowfin tunas tracked off Southern California. Taken from Block et al. (1997).

anti-parallel to the earth's current main field because volcanic eruptions happened during different pole reversals (Parker et al. 1987). Another pattern, ubiquitous to all ocean basins, is the mosaic of north–south directed bands of weak and strong magnetization to either side of the centers of the oceans where the crustal plates are constantly diverging. Both the dipole nature of the earth's main field and local distortions in it such as dipoles and lineations would be of great value in the ocean for guiding the movements of migratory animals. The main field would be an ideal directional reference while the local distortions would be an ideal spatial reference.

At the surface, the local distortions to the overall dipole moment are small. However, with increasing depth these small field 'anomalies' increase because the contribution to the total field from the crust, only 4 km from the surface, increases disproportionately to that of the core, 2900 km from the surface (Press & Siever 1986). This is evident from the comparison of two curves of magnetic intensity, one of which is derived from the crust and the other from the core (Figure 15). The curve depicting the magnetic contribution from the crust passes across the curve for core as depth increases (see two lines on upper right inset). The direction of the maximum total field gradient rotates from latitudinal (north–south axis of the main field) to longitudinal (east–west axis between magnetic lineations). The magnetic anomaly across a 3 km transect perpendicular to the polarity reversal zone at the East Pacific Rise recorded by a submersible moving at a height of 10 m from the bottom was 1400 nT in comparison to 400 nT at the surface (Macdonald et al. 1980).

Klimley (1993) argued that scalloped hammerhead sharks would be better able to detect guiding magnetic topography by descending in the water column, when migrating to and from a seamount. Individuals could distinguish the local gradients from the main field by gliding downward until the field rotates and increases so that magnetic dipole or lineation is perceptible above the main field. Klimley (op. cit.) found a hammerhead shark swimming in a yo-yo pattern and presumably orienting to a magnetic lineation at that point in the water column where the local magnetic intensity was highest. The individual would have to periodically rise in order to re-establish its field of reference. He predicted that sharks basking at the surface would swim in a straight line while orienting to the earth's main field, and those swimming up and down would swim along sinuous paths while following local magnetic topography. The lateral enlargement of the rostrum of the hammerhead shark would optimize magnetic sensitivity by maximizing the intensity gradient perceived between bilaterally separated receptors (Figure 16).

Surface swimming

The bouts of surface swimming by the white and mako sharks varied in duration but were as long as 30 min. This behavior is common among cartilaginous and bony fishes. Surface swimming has been recorded for mako (Holts & Bedford 1993), white (Strong et al. 1992), blue (Carey & Scharold 1990), and scalloped hammerhead sharks (Klimley 1993). Similar behavior has been observed in salmon (Westerberg 1982b), blue marlin (Holland et al. 1990, Block et al. 1992), and yellowfin tuna (Holland et al. 1990, Block et al. 1997, Brill et al. 1999).

Why do pelagic fishes swim at the surface? As mentioned before, this is where it would be easiest to use the earth's main dipole field as a reference. The shark could swim in a single direction by either keeping the induced field perceived by its receptors constant or maintaining the differential between fields detected by bilaterally separated receptors. The main field is most uniform at the surface of the ocean and could best guide the shark in a straight line here. Another impetus for swimming

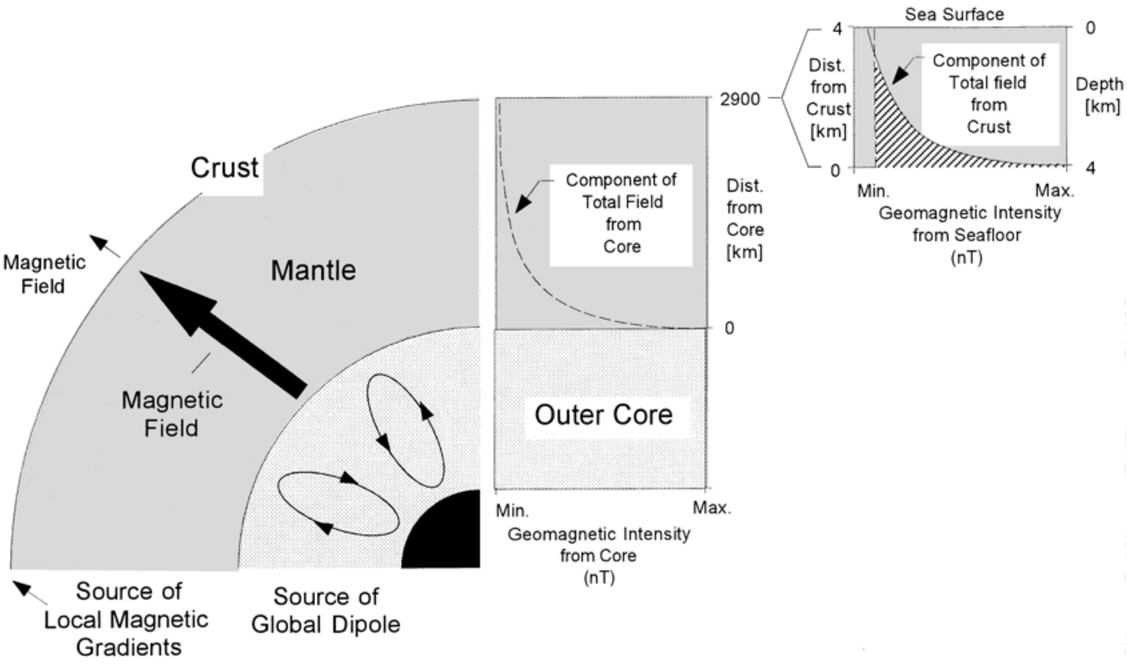

Figure 15. Illustration of the greater proportional increase with depth between the contribution to the total magnetic field of the earth's crust versus its core. The ocean is distant from the core (ca. 2896 km) and its field attenuates little over the next 4 km of ocean relative to the field from the adjacent crust that originates 4 km from the surface.

at the surface would be to see the sun or moon or detect polarized irradiance and use them as a directional reference. It would, of course, also be adaptive for an endothermic fish to rest at the surface on warm days in order to conserve energy.

Experimental imperative

We need to discriminate between the hypotheses described above based on empirical observations with well crafted laboratory and field experiments. How would one experimentally verify the importance of thermoregulation to pelagic fishes?

Thermoregulation

One could examine the relationship of thermoregulation to oscillatory swimming by ascertaining whether individuals remain longer in the cool depths when the part the brain that processes input from heat receptors were to be artificially heated by passing current through a low-value resistor placed near a rete important to thermoregulation. Conversely, one could determine whether a fish refrains from diving, if one were to cool the same areas of the brain with a chemical coolant.

Olfactory orientation

One could monitor the diving pattern of a shark in response to an odorant injected into a specific layer of water. One would have to firstly identify a water stratum containing a chemical attractant. One would need to track individuals, record their diving oscillations, and sample the physical properties of the water column. The objective would be the identification of a margin between two water masses where the attractive chemical would be present and across which the shark would oscillate. One would then collect water at this depth and inject it into another water mass at a different depth in order to ascertain whether the shark would modify its pattern of diving to orient to the experimental stimulus.

Magnetic orientation

With regard to magnetic orientation, one could create a slowly changing gradient between two coils attached to a surface swimming individual that would indicate the shark was passing over a local magnetic feature in the ocean. The shark would be predicted to deviate from a uniform course. Alternately, one could have the magnets induce a strong dipole when an individual

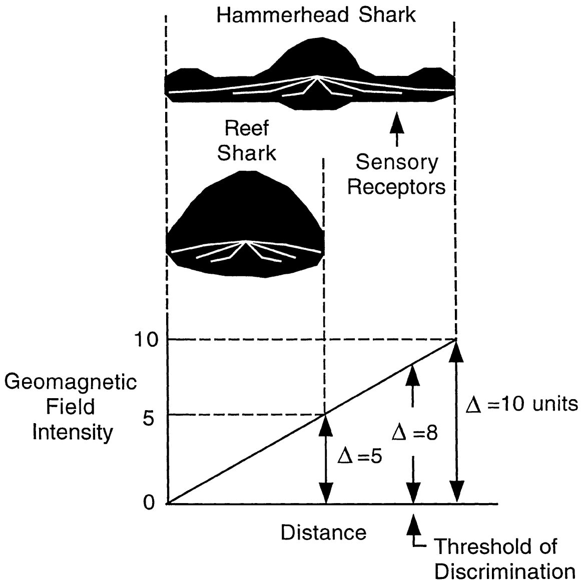

Figure 16. Diagram depicting the adaptive advantage of a widened over a narrow rostrum in the hammerhead shark. The difference between the magnetic intensities at the outermost receptors of a hammerhead shark (10 units) is greater than for a reef shark (5 units) for the same change in intensity per distance. If the receptor threshold of both sharks were eight units, the hammerhead would be able to detect the gradient while the reef shark would be unable to detect the same gradient.

swims at great depths, where it would be expected to follow a convoluted path following a local magnetic pattern. One would predict that the shark would alternatively swim in a straight line. However, it is difficult to fool animals with false magnetic fields created on them with electronic coils. Even the results of the most elegant experiment on magnetic sensing to date were equivocal (see Walcott & Green 1974). Although the departure bearings of homing pigeons armed with magnets oriented parallel and anti-parallel to their body axis differed, all of the experimental subjects eventually returned to the roost from which they were displaced.

It is preferable to modify the environment, in which an individual exhibits an oriented response. One approach would be to record the location of hammerhead sharks before and after reversing the polarity of a seamount by energizing a large coil of wire wound around the base of the seamount. Hammerhead sharks remain within a small area (200 × 200 m) to one side of a seamount during daytime (Klimley & Nelson 1984, Klimley et al. 1988) despite foraging widely in the surrounding pelagic waters during nighttime (Klimley 1993). Would the sharks move to the other side of the seamount if one switched the polarity of the coil to produce a concomitant reversal to the dipole moment to the seamount? Alternatively, one might modify the large-scale magnetic lineation, which exists at the edge of the seamount.

A more plausible approach would be to artificially alter a small-scale magnetic feature. One might condition sharks to swim along a magnetic 'ridge', created by a subsurface solenoid in a 'Y' maze. The magnetic stimulus could be paired with an acoustic one to attract the sharks into a specific arm of the maze where they would be fed. Would the shark move into proper arm of the maze once deprived of the acoustic stimulus and given only the magnetic stimulus? We should use our imagination and ingenuity in designing future experiments, which will identify the mechanism(s) by which animals orient in the apparently featureless open ocean. The answer will become one of the revelations of modern marine biology.

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