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RESEARCH ARTICLE

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Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight

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Abstract Acoustic telemetry was used to track vertical and horizontal movement patterns and to monitor the stomach temperatures of seven juvenile shortfin mako sharks (*Isurus oxyrinchus* Rafinesque) in the Southern California Bight from July to November 2002. Makos (80–145 cm fork length, FL) were attracted to the tracking vessel, where they were fed a mackerel containing an acoustic transmitter that reported temperature and pressure. Tracks ranged from 6.8–45.4 h. Collectively, the mako sharks spent 80% of the track record at 0–12 m, 15% at 12–24 m, and 5% at depths >24 m. The average horizontal swimming speed was 2.3 km h^{-1} or 0.55 FLs s^{-1}, and the greatest distance traveled was 145 km in 45.4 h. For the six tracks >21 h, there was a positive correlation between body size and maximum depth. Makos used more of the water column during daylight hours. Mean stomach temperature was 3.8 ± 1.5°C above ambient, and body size was positively correlated with both maximum and average stomach temperature. Stomach content analyses of four makos captured at the end of tracking verified the occurrence of feeding events as indicated by changes in stomach temperature.

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Introduction

This study examined the movements of the shortfin mako shark (*Isurus oxyrinchus*) in the Southern California Bight (SCB). The mako belongs to the family Lamnidae, a group that is capable of elevating the temperatures of their aerobic locomotor musculature (red muscle, RM), brains, and stomachs above ambient (Carey and Teal 1969; Carey et al. 1971; McCosker 1987; Goldman 1997; Bernal et al. 2001a, 2001b). The mako, like the other lamnids, is an active species with a relatively high metabolic rate (Graham et al. 1990).

Makos occurring within the SCB are of special concern because this region is one of the few documented nursery habitats in the North Pacific (Hanan et al. 1993). Makos harvested in the SCB are predominantly juveniles [year classes 0–3 (13–27 kg, 1–1.5 m fork length, FL)] (Cailliet and Bedford 1983; Cailliet et al. 1983; Pratt and Casey 1983; Holts and Bedford 1993; Hanan et al. 1993; O'Brien and Sunada 1994), which are present seasonally from May to October. Although commercially fished, there is little information about the population dynamics, migratory patterns, or fine-scale movements of makos within the SCB.

Mako movement patterns have been studied through conventional tagging (release and recapture) (Casey and Kohler 1992; California Department of Fish and Game 2001), commercial catch information (Stillwell and Kohler 1982; Cailliet and Bedford 1983), and acoustic telemetry (Carey et al. 1981; Holts and Bedford 1993; Klimley et al. 2002). The latter technique has been used to document fine-scale movements in relation to temperature, depth, and other physical factors. However, in the present study, to eliminate the possibility that capture and transmitter attachment may affect the shark's behavior (Carey et al. 1981; Holts and Bedford 1993), we used a non-invasive tag attachment technique, whereby the sharks volitionally ingested the transmitter.

This study addresses the following questions. How do physical conditions within the track area (i.e. submarine topography, sea surface temperature, time of day) and factors such as body size and stomach temperature relate to mako swimming depth and habitat utilization? How do the track results from this study compare with previous studies (Carey et al. 1981; Holts and Bedford 1993; Klimley et al. 2002)? Are there differences in habitat utilization among the different mako year classes (years 0, 1, 2) most frequently found in the SCB?

Materials and methods

Mako shark capture and tagging procedure

Seven mako sharks (*Isurus oxyrinchus* Rafinesque) were tracked from July to November 2002. Makos were attracted to the 6-m tracking vessel, R.V. "Spilunky", using ground chub mackerel (*Scomber japonicus*) as chum. Once near the vessel, the size of the mako to be tracked was estimated and it was offered a mackerel in which an acoustic transmitter was embedded. The transmitter package consisted of a 6/0 fishing hook (which was intended to prevent immediate regurgitation) that was set in the mackerel and attached to a 10-cm-long (100 kg) monofilament leader spliced to a light (10 kg) main line. The heavy monofilament prevented a premature severing of the line until the package was at least 10 cm into the mako's esophagus. During ingestion, care was taken not to put any tension on the main line or to make any sudden movements that might affect the shark's behavior. Once the transmitter was swallowed, tracking commenced.

Four of the tracked makos were captured at the end of the study. Necropsy results provided data on gut contents, transmitter position, and body size (mass and FL).

Transmitters, receiving platform, and thermal profiles

We used Vemco Electronics (Armdale, Nova Scotia) V22 TP (22 mm diameter, temperature and pressure) 50-kHz transmitters, with the extra power option and an external reed switch. The rated accuracy of the transmitters was ±6.12 m (3% of total scale, 204 m) and temperature at ±1°C.

Signals were received and decoded by a Vemco VR60 receiver or a VR28 tracking system. The former used a V10 hydrophone (150 of the 167 total tracking hours) that was attached to a 2.5-cm-diameter steel pipe that extended 1.5 m below the lowest point of the hull of the tracking vessel. The pipe could be rotated 360° as to determine the shark's relative bearing. The VR28 used a V41 hydrophone side-mounted approximately 1 m below the hull of the 7-m tracking vessel (R.V. "Ernest"). The horizontal position estimates for each track were recorded periodically (approximately every 3–30 min) using a handheld GPS (Garmin model 72) and downloaded using the Map Source software package.

Water column thermal profiles and ambient track conditions were measured with a Sea Bird Electronics micro-bathythermograph (model SBE-39), which was deployed with a fishing reel at the initial tagging site and at 1- to 3-h intervals over the duration of the track.

Data analysis

Three terms are used to describe mako stomach temperatures. T_S is the observed stomach temperature and T_{SX} is the difference between T_S and the ambient water temperature at which the shark was swimming (T_A, extrapolated from the thermal profile data). In order to compare our study to previous work (Carey et al. 1981; Bernal et al. 2001b), we also used T_X, which is defined as the difference between T_S and the sea surface temperature (SST; $T_X = T_S - T_{SST}$).

Two methods were used to estimate swimming speeds. The first was an over-ground estimate determined from the GPS data from the tracking-vessel position. The second, which incorporated the shark's horizontal and vertical movements, required calculation of each vertical vector and combining them with the over-ground distance estimate to construct two legs of a right triangle, of which the calculation of the hypotenuse and the track time provided the combined speed estimate (Marcinek et al. 2001).

Daylight hours were defined as 30 min before sunrise to 30 min after sunset. Diurnal movement patterns for each shark were analyzed for differences in average depth using a two-sample *t*-test, and depth range was analyzed using a paired Wilcoxon rank test, one-sided. All values are indicated as means ± SE.

The presence of acoustic noise (i.e. cetaceans, scattering layer organisms, and depth recorders that use 50 kHz) and interruptions in data transmission (spurious data points) provided occasional erroneous temperature and depth measurements. These data points accounted for <4% of the entire data set and were filtered from the records. The criteria for the removal of such data points included: (1) if the recorded values were not within the transmitter specifications [depth (0–204 m) and temperature range (−5°C to 35°C)]; (2) if consecutive data points in the depth record deviated by >12 FLs s^{-1}; and (3) if consecutive temperature data points deviated by $>2°C\ s^{-1}$.

Results

Data for the seven tracked mako sharks (*Isurus oxyrinchus*) are given in Table 1 and Appendix 1 of the Electronic Supplementary Material to this paper. The mean over-ground speed was 2.3 ± 0.2 km h^{-1}or 0.55 ± 0.04 FLs s^{-1} and the combined vertical and horizontal speed estimate was 6.7 ± 1.2 km h^{-1}. The com-

Table 1 *Isurus oxyrinchus*. Details for seven mako sharks tracked in the Southern California Bight in 2002 (*M* male; *F* female; *n*/*a* data not available)

Fish no.	Date	Fork length (m)	Mass (kg)	Gender	Start location (DD)	Track duration (h)	Distance traveled (km)	Mean speed (km h^{-1})	Max. depth (m)	Capture
1	25 Jul	~1.15	~16	n/a	32.839N; 117.357W	6.8	18	2.6	17	No
2	20 Sep	1.15	16.0	F	32.833N; 117.376W	25	49	2.0	101	Yes
3	29 Sep	1.2	18.0	F	32.888N; 117.405W	23	55	2.4	168	Yes
4	8 Oct	~1.25	~20	n/a	32.854N; 117.499W	21	32	1.5	80	No
5	15 Oct	0.83	7.0	M	32.899N; 117.389W	23.2	50	2.15	32	Yes
6	22 Oct	~1.45	~32	n/a	33.108N; 117.454W	45.4	145	3.2	201	No
7	6 Nov	0.80	5.0	F	32.846N; 117.442W	23.2	37	1.6	35	Yes

bined depth records show that 80% of the track record (given as a percent of total data points recorded) was spent at depths from 0 to 12 m, 15% at 12–24 m, and 5% at depths >24 m (Fig. 1). For the six tracks spanning both day and night hours (makos 2–7), the average swimming depth and overall depth range were significantly greater during the day than at night (paired Wilcoxon rank test; $P<0.05$). The greatest distance traveled by any mako was 145 km in 45.4 h (mako 6), and the greatest depth penetrated was 201 m (mako 6). Makos 2–7 showed a positive correlation ($r^2=0.86$; $P<0.05$) between body length and maximum depth penetration (Fig. 2). The mean T_{SX} for each shark ranged from 1.7°C to 5.7°C, with a mean of 3.8 ± 1.5°C. When the T_{SX} data were examined in relation to body size, positive correlations were found between body mass and maximum T_{SX} ($T_{SX\max}=2.847e^{0.029\text{mass}}$; $r^2=0.56$) and average T_{SX} ($T_{SX}=0.568e^{1.62\text{mass}}$; $r^2=0.61$).

Individual tracks

Mako 1 remained at depths between 0 and 12 m for 99% of the track record (Fig. 3a). The average T_S was 25.9 ± 1.2°C, and the SST was approximately 21.3°C. The maximum T_X for this mako was 5.8°C. (The thermal profile of the water column was not measured during this tracking session.) This shark was fed a mackerel (ca. 300–400 g) near the end of the track session (~1620 hours) in order to quantify the reduction in T_S caused by food ingestion. A T_S decrease of 0.12°C min^{-1} was recorded immediately after swallowing the mackerel (Fig. 3a, 1620 hours). For all subsequent tracks, we interpreted abrupt T_S changes of this magnitude or greater as indicative of feeding. We identified six presumptive feeding events.

Mako 2 spent 91% of its track record shallower than 12 m, 7% at 12–24 m, and 2% deeper than 24 m (Fig. 3b). Diurnal trends were not obvious in the track record of mako 2. The mean T_S was 23.6 ± 1.4°C at an average SST of 20.3 ± 0.05°C. Its average T_{SX} was 4.2 ± 1.7°C. The T_S record indicated two feeding events. The first was at 1840 hours, about 2.5 h after the track began. The second occurred the following afternoon when, at approximately 1340 hours, it abruptly descended to 101 m. This shark was captured soon thereafter, and we found six (~0.4 kg total mass) nearly undigested Pacific saury (*Cololabis saira*). We also found the transmitter to be in the posterior portion of the stomach and that the transmitter hook had not pierced the stomach wall.

Mako 3 spent ~82% of the track record at 0–12 m, 4% at 12–24 m, and 14% deeper than 24 m (Fig. 3c). The depth record indicated a strong diurnal pattern in

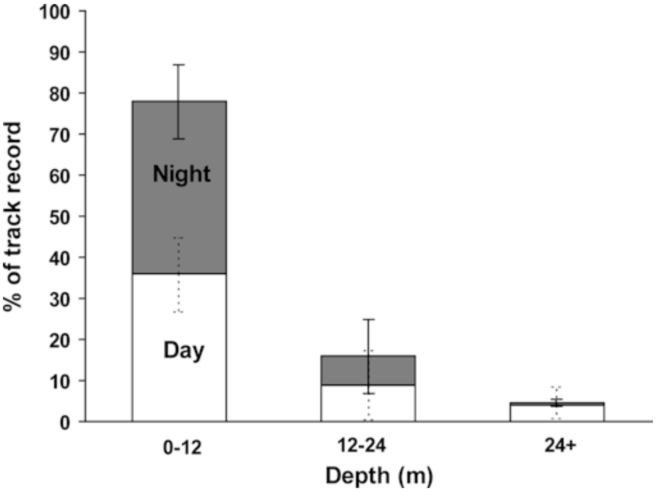


Fig. 1 *Isurus oxyrinchus*. Combined depth distribution data (presented as percentage of track record) for six makos (makos 2–7). Day (*white*) and night (*shaded*) hours indicated for three depth categories: surface–12 m, 12–24 m, and >24 m

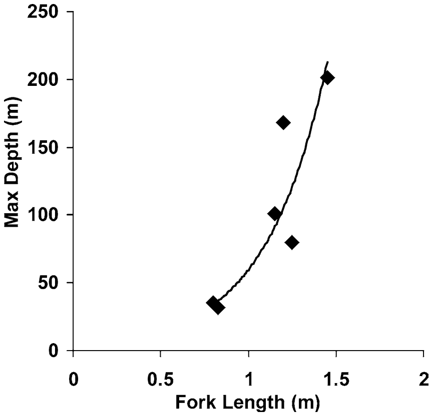


Fig. 2 *Isurus oxyrinchus*. Maximum depth penetration (*D*, m) as a function of fork length (FL, m) ($D=3.539e^{2.823\text{FL}}$; $r^2=0.86$)

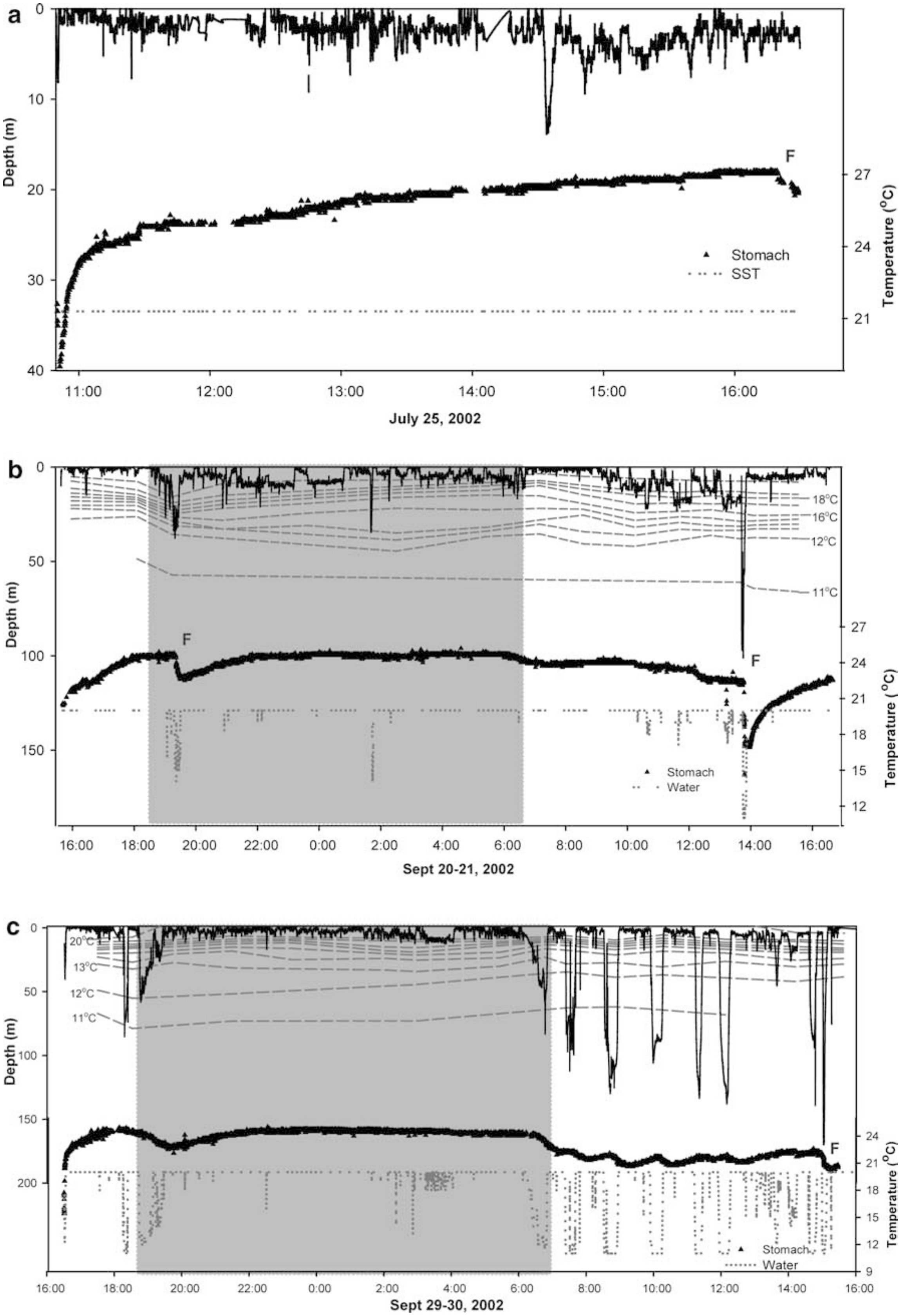
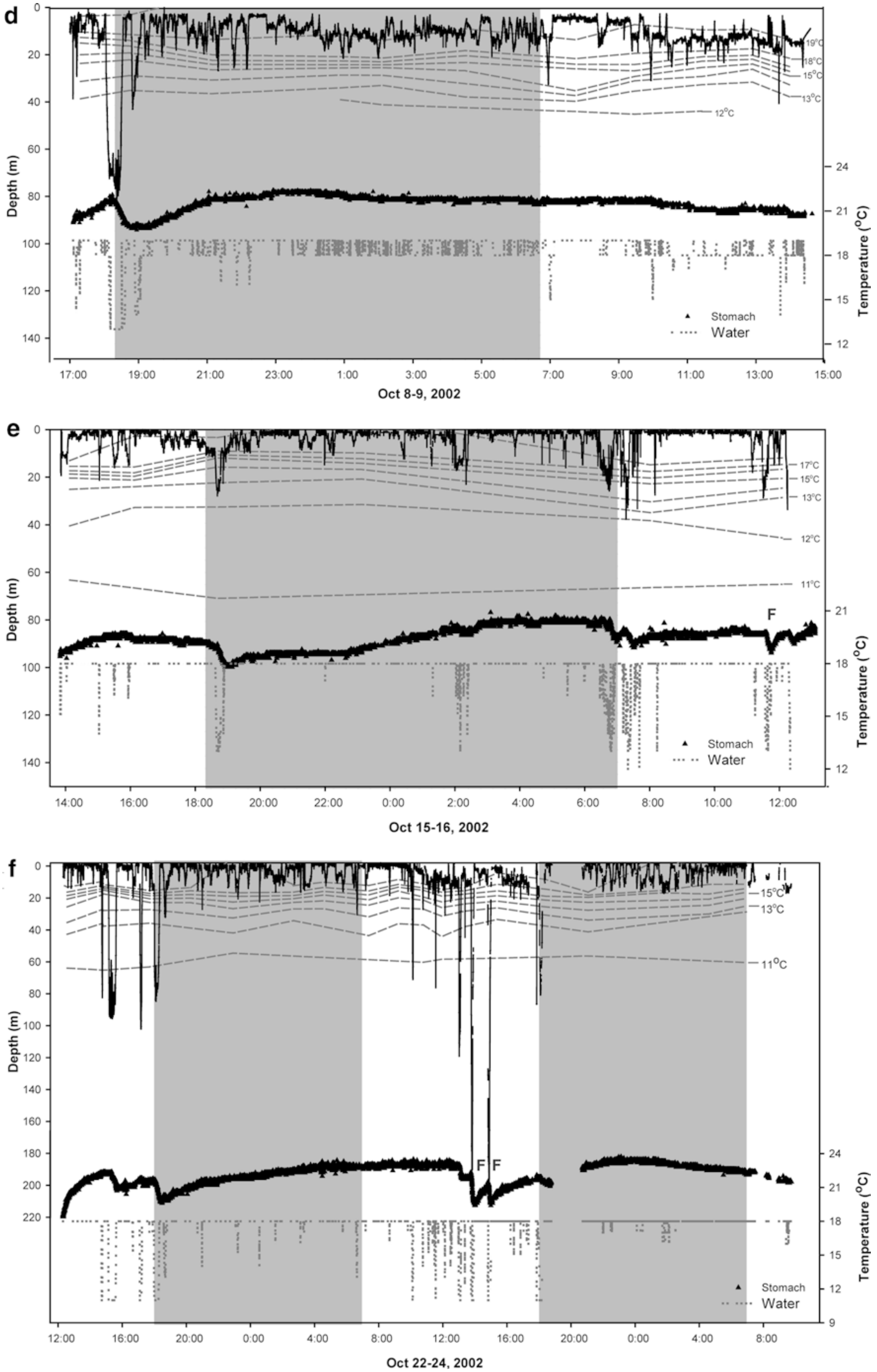

a
Depth (m)
0
10
20
30
40
F
Stomach
SST
27
24
21
Temperature (°C)
11:00
12:00
13:00
14:00
15:00
16:00
July 25, 2002
b
Depth (m)
0
50
100
150
18°C
16°C
12°C
11°C
F
F
27
24
21
18
15
12
Temperature (°C)
Stomach
Water
16:00
18:00
20:00
22:00
0:00
2:00
4:00
6:00
8:00
10:00
12:00
14:00
16:00
Sept 20-21, 2002
c
Depth (m)
0
50
100
150
200
20°C
13°C
12°C
11°C
F
24
21
18
15
12
9
Temperature (°C)
Stomach
Water
16:00
18:00
20:00
22:00
0:00
2:00
4:00
6:00
8:00
10:00
12:00
14:00
16:00
Sept 29-30, 2002

Fig. 3 (Contd.)


d
Depth (m)
Temperature (°C)
19°C
18°C
15°C
13°C
12°C
Stomach
Water
17:00
19:00
21:00
23:00
1:00
3:00
5:00
7:00
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Oct 8-9, 2002
e
17°C
15°C
13°C
12°C
11°C
F
Stomach
Water
14:00
16:00
18:00
20:00
22:00
0:00
2:00
4:00
6:00
8:00
10:00
12:00
Oct 15-16, 2002
f
15°C
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11°C
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Stomach
Water
12:00
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20:00
0:00
4:00
8:00
Oct 22-24, 2002

Fig. 3 (Contd.)

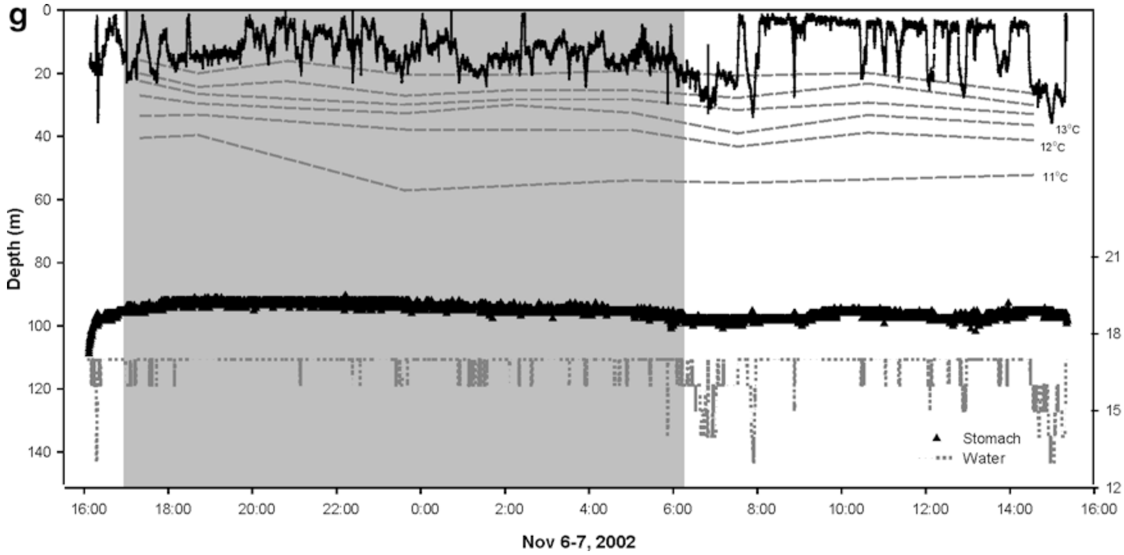

Fig. 3a–g *Isurus oxyrinchus*. Vertical movements and stomach temperatures for seven sharks (**a–g**: makos 1–7, respectively) tracked in the Southern California Bight. *Top to bottom*: swimming depth (*solid line*), ambient isotherms (*dashed lines*), stomach temperature (*triangles*) and corresponding water temperature (*dotted lines*) plotted over time. *Shaded areas* indicate hours between sunset and sunrise. Suspected feeding events (*F*)

which the shark remained at or near the surface at night and went deeper during the day. Mako 3 had an average T_S of 23.3 ± 1.3°C (SST 19.7 ± 0.4°C), and the average T_{SX} was 5.1 ± 2.7°C. The T_S record suggested only one feeding event at ~1500 hours (30 min before capture). Necropsy results revealed one 90 g nearly undigested Pacific sardine (*Sardinops sagax*) and, as with mako 2, that the transmitter was in the posterior stomach and that the hook had not penetrated the stomach wall.

Mako 4 ranged between the surface and 80 m (Fig. 3d). It spent 60% of the track record at 0–12 m, 36% at 12–24 m, and 4% deeper than 24 m, and did not demonstrate any clear diurnal dive patterns. The average T_S was 21.5 ± 0.5°C at an average SST of 19.6 ± 0.4°C. The average T_{SX} was 3.3 ± 1.4°C, and there were no feeding events.

Mako 5 spent 93% of the track record at 0–12 m, 6% at 12–24 m, and 1% deeper than 24 m (Fig. 3e). While there were no diurnal trends, the shark did spend ~50% of the track within 1 m of the surface. The average T_S was 19.5 ± 0.6°C (SST 18.3 ± 0.3°C), and the average T_{SX} was 1.7 ± 1°C. One feeding event occurred at 1130 hours (~1.5 h before capture), which was a 100 g Pacific sardine. The necropsy revealed that the transmitter was in the posterior stomach and that there was no hook penetration.

Mako 6 was the largest shark tracked. It ranged from the surface to 201 m (Fig. 3f) and spent 89% of its track record at 0–12 m, 5% at 12–24 m and 6% deeper than 24 m. Mako 6 exhibited a diurnal dive pattern similar to that of mako 3, in that it remained near the surface throughout the night and undertook deeper dives during the day. The average T_S was 22.1 ± 1°C (SST 18.2 ± 0.2°C), and the average T_{SX} was 4.5 ± 1.9°C. The T_S record indicated two feeding events (at ~1400 and 1500 hours on day 2). Mako 6 was not captured at the end of the study.

Mako 7 spent 50% of the track record at 0–12 m, 45% at 12–24 m, and 5% deeper than 24 m (Fig. 3g). Although it made frequent vertical excursions between 0 and 35 m, mako 7 did not display any obvious diurnal depth trends. The average T_S was 18.9 ± 0.3°C (SST 17.5 ± 0.2°C), and the average T_{SX} was 2.1 ± 0.6°C. Mako 7 did not feed during the time that it was followed. Necropsy results indicated the absence of prey, the transmitter in the posterior stomach, and that the hook had not pierced the stomach wall.

Discussion

This study provides information on the movement patterns and stomach temperatures of seven juvenile mako sharks (*Isurus oxyrinchus*) tracked in the SCB using a non-invasive tagging procedure. Using the T_S we were able to record feeding events for free-swimming makos. The post-track capture and subsequent gut content analyses of four of the sharks verified the feeding signal in the T_S record. This work on non-stressed makos suggests that juveniles may spend as much as 80% of the time in surface waters (<12 m depth) and that excursions into deeper, cooler waters are more frequent during the day. When coupled with earlier mako telemetry studies (Holts and Bedford 1993; Klimley et al. 2002), it is evident that SCB juveniles frequent the upper mixed layer. Our study also confirms previous observations that makos undergo frequent vertical oscillations (Carey et al. 1981; Holts and Bedford 1993; Klimley et al. 2002), routinely entering waters cooler (<11°C) than those previously described as the mako thermal boundary (14°C; Klimley et al. 2002). Additionally, this study indicates that larger makos swim to greater maximum depths than do smaller makos (Fig. 2).

Feeding the transmitter to the mako sharks avoided capture and restraint for tag attachment. Capture and handling can alter blood and body biochemistry (i.e. elevated plasma and muscle lactate; catecholamines; glucose), which may influence the shark's behavior (Arthur et al. 1992; Milligan 1996; Bernal et al. 2001b). Telemetry studies on both blue (*Prionace glauca*) and mako sharks that were hooked and restrained prior to their tracking have shown a distinct post-handling dive immediately upon release (Carey and Scharold 1990; Holts and Bedford 1993; Klimley et al. 2002), something we did not observe in this study. This suggests that there was little stress induced by the initial feeding of the transmitter to the sharks. Other indications that these makos were not adversely affected by the tagging procedure were the records of natural feeding events, the relatively slow swim speeds observed throughout the tracks (even immediately after tag ingestion), and the subsequent capture of post-track individuals when presented with a baited hook.

The maximum T_X (T_S–T_{SST}) range for the seven tracked makos (1.9–5.7°C) was slightly warmer than those determined by Bernal et al. (2001b; 1–3°C) for similar sized makos in a swim tunnel, but less than the values of Carey et al. (1981; 6–8°C) for larger makos in the West Atlantic. The degree to which lamnids can control T_S is not known. However, Goldman (1997) has determined that large white sharks (*Carcharodon carcharias*) can maintain a relatively constant T_S (24°C) in cool water (~14°C SST). In the present study, we observed T_S records that remained relatively stable over periods as long as 23 h (Fig. 3g), but abrupt changes in the T_S records were also common. These abrupt changes were associated with both verified feeding events and penetration into cooler waters. An unstable T_S record may be more representative of wild juvenile (0.80–1.45 m) makos that are feeding and regularly traversing the thermocline.

The criterion used to define the T_S feeding signal was based on the temperature change associated with the ingestion of a 300–400 g mackerel. Therefore, we may be underestimating the number of actual feeding events, in that smaller prey undoubtedly result in a smaller decrease in T_S. Six suspected feeding events were recorded using our conservative criteria, three of which (makos 2, 3, and 5) were confirmed through gut content analyses.

The swimming behaviors and diurnal patterns we observed resemble those previously recorded for the blue shark in the Atlantic and Pacific (Carey and Scharold 1990), for makos in the Atlantic (Carey et al. 1981), and a juvenile white shark fitted with a "pop-off" satellite tag in the SCB (Dewar et al. 2004). For all tracked makos the greatest depth always occurred during daylight hours, and, for makos 3 and 6, there was a consistent pattern of repetitive deeper dives during the day, with the shark remaining near the surface at night. Although these trends are consistent with those described for other pelagic species known to follow and prey on the vertically migrating deep scattering layer (DSL) (Carey and Robinson 1981; Holland et al. 1990; Dagorn et al. 2000; Schaefer and Fuller 2002), all but one of the suspected mako feeding events took place during the day and gut inspection did not reveal mesopelagic prey (species common to the DSL). One explanation for the diurnal movements may be that makos rely heavily on vision for locating prey and, thus, penetrate to greater depths during the daylight hours when visibility is the greatest.

Other trends in the dive records included repeated vertical oscillations throughout the tracks. Oscillatory swimming is well described for fishes (Carey et al. 1981; Carey and Scharold 1990; Holland et al. 1992; Holts and Bedford 1993; Brill et al. 2002; Klimley et al. 2002). Despite individual variation, the oscillatory swimming we observed seemed to fit into two distinct categories: one in which the swimming pattern included repeated shallow oscillations as if the sharks were searching a small section of the water column and the second in which the oscillations seemed to be directed descents into deeper waters followed by rapid ascents, or "bounce dives". These "bounce dives" were frequently associated with successful feeding events.

Several hypotheses have been put forth as to why fish might make frequent vertical oscillations. Carey and Scharold (1990) suggested that this pattern might provide for optimal foraging of the water column. In the case of the mako, frequent excursions may enable them to use their counter-shading and burst capabilities to overtake prey from below, as has been shown for the white shark (Klimley 1994). The makos may also undertake frequent excursions to deeper, colder waters and use the warmer surface waters to regain lost heat and hence behaviorally thermoregulate (Holland et al. 1992; Bernal et al. 2001a; Klimley et al. 2002). Weihs (1973) has proposed that swimming in an oscillatory manner (bursting upward and gliding downward) is a more efficient form of locomotion as opposed to swimming in a straight line. However, Weihs' (1973) model requires a shallower angle of descent than ascent, the opposite of what we observed in this study. Other explanations of oscillatory swimming include a potential role in navigation (Klimley et al. 2002), or possibly in sensing different water masses for directional information (Westerberg 1982; Klimley 1993; Klimley et al. 2002).

All track records were plotted on a high-resolution topographical map to determine if their horizontal movements tracked the submarine topography of the SCB (Appendix 1, Electronic Supplementary Material). Although we observed our tracked makos associating with topographic features and at times following specific bathymetric contours, we cannot conclude whether these movements were directed towards these features, or if the intricate topography of the SCB is such that they encountered these by chance.

Recent management decisions to close part of the central and northern California coastline to the gillnet fleet (2001 temporal and regional closures to the California gillnet fishery for swordfish and thresher shark, Federal Register 2001) have redistributed the gillnet effort within the SCB. This fishery is more than 20 years old and accounts for more than half of the California annual mako harvest (Taylor and Bedford 2001). Better understanding of mako fine-scale movement patterns may provide managers with the habitat utilization data necessary for managing the target species of the fishery as well as reducing the bycatch. Our data suggest that juvenile makos spend up to 80% of their time in surface waters (< 12 m) and that excursions into deeper, cooler waters are more frequent during the day. Considering the current gillnet depth restrictions employed to reduce interactions with marine mammals [36-foot sub-surface extenders and daytime fishing prohibited (California Department of Fish and Game 2003)] it may be that the management decisions already in place cause the gillnet fishery to have a reduced juvenile mako catch. Further study of a larger size range of makos and tracking of the target species of the gillnet fishery (thresher sharks, *Alopias* spp., and swordfish) are needed to better understand how these apex predators partition the SCB.

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References

Arthur PG, West TG, Brill RW, Shulte PM, Hochachka PW (1992) Recovery metabolism of skipjack tuna, *Katsuwonus pelamis,* white muscle: rapid and parallel changes of lactate and phosphocreatine after exercise. Can J Zool 70:1230–1239

Bernal D, Dickson KD, Shadwick RE, Graham JB (2001a) Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. Comp Biochem Physiol 129:695–726

Bernal D, Sepulveda CA, Graham JB (2001b) Water-tunnel studies of heat balance in swimming mako sharks. J Exp Biol 204:4043–4054

Brill RW, Lutcavage M, Metzger G, Bushnell P, Arendt M, Lucy J, Watson C, Foley D (2002) Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry. Fish Bull (Wash DC) 100:155–167

Cailliet GM, Bedford DW (1983) The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. CalCOFI (Calif Coop Ocean Fish Investig) Rep 24:57–59

Cailliet GM, Martin LK, Harvey JT, Krusher D, Welden BA (1983) Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. NOAA Tech Rep 8:179–188

California Department of Fish and Game (2001) Shark tagging news. California Department of Fish and Game, Long Beach, Calif. (News Letter Series)

California Department of Fish and Game (2003) Commercial fishing regulations: Marine Mammal Protection Act section 118. Available at http://www.dfg.ca.gov/licensing/pdffiles/2003CommFishDigest/MMProtectionAct.pdf

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

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

Carey FG, Teal JM (1969) Mako and porbeagle: warm bodied sharks. Comp Biochem Physiol 28:199–204

Carey FG, Teal JM, Kanwisher JW, Lawson KD (1971) Warm bodied fish. Am Zool 11:135–145

Carey FG, Teal JM, Kanwisher JW (1981) The visceral temperatures of mackerel sharks (Lamnidae). Physiol Zool 54:334–344

Casey JG, Kohler NE (1992) Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the western North Atlantic. Aust J Mar Freshw Res 43:45–60

Dagorn L, Bach P, Josse E (2000) Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. Mar Biol 136:361–371

Dewar H, Domier M, Nasby-Lucas N (2004) Insights into young of the year white shark (*Carcharodon carcharias*) behavior in the Southern California Bight. Environ Biol Fishes (in press)

Federal Register (2001) Endangered and threatened wildlife; sea turtle conservation requirements; taking of threatened or endangered species incidental commercial fishing operations. Federal Register 166:165, microfiche

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

Graham JB, Dewar H, Lai NC, Lowell WR, Arce SM (1990) Aspects of shark swimming performance determined using a large water tunnel. J Exp Biol 151:175–192

Hanan DA, Holts DB, Coan AL Jr (1993) The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. Fish Bull (Wash DC) 175:89–95

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

Holland KN, Brill RW, Chang RKC, Sibert JR, Fournier D (1992) Physiological and behavioral thermoregulation in bigeye tuna, *Thunnus obesus*. Nature 358:410–412

Holts DB, Bedford DW (1993) Horizontal and vertical movements of the shortfin mako, *Isurus oxyrinchus,* in the Southern California Bight. Aust J Mar Freshw Res 44:45–60

Klimley AP (1993) Highly directional swimming by the scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry and geomagnetic field. Mar Biol 117:1–22

Klimley AP (1994) The predatory behavior of the white shark. Am Sci 82:122–133

Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environ Biol Fishes 63:117–135

Marcinek DJ, Blackwell SB, Dewar H, Freund EV, Farwell C, Dau D, Seitz AC, Block BA (2001) Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. Mar Biol 138:869–885

McCosker JE (1987) The white shark, *Carcharodon carcharias*, has a warm stomach. Copeia 1987:195–197

Milligan CL (1996) Metabolic recovery from exhaustive exercise in rainbow trout. Comp Biochem Physiol A 113:51–60

O'Brien JW, Sunada JS (1994) A review of the southern California experimental drift longline fishery for sharks, 1988–1991. CalCOFI (Calif Coop Ocean Fish Investig) Rep 35:222–229

Pratt HL, Casey JG (1983) Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can J Fish Aquat Sci 40:1944–1957

Schaefer KM, Fuller DW (2002) Movements, behavior and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. Fish Bull (Wash DC) 100:765–788

Stillwell CE, Kohler NE (1982) Food, feeding habits, and estimates of daily ration of the shortfin mako *(Isurus oxyrinchus*) in the North Atlantic. Can J Fish Aquat Sci 39:407–414

Taylor VB, Bedford DW (2001) Shortfin mako shark. In: Leet WS, Dewees CM, Klingbeil R, Larson EJ (eds) California's living marine resources: a status report. California Department of Fish and Game, Resource Agency, Long Beach, pp 336–341

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

Westerberg H (1982) Ultrasonic tracking of Atlantic salmon (*Salmo salar*). I. Movements in coastal regions. Inst Freshw Res Drottningholm Rep 60:81–98