

Homeothermy in adult salmon sharks, *Lamna ditropis*

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Synopsis

Salmon sharks, *Lamna ditropis*, belong to a small group of sharks that possess vascular counter-current heat exchangers (*retia mirabilia*) allowing retention of metabolically generated heat, resulting in elevated body temperatures. The capacity of free-swimming lamnid sharks to regulate rates of heat gain and loss has not been demonstrated. Using acoustic telemetry, we recorded swimming depth and stomach temperature from four free-swimming salmon sharks in Prince William Sound, Alaska. Temperature data were obtained over time periods ranging from 3.8 to 20.7 h. Temperature profiles of the water column were obtained concurrently for use as estimates of ambient temperature. Mean stomach temperature among four individuals tracked ranged from 25.0 to 25.7°C. These sharks defended specific elevated temperatures regardless of changes in ambient temperature, which ranged from about 5–16°C. The maximum observed elevation of stomach temperature over ambient was 21.2°C. Because stomach temperatures were so strictly maintained relative to changes in ambient temperature, a thermal rate coefficient, k , ($^{\circ}\text{C min}^{-1} \text{ } ^{\circ}\text{C thermal gradient}^{-1}$) for cooling of 0.053 min^{-1} was obtained via a ‘control’ experiment with a dead salmon shark. We show that free-swimming adult salmon sharks maintain a specific stomach temperature independent of changes in ambient temperature through a combination of physical and physiological means, and essentially function as homeotherms. This unique ability is probably the underlying factor in the evolutionary niche expansion of salmon sharks into boreal waters and in their ability to actively pursue and capture highly active prey such as salmon.

Introduction

The salmon shark, *Lamna ditropis* (Family Lamnidae), occurs in the boreal and cool temperate coastal and oceanic waters of the north Pacific Ocean (Strasburg 1958, Blagoderov 1994, Nakano & Nagasawa 1994, Compagno 2001). It is a large apex predator that can reach 260 cm total length (TL) and weigh 220 kg (Tanaka 1980, Goldman 2002, Goldman & Musick 2005).

As with all other lamnids, salmon sharks are known to be endothermic based on their posses-

sion of vascular counter-current heat exchangers (*retia mirabilia*) that allow the retention of heat created by their own oxidative metabolism (Hochachka et al. 1978, Carey et al. 1985, Fudge & Stevens 1996, Bernal et al. 2001a). The first descriptions of *retia* in lamnid sharks were by Eschricht & Müller (1835a, b). Burne (1923) provided a detailed description of the *retia* in the porbeagle shark, *Lamna nasus* (as *Lamna cornubica*). *Retia* in salmon sharks are located in the cranium near the eyes (orbital *retia*), in locomotor musculature (lateral cutaneous *retia*), and viscera

(suprahepatic and kidney *retia*). Temperature probe data (from moribund and recently dead animals) has shown temperature elevations of 15.6°C over sea surface temperature (Smith & Rhodes 1983, Anderson & Goldman 2001).

Due to the inevitable linkage of aerobic heat production and heat loss via the gills and body surface, the steady state body temperature (T_b) of most fishes is virtually identical to ambient water temperature (T_a) (Brill et al. 1994). However, lamnid sharks (Family Lamnidae) and tunas (Family Scombridae, tribe Thunnini) show a convergent evolution in their capacity to conserve metabolic heat thereby maintaining a steady state $T_b > T_a$ (Brill et al. 1994, Bernal et al. 2001a). Perhaps the major (and most intriguing) physiological questions surrounding fishes that have elevated body temperatures are: Are they able to control rates of heat gain and heat loss? If so, to what degree?

Studies with captive juvenile mako sharks, *Isurus oxyrinchus*, and several species of tunas have demonstrated that these fishes regulate rates of heat transfer with the environment (Neill et al. 1976, Dewar et al. 1994, Bernal et al. 2001b). Free-swimming juvenile bigeye, *Thunnus obesus*, and bluefin tunas, *Thunnus thynnus*, have also been shown to possess this ability (Holland et al. 1992, Holland & Sibert 1994, Kitagawa et al. 2001). However, when subjected to changes in T_a , small mako sharks and tunas (even large bluefin) are unable to defend a specific body temperature (Carey & Lawson 1973, Brill et al. 1994, Bernal et al. 2001b, Block et al. 2001). At a given T_a , small mako sharks and tunas all possess an equilibrium body temperature (T_e) that is several degrees above T_a . Rapid changes in T_a result in a shift in T_b , and ultimately a new T_e . Their excess body temperature (T_x , where $T_x = T_e - T_a$) before and after changes in T_a is, however, generally maintained within a fairly narrow range (i.e., T_x is relatively constant with respect to T_a) (Neill & Stevens 1974). While adult bluefin tuna show the least fluctuations of body temperature relative to ambient temperature fluctuations (Carey & Lawson 1973, Stevens et al. 2000), no tuna species has been shown to defend a specific body temperature. Alternatively, data from adult lamnid sharks has shown that their T_x is not constant with respect to T_a , and that body temperatures appear to be

maintained regardless of ambient water temperatures (Carey et al. 1981, Goldman 1997, Lowe & Goldman 2001, Goldman 2002).

Although they possess elevated body temperatures (Carey et al. 1985, Goldman 1997), the capacity of free-swimming lamnid sharks to regulate rates of heat gain and loss has not been demonstrated. This is due to a number of factors including their size, logistical difficulties in studying them, and the serendipity involved in obtaining field data that can serve as a surrogate for a laboratory experiment. We present results from 47.7 h of stomach temperature telemetry data obtained from four free-swimming salmon sharks, and data from a 'control' experiment with a dead salmon shark which was necessary to examine the rate of heat loss. Herein, we provide evidence that adult salmon sharks regulate rates of heat gain and loss in order to defend a specific body temperature, and that this is achieved through a combination of physiological thermoregulation and thermal inertia. We examine the data relative to the physiological ecology of salmon sharks and address the 'homeothermy hypothesis' presented by Lowe & Goldman (2001).

Materials and methods

We obtained stomach temperature data via acoustic telemetry from four free-swimming salmon sharks in Prince William Sound, Alaska, during July 1999 and July and August 2000. Sharks #1 and #4 were tracked in the 'Port Gravina' fjord (60°40.0' N; 146°20.0' W). Sharks #2 and #3 were tracked near Windy Bay on the north side of Hawkins Island (60°34.5' N; 145°59.8' W). We measured length and determined sex at time of capture (shark #1), or by repeated observations of the shark from a small tracking vessel and underwater videos obtained when the transmitter was fed to the individual (shark #2). Based on the high degree of sexual segregation in this species and documented lengths in Alaska waters, it is highly likely that sharks #3 and #4 were also female and approximately 180 cm precaudal length (PCL), the mean PCL of salmon sharks in Alaska (Goldman & Musick 2005).

Acoustic transmitters were manufactured by VEMCO Ltd. (Halifax, Nova Scotia, Canada –

model V22-TP) and by Sonotronics (Tucson AZ – model CHP-87-LT). Transmitters operated at frequencies of 34.0, 42.5 or 50.0 kHz. VEMCO transmitters were ‘multiplexed’ possessing both a thermistor and depth sensor with ranges of 0–30°C and 0–200 m respectively. They had a life of 9–10 days, and a range of approximately 1 km at the study sites (based on manufacturers estimates and a single range test). Sonotronics transmitters possessed thermistors, with a range of 0–30°C. They had a life of approximately 60 days and were audible from about one-half the distance of the VEMCO transmitters.

Manufacturers made initial temperature calibrations on all transmitters. We verified temperature calibrations in a digital readout water bath, using a Fluke K/J 51 thermometer as a backup. These two devices were always within 0.1°C of each other. Transmitter readings were always within 0.2°C of the manufacturer’s calibrations. The accuracy (and precision) of the two VEMCO transmitter calibrations were verified a final time as they were regurgitated after 28.3 and 22.4 h by sharks #2 and #4, respectively. (Water temperature readings at the depth where transmitters settled on the bottom were identical to temperature calibrations made in the lab).

We fed transmitters to sharks by catching them in a purse seine and inserting the transmitter in a herring bait into the stomach via a small PVC tube (shark #1) or by lowering the transmitter in a bait into the water column via rod and reel for a shark to consume (sharks #2, 3, and 4). Sharks #1 and #3 were fed Sonotronics temperature transmitters. Sharks #2 and #4 were fed multiplex (temperature and depth) VEMCO transmitters allowing swimming depth data to be obtained. No swimming depth data were obtained from shark #3.

Immediately upon ingestion of a transmitter, we monitored sharks using a directional hydrophone (Dukane Corporation, St. Charles, Illinois, model N30A5A with an analog to digital converter from Ultrasonic Telemetry Systems, Brea, California, or a VEMCO model VR-10 with VR-60 receiver). We conducted three tracks from small (approximately 3 m) skiffs and one from the Alaska Department of Fish and Game’s (17.7 m) R/V Montague. A member of the tracking crew constantly monitored the acoustic signal, and data values were recorded every 5 min. We tracked each telemetered shark

until the signal was permanently lost or until the transmitter was regurgitated.

Temperature-depth profiles have been shown to provide valid estimates of T_a at swimming depth (Goldman 1997). Profiling the water column with a temperature-depth transmitter prior to, during, and-or after tracks and comparing the profile to the swimming depth of the shark provided estimates of T_a for sharks #2 and #4. Ambient water temperature and swimming depth data were obtained from shark #1 via a National Geographic ‘Critter Cam’ camera attached to its first dorsal fin. The camera came off (prematurely) after 2.4 h after which sea surface temperature (SST) was used for comparison with stomach temperature. We compared T_b for shark #3 to T_a at 25 m, which was obtained from a transmitter regurgitated by shark #2.

In adult lamnid sharks, stomach temperature appears to be an excellent indicator of body core temperature (Carey et al. 1981, Goldman et al. 1996, Goldman 1997). The stomach is not only centrally located within the visceral cavity, but is surrounded by *retia*; lying ventral to the subcutaneous lateral *rete* and dorsal (and slightly posterior) to the suprahepatic *rete*, which make it relatively unsusceptible to changes in ambient water temperature (Goldman et al. 1996, Goldman 1997). Alternatively, a thermistor placed in the musculature anywhere between the body wall and the deepest red muscle would be subject to conductive heat gradients that naturally exist between a warm body core and a cooler body wall. However, the ingestion of seawater while feeding has been shown to cause a temporary reduction in stomach temperature that may significantly affect the statistical analysis of stomach temperature for use as an index of T_b (McCosker 1987, Goldman 1997, Lowe & Goldman 2001). In addition to consuming the baited transmitters, sharks #2 and #3 each fed during the time period tracked. Those temperature data are reported here, but were not used in any calculation or statistical analysis presented. We used paired t-tests to compare T_b with T_a (and estimates of T_a at swimming depth), and we calculated cross-correlations to see if T_a had a lag-time effect on T_b .

Heat loss (or gain) in fishes with counter-current heat exchangers is proportional to the difference between T_e and T_b , not between T_a and T_b , because $T_b > T_a$ (i.e., a T_x is present therefore T_b

will not reach T_a) (Neill & Stevens 1974, Neill et al. 1976, Brill et al. 1994). The equation describing the rate of change in body temperature is:

$$dT_b/dt = k(T_e - T_b) + H_p \quad (1)$$

where dT_b/dt = rate of change of T_b with time, k is the thermal rate coefficient ($^{\circ}\text{C min}^{-1} \text{ } ^{\circ}\text{C thermal gradient}^{-1}$) – an empirically determined descriptor of heat transfer from the body to the environment, and H_p = internal heat production ($^{\circ}\text{C per minute}$). Equation (1) and its solution (Neill et al. 1976, Brill et al. 1994, Bernal et al. 2001b) are appropriate to use for tuna and small mako sharks because changes in T_a result in a new T_e . However, equation (1) is unable to provide realistic estimates of k when a specific body temperature is defended (i.e., because $T_e \cong T_b$ for all observed T_a values), and is therefore inappropriate for our salmon shark data (see results).

On 9 September 2001, we conducted a control experiment to examine the rate of heat loss from the body core of an adult salmon shark (through the body surface) in 5.5°C water, thus allowing estimation of a minimum cooling k (no estimation of a warming k was made). A 187 cm PCL, 157 kg salmon shark (similar to the size of the tracked sharks) was caught hook and line and killed with buffered MS-222. To ensure no heart activity (i.e. no residual heat production), we injected the shark with 50 cc of potassium chloride via a cardiac puncture. We inserted a VEMCO V22-TP acoustic transmitter into the stomach to measure temperature and pressure. We then lowered the shark to a depth of 85 m where ambient temperature was 5.5°C , and monitored T_b for 3.92 h. The equation describing the rate of change in body temperature in the dead shark is:

$$dT_b/dt = -k(T_b - T_e) \quad (2)$$

which when solved yields:

$$T_b(t) - T_b(e) = (T_b(0) - T_b(e)) \cdot e^{(-kt)} \quad (3)$$

where $T_b(t)$ = body temperature at time t , $T_b(e)$ = equilibrium body temperature for the dead shark, which is equal to ambient water temperature (T_a), $T_b(0)$ = initial body temperature (prior to change in T_a), and t = time. While a T_x is initially present for the dead shark, T_b will equilibrate with T_a , so ($T_b(e) = T_a = 5.5^{\circ}\text{C}$).

Results

We obtained a total of 4.03 continuous hours of stomach temperature data from shark #1 on 25 July 1999 (Figure 1a). The track was terminated as the research cruise time ended. Stomach temperature for the entire track ranged from 22.8 to 26.2°C with a mean of 25.2°C . Stomach temperature became stable 35 min after ingesting the transmitter (Figure 1a), and a mean stomach temperature of 25.7°C was subsequently maintained. The maximum difference observed between stomach and ambient temperatures was 21.2°C (Table 1). Ambient water temperature ranged from approximately 5.0 – 15.9°C , and was 12.4°C at the shark's mean swimming depth. Sea surface temperature during the time tracked was 15.0 – 15.9°C .

We obtained temperature data for 19.2 h from shark #2 over a 28.3 h time period on 25 and 26 July 2000 (Figure 1b). The track was terminated due to the regurgitation of the transmitter. Stomach temperature for the entire track ranged from 20.1 to 26.0°C with a mean of 25.0°C . Stomach temperature became stable 56 min after ingesting the transmitter (Figure 1b). After that time, and not including the reduction and subsequent rise in stomach temperature associated with feeding at 20:45 h, the shark maintained a constant body temperature with a mean of 25.1°C . The maximum difference observed between stomach and ambient temperatures was 19.5°C (Table 1). Ambient water temperature ranged from 5.7 to 14.1°C , and was 9.2°C at the shark's mean swimming depth. Sea surface temperature during the time tracked was 13.8 – 14.1°C .

We obtained temperature data for 3.8 continuous hours from shark #3 on 28 July 2000 (Figure 1c). The track was terminated after losing the signal and not relocating it during 2 days of searching. Stomach temperature for the entire track ranged from 20.8 to 25.9°C with a mean of 24.4°C . Stomach temperature became stable 22 min after ingesting the transmitter (Figure 1c). After that time, and not including the reduction and subsequent rise in stomach temperature associated with feeding at 21:00 h, the shark maintained a constant body temperature with a mean of 25.4°C . The maximum difference observed between stomach temperature and ambient

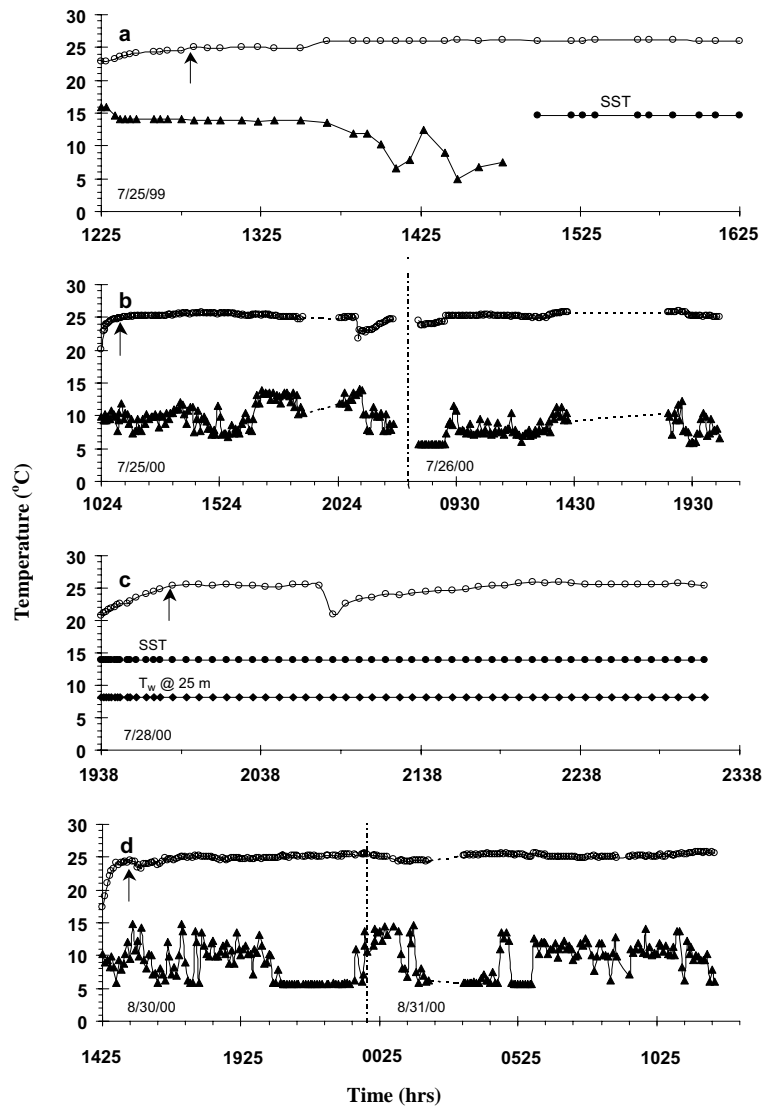


Figure 1. Temperature data for four salmon sharks tracked in Prince William Sound, Alaska. (a) shark #1, (b) shark #2, (c) shark #3, and (d) shark #4. Open circles: stomach temperature; solid circles: sea surface temperature (SST); solid triangles: ambient water temperature (or estimated ambient water temperature via temperature-depth profiles); solid diamonds: water temperature at 25 m. Small vertical arrows indicate the time when stomach temperature became stable. Vertically dashed lines separate days.

temperature at 25 m was 17.8°C (Table 1). Ambient water temperature at 25 m was 8.1°C and SST was 13.9°C.

We obtained temperature data for 20.7 h from shark #4 over a 22.4 h time period on 30 and 31 August 2000 (Figure 1d). The track was terminated due to the regurgitation of the transmitter. Stomach temperature ranged from 17.4 to 25.8°C with a mean of 24.1°C. Stomach temperature be-

came stable 60 min after the transmitter was ingested (Figure 1d), and a mean stomach temperature of 25.0°C was subsequently maintained. The maximum difference observed between stomach and ambient temperatures was 19.7°C (Table 1). Ambient temperature ranged from 5.7 to 14.9°C, and was 9.3°C at the shark's mean swimming depth. Sea surface temperature during the time tracked was 14.8 to 15.1°C.

Table 1. Salmon shark body temperature (T_b) ranges and means (w/standard deviations), ambient water temperature (T_a) ranges and means (in parentheses), and the maximum difference observed (X_d) between T_b and T_a .

Shark #	T_b range	Mean T_b^a	T_a range	X_d	Time tracked(h)
1	22.8–26.2	25.7 ± 0.5	< 5.0–15.9 (12.4)	21.2	4.03
2	20.1–26.0	25.1 ± 0.5	5.7–14.1 (9.2)	19.5	19.2
3	20.8–25.9	25.4 ± 0.4	8.1–13.9 (11.0)	17.8 ^b	3.8
4	17.4–25.8	25.0 ± 0.5	< 5.7–14.9 (9.3)	19.7	20.7

All temperatures are in °C.

^aDoes not include initial rise to stable T_s or decreases and subsequent rise back to stable T_s due to feeding.

^b= T_a at 25 m used in calculations.

Stomach temperature elevations over water temperature for all four sharks were considerable (max. = 21.2°C), and mean stomach temperatures differed among the four individuals by only 0.7°C (Table 1). Body temperature elevations over ambient temperature, estimates of ambient temperature or SST were all statistically significant (paired *t*-tests, all *p* values < 0.0005). Changes in T_a (< 5.0–15.9°C) had no apparent effect on T_b – they were uncorrelated (maximum individual $r^2 = 0.25$), and lag effects from T_a on T_b were not present (maximum cross-correlation value for an individual, $r^2 = 0.39$).

The initial stomach temperature recorded for the control shark (after capture and death) was 20.5°C, which fell to 17.7°C after 3.92 h. The *k* coefficient calculated for cooling (equation (3)) was 0.053 min⁻¹. This value represents an assessment of a minimum *k* when applied to a living shark because we were unable to include heat loss via the gills in a free-swimming salmon shark.

Discussion

All four salmon sharks maintained elevated stomach temperatures within a very narrow range, while measured ambient temperatures ranged from below 5.0 to 15.9°C (Figure 2). Each individual showed an increase in stomach temperature after ingesting a transmitter, and two individuals showed decreases followed by similar increases after either consuming either a bait or a natural prey item during the course of the track (Figures 1b and 1c). These observations are virtually identical to those observed in white sharks and are likely caused by ingestion of small amounts of seawater with either cold bait and/or prey

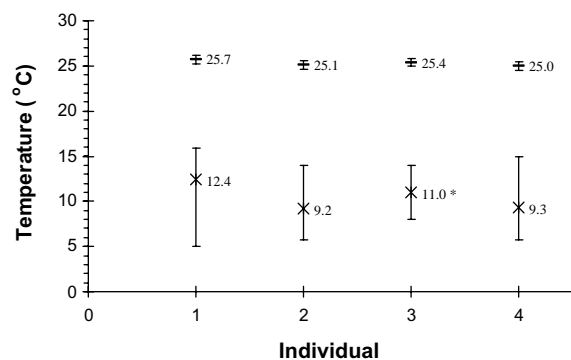


Figure 2. Mean stomach temperature with standard deviation for four salmon sharks tracked in Prince William Sound, Alaska. Mean (* or median) water temperatures and ranges are shown below body temperature data for each individual.

(McCosker 1987, Goldman 1997). Interestingly, white shark stomach temperature becomes fairly stable after 3–6 min, but then takes several hours to reach a stable stomach temperature (Goldman 1997) while salmon shark stomach temperature achieved stability in 22–60 min. This may be due to a number of factors including differences in heat production and conservation ability (e.g. salmon sharks possess a kidney *rete*, white sharks do not), differences in body size between the two species, temperature and volume of the seawater ingested, temperature and mass of the prey ingested or a combination of these factors.

Salmon sharks made regular vertical movements in the water column, sometimes exceeding 140 m. Shark #4 exhibited this behavior in a manner that enabled us to test for the occurrence of physiological thermoregulation. Over 30 min (beginning at 20:05 h – Figure 1d), this shark dove from 9.6 m, where T_a was 13.2°C, to 123.8 m where T_a was ≤ 5.7°C. The shark remained at T_a ≤ 5.7°C (between

56 and 124 m) for 3.3 h during which time no decrease in T_b was observed (Figure 1d). In fact, instead of decreasing in response to the decrease in T_a , T_b actually increased slightly (from 24.8 to 25.5°C, mean of 25.0°C). Stomach temperature from shark #2 when relocated at 08:09 h on 26 July 2000, appears to be correlated with water temperature. However, these data appear similar to the end of other feeding events and could be the result of a feeding event that occurred prior to our relocating the signal, but we cannot be certain. Not knowing the stomach temperature prior to relocating the signal, along with the short duration of the decrease does not allow us to use these data to test for physiological thermoregulation. The data from shark #4 provides a longer time frame for testing thermal ability, and we have stomach temperature data prior to the change in ambient temperature.

In fishes with elevated T_b 's, k , H_p or both may change as a function of T_a (Neill & Stevens 1974, Dewar et al. 1994). While tracking the salmon sharks, we found they maintained constant horizontal swimming speeds during rapid and long duration changes in T_a , indicating that H_p was relatively constant during these periods (i.e., equivalent to metabolic heat production). Since equation (1) does not provide realistic estimates of k when $T_e = T_b$, we used the data from the control shark and from the free-swimming shark's 3.3 h excursion into cold water to assess whether physiological thermoregulation was occurring or whether T_b was maintained solely due to thermal inertia (Neill & Stevens 1974).

It is reasonable to assume that the free-swimming shark's T_b should have decreased (during its 30 min dive and 3.3 h excursion) at a rate similar to the 0.053 min^{-1} exhibited by the control shark under virtually identical changes in ambient temperature, yet it was maintained and actually increased during that time (Figure 3). Therefore, thermal inertia alone could not be responsible for our observations. Our data demonstrate that adult salmon sharks maintain elevated stomach temperatures independent of ambient temperature, and that they possess the ability to regulate heat balance by altering their thermal conductance (whole-body thermal rate coefficient). The degree of their thermoregulatory ability, however, cannot be determined by our experiment. Changes in k that are independent of activity indicate physio-

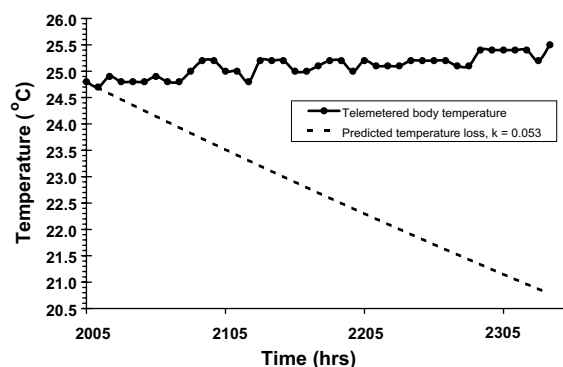


Figure 3. Stomach temperature of shark #4 during 3.3 h excursion into water $\leq 5.7^\circ\text{C}$ (solid circles and line) compared with the predicted temperature loss based on the control shark (dashed line) ($k = 0.053 \text{ min}^{-1}$).

logical thermoregulation (Holland et al. 1992, Dewar et al. 1994), as does the fact that T_x was not constant with respect to T_a (Neill & Stevens 1974).

As with mako and white sharks, salmon sharks can apparently also alter routes of blood flow through vascular shunts (Carey et al. 1981, Bernal et al. 2001a, Goldman et al. unpublished data). This would provide a mechanism for regulating rates of heat gain and loss. A hepatic sinus bypasses the suprahepatic *rete* (at the forefront of the liver). The anatomy of the sinus suggests that it can be opened and closed in the living animal, thereby regulating the amount of heat retained within the system (Carey et al. 1981, Bernal et al. 2001a, Goldman et al. unpublished data). Additionally, cool blood from the dorsal aorta flows around the suprahepatic *rete* into the viscera (Carey et al. 1981).

An animal able to maintain an elevated and uniform body temperature independent of changes in ambient temperature is defined as a homeotherm (Hickman et al. 1984). Telemetered temperature data on free-swimming lamnid sharks led Lowe & Goldman (2001) to hypothesize that adult mako and white sharks may be homeotherms. Our data demonstrate that adult salmon sharks essentially function as homeotherms, in a way analogous to mammals, through a combination of thermal inertia and physiological thermoregulation. The thermal buffer to the environment created by the combination of physical and physiological thermoregulation is probably one of the major underlying factors in the evolutionary

niche expansion of salmon sharks into boreal waters and allows them to range throughout the water column in search of prey.

Circadian cycles of body temperature are an additional feature of homeotherms. Our data do not indicate the presence of a circadian body temperature cycle, which is present in birds and mammals, but more diel tracking data may reveal such a cycle.

Based on temperature measurements, known geographical distribution and a small amount of comparative anatomical data from the viscera and musculature of lamnid sharks, Carey et al. (1985) predicted that salmon sharks should rank atop this endothermic family in their 'ability to maintain an elevated temperature'. Telemetered stomach temperature data from shortfin mako, white, and salmon sharks strongly support this ranking. Whereas white sharks possess a slightly higher mean body temperature than other lamnids, the maximum reported elevation of stomach temperature over ambient water temperature is 8.0°C for shortfin mako sharks (Carey et al. 1981), 14.3°C for white sharks (Goldman 1997), and 21.2°C for salmon sharks (this study).

The data presented here support the homeothermy hypothesis of Lowe & Goldman (2001). However, all of the telemetered T_b 's reported from free-swimming lamnid sharks to date have been obtained from adult specimens. It is important to obtain similar data from across size classes, particularly small individuals, in order to examine possible ontogenetic changes in thermoregulatory ability and changes in thermal inertia, and thereby define the limits of homeothermy in lamnid sharks. The relationship between body size, heat production, and heat loss in these sharks is almost certainly a key component in addressing and answering these questions.

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