Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean

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ABSTRACT: Acoustic telemetry was used to identify the short-term horizontal and vertical movement patterns of the bigeye thresher shark *Alopias superciliosus* in the eastern tropical Pacific Ocean during the summer of 1996. Two immature female sharks, 175 and 124 cm PCL (precaudal length), were tracked for 96 and 70 h, respectively, demonstrating very distinct crepuscular vertical migrations similar to those reported for the megamouth shark. The bigeye threshers stayed at 200 to 500 m depth during the day and at 80 to 130 m at night. The deepest dive extends the known depth distribution of the species to 723 m. No 'fly-glide' behavior (rapid ascents followed by slower acute-angled descents) was observed for the 2 sharks. However, the opposite behavioral pattern of slow ascents and relatively rapid descents during the night was observed. Since bigeye threshers have large eyes extending upwards onto the dorsal surface of the cranium, it may be more efficient for them to hunt prey which are highlighted against the sea surface from below. Estimated mean swimming speed over the ground ranged from 1.32 to 2.02 km h^{-1}, similar to swordfish and megamouth sharks, and slower than that reported for tunas, billfishes, and other pelagic sharks.

KEY WORDS: Shark · Acoustic telemetry · Vertical movement · Diel cycle

INTRODUCTION

The bigeye thresher shark *Alopias superciliosus* is a deep-water pelagic species, but is also found in coastal waters over continental shelves in tropical and subtropical waters worldwide (Gruber & Compagno 1981, Compagno 1984). This shark is a strong swimmer and can reach 461 cm total length (Gruber & Compagno 1981). Its vertical distribution ranges from the surface to about 500 m (Gruber & Compagno 1981). As individuals are often tail-hooked on longline fishing gear, it is believed that this shark stuns its prey with its long caudal fin. Prey includes pelagic aulopoids (lancetfishes), scombroids, small istiophorids, demersal fishes and squids (Stillwell & Casey 1976).

Although high-seas longline fisheries catch many species of pelagic sharks, including bigeye thresher sharks, little is known about the ecology of many of these species, including their diel behavior and movement patterns. This ecological information is important both for management purposes and for understanding the factors influencing longline catches, with regard to reducing incidental catches of non-target species.

Acoustic telemetry has been used to study free-swimming large pelagic sharks including the blue shark *Prionace glauca*, the shortfin mako shark *Isurus oxyrinchus*, and the white shark *Carcharodon carcharias* (Sciarrotta & Nelson 1977, Carey & Scharold 1990, Strong et al. 1992, Holts & Bedford 1993). In order to understand the ecology and behavior of pelagic sharks, it is necessary to have information about their horizontal and vertical movement patterns and habitat preferences. For example, telemetry studies of the blue shark indicated significant differences in diurnal and nocturnal movement patterns, and studies of the shortfin mako shark revealed that this species was the fastest swimmer among 3 pelagic species studied. In the present study, we used acoustic telemetry to gain insights into the diel behavior patterns of the bigeye thresher shark. We present information on

horizontal and vertical movement patterns, and suggest that changes in course and speed may be related to temperature preferences.

MATERIALS AND METHODS

Acoustic tracking experiments on 2 bigeye thresher sharks were conducted during the research cruise of the RV 'Shoyo-maru' (Fisheries Agency of Japan), in July 1996, in the eastern tropical Pacific Ocean. The study area was located approximately 1500 to 2700 km WSW of the Galapagos Islands. Sharks were caught by longline gear and lifted to deck level by means of a 'scooper' (a square basket-like retrieving device used for tuna). Sharks were sexed and measured to the nearest cm precaudal length (PCL) with a wooden caliper. The acoustic transmitter was attached by spearhead to a conventional shark tag inserting into the dorsal musculature near the edge of the first dorsal fin using a standard tagging pole. The transmitters (VEMCO) had a nominal life span of 5 d and a maximum working pressure of 1000 psi. Sharks were kept tethered with 200 m of line and a radio buoy until longline fishing operations were finished. Subsequently the tagged sharks were slowly hauled to the surface and then released by cutting the tether near the mouth. The behavior of the shark immediately following release was monitored and judged to return to normal condition by the initiation of cyclic behavior (regular up and down swimming).

The signal, encoding depth information by variable pulse interval, was received on board the ship by a VEMCO VR-60 ultrasonic receiver and recorded digitally by a PC that simultaneously monitored the vertical movements. The ship followed above the shark as closely as possible, thus the ship's position was assumed to be the same as that of the shark. Positional information was obtained on board by Global Positioning System (GPS) satellite receivers (GP-500, FURUNO Electronic Corporation) every 15 min. Average swimming speed of the sharks, taken as speed over ground (SOG), was calculated as the straight-line distance between the geographical positions of the ship taken every hour. The estimated error of the GPS, and therefore the position of the ship, was approximately 50 to 100 m. These positional errors result in errors of 4.9 to 8.2% in the estimated swimming speeds. Depth and temperature profiles were collected by CTD casts just prior to release of the sharks and just after tracking ended. Expendable bathythermograph (XBTs) probes were deployed every 6 h during the study. Oceanic current data were collected every 5 min in 8 m intervals from 20 to 524 m by an Acoustic Doppler Current Profiler (ADCP, RD Instruments). We calculated the mean heading of sharks during day and night. Mean current direction at 84 m depth (day) and 252 m depth (night), and 84 m (day) and 452 m depth (night), were also calculated in order to compare the shark headings with the current directions at the preferred depths for Sharks 1 and 2, respectively. The directionality of both shark heading and current were checked by the Rayleigh test (Zar 1999).

RESULTS

Shark 1, a female, measuring 175 cm PCL (195 cm fork length (FL), and 332 cm total length (TL)) was caught on 4 July 1996. This shark was released at 6° 30′ S, 103° 32′ W about 1500 km WSW from the Galapagos Islands and tracked for 96 h, covering approximately 158 km. Shark 2, also a female, measuring 124 cm PCL (142 cm FL, 240 cm TL) was caught on 12 July 1996, released at 9° 25′ S, 112° 46′ W about 2700 km WSW from the Galapagos Islands, and tracked for 70 h, covering about 85 km. Length measurements were converted to weights using the formula of Liu et al. (1998).

Vertical movements of the sharks and simultaneously gathered depth-temperature data are shown in Figs. 1 & 2. Both sharks exhibited 'normal' regular diving patterns from the second day onward. It is evident from Figs. 1 & 2 that the tracked bigeye thresher sharks exhibited acute depth preferences predicated on a diel cycle. Shark 1 spent most of the day at depths between 200 and 300 m and the night at depths between 50 and 80 m. Shark 2, the smaller of the two, swam at depths between 400 and 500 m in the daytime and at depths between 80 and 130 m at night. These sharks made regular 'deep dives' at dawn and 'surface night dives' at dusk, and the timing of these diurnal/ nocturnal events was very predictable. For example, descending and ascending movements occurred about 30 min immediately before or after sunrise and sunset, respectively. There was only a single deviation from this crepuscular behavior which occurred when Shark 1 was released at 20:40 h on the first evening and started her dive the next morning at 10:35 h, about 3.5 h after sunrise. At night, the sharks displayed extensive vertical oscillations that traversed the thermocline. This was considerably different to the daytime in which the sharks maintained a steady position in the water column. Shark 1 showed a sudden dive from 300 m to 723 m in the daytime on the 4th day, ascending back to a depth of about 300 m 4 h later. During the day, Shark 1 spent most of the time in water temperatures of about 11°C except during the deep dive when she experienced water temperatures as cold as 5°C. At night, the shark made vertical movements
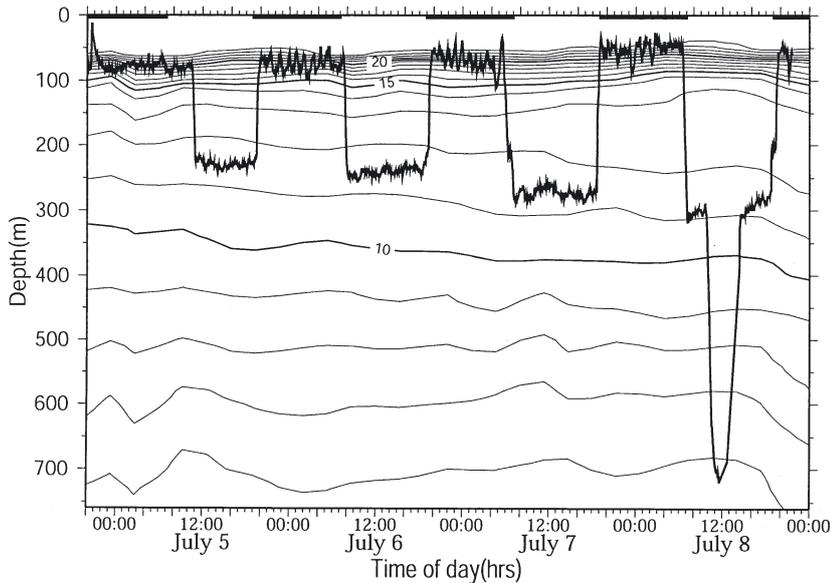
Fig. 1. *Alopias superciliosus*. Vertical movement of bigeye thresher Shark 1 superimposed on a 1°C isotherm plot drawn from expendable bathythermograph casts. Black bold lines along upper horizontal axes indicate nighttime

Horizontal movements of the 2 sharks are shown in Figs. 4 and 5. Shark 1 was released at 6° 30' S, 103° 32' W and started on a southwesterly course, with mean heading ranging from 230 to 275°, and then later changed to a northwesterly course ranging from 301 to 347° (Table 1). After 3 d of tracking, the shark returned to a southwesterly course. Since different depth layers were frequented during the day and night, current vectors were estimated at 84 m and 252 m for Shark 1, to determine whether they may have influenced the movements of the shark. Mean current directions for both day and night indicated a northeasterly direction (ranging from 89 to 90°) in most cases; thus, shark headings and current directions differed. While swimming on the first southwesterly course, Shark 1 was observed swimming diagonally upcurrent during both night and day. Mean current velocities were 6.5 cm s⁻¹ (0.23 km h⁻¹) at the depth of 84 m and 15.0 cm s⁻¹ (0.54 km h⁻¹) at the depth of 252 m. There was no ADCP data for the second day of tracking due to instrument problems. Shark 2 moved westwards after being released at 9° 25' S, 112° 46' W, and then she switched to a southwesterly course, ranging from 225 to 298°, until the end of the track. Current vectors were estimated at 84 m
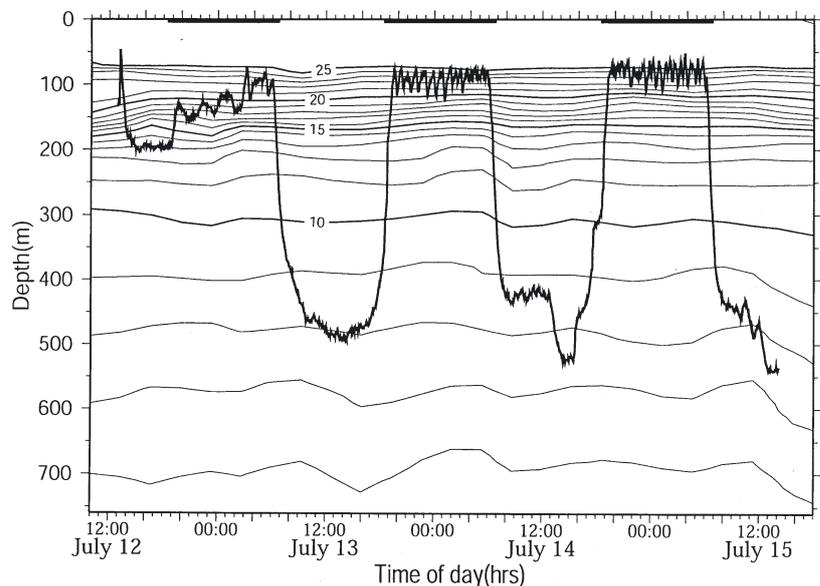
that traversed the mixed layer where water temperatures ranged from 15 to 24°C. Although Shark 1 dived deeper on consecutive days, she was always observed at temperatures around 11°C. From a physiological and behavioral standpoint, the 11°C thermocline may indicate the sharks' preferred position in the water column. Shark 2 displayed almost the same diving pattern as Shark 1, but was usually found at temperatures of 7 to 8°C in the daytime, and at night she traversed the mixed layer experiencing temperatures of 19 to 26°C.

Swimming behavior traversing the mixed layer at night was compared to daytime swimming. Fig. 3 shows the swimming patterns from 00:00 to 04:00 h and from 12:00 to 16:00 h on the second day of tracking for both sharks. At night, the frequency of oscillations was quite regular (approx. 0.8 to 1.2 oscillations h⁻¹). The ranges of oscillations were approximately 20 to 40 m at 60 to 100 m depth for Shark 1 and 80 to 120 m for Shark 2. It usually took more time to ascend than it did to descend. The sharks demonstrated slow and continuous ascending and descending behavioral cycles approximately 10 times during the night. In the daytime, pronounced ascending and descending dives were not evident.

Fig. 2. *Alopias superciliosus.* Vertical movement of bigeye thresher Shark 2 superimposed on a 1°C isotherm plot drawn from expendable bathythermograph casts. Black bold lines along upper horizontal axes indicate nighttime
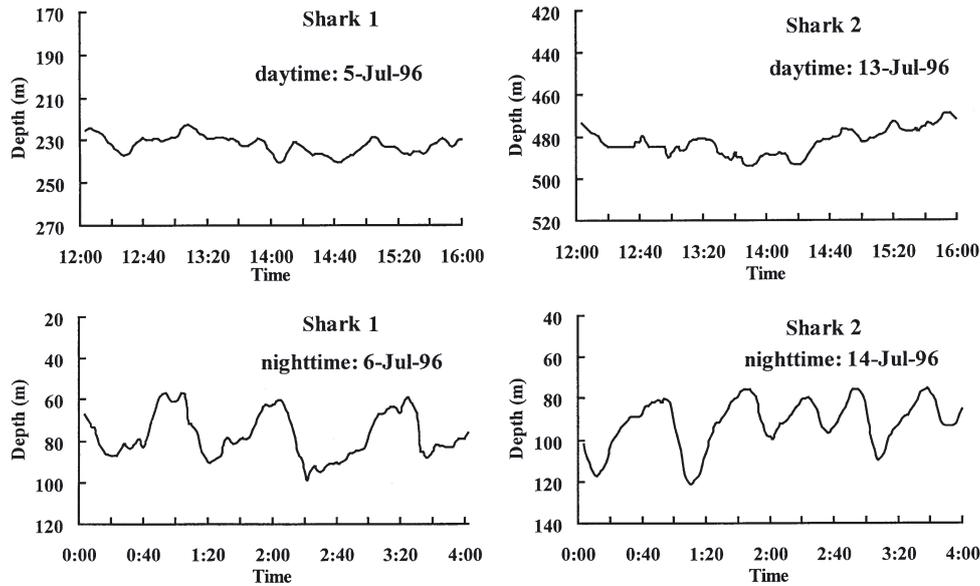
Fig. 3. *Alopias superciliosus.* Recordings of bigeye thresher shark movements over a 4 h period, day and night. Oscillatory swimming patterns were recognized at night only. Lines represent a moving average of 3 records

and 452 m for Shark 2 with current flows toward the south to southwest (179 to 186°). Mean current velocities were 16.4 cm s^{-1} (0.59 km h^{-1}) at the depth of 84 m and 6.5 cm s^{-1} (0.23 km h^{-1}) at the depth of 452 m. Shark 2 was observed swimming diagonally down-current.

We estimated average swimming speeds over ground of the sharks to be approximately 1.69 km h^{-1} (SD = 0.42, median 1.82 km h^{-1}, n = 43) during the day

and about 2.02 km h^{-1} (SD = 0.57, median 2.09 km h^{-1}, n = 41) during the night for Shark 1, and 1.34 km h^{-1} (SD = 0.72, median 1.40 km h^{-1}, n = 30) during the day and 1.32 km h^{-1} (SD = 0.48, median 1.47 km h^{-1}, n = 33) during the night for Shark 2. Differences in swimming speeds between day and night were tested using the Mann-Whitney test. Statistically significant differences were observed between day and night swimming speeds for Shark 1 only (U = 1276.5, p = 0.0005 for

Table 1. *Alopias superciliosus.* Mean directions of shark heading and current, number of observations, z-values of Rayleigh test and probability (p) in each tracking day and night. *: not significant; **: Rayleigh's z not available; na: not applicable

| Date (mo/d)		Heading direction (°)	n	z-value	p	Current direction (°)	n	z-value	p
Shark 1									
7/5	Night	229.7	10	7.40	p < 0.001	90.1	119	59.99	p < 0.001
7/6	Day	274.6	11	6.87	p < 0.001	90.0	115	1.15	0.20 < p < 0.50*
	Night	308.4	11	5.39	0.002 < p < 0.005	na			
7/7	Day	322.1	12	11.52	p < 0.001	na			
	Night	324.4	12	10.38	p < 0.001	88.8	139	80.29	p < 0.001
7/8	Day	347.0	12	11.29	p < 0.001	90.0	144	141.13	p < 0.001
	Night	301.7	12	8.07	p < 0.001	90.0	144	101.61	p < 0.001
7/9	Day	211.5	12	9.29	p < 0.001	90.1	115	112.71	p < 0.001
Shark 2									
7/13	Day	297.7	4	2.62	na**	180.0	39	29.52	p < 0.001
	Night	283.9	12	7.11	p < 0.001	179.5	139	53.43	p < 0.001
7/14	Day	263.0	12	10.16	p < 0.001	180.4	144	116.64	p < 0.001
	Night	229.3	12	11.52	p < 0.001	179.3	144	138.30	p < 0.001
7/15	Day	249.8	12	9.72	p < 0.001	180.2	144	48.44	p < 0.001
	Night	224.6	12	9.94	p < 0.001	178.7	139	128.10	p < 0.001
7/16	Day	276.9	7	4.82	0.002 < p < 0.005	186.4	73	11.10	p < 0.001
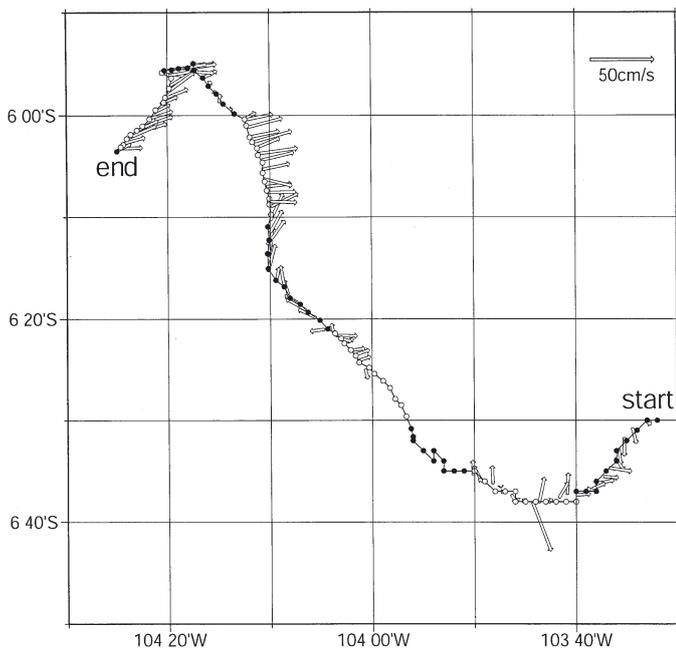
Fig. 4. *Alopias superciliosus.* Tracking position of bigeye thresher Shark 1 and current vector of 84 m at night and 252 m in the daytime. White and black circles indicate the position by hour during day and night, respectively

Shark 1, U = 439, p = 0.50 for Shark 2). Since bigeye thresher sharks demonstrate distinct crepuscular vertical migration at dawn and dusk, the swimming speeds of these movements were also examined by the Mann-Whitney test with respect to the horizontal and vertical distances traveled. Our estimated average vertical descending speed was 1.66 km h^{-1} (SD = 0.69, median 1.87 km h^{-1}, n = 5) and ascending speed was 1.54 km
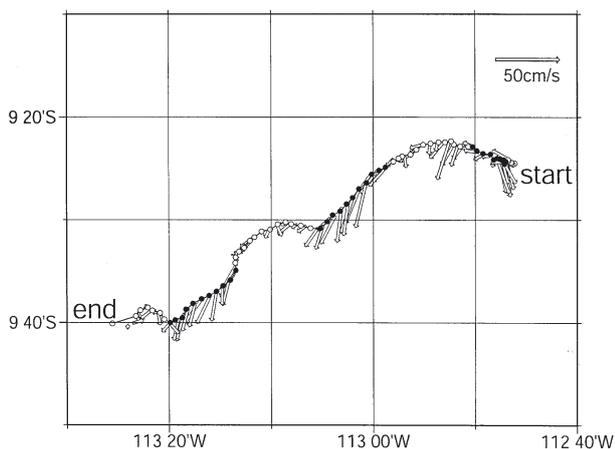

Fig. 5. *Alopias superciliosus.* Tracking position of bigeye thresher Shark 2 and current vector of 84 m at night and 452 m in the daytime. White and black circles indicate the position by hour during day and night, respectively

h^{-1} (SD = 0.29, median 1.58 km h^{-1}, n = 5) for Shark 1. For Shark 2, the average vertical descending speed was 1.28 km h^{-1} (SD = 0.43, median 1.26 km h^{-1}, n = 3) and the ascending speed was calculated as 1.14 km h^{-1} (SD = 0.002, median 1.14 km h^{-1}, n = 2). The vertical ascending and descending speeds were not significantly different for either shark (U = 10, p = 0.452 for Shark 1, U = 2.0, p = 0.40 for Shark 2).

DISCUSSION

The bigeye thresher shark is a deep-water species and is found in both coastal waters and the high seas, from the surface to near the bottom at depths greater than 500 m (Gruber & Compagno 1981). Direct observation of vertical movements recorded by acoustic tracking has given us new insight into the behavior and thermal ecology of the species. The observed maximum recorded depth of 723 m is the deepest ever recorded for this species, and the water temperature 5°C at this depth suggests a behavioral and physiological capacity for thermo-tolerance.

Diel vertical movement patterns suggest that the bigeye thresher is predominantly a nocturnal species. Pronounced vertical oscillations at night, which traverse the mixed layer, are hypothesized to be a possible hunting tactic. The belief that thresher sharks stun small prey fish using the long caudal fin is based on the frequent occurrence of tail-hooked thresher sharks in longline fisheries. Nighttime feeding behavior may provide some advantage in hunting prey. Use of deep habitat during the daytime may help bigeye threshers avoid predation by other large animals. Marked changes in depth between day and night have been observed in several large pelagic species such as bigeye tuna *Thunnus obesus*, yellowfin tuna *Thunnus albacares*, blue marlin *Makaira mazara*, swordfish *Xiphias gladius*, blue shark *Prionace glauca*, and shortfin mako shark *Isurus oxyrinchus* (Carey & Robison 1981, Carey 1983, Carey & Scharold 1990, Holland et al. 1990a,b, Cayré 1991). In addition, distinct crepuscular vertical migrations, e.g. descending migration at sunrise and ascending migration at sunset, have been observed in the megamouth shark *Megachasma pelagios* (Nelson et al. 1997) and swordfish *Xiphias gladius* (Carey & Robison 1981). Whereas the megamouth shark maintains a shallower depth during the night, the bigeye thresher shark demonstrates active oscillatory movements more like that of swordfish. The reason for this different behavior may be that the megamouth shark is a plankton feeder and its feeding is passive, whereas the bigeye thresher shark and swordfish feed on larger prey items which require an active feeding strategy.

No 'fly-glide' behavior (rapid ascents, slower acute angle descents) (Weihs 1973, Carey & Olsen 1982) was observed for the 2 bigeye thresher sharks during the night. However, they demonstrated an opposite behavioral pattern of low angle and prolonged ascents and high angle and short time descents. The upward-facing large eyes of the bigeye thresher may be an evolutionary adaptation for increasing visual detection of prey as they slowly ascend.

The frequency of depth oscillations by the bigeye thresher sharks at night in this study was regular at a rate of 0.8 to 1.2 oscillations h^{-1} and they remained in certain layers (60 to 100 m for Shark 1 and 80 to 120 m for Shark 2). Similar nighttime oscillations have been reported and estimated for other species, e.g. shortfin mako sharks, which dive on average 3.5 times per hour whereas bigeye tuna dive every 57.7 min, but these dives were found to be rather irregular and not confined to certain depth intervals (Holland et al. 1990b, Holts & Bedford 1993). Observations suggested that sharks seem to prefer certain depth layers. It is possible that these layers contain the deep scattering layer (DSL) or small planktivorous fish associated with the DSL. If this is true, the observed slow and continuous ascending and descending behavior may be the appropriate adaptation to search for prey around the DSL.

The bigeye thresher sharks tracked remained in water temperatures ranging from 6 to 11°C during the day and shifted to the mixed layer at night in temperatures from 15 to 26°C. This species can apparently maintain its position within distinct water temperature ranges during day and night. Sharks belonging to the family Lamnidae can maintain body temperatures 5 to 10°C above the ambient water and are well known as endothermic species (Carey et al. 1971, 1982, Goldman 1997). The endothermic ability of the thresher shark was suggested by measurement of body temperature (Carey et al. 1971), anatomical observation of the retial system of locomotor muscles (Bone & Chubb 1983), and presence of the orbital *rete mirabile* in all lamnid sharks and 2 thresher sharks of the family Alopiidae (Block & Carey 1985). However, there are no published data on the body temperatures of free-swimming bigeye threshers. Ambient water temperature in bigeye thresher habitat was observed to vary considerably between day and night, but the endothermic ability of the species is yet to be verified. The depths reached by our tracked sharks at night varied between the different sized individuals, but both stayed within the confines of the mixed layer. It appeared that the sharks orientated themselves based on temperature rather than depth.

Movement was mostly in a northwesterly direction for Shark 1 and southwesterly direction for Shark 2 during the study. Since the current flowed east for Shark 1 and west for Shark 2, the sharks seemed to orient in a westward direction under the influence of either current. The bigeye thresher shark has a circumglobal distribution extending through tropical and subtropical waters; it is possible that the directed westward movements observed in this study may be part of their annual migration. However, the distribution of individuals by size and sex and the implications of this for migration are not fully understood. Further studies of the distribution and migration of the species are therefore necessary.

The observed swimming speeds of the bigeye thresher shark (1.14 to 2.02 km h^{-1}) were considerably slower than those reported for tunas (2.96 to 7.41 km h^{-1} for yellowfin, 2.85 for bigeye, 2.22 to 7.96 km h^{-1} for skipjack; Yuen 1970, Holland et al. 1990b, Cayré 1991, Block et al. 1997), and billfishes (1.21 to 9.72 km h^{-1} for blue marlin, 1.30 to 7.22 km h^{-1} for striped marlin; Holland et al. 1990a, Block et al. 1992, Brill et al. 1993), but similar to swordfish (1.00 to 3.20 km h^{-1}; Carey & Robison 1981). Among the swimming speeds calculated for pelagic sharks, the bigeye thresher shark is very similar to the megamouth shark (1.5 to 2.1 km h^{-1}; Nelson et al. 1997). Although the range of swimming speeds overlapped, the maximum speed of the bigeye thresher is slower than the blue shark (1.20 to 3.67 km h^{-1}; Sciarrotta & Nelson 1977, Carey & Scharold 1990), the shortfin mako shark (1.31 to 4.44 km h^{-1}; Holts & Bedford 1993), and the great white shark (3.20 km h^{-1}; Strong et al. 1992).

The similarity of diel vertical migration patterns and swimming speeds among swordfish, megamouth sharks and bigeye thresher sharks suggests that these species have similar ecological niche preferences which differ from those of other large pelagic species. Utilizing the shallow mixed layer at night might provide these species with some ecological advantage while feeding and/or for avoiding attack. Other morphological features common to both swordfish and bigeye thresher sharks are relatively large eyes and specialized hunting tactics whereby prey is stunned using either a broad-bill or long tail.

Bigeye thresher sharks are usually caught by the Japanese longline fleet at night. Although at present fishermen consider this species a secondary target and there is thus little incentive to minimize catches, understanding the behavioral patterns of the bigeye thresher nevertheless provides useful information for pelagic fisheries and their management. Given the strong diel patterns in the vertical habitat preferences of bigeye thresher sharks, it should be possible to avoid incidental catches of this species. For example, limiting longline sets in shallow waters to daytime hours could drastically reduce incidental catches of bigeye threshers if necessary for fishery management.

LITERATURE CITED

Block BA, Carey FG (1985) Warm brain and eye temperatures in sharks. J Comp Physiol B 156:229–236

Block BA, Booth DT, Carey FG (1992) Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. Mar Biol 114:175–183

Block BA, Keen JE, Castillo B, Dewar H, Freund EV, Marcinek DJ, Brill RW, Farwell C (1997) Environmental preference of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. Mar Biol 130:119–132

Bone Q, Chubb AD (1983) The retial system of the locomotor muscles in the thresher shark. J Mar Biol Assoc UK 63:239–241

Brill RW, Holts DB, Chang RKC, Sullivan S, Dewar H, Carey FG (1993) Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. Mar Biol 117:567–574

Carey FG (1983) Experiments with free-swimming fish. In: Brewer PG (ed) Oceanography: the present and future. Springer-Verlag, New York, p 57–68

Carey FG, Olsen RJ (1982) Sonic tracking experiments with tunas. ICCAT CVSP XVII:458–466

Carey FG, Robison BH (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish Bull 79(2):277–292

Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. Mar Biol 106:329–342

Carey FG, Teal JM, Kanwisher JW, Lawson KD, Beckett JS (1971) Warm-bodied fish. Am Zool 11:137–145

Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HL Jr (1982) Temperature and activities of a white shark, *Carcharodon carcharias*. Copeia 1982(2):254–260

Cayré P (1991) Behavior of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish ag- gregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. Aquat Living Resour 4:1–12

Compagno LJV (1984) Sharks of the world. FAO species catalog, Vol. 4, Part 1. Fisheries Synopsis No. 125. FAO, Rome

Goldman KJ (1997) Regulation of body temperature in the white shark, *Carcharodon carcharias*. J Comp Physiol B 167:423–429

Gruber SH, Compagno LJV (1981) Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus.* Fish Bull 79(4):617–640

Holland KN, Brill RW, Chang RKC (1990a) Horizontal and vertical movements of pacific blue marlin captured and released using sportfishing gear. Fish Bull 88:397–402

Holland KN, Brill RW, Chang RKC (1990b) Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish Bull 88:493–507

Holts DB, Bedford DW (1993) Horizontal and vertical movement of the shortfin mako shark, *Isurus oxyrinchus*, in the southern California bight. Aust J Mar Freshw Res 44:901–909

Liu K, Chiang P, Chen C (1998) Age and growth estimate of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters. Fish Bull 96:482–491

Nelson DR, McKibben JN, Strong WR Jr, Lowe CG, Sisneros JA, Schroeder DM, Lavenberg RJ (1997) An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. Environ Biol Fish 49:389–399

Sciarrotta TC, Nelson DR (1977) Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. Fish Bull 73(3):519–528

Stillwell CD, Casey JG (1976) Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic. Fish Bull 74:221–225

Strong WR Jr, Murphy RC, Bruce BD, Nelson DR (1992) Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. Aust J Mar Freshw Res 43:13–20

Weihs D (1973) Mechanically efficient swimming techniques for fish with negative buoyancy. J Mar Res 31:194–209

Yuen HS (1970) Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J Fish Res Board Can 27(11):2071–2079

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River, NJ