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ELSEVIER

Journal of Experimental Marine Biology and Ecology 352 (2007) 114–128

**Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY**

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Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation?

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Received 7 October 2006; received in revised form 26 October 2006; accepted 14 July 2007

Abstract

The leopard shark, *Triakis semifasciata*, is an abundant nearshore elasmobranch, ranging from Baja California, Mexico to Oregon, USA. Mature female leopard sharks have been observed aggregating in shallow embayments throughout California; however, it is unclear why only females aggregate in these shallow areas. The goal of this study was to determine if mature female leopard sharks selectively occupy the warmest areas of a shallow embayment, if free-ranging leopard sharks' body temperatures are significantly warmer during the day than at night, and to quantify temporal use of these shallow habitats. Visual observations of sharks' fine-scale movements within the shallows of Big Fisherman's Cove Marine Life Refuge (Santa Catalina Island) aggregation site indicated that sharks preferred the warmest areas of the embayment and moved to warmer locations over the course of the day ($p < 0.05$). Active and passive acoustic tracking, along with archival transponder technology (Vemco: V13, V13-R256, VX32TP-CHAT tags respectively) of 16 sharks caught and tagged within this aggregation were used to monitor core body temperature, swimming depth, and movements. Sharks had significantly higher core body temperatures in the late afternoon (1700 h–2000 h) during the summer, showed increased fidelity to thermal refuges during the day and increased movement away from these refuges at night ($\chi^2, p < 0.05$). Seasonal variations in warm, shallow water usage were also observed. Elevated core body temperature of mature female leopard sharks using warm shallow embayments will likely augment metabolic and physiological functions such as digestion, somatic growth, and possibly reproduction.

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Keywords: Acoustic telemetry; Behavior; CHAT tags; Elasmobranch; Site fidelity

1. Introduction

The leopard shark, *Triakis semifasciata*, is a nearshore elasmobranch that ranges from Baja California, Mexico to Oregon, USA, and is particularly common in estuaries and bays throughout California (Miller and Lea 1977; Cailliet 1992). Leopard sharks feed opportunistically on

benthic invertebrates, small fish, and fish eggs in the intertidal and subtidal zones (Webber and Cech 1998; Smith 2001; Ebert and Ebert 2005) and adults are typically found in waters less than 1 m to depths of 100 m (Eschmeyer et al., 1983; Love 1996). Males reach sexual maturity at 7 years (90 cm TL), whereas females reach maturity at 10 years (100 cm TL) (Smith 1984; Kusher et al., 1992) and produce 1–37 offspring per annual breeding cycle (Smith and Abramson, 1990; Au and Smith, 1997). Adult female leopard sharks are known to

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aggregate in large numbers in shallow bays and estuaries, particularly in summer months; however, the function of these aggregations has been unclear (Manley 1995; Capuzzo 2001; Smith 2004). Because these shallow areas are typically warmer than other adjacent habitats during the summer (Babel 1967), the goal of our study was to determine if mature female leopard sharks are utilizing these shallow waters to increase their core body temperatures.

Previous studies of leopard shark behavior have indicated that they exhibit tidally influenced movement patterns as well as diel movement patterns. Ackerman et al. (2000) acoustically tracked adult leopard sharks in Tomales Bay, California, and found that they moved in and out of the bay with the tides. These movement patterns were thought to allow sharks to exploit intertidal mud flats during high tides in the inner bay. As in many other elasmobranchs, there was a significant increase in the rate of movement at night. Manley (1995) acoustically tracked adult female leopard sharks in Big Fisherman's Cove (BFC), Santa Catalina Island, California, focusing on their diurnal movement patterns in and out of the shallowest area of the cove. Manley (1995) found that mean nighttime activity of leopard sharks was significantly greater than mean daytime activity, and suggested that sharks were leaving the shallow areas to forage at night. Some individuals dispersed up to 10 km from the shallow cove at night, and then returned the following morning. Because shallow waters of the embayment were notably warmer than surrounding waters, he suggested that these mature sharks might be returning to the same location each morning to warm and that mature female leopard sharks could be utilizing the shallow embayment of BFC during the day to gain some thermal advantage, since there was little evidence of sharks feeding in these shallow areas during the day.

Although a small proportion of elasmobranch species have been found to physiologically regulate their body temperature to some degree (Casterlin and Reynolds 1979; Anderson and Goldman 2001; Lowe and Goldman 2001; Bernal et al., 2001; Dickson and Graham, 2004), evidence for behavioral thermoregulation has been documented in only a few ectothermic elasmobranchs. Blue sharks (*Prionace glauca*) have been found to move to surface waters apparently to warm swimming muscles after prolonged periods at cooler depths, which is thought to enable them to exploit vertically migrating prey without significant loss of muscle performance due to cooling (Carey and Scharold 1990). Similar observations have been made for ectothermic teleosts, such as the ocean sunfish (*Mola mola*), which was observed to spend longer periods of

time at the surface after prolonged dives through the thermocline (Cartamil and Lowe 2004). Bat rays (*Myliobatis californica*) in Tomales Bay, California were found to forage over mud flats during times of day when water temperatures are elevated, then move to cooler water after feeding, which has been hypothesized to increase energy efficiency by lowering gastric evacuation rates and decreasing metabolic rate (Matern et al., 2000). Collectively, these studies have shown that these fishes may be selectively moving through their environments in a way that conveys some energetic advantage to these ectotherms, resulting in a beneficial increase or decrease in physiological function.

Because rates of physiological functions are directly affected by changes in temperature (Schmidt-Nielsen 1990), leopard sharks may be aggregating to achieve some energetic advantage that might be particularly beneficial to sexually mature females. This sort of behavior has been observed in other species of elasmobranch and has been hypothesized to speed up rates of embryo development and gestation (Taylor 1993; Economakis and Lobel 1998; Wallman and Bennett 2006).

We hypothesize that mature female leopard sharks show diurnal and seasonal fidelity to the shallow embayments of Santa Catalina Island, and when possible, mature female leopard sharks utilize warmer shallow embayments of Santa Catalina Island to increase their core body temperature. Therefore, the three primary goals of this study were to determine: 1) if adult female leopard sharks selectively occupy the warmest areas of a shallow embayment within Big Fisherman's Cove (BFC), Santa Catalina Island during the summer months, 2) if free-ranging leopard sharks' internal body temperatures are significantly warmer during the day than at night, and 3) to what degree mature female leopard sharks utilize BFC and other shallow embayments around Santa Catalina Island over daily and seasonal periods.

2. Materials and methods

2.1. Study site

The primary location of this study was Big Fisherman's Cove, Santa Catalina Island, California (33° 26' N, 118° 29' W), which is a state marine life refuge located approximately 40 km from the southern California mainland (Fig. 1, inset A & B). Big Fisherman's Cove is approximately 200 m by 300 m with most of the coastline composed of rock reef and rock cobble. The northwest wall is a steep rock reef that extends from 0 to 40 m in depth and is largely covered with macroalgae such as *Macrocystis pyrifera*. This continuous rock wall

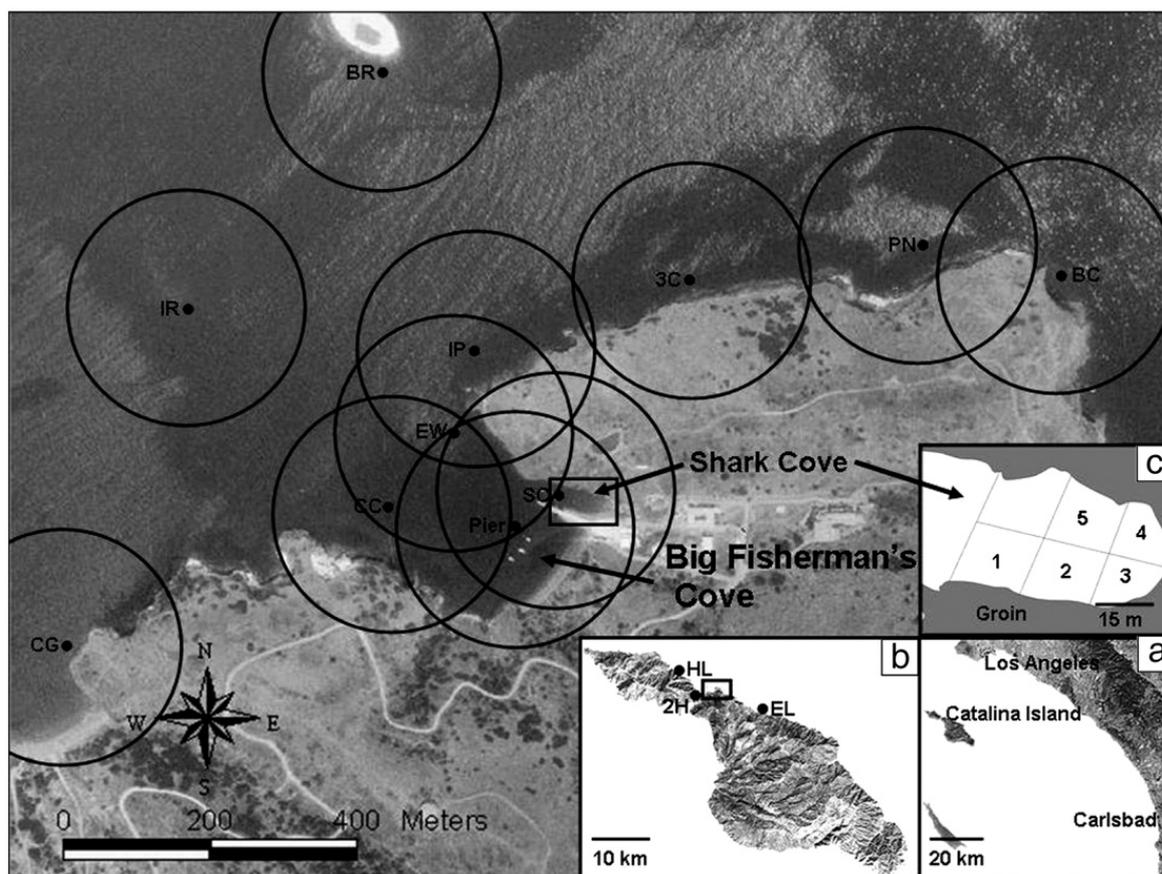


Fig. 1. Aerial photograph of Big Fisherman's Cove ($33^{\circ}26' N$, $118^{\circ}29' W$) and adjacent areas. Black dots indicate location of automated acoustic VR1 receivers and black rings depict with their 150 m radius detection ranges. CG = Camp Ground, IR = Isthmus Reef, BR = Bird Rock, CC = Chalk Cliffs, SC = Shark Cove, EW = East Wall, IP = Intake Pipes, 3C = Three Caves, PN = Pumpnickel, and BC = Blue Cavern. Inset A shows the location of Santa Catalina Island in relation to southern California, inset B shows the Big Fisherman's Cove (BFC) area in relation to Howlands Landing (HL), Empire Landing (EL), and Two Harbors (2H), and inset C shows an enlarged view of Shark Cove (SC), which is located in the northeast corner of Big Fisherman's Cove. The numbers within the gridded area in inset C indicate the behavioral observation zones.

extends well outside BFC to the north, where it drops to depths of 50 m before reaching the gradually sloping sand substratum. To the east, this rock wall progressively becomes shallower, ending in a semi-enclosed area called Shark Cove (SC), which is approximately 35 m wide by 70 m long. Shark Cove ranges in depth from 0 to 5 m with a sand/mud substratum interspersed with rock cobble, particularly in the shallowest area. Shark Cove is separated from the rest of BFC by a groin that was built to support a pier and dock. This groin is approximately 5 m above sea level and provides an excellent vantage point over most of SC, except for the deepest area farthest from the groin. The opposing side of the groin is a northwest-facing beach that is 130 m long and composed of small to medium sized rock cobble. The southwest border to the cove is rock reef ranging in depth from a few meters to 40 m. The middle of BFC (depth range: 5–30 m) is composed mostly of sand/mud substratum with a small rock reef in the southwest region at the Chalk Cliffs (CC) area (Fig. 1).

Two additional aggregation sites included in this study are Howland's Landing (HL) and Empire Landing (EL) (Fig. 1). Howland's Landing ($33^{\circ} 27' N$, $118^{\circ} 31' W$) is located approximately 4 km west of BFC and is a 260 m wide shallow sand/mud cove surrounded on either end by rock cobble and kelp beds. Empire Landing ($33^{\circ} 25' N$, $118^{\circ} 26' W$) is a more exposed shallow embayment with no defining borders, located approximately 6 km to the southeast of BFC. This sand beach extends a length of 400 m and ranges in depth from 0 to 20 m. Adult leopard sharks have historically been observed aggregating at both of these sites as well as in BFC.

2.2. Behavioral observations

Visual observation of the fine-scale movement and distribution patterns of aggregating leopard sharks in the SC area were made from late July to August 2003. Shark Cove was divided into five equal sampling zones, each 10 m wide by 15 m long, using physical references and

rock outcroppings (Fig. 1, inset C). Seafloor water temperatures of each sampling zone were continuously monitored using temperature data loggers (HOBO Stowaway TidbiT -4 °C to $+37$ °C, Onset Computers) to record changes in ambient water temperature every 5 min (± 0.1 °C). Zones 1 through 5 were clearly visible from the top of the groin and allowed for accurate counts of the leopard sharks with minimal disturbance to the sharks' behavior. The number of leopard sharks in each sampling zone was counted during 1-hour intervals randomly chosen from 0600 h to 2000 h, 3 times a day. Counts included records of the time of day and the leopard sharks' locations in relation to the 5 sampling zones of SC. The mean seafloor water temperature of each sampling area was determined by taking an average of the 12 temperatures logged by the HOBO TidbiT during that particular hour of observation. Along with counts of sharks, estimates of sex and size were also made. Four 30 cm white plastic disks were affixed to the seafloor in the cove to aid in size estimates of sharks as they swam close to these disks. Sharks were also observed for the presence of claspers to determine sex. Weekly snorkel observations were made to further verify the sex of the sharks frequenting the SC area.

To determine if the leopard sharks in SC were selectively occupying the warmest water, a correlation was used to quantify the relationships between water temperature and the number of sharks present in SC. Rank correlation was used to evaluate whether sharks preferentially occupied the warmest zone of SC at each hour interval. Non-linear regressions were used to compare the average number of sharks versus the time of day, and the average ambient seafloor water temperature versus the time of day. Peaks in the resulting parabolic curves were compared to determine if peak shark abundance corresponded to peaks in ambient seafloor temperature.

2.3. Monitoring internal body temperature

Six mature female leopard sharks were fitted with internal archival temperature/depth acoustic transponders, "Communicating Histogram Acoustic Sensors" (CHAT Tags: Vemco model VX32TP), and externally attached continuous pulse acoustic transmitters (Vemco model V-13). CHAT tags were programmed to sample body temperature (-5 °C to $+35$ °C ± 0.3 °C) and depth (± 0.5 m) every 10 s and retrieved information was then averaged every 30 min. Archived data included 1) the temperature and minimum depth for the 30 minute interval, 2) the temperature at the maximum depth for the 30 minute interval, and 3) the average temperature

for the 30 minute interval. With this sampling rate, up to 42 days of data could be archived for retrieval at a later date and time. Retrieval of archived data occurs via a two-way communication with a CHAT tag receiver (VR-20CXP, Vemco Ltd.). The CHAT tags emitted an interrogate pulse every few minutes in order to establish communication with a nearby VR-20 receiver. This VR-20 receiver was placed in the SC area in BFC where data on body temperature and swimming depth were automatically downloaded when sharks moved within acoustic detection range and an interrogate pulse was detected by the VR-20 receiver. The estimated range of CHAT tags was approximately 500 m based on range tests and the topographic features of BFC. VR-20 receiver gain was set at 3 dB, the lowest possible setting.

For implanting CHAT tags all leopard sharks were collected in the SC area of BFC between 23 April and 6 July 2004. A large barrier net was used to contain sharks aggregated in the shallow end of the cove and a smaller beach seine net was used to corral individual sharks. Once captured, each shark was transported in a canvas sling to a holding tank onshore. Each shark was held inverted in the holding tank and tonic immobility was induced, while being bathed in an anesthetic of tricaine methanesulfonate (MS222, 70 mg/L). CHAT tags (model VX32TP, 32 mm by 150 mm; nominal battery life 1 year) were coated with a combination of beeswax and paraffin (1:2.33) and were surgically inserted through a 3 cm incision into the shark's body cavity (Holland et al., 1999). The incision was closed using dissolvable suture (Chromic Gut CT-2, Ethicon Inc.) and the wound was treated with a topical antibiotic (Neosporin, Pfizer). In addition, a continuous pulse acoustic transmitter (Vemco model V-13, 13 mm by 36 mm; nominal battery life 36 days) was externally attached to the dorsal fin, using corrosible wire that would allow the transmitters to be shed after several months. These transmitters allowed for manual tracking of instrumented sharks from a small, customized tracking skiff (Lowe et al., 2003), providing information on fine-scale movements. Prior to release, all sharks were measured, sexed, and an external California Department of Fish & Game nylon dart tip spaghetti tag was placed in the left dorsal musculature next to the first dorsal fin. This facilitated visual recognition of instrumented sharks in the field (Table 1). Surgery and tagging took approximately 10 min per shark and, after tagging; all sharks were released inside the barrier net and monitored for 30 min before being released back into the wild.

Leopard sharks were initially tracked immediately after leaving the SC or after being relocated within the

Table 1
Summary of leopard shark fitted with acoustic transmitters

Tag #	Sex	Tagging date	Tag type	Total length (cm)	Fork length (cm)
221	F	23-Apr-2004	V13-1L-R256	155	134
224	F	07-May-2004	V13-1L-R256	190	173
222	F	08-May-2004	V13-1L-R256	139	123
225	F	09-May-2004	V13-1L-R256	135	120
228	F	12-Jun-2004	V13-1L-R256	140	120
229	F	12-Jun-2004	V13-1L-R256	145	125
230	F	12-Jun-2004	V13-1L-R256	150	131
223	F	12-Jun-2004	V13-1L-R256	132	115
226	F	12-Jun-2004	V13-1L-R256	151	129
227	F	12-Jun-2004	V13-1L-R256	150	129
575	F	12-Jun-2004	VX32TP and V13-1H	146	125
511	F	12-Jun-2004	VX32TP and V13-1H	150	130
559	F	12-Jun-2004	VX32TP and V13-1H	157	128
527	F	06-Jul-2004	VX32TP and V13-1H	145	125
543	F	06-Jul-2004	VX32TP and V13-1H	155	135
495	F	06-Jul-2004	VX32TP and V13-1H	155	135

Tag # represents the acoustic tag identification number. Sex, tagging date, tag type, total length, and fork length of 16 leopard sharks tagged in Shark Cove. Acoustic transmitter types are coded transmitters (V13-1L-R256), CHAT tag transmitters (VX32TP), and continuous pulse acoustic transmitters (V13-1H).

first week of release using a Vemco model VR-60 acoustic receiver. In some cases, the VR-20 receiver was taken to other locations where tagged sharks had been relocated so that CHAT tags could be downloaded at these relocation sites. To compare mean internal body temperature (1 h intervals) with time of day, 30 min sampling intervals were averaged. An analysis of variance was used to test for differences in mean internal body temperature with time of day and to compare swimming depth versus time of day (ANOVA, $\alpha=0.05$).

2.4. Thermal inertia

Thermal inertia, or the measure of a material's response to temperature change, was determined by

calculating the thermal rate coefficient (k) for four captive leopard sharks. This value is important in determining how leopard sharks' metabolism can vary with an increase or decrease in temperature. To determine the thermal inertia of adult leopard sharks, body temperatures were measured for two male and two female sharks by rapidly transferring them between two 7500 L holding tanks of known water temperature. Both the sharks' core body temperatures and the holding tank temperatures were measured using small calibrated temperature data loggers (iBCodZ: Alpha Mach Inc., 44 mm by 12 mm, $-5\text{ }^{\circ}\text{C}$ to $26\text{ }^{\circ}\text{C}\pm 0.05\text{ }^{\circ}\text{C}$). Sedated sharks were force fed wax coated temperature data loggers by gently inserting a lubricated 3 cm diameter PVC tube through the mouth into the stomach. The small temperature data logger was then inserted into the stomach of the shark through the PVC tube and the tube was removed (Papastamatiou and Lowe 2004). Each shark was measured and weighed immediately following the data logger insertion and was placed in a 7500 L holding tank of known temperature ($16\text{ }^{\circ}\text{C}\pm 0.5\text{ }^{\circ}\text{C}$). The shark was left to adjust to this water temperature for 2 h, and then was rapidly transferred to a neighboring holding tank $3\text{ }^{\circ}\text{C}\pm 0.5\text{ }^{\circ}\text{C}$ warmer ($19\text{ }^{\circ}\text{C}\pm 0.5\text{ }^{\circ}\text{C}$) than the original holding tank for an additional 2 h. After which each shark was then rapidly transferred back to the original tank (cooler water) for another 2 h period. Activity was observed throughout the temperature trials to determine the percentage of time that the shark was swimming or resting on the bottom of the tank. The water chemistry of each holding tank was kept as constant as possible to ensure that the only change the sharks were experiencing was a temperature change. Once the temperature trial was complete, the temperature data logger was removed using the same method as for insertion and sharks were returned to their display tank and monitored for a minimum of 30 min.

The thermal rate coefficient (k) was calculated for each individual shark when transferred from colder to warmer water and also in the reverse direction using the exponential equation:

$$T_{\text{stomach}} = T_{(t=0)} + e^{k(t)}$$

where T_{stomach} is the shark's core body temperature ($^{\circ}\text{C}$) at given time, $T_{(t=0)}$ is the original temperature of the shark's body ($^{\circ}\text{C}$) at time 0, k is the thermal rate coefficient ($^{\circ}\text{C min}^{-1}$), and t is time (min). Captive sharks' lengths and weights were compared to the expected weights for wild sharks of the same lengths using the equations of Ackerman (1971) derived for male and female leopard sharks of Elkhorn Slough,

California. The thermal rate coefficients were calculated for each shark of known mass.

2.5. Site fidelity and passive tracking

To determine the periodicity of occurrence and fidelity of adult female leopard sharks to the warm shallow embayments and adjacent areas of Santa Catalina Island, an additional ten sharks collected in BFC were surgically fitted with coded acoustic transmitters (Vemco model V13-1L-R256, 13 mm by 36 mm, frequency 69 kHz). These sharks were collected and tagged concurrently with the sharks outfitted with CHAT tags.

Sharks fitted with coded transmitters were passively tracked via an array of 14 automated omnidirectional underwater acoustic receivers (Vemco model VR1) placed throughout BFC, several deeper water sites adjacent to BFC, Howland's Landing, and Empire Landing aggregation sites (Fig. 1, inset B). All VR1 receivers were affixed via cables to sand screws anchored in the seafloor and receivers were placed at approximately 10 m depth. Estimated acoustic range of each receiver was approximately 150 m radius. When a tag was in range of a VR1 receiver, the date, time and identification number of the shark was recorded. The Pier, Shark Cove (SC), Empire Landing (EL), and Howlands Landing (HL) VR1 receivers were in known aggregation sites of leopard sharks. Due to the shallow

nature of these areas each monitor was set in less than 10 m of water. The Chalk Cliffs (CC) receiver had an overlapping range with the Pier receiver, but the majority of its detection range was in water greater than 10 m depth and it did not detect sharks in the shallowest areas of BFC. Campground (CG), Two Harbors (2H), and Pumpnickel (PN) receivers had detection ranges that included shallow water sites but were not known aggregation sites for leopard sharks. The remaining receivers, East Wall (EW), Bird Rock (BR), Intake Pipes (IP), 3 Caves (3C), Isthmus Reef (IR), and Blue Caverns (BC), were all mounted to sand screws set in water deeper than 30 m and along areas with steep rock walls.

The numbers of detections at each VR1 receiver were recorded to determine day/night periodicity, daily fidelity to a particular area, and seasonal fidelity to BFC (Pier and SC), EL, and HL. Detections are expressed as detections per functional day to control for periods when there was no receiver coverage for a particular area. Normalized data from these receivers were divided into 0600–1800 h (daytime) and 1800–0600 h (nighttime) sampling periods over all seasons. To determine the day/night periodicity of sharks to shallow embayment areas a χ^2 Goodness of Fit test was performed to determine if sharks utilized the embayments more during the day than at night. The percentages of detections per month for Pier, CC, and HL receivers were calculated to determine daily and seasonal fidelity to these shallow areas, and the numbers of sharks

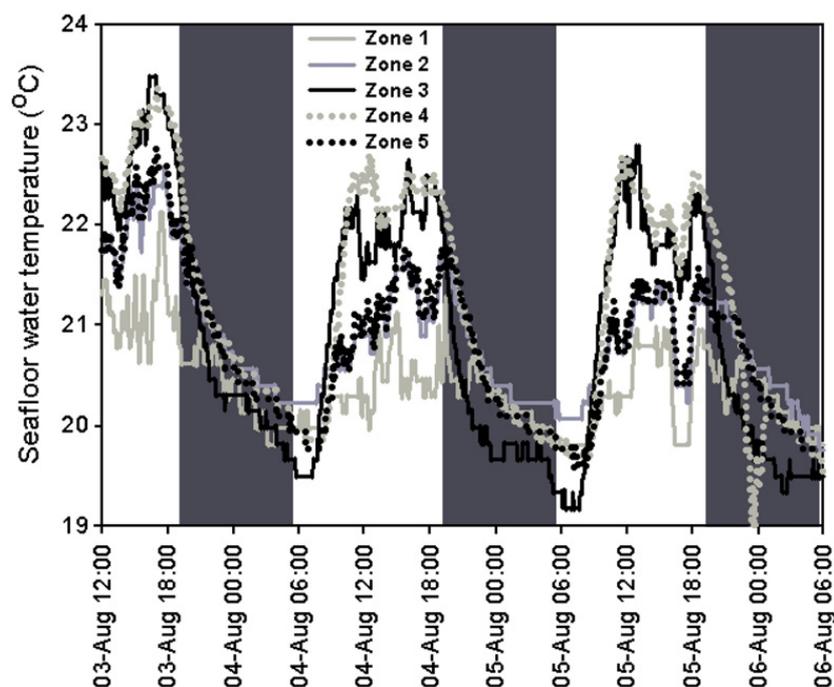


Fig. 2. Seafloor water temperatures within each of the five sampling zones in Shark Cove over three consecutive days in August 2003. Dark gray bars represent nighttime periods from dusk until dawn.

contributing to these percentages were recorded to determine the degree of fidelity of individuals to these sites. Two known aggregation sites, Pier and HL, with the most consistent receiver coverage, were evaluated to determine seasonality. The mean number of total detections at each aggregation site was compared by season.

3. Results

3.1. Behavioral observations

During late July and August of 2003, sharks were counted in Shark Cove (SC) three times a day for 34 days at random time intervals between the hours of 0600 h and 2000 h ($n=102$ observations). The maximum number of sharks observed frequenting the shallows of SC across all zones was 36 sharks (22 ± 8 ; mean \pm SD). Seafloor water temperatures in all sampling zones of SC ranged from 17.8 °C to 25.8 °C (mean= 21.8 ± 1.2 °C) with little hourly variation within each zone. Daytime temperature increased as the day progressed, with the shallowest parts of the embayment being up to 1.5 °C warmer than the deeper sampling zones (Fig. 2). Ambient water temperatures peaked between 1400 h and 1700 h each day, then cooled in the evening ($n=37$, $r^2=0.61$, $p<0.05$, Fig. 3). The number

of sharks in SC followed a similar trend, increasing during the day and then decreasing after 1500 h ($n=37$, $r^2=0.69$, $p<0.05$, Fig. 3). In addition, significantly more sharks were found in the warmest zone of SC throughout the day (ranked correlation: $n=191$, $r=0.83$, $p<0.05$).

3.2. Monitoring internal body temperature

Five mature female leopard sharks were tagged in the SC area of Big Fisherman's Cove (BFC). The tagged sharks ranged in size from 145 cm to 157 cm (mean= 153 ± 5 cm). Core body temperature and depth data were acquired for two of the five sharks carrying CHAT tags. Shark # 511 yielded 11 consecutive days of data from 12 June to 22 June 2004, and shark # 575 yielded ten consecutive days of data from 12 June to 21 June 2004. Body temperatures of shark # 511 ranged from 18.0 °C to 25.9 °C ($n=461$, mean= 19.5 ± 0.98 °C). This shark reached a maximum depth of 27.6 m once and the minimum depth recorded was 0 m, with a mean depth of 1.9 ± 0.07 m. Shark # 575's core body temperature ranged from 18.0 °C to 21.8 °C ($n=545$, mean= 19.3 ± 0.67 °C) and this shark reached a maximum depth of 18.1 m and a minimum depth of <1 m, with a mean depth of 1.5 ± 1.1 m.

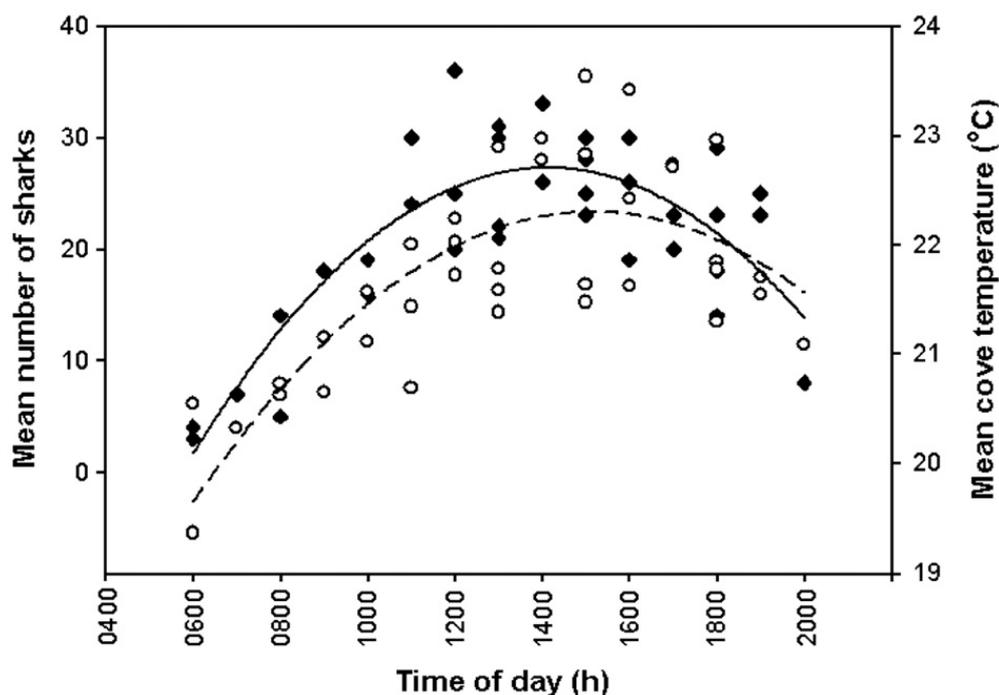


Fig. 3. The relationship between the mean number of leopard sharks ($n=36$, mean= 21.5 ± 18.7) in Shark Cove and the mean seafloor water temperature in the cove (mean= 21.8 ± 1.2) by time of day. Black diamonds represent mean number of sharks and open circles represent the mean seafloor cove water temperatures. Solid line represents the best fit curve for mean number of sharks and dashed line represents the best fit curve for mean seafloor cove water temperature.

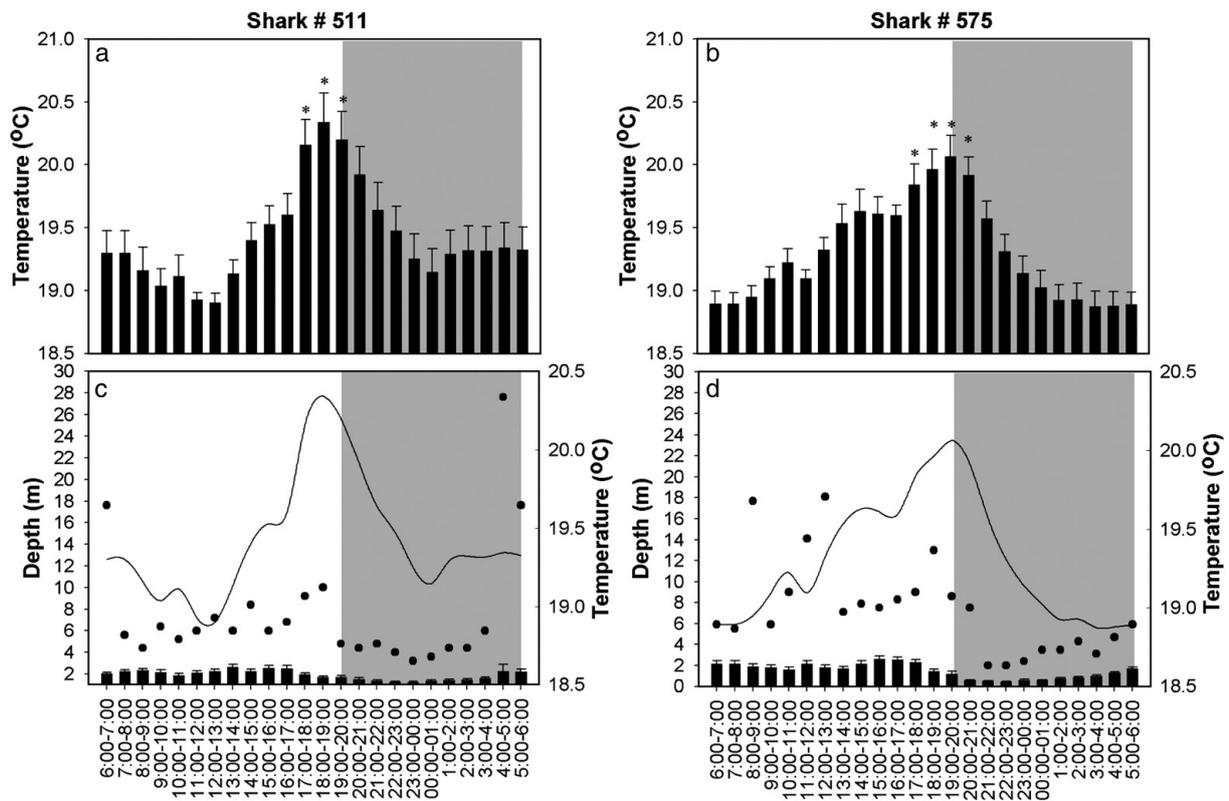


Fig. 4. a. Shark # 511—mean (\pm SD) core body temperature ($^{\circ}$ C) in 1 h intervals over 11 consecutive days. b. Shark # 575 mean (\pm SD) core body temperature ($^{\circ}$ C) in 1 h intervals for 10 consecutive days. Asterisks represent time periods of significantly higher body temperatures. c. Depth (m) and core body temperature ($^{\circ}$ C) profile for shark # 511. d. Depth and temperature profile for shark # 575. Black bars represent mean (\pm SD) depth of sharks, black dots represent maximum depths recorded during those time periods, and the black line represents the sharks' mean core body temperature ($^{\circ}$ C). Gray background represent nighttime period from dusk until dawn.

Shark # 511 exhibited significantly higher core body temperature from 1700 h to 1900 h than any other times of day (ANOVA: $p < 0.05$, $f = 4.05$, $df = 23$, Fig. 4a). The same trend was also observed for shark # 575, except this shark showed significantly higher body temperature from 1700 h to 2000 h (ANOVA: $p < 0.05$, $f = 9.62$, $df = 23$, Fig. 4b). Depth profiles for both sharks, although expected to have a reciprocal trend to temperature, did not show a significant change in depth throughout the day. Sharks did occasionally make deeper dives; however, there was no apparent diel pattern to changes in swimming depth (Fig. 4c and d).

3.3. Thermal inertia

Core body temperatures of two male leopard sharks (weights: 12.7 kg and 7.7 kg; TL: 147 cm and 123 cm) and two female (weights: 18.2 kg and 17.3 kg; TL: 165 cm and 160 cm) leopard sharks were monitored in relation to ambient water temperature changes. The mass/length ratios for these four sharks were not significantly different from wild caught leopard sharks of comparable length.

All four sharks took approximately 60 min to change body core temperature by 3 °C. The mean (\pm SD)

thermal rate coefficient (k) for all sharks during the descending temperatures was 0.0054 ± 0.001 °C min⁻¹ and 0.0051 ± 0.0006 °C min⁻¹ for the ascending temperature. There was no significant difference in the thermal rate coefficient (k) when the sharks were transferred from cold to warm compared to when they were transferred from warm to cold water. Both male sharks spent 80–90% of their time swimming, while females spent only 25–30% of their time swimming during the temperature trial.

3.4. Site fidelity

Ten adult female leopard sharks were captured, tagged, and passively tracked using 14 VR1 acoustic receivers located throughout BFC and at Howlands Landing (HL) and Empire Landing (EL) from 6 June 2004 to 6 June 2005. All captured and tagged sharks were mature females ranging in size from 132 cm to 190 cm (mean: 148.7 ± 16.3 cm; Table 1). All 10 sharks were detected over the 1-year sampling period, except for shark # 221, which was detected only sporadically during the first few months of the study. Although continuous monitoring at all 14 locations was attempted, most of the VR1 receivers were functional year round

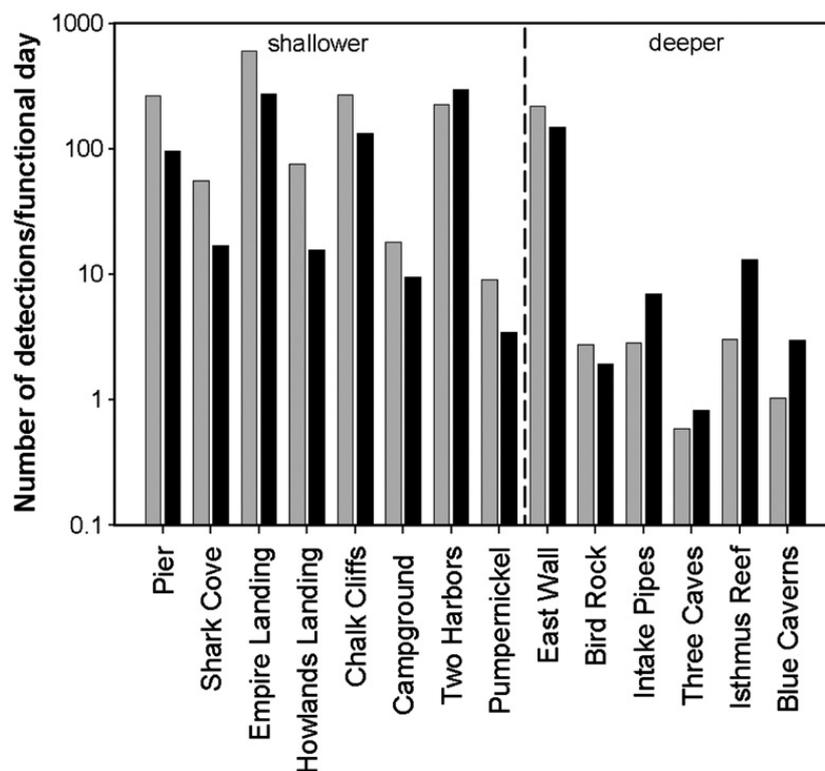


Fig. 5. Number of detections per functional day at each location for all leopard sharks fitted with coded acoustic transmitters. Gray bars represent daytime detections between the 0600 and 1800 h and black bars represent nighttime detections between 1801 and 0559 h. Locations to the left of the dashed line are receivers positioned in shallow areas and locations to the right of the dashed line represent receivers in deeper water.

except for a 1-month gap in December 2004. The Pier receiver and HL receiver had the most continuous coverage of shallow sites.

Acoustic detections at the shallow aggregation site, such as Pier, SC, and HL, occurred during daytime periods but the sharks tended to disperse away from these areas at night (Fig. 5). There was a significantly greater proportion of acoustic detections of tagged sharks during daytime periods at shallow sites than at night ($p < 0.05$, $\chi^2 = 7906$, $df = 9$). Due to the topography of HL, the receiver range is confined to the shallow depths and could not detect tagged sharks when they left the shallow embayment area. Of the ten sharks fitted with coded acoustic transmitters, three sharks showed a distinct diurnal pattern of use at the HL site. A representative of this pattern can be seen in detection records for Shark # 227 (Fig. 6), where 93% of all detections for this individual at HL were between 0600 h and 1800 h. There was no difference in the proportion of detections of tagged sharks during the day and night by VR1 receivers located in deeper water.

Movements between locations (loss of detections) occurred primarily during nighttime periods. Sharks passively tracked at HL were found to leave this site after 1900 h and were detected the follow morning at another site. In addition, observational data from SC indicated a reduction in the number of sharks in the cove after 1500 h. All ten sharks were detected at the other acoustically monitored aggregation sites (HL and EL) after tagging at BFC, and were often detected at these locations for more than four weeks at a time.

Aggregations of sharks (>25 individuals) were observed in BFC only during the summer months. The Pier receiver and the CC receiver had some overlap in acoustic detection range. The Pier receiver detection range encompassed the NW facing beach of BFC, while the CC receiver only detected sharks in water that was greater than 10 m deep (Fig. 1). Both receivers had a similar number of total detections (>120,000 detections), but the Pier receiver had the greatest proportion of detections from April to June 2005, whereas detections were more evenly distributed over seasons at the CC monitor. Although tagged sharks were detected by Pier and CC receivers year round, monthly detection patterns indicate that sharks were primarily utilizing the warmer shallow waters of BFC in the summer months (Fig. 7). Of the 10 sharks fitted with coded transmitters from BFC, only five were found to return to BFC the following summer.

Although VR1 receivers were placed only at known aggregation sites on the north side of Santa Catalina Island, two sharks have been detected along the mainland coast south of the Santa Catalina Island. Detailed searches for all tagged sharks (CHAT tags, standard transmitters, and coded transmitters) were conducted during all seasons along the entire north coast of Santa Catalina Island (>65 km), along with occasional searches along the south coast, yielding relocations of only six individuals out of 16 sharks tagged over the course of the study period. Shark # 222 tagged May 2004 was detected at BFC and EL until 30 March 2005. Seven days later on 6 April 2005 this

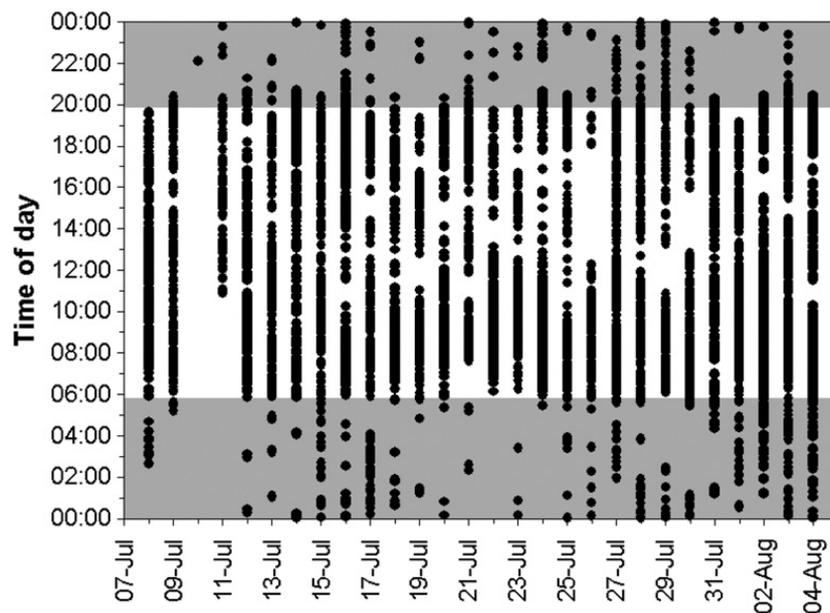


Fig. 6. Time of detections for Shark # 227 at Howlands Landing from 8 July to 4 August 2004. Gray background represents nighttime period from dusk until dawn.

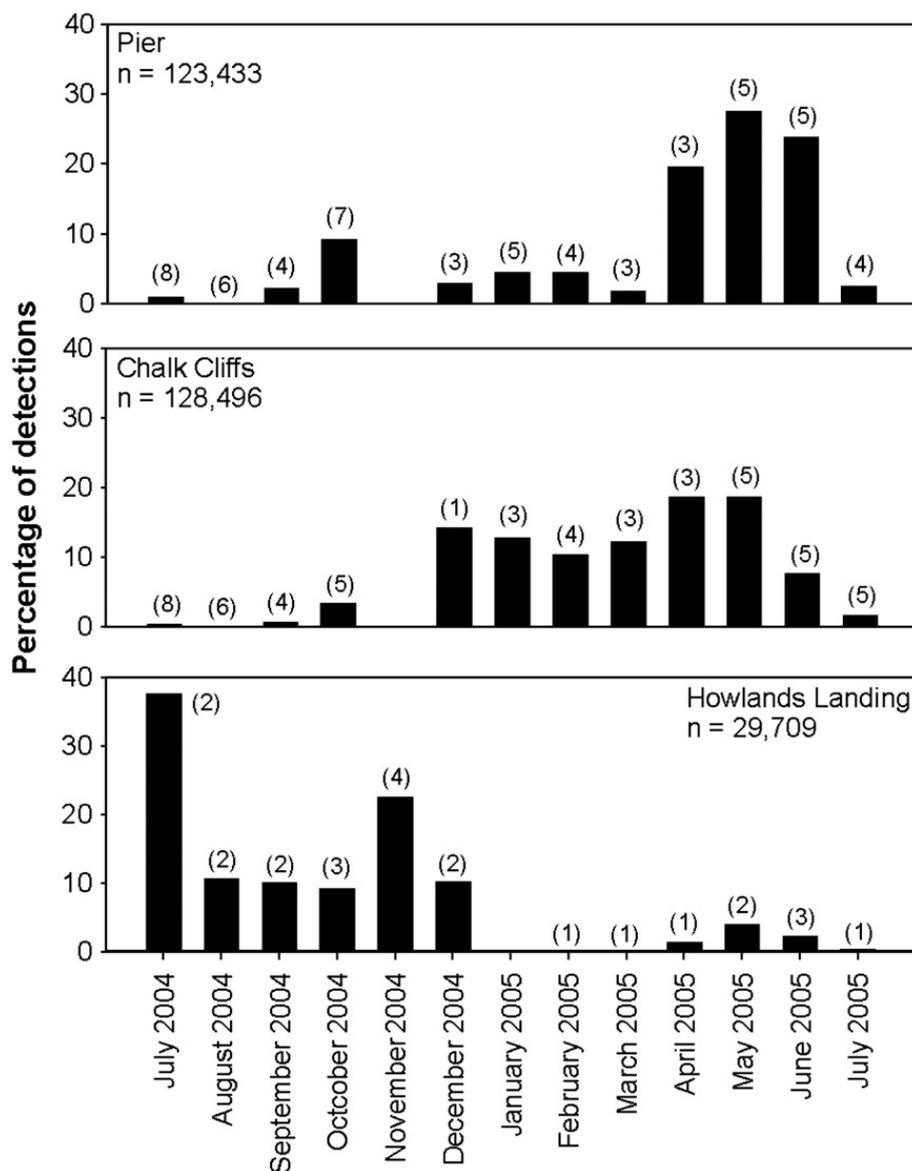


Fig. 7. Percentage of total annual detections for Pier, Chalk Cliffs (CC), and Howland's Landing (HL) acoustic receivers. *N* represents the total number of annual detections at each location and the number in parentheses at the top of each bar represents the number of sharks detected that month. The Pier and CC monitors were not functional in November and the HL receiver was not functional in January.

individual was detected 105 km away along the mainland coast at Carlsbad, California (33° 09' N, 117° 20' W) at another passive receiver array maintained by Hubbs-SeaWorld San Diego. This shark was detected at Carlsbad for three consecutive days and then was detected back at Santa Catalina Island 27 days later, where it was most frequently detected at EL. Shark # 227 tagged June 2004 was detected on Santa Catalina Island until the end of the study period in 2006. This shark was detected along the mainland coast in Anaheim Bay (33° 44' N, 118° 03' W), by a passive receiver array maintained by the CSULB Shark Lab at California State University, Long Beach, from 20 March to 22 March 2007.

4. Discussion

An increase in core body temperature of ectothermic organisms can benefit animals physiologically by increasing muscle performance, digestive rate, metabolic rate, and gestation rates (e.g., Carey and Scharold 1990; Economidis and Lobel 1998; Matern et al., 2000). Two of the five CHAT tagged adult female leopard sharks found aggregating in warm, shallow areas of Big Fisherman's Cove (BFC) showed significantly warmer core body temperatures during the day, while in shallow water, than at night. As a result these sharks increased their core body temperature by an average of 1 °C, for 3–4 h each afternoon. Miklos et al. (2003) found that leopard sharks

exhibit a Q_{10} of 2.51 over a temperature range of 12–24 °C. Therefore, a 1 °C increase in core body temperature for 4 h would result in an 8% increase in metabolic rate during that period. Because water temperature in Shark Cove (SC) was found to change up to 3 °C over the course of a day, it is likely that the sharks using this area of BFC would have increased their body temperature by up to 3 °C, which would result in a 17% increase in metabolic rate.

The daily increase in the sharks' internal body temperatures followed the cyclic daily increase in ambient water temperature in shallow areas; however, because of their mass it may take individuals more than 1 h for body temperature to match that of ambient water temperature. Laboratory experiments of thermal inertia indicated that adult leopard sharks (10–18 kg) had thermal rate coefficients ranging from 0.0044 to 0.0068 °C min⁻¹. The speed of the sharks' core body temperature change from warmer to colder and vice versa was similar, which is not the pattern observed in other ectothermic species such as the blue shark and swordfish (*Xiphias gladius*), where muscle warms more quickly than it cools due to changes in blood flow rates (Carey and Gibson 1987, Brill et al., 1994). This lack of pattern observed in leopard sharks may be attributed to their metabolic heat production being too low to make a measurable contribution in the warming of their tissues.

Because of their thermal inertia, leopard sharks can make short excursions below the upper mixed layer of water and not experience a marked change in internal body temperature. Previous research found that leopard sharks leave BFC at night, showing increased movement, possibly to forage in deeper water (Manley 1995). Both increased activity and distance traveled was observed at night via manual acoustic tracking; however, CHAT tagged sharks were generally found in the upper 3 m of the water column, and were closest to the surface during the evening hours (2000 h to 0100 h). Although these sharks spent a majority of their time in <3 m of water, they were also observed to make occasional deeper dives (27 m). This pattern of shallow water usage suggests that sharks rarely leave the upper mixed layer of water during the day or night, and that daytime warming of a shark's body is most likely due to solar warming of the water in calm shallow areas.

If leopard sharks do gain some energetic advantage from diurnal warming of core body temperature, then they may be expected to seek the warmest areas and follow these warm cells of water over the course of the day. Leopard sharks in the SC area of BFC were observed in the highest numbers in the warmest waters of the cove during summer months. Although SC is relatively small (2450 m²) compared to BFC

(60,000 m²), observations of leopard sharks in the SC indicate that they have the ability to detect and follow fine-scale changes in water temperature in the cove over the course of the day. Sharks were observed laying on the seafloor at the entrance of the cove during morning hours, when water temperature in each zone of the cove was not significantly different. Sharks penetrated further into the shallower portions of the cove over the course of the day and darkened in skin color. By late afternoon, most sharks were aggregated in the northeast corner of the cove, which receives direct afternoon sunlight. This behavior of selectively occupying the warmest water has also been documented in other ectothermic vertebrates. For instance, tadpoles aggregate in the warmest area of a pond, achieving higher body temperatures and in turn increased metabolic rates resulting in early metamorphosis (Brattstrom 1962). In addition, tadpoles were found to disperse from aggregations when water temperatures decreased. The same behaviors have been observed for leopard sharks in SC, where by late afternoon and early evening, sharks begin to leave the cove. Because water temperature cools faster in the shallowest portions of the cove, the sharks' departure may be because of the reduction in thermal benefit.

Visual observations of leopard sharks were limited to daytime periods during summer months. Therefore, it could not be determined how often sharks utilize SC and whether they exhibited daily and seasonal fidelity to SC and other aggregation sites. Active and passive acoustic tracking of these sharks over a 1-year period revealed a more complex pattern of diurnal usage of shallow embayments and of seasonal presence. As hypothesized and inferred from observational data, sharks showed diurnal fidelity to BFC, and a similar pattern was observed at other known aggregation sites. Like many elasmobranchs, leopard sharks have an increased rate of movement at night and also travel great distances at night, often arriving at a different aggregation site the following morning (Klimely and Nelson 1984; Holland et al., 1993). Sharks were detected at all monitors year round, but more often at shallow water sites (known aggregation sites) during the summer and early fall. This is consistent with visual observations from SC, and corresponds with seasonal peaks in water temperature.

Previous visual observation and active acoustic tracking data (Manley 1995) of leopard sharks in BFC, suggested that the same individuals were using the cove daily throughout the summer, and therefore, it was hypothesized that the same individuals were returning each summer. All leopard sharks caught and tagged from SC were detected at two other known aggregation sites along the north coast of Santa Catalina

Island. In addition, sharks tagged in SC were not found to return daily. Although it is possible that sharks did not resume their daily use of SC because of trauma resulting from the tagging event, CHAT tag data suggest that sharks continued their thermoregulating behavior within a day following tagging, but at locations other than SC. In addition, numerous studies have shown that fishes behaviorally recover within hours after the tagging event (e.g., Holland et al., 1999; Starr et al., 2000; Lowe and Bray 2006). Even if sharks were traumatized as a result of the tagging, some individuals may not return to the cove for the rest of the season. However, it is unlikely that this would influence sharks from returning to SC the following season. Of the ten sharks originally fitted with coded tags, only five returned to BFC the following year, suggesting that annual aggregations are not composed of specific individuals. This finding could explain the variation in number of individuals at aggregation sites each year. This suggests that leopard sharks do not show any specific site fidelity to a particular thermal refuge.

Leopard sharks were found to travel at least 7 km between known aggregation sites over a single night; however, it is likely that there are more thermal refuges other than those monitored during this study. Acoustic searches for tagged sharks were conducted from the east to west ends of Santa Catalina Island (>65 km) during each season and only six of the 16 sharks were relocated. Most of these sharks were relocated at either HL or EL. The leopard sharks may be circumnavigating the island or leaving the island. Two of the sharks tagged at BFC with coded transmitters were detected at mainland locations in the spring, indicating movements across open water in excess of 100 km. Because of the timing of these large-scale movements, it is possible the sharks are migrating to pup or mate. Both mainland locations where sharks were detected are known mating sites for leopard sharks and leopard shark neonates are often caught along the shoreline or within estuaries in southern California (Smith 2004).

Although behavioral observations and direct measurements of body temperature relative to water temperature indicate that adult female leopard sharks are increasing their core body temperature by moving into warmer areas, it is unclear why only mature females exhibit this behavior. Visual observations and tagging data confirm that aggregations are composed solely of sexually mature sized females. Sexual segregation is common in elasmobranchs, in which females are typically found at shallower depths than males (Klimely 1987; Wetherbee et al., 1997). Sexual segregation is thought to be related to mate avoidance, where females

may seek refuge from more aggressive males (Economakis and Lobel 1998; Sims et al., 2001). Economakis and Lobel (1998) observed large female gray reef sharks aggregating in the shallow waters of Sand Island, Johnston Atoll. These shallow water aggregations were thought to provide refuge for pregnant females from aggressive males. Female leopard sharks may be using these shallow areas as refuges from males; however, aggressive interactions have rarely been observed in this species (Smith 1984). In addition, females may actually be more susceptible to predation using these shallow areas such as SC. In the summer 2001, a male California sea lion (*Zalophus californianus*) killed 12 adult leopard sharks in SC by chasing sharks up onto the beach while they were in the shallows (S. Anderson, pers. comm.; C. Lowe pers. obs.).

As long as food is readily available, an increase in core body temperature could slightly increase metabolic rate, in turn increasing the rate of digestion, assimilation of food, and somatic growth rates. Economakis and Lobel (1998) also hypothesized that adult female gray reef sharks may be using the warm shallow waters at Johnston Atoll to increase their somatic growth rate. Ebert and Ebert (2005) found that female leopard sharks of larger size were more fecund regardless of age. Because female leopards are known to grow larger than males (Kusher et al., 1992), it is possible that adult female leopard sharks aggregate in warmer water to increase their growth. However, this does not explain why juvenile or subadult females are not observed in these aggregations.

Therefore, it is most likely that this increase in core body temperature serves some reproductive function that is of greater advantage to females than males. Female sharks may aggregate in warmer waters to increase the rate of embryonic development (Taylor 1993). In laboratory studies, dogfish embryos develop almost twice as fast in 4 °C warmer water (Harris 1952). Wallman and Bennett (2006) found that 1 °C increase in water temperature could decrease gestation period of pregnant Atlantic stingrays (*Dasyatis sabina*) by as much as two weeks. Mating in leopard sharks occurs in early summer after parturition, with pregnant females in gestation for ten months (Smith 1984). Leopard shark aggregations peak in number in August, which might mean that females are in early stages of gestation. Unfortunately, it is unknown whether the females within these aggregations are gestating during this period. Future studies confirming female reproductive state are needed to support this hypothesis.

Studies on leopard sharks have shown that they are wide ranging and may travel 100s of km (Smith and

Abramson, 1990; Smith 2001). Typically, these types of movement patterns reduce the probability of over harvesting because animals are more dispersed. However, because of the behavioral affinity that adult female leopard sharks exhibit for warm, shallow water sites and the large numbers of sharks within these aggregations, they become particularly vulnerable to over fishing while in these areas. Therefore, it may be prudent to establish marine protected areas that incorporate shallow water aggregation sites that leopard sharks utilize.

Acknowledgements

We would like to thank the Wrigley Marine Science Center and the Long Beach Aquarium of the Pacific for the use of their facilities and the support from their staff especially K.A. Miller, D. Smith, G. Smith, L. Garske, M. Iacchie, L. Adams, and P. Hampton. Thanks also to K. Goldman, H. Dewar and K. Young for the support and sage advice. We thank the numerous graduate and undergraduate volunteers for their many hours diving and searching for sharks, particularly, M. Blasius, L. Hale, J. Vaudo, L. Bellquist, J. May, and J. King. We thank K. Holland of Univ. of Hawaii for the use of his VR-20 acoustic CHAT tag receiver. Funding for this study was provided by USC Sea Grant, PADI project AWARE, Blue Planet Foundation, the Boeing-CNSM Graduate Fellowship, SCTC Marine Biology Education Foundation, the CSULB Richard B. Loomis Award, and the Southern California Academy of Sciences. [SS]

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