

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/226319337>

Regulation of body temperature in the white shark, *Carcharodon carcharias*

Article in *Journal of Comparative Physiology B* · January 1997

DOI: 10.1007/s003600050092

CITATIONS

86

READS

428

1 author:



[Kenneth J. Goldman](#)

Alaska Dept. Fish and Game, Homer, Alaska

44 PUBLICATIONS 1,669 CITATIONS

SEE PROFILE

ORIGINAL PAPER

Kenneth J. Goldman

**Regulation of body temperature in the white shark,
*Carcharodon carcharias***

Accepted: 17 February 1997

Abstract Stomach temperatures of three white sharks, *Carcharodon carcharias*, (one reported previously and two new individuals) were intermittently recorded by acoustic telemetry at the South Farallon Islands, central California. Temperature profiles of the water column were obtained concurrently. Stomach temperatures were elevated over ambient water temperatures by as much as 14.3 °C. Stomach temperatures varied within a narrow range while ambient water temperature fluctuated over a much larger range, showing that this species regulates its body temperature. These data, in combination with previous work on the physiology and anatomy of white sharks, indicate that the white shark is endothermic. It appears that the heat retention system in lamnid sharks has allowed them to inhabit cold water and remain active predators of swift and agile prey.

Key words *Carcharodon carcharias* · South Farallon Islands · Telemetry · Stomach temperature · Thermoregulation · Endothermy

Abbreviations *SFI* South Farallon Islands · *SST* sea surface temperature

Introduction

White sharks, *Carcharodon carcharias*, belong to a very small group of lamnoid sharks (Order Lamniformes)

that possess vascular counter-current heat exchangers (Bone and Chubb 1983; Carey et al. 1981). These allow individuals to retain metabolically-generated heat instead of losing that heat to the ambient water during oxygenation of the blood at the gill lamellae. The masses of parallel arteries and veins making up these retia mirabilia were first described in the related porbeagle shark *Lamna nasus* [as *Lamna cornubica* (Burne 1923); see also Smith and Rhodes (1983)]. They are located in the brain (orbital rete), musculature (subcutaneous lateral rete), and viscera (suprahepatic rete), and function to elevate the shark's body temperature over the ambient water temperature. White sharks have been shown to possess elevated muscle, brain, eye, and stomach temperatures (Carey et al. 1982; Tricas and McCosker 1984; Block and Carey 1985; Carey et al. 1985; McCosker 1987; Wolf et al. 1988; Goldman et al. 1996).

The first stomach temperature data were obtained from a white shark in South Australia by McCosker (1987), who suggested that "further study might be directed toward the hypothesis that *Carcharodon* can control its stomach temperature." A second individual tagged off California in 1991 (Goldman et al. 1996) generated the hypothesis that white sharks maintain an "optimal physiological operating temperature with minimal effects from ambient water temperature." The purpose of this paper is to examine newly obtained stomach temperature data along with all previous temperature and anatomical data in order to test the hypotheses of physiological thermoregulation and endothermy in the white shark. I then briefly discuss the relationship of body temperature to the physiological ecology of this species.

Materials and methods

This paper presents data on stomach temperatures from three free-swimming adult male white sharks at the South Farallon Islands (SFI) (37°42'N, 123°00'W), a small group of rocky islands located 30 km west of San Francisco, California. One shark, an approximately 4.3 m (total length) individual, reported in Goldman et al.

K.J. Goldman¹
Department of Biology,
San Francisco State University,
1600 Holloway Avenue,
San Francisco, CA 94132, USA

Present address:

¹ The College of William and Mary, School of Marine Science,
Virginia Institute of Marine Science,
P.O. Box 1346, Gloucester Point,
VA 23062, USA
e-mail: keng@vims.edu

(1996), was observed in 1991 and is referred to as shark #1. The two additional individuals were observed in 1993. One shark (#2) was approximately 4.9 m total length, and the second shark (#3) was approximately 3.7 m total length. All observations took place at SFI during October–November, when white shark predation on pinnipeds is common (Ainley et al. 1981; Ainley et al. 1985; Klimley et al. 1992; Anderson et al. 1996a). Gender was determined by using underwater videos obtained when the transmitter was fed to the individual or when it was attracted to an unbaited decoy which housed a video camera [see Anderson et al. (1996b) for description of decoy study]. Total lengths of individuals were estimated from repeated observations of the sharks next to the 5.4 m tracking vessel or at a decoy in close proximity to the tracking vessel (K.J. Goldman, S.D. Anderson, P. Pyle, unpublished observation). Stomach temperature data were obtained from acoustic transmitters that were fed to sharks during the course of natural predatory attacks on pinnipeds. All data are diurnal and were gathered intermittently over multi-day periods.

Transmitters were manufactured by VEMCO Ltd. (Halifax, Nova Scotia, Canada – model V4TP-8H) and operated at frequencies of 30.000 and 32.768 kHz. They possessed thermistors and depth sensors with ranges of 0–30 °C and 0–200 m, had a life of 57–91 days, and a maximum range of 1.1 km at SFI (based on range tests conducted in the field). All transmitters were calibrated by the manufacturer; I verified thermistor readings on four separate occasions in a digital readout waterbath, using a Fluke K/J 51 thermometer as a backup. These two devices were always within 0.1 °C of each other. The VEMCO calibrations and my waterbath recalibrations were always within 0.2 °C. One transmitter's calibrations were further verified after it was regurgitated by shark #3 in 1993. Calibrations were unchanged during this biological excursion. It was fed to another white shark (approximately 4.0 m TL female) at the North Neptune Islands (35°14'S, 136°03'E), Spencer Gulf, South Australia on January 29, 1994 (see Results and Discussion).

Each shark at SFI was fed a piece of blubber (3–4 kg) from an elephant seal, *Mirounga angustirostris*, with transmitter attached, that had been placed in the water during a feeding event resulting from a predatory attack. This procedure was followed so the shark would ingest it during the course of its natural predatory and feeding behavior. No attractants (e.g. blood or fish parts) were used to avoid altering the natural behavior of the sharks at SFI.

Immediately upon ingestion of a transmitter, sharks were monitored using a directional hydrophone (Dukane Corporation, St. Charles Illinois, model N3OA5A) from a 5.4-m “Boston Whaler” skiff. Data (acoustic signal) were recorded on audio tape (Panasonic model RQ-L340) and later decoded by playing the tape through an analog to digital converter (Ultrasonic Telemetry Systems, Brea, California). Four data points per minute (at 0, 15, 30, and 45 s) were read, manually by the author, from the converter and entered into a computer spreadsheet.

Temperature-depth profiles of the water column were obtained by lowering another transmitter early during the tracking period and again at the end. They were conducted at the buoy on the south-south-east side of the islands, where sea conditions were sufficiently calm, allowing water temperature to be measured to a depth of 20–25 m. The two profiles never varied by more than 0.1 °C. Sea surface temperature was taken at various times and locations around the islands during tracking sessions, and they never differed from the temperature-depth profile site by more than 0.1 °C. Considering the small differences between water temperature at the surface and at 20–25 m (maximum of 1.5 °C), and the lack of a difference in sea surface temperature around the islands, the profiles provide valid estimates of water temperature at a shark's mean swimming depth [for further description see Goldman et al. (1996)]. Comparing stomach temperature with estimates of water temperature at mean swimming depth gives a more precise representation of the true difference, whereas using sea surface temperature would underestimate it.

During each tracking session the telemetered shark (or sharks) were followed for as long as conditions around the island permitted or until dusk. Weather permitting, attempts were made to relocate the shark the next day. Searches were conducted by checking the area where the animal was last tracked and proceeding around the

island in an inshore/offshore star pattern to maximize the chances of hearing the acoustic signal. These searches covered a radius around the island of approximately 3 km.

Stomach temperatures were compared to estimated water temperatures at a shark's mean swimming depth. On feeding days, stomach temperatures were reduced, presumably because of sea water ingested with food (and/or transmitter and bait). Temperatures for those days are presented but were not used in any calculation or statistical analysis (Tables 1 and 2). Data from the adult male white shark at SFI in 1991 (Goldman et al. 1996) were used with data from the two new individuals to test the thermoregulation hypothesis of Goldman et al. (1996).

Results

Temperature data were successfully obtained from three individual white sharks at SFI, one in 1991 (Goldman et al. 1996), and two in 1993 (new data reported here). Additional data were obtained in 1995 from an individual at the North Neptune Islands, South Australia. This shark, however, was injured and appeared to be in poor condition. Its stomach temperature was lower than would be expected: 2.1 °C above surface water temperature. The data from that shark are not presented here. All individuals from SFI [Goldman et al. (1996) and the two from 1993] were uninjured and apparently in good condition.

A total of 5.5 h of data were obtained from shark #1 (Goldman et al. 1996) on 5 days over the 8-day period of 17–24 October 1991. Stomach temperature for the time periods tracked ranged from 23.4 to 27.6 °C (Table 1). Mean stomach temperatures ranged from 24.6 to 27.3 °C, and the overall mean was 26.6 °C (Table 2). Sea surface temperatures (SST) ranged from 13.3 to 16.4 °C and water temperatures at mean swimming depth ranged from 12.3 to 13.9 °C. Differences between mean stomach temperatures and water temperatures at mean swimming depth ranged from 10.9 to 14.1 °C (Table 2).

A total of 7.3 h of data were obtained from shark #2 on 10 days over the 17-day period of 12–28 October

Table 1 Stomach temperature ranges (T_s) and sea surface temperatures (SST), in °C, from three white sharks at South Farallon Islands

Day no.	Shark #1 ^a		Shark #2		Shark #3	
	T_s Range	SST	T_s Range	SST	T_s Range	SST
1	23.4–25.9 ^b	14.7	23.4–25.2 ^b	15.9	23.8–26.1 ^b	13.8
2	25.8–26.8	14.6	26.0–27.0	15.5	26.2–27.1	13.7
3	25.4–27.4	16.4	25.8–26.9	15.8	25.7–26.7	13.9
4	26.8–27.6	14.4	25.6–26.5	14.4	26.0–27.1	15.8
5	26.2–26.6	13.3	25.5–26.5	14.0	25.8–27.0	15.9
6			25.7–26.6	14.0	25.3–26.3	16.0
7			25.5–26.5	13.9	24.2–25.3 ^b	16.1
8			25.9–26.8	15.8		
9			25.9–26.9	15.9		
10			25.8–26.7	16.0		

^a Data from Goldman et al. 1996

^b Indicates values are low owing to probable ingestion of sea water with prey and/or transmitter and bait at a feeding event

Table 2 Thermal data (in °C) from three white sharks fall of 1991 and 1993 at South Farallon Islands. Daily and overall mean stomach temperatures (T_s) are given along with daily water tem-

peratures at mean swimming depth (T_wD_s) and differences between T_s and T_wD_s (X_d). Standard deviations are given for all mean T_s values. n values of T_s are at four observations per minute

Day no.	Shark #1 ^a				Shark #2				Shark #3			
	n	T_s	T_wD_s	X_d	n	T_s	T_wD_s	X_d	n	T_s	T_wD_s	X_d
1	377	24.6 ± 0.3 ^b	13.7	10.9	140	24.8 ± 0.4 ^b	14.5	10.3	224	25.1 ± 0.4 ^b	13.5	11.6
2	177	26.2 ± 0.2	13.2	13.0	191	26.5 ± 0.2	14.3	12.2	144	26.8 ± 0.2	12.9	13.9
3	448	26.5 ± 0.2	13.8	12.7	196	26.3 ± 0.3	14.9	11.4	180	26.2 ± 0.2	13.0	13.2
4	198	27.3 ± 0.2	13.9	13.4	144	26.1 ± 0.2	12.9	13.2	184	26.5 ± 0.2	14.0	12.5
5	107	26.4 ± 0.1	12.3	14.1	208	25.9 ± 0.2	13.0	12.9	156	26.4 ± 0.2	15.3	11.1
6	—	—	—	—	204	26.2 ± 0.2	13.5	12.7	244	25.9 ± 0.3	15.0	10.9
7	—	—	—	—	192	25.9 ± 0.2	13.0	12.9	130	24.7 ± 0.3 ^b	15.0	9.7
8	—	—	—	—	140	26.4 ± 0.2	14.0	12.4	—	—	—	—
9	—	—	—	—	160	26.4 ± 0.2	15.3	11.1	—	—	—	—
10	—	—	—	—	176	26.3 ± 0.2	15.0	11.2	—	—	—	—
Overall T_s^c	930	26.6 ± 0.5	—	—	1611	26.2 ± 0.2	—	—	908	26.3 ± 0.3	—	—

^a Data from Goldman et al. (1996)

^b Indicates value is low owing to probable ingestion of sea water with prey and/or transmitter and bait at a feeding event (values are not used in statistical analysis)

^c Overall T_s values do not include days where sharks feed

1993. Stomach temperature for the time periods tracked ranged from 23.4 to 26.9 °C (Table 1). Mean stomach temperatures ranged from 24.8 to 26.5 °C, and the overall mean was 26.2 °C (Table 2). Water temperatures at mean swimming depth ranged from 12.9 to 15.3 °C and SST ranged from 13.9 to 16.0 °C. Differences between mean stomach temperatures and water temperatures at mean swimming depth ranged from 10.3 to 13.2 °C (Table 2).

A total of 5.3 h of data were obtained from shark #3 on 7 days over the 9-day period of 21–29 October 1993. Stomach temperature for the time periods tracked ranged from 23.8 to 27.1 °C (Table 1). Mean stomach

temperature ranged from 24.7 to 26.8 °C, and the overall mean was 26.3 °C (Table 2). Water temperatures at mean swimming depth ranged from 12.9 to 15.3 °C and SST ranged from 13.7 to 16.1 °C. Differences between mean stomach temperatures and water temperatures at mean swimming depth ranged from 9.7 to 13.9 °C (Table 2).

The sharks at SFI maintained elevated stomach temperatures within a very narrow range, while water temperatures fluctuated over a wider range. All three showed a small initial increase in stomach temperature after ingesting the transmitter, which became stable within 3–6 min (Fig. 1), and showed stable elevated

Fig. 1 Initial rise and subsequent stabilization of stomach temperature of three white sharks at South Farallon islands after a feeding event. All time periods are in 3-min intervals

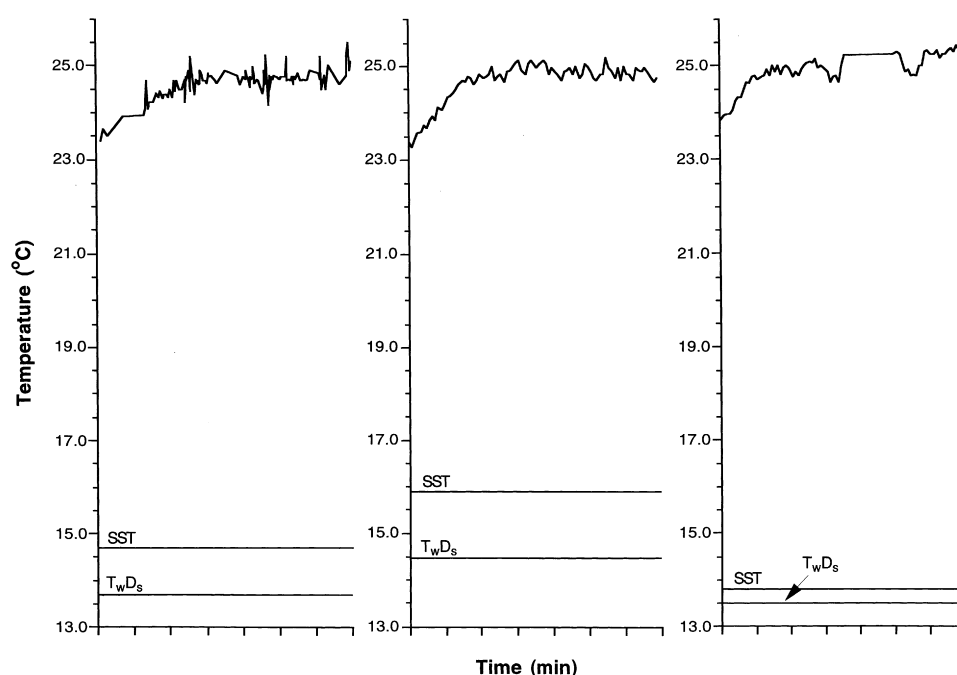
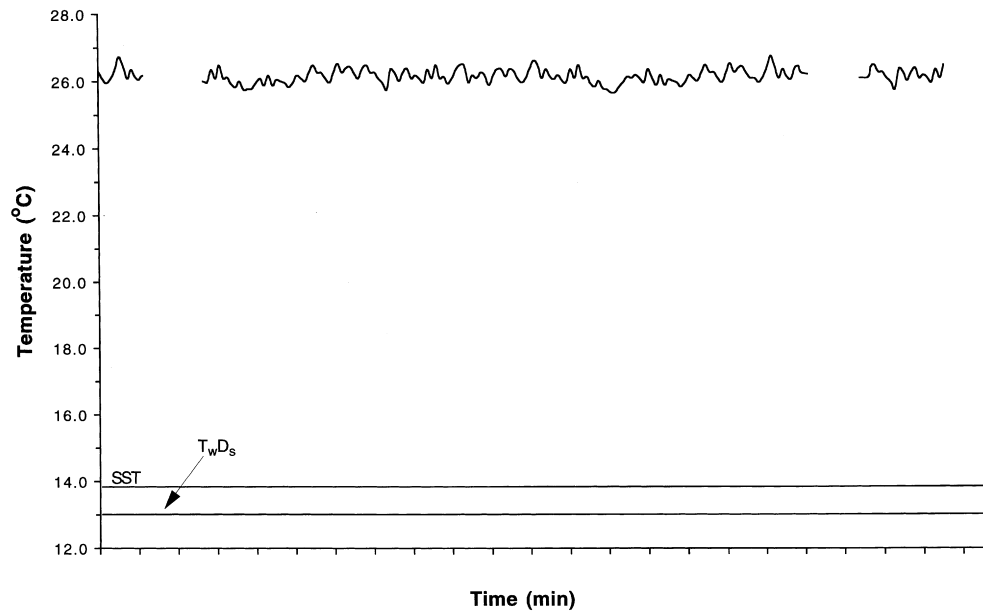


Fig. 2 An example showing maintained elevated stomach temperature (from shark #3, day #3) on a non-feeding day. Mean stomach temperature for this track was 26.2 °C. All time periods are in 3-min intervals

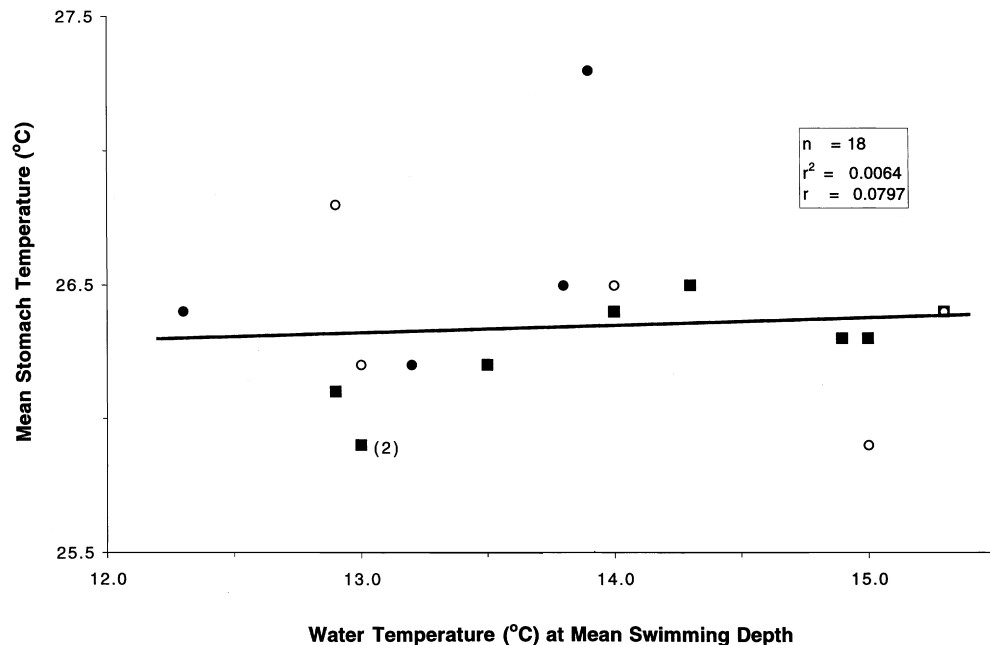


temperatures during each subsequent track (Fig. 2). Not including days on which sharks fed, stomach temperature showed a maximum elevation of 14.3 °C over water temperature at mean swimming depth (13.4 °C over SST), and ranged 2.1 °C. Mean stomach temperatures showed a maximum elevation of 14.1 °C over water temperature at mean swimming depth (13.4 °C over SST), and ranged only 1.4 °C. Water temperature at mean swimming depth ranged 3.0 °C while SST ranged only 3.1 °C (see Tables 2 and 1, respectively). All stomach temperatures were significantly higher (statistically) when compared to both water temperature at

mean swimming depth or SST (*t*-tests; all *P* values < 0.0005). Stomach temperatures of the three individuals were similar (Table 1) and their overall mean stomach temperatures differed by only 0.4 °C, which is not statistically significant (unbalanced, nested ANOVA; *df* = 2, 15; *F* = 2.31; 0.25 < *P* < 0.10) (Table 2).

Changes in water temperature at SFI had no apparent effect on stomach temperature, and virtually all of the observed differences between the two were caused by changes in water temperature and not by changes in stomach temperature. Mean stomach temperatures (per track) were uncorrelated with water temperatures at

Fig. 3 Stomach temperatures (per track) versus water temperatures at mean swimming depth for three white sharks at South Farallon Islands (closed circles = shark #1, closed squares = shark #2, open circles = shark #3)



mean swimming depth (regression ANOVA; $df = 1, 16$; $F = 0.102$; $P = 0.75$) (Fig. 3).

Discussion

Stomach temperatures varied only slightly, both among days and among individuals. The variations may be similar to minor temperature fluctuations observed in other thermoregulating animals, such as bluefin tuna and humans (Carey et al. 1984; Langley et al. 1980; Vander et al. 1990).

Other studies have shown significant (positive) correlations between muscle temperature and ambient water temperature in lamnid sharks (Family Lamnidae). The muscle temperature of shortfin mako sharks (*Isurus oxyrinchus*), porbeagle sharks (*Lamna nasus*), and white sharks has been observed to change in response to changes in ambient water temperature (Carey et al. 1982; Tricas and McCosker 1984; Carey et al. 1985).

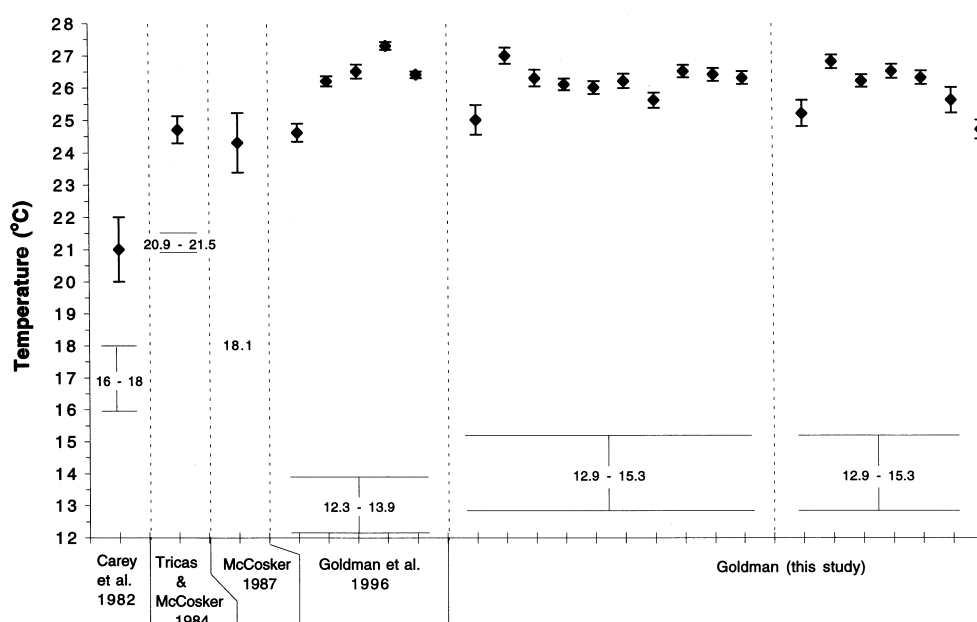
Thermistor location was probably responsible for the greater responsiveness of muscle temperature to changes in ambient water temperature. Carey et al. (1982) described a change in muscle temperature following a change in water temperature after a brief lag time (see also Tricas and McCosker 1984). I observed no such changes when the thermistor was in the stomach. The location of the stomach, ventral to the subcutaneous lateral rete and dorsal (and slightly posterior) to the suprahepatic rete, may make it relatively unsusceptible to changes in ambient water temperature (Goldman et al. 1996). 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 (see Carey and Teal 1969). This would explain why muscle temperature changed in response to

changes in ambient water temperature, and why the elevation of muscle temperature over water temperature was only 3–5 °C in a white shark from the north-western Atlantic and another from the southern Indian Ocean (Carey et al. 1982; Tricas and McCosker 1984) (Fig. 4).

Stomach temperature appears to be a good indicator of body core temperature, whereas epaxial muscle temperature is not (Fig. 4). This may be significant in approaching the determination of thermoregulation and endothermy in other animals. The elevation of body core temperature relative to muscle temperature, along with changes in muscle temperature, but not body core temperature, with changes in ambient temperature would be considered typical conditions for a physio-thermoregulating animal (Schmidt-Nielsen 1990). Therefore, while results from previous muscle temperature data initially appear inconsistent with stomach temperature data, taken together they support thermoregulation in this species.

It is noteworthy that stress can apparently cause lamnid sharks to lose their ability to maintain elevated body temperatures. Stress and trauma resulting from capture and tagging may have been the cause of low muscle and stomach temperatures observed in mako sharks (Carey et al. 1981). Additionally, stress resulting from physical trauma may have been the cause of the low stomach temperatures (21–22 °C, sea surface temperature = 19.4 °C) I obtained from the white shark in South Australia in 1995. This shark had a deep hook and line wound and large white shark bites near her head. She was observed on two more occasions over the following 2 weeks appearing more sluggish in her swimming on each occasion. On the last occasion (approximately 4 h of observation) she possessed additional white shark bites and the old ones had been re-opened and appeared infected. She was unable to maintain a horizontal plane while swimming (tail hanging down).

Fig. 4 All muscle and stomach temperatures taken from white sharks. Standard deviations are shown for all shark temperatures. Ranges of water temperatures are shown beneath shark temperatures. Dotted vertical lines separate studies and/or individuals



Small differences exist between stomach temperatures from this study and the stomach temperature values from the white shark tagged by McCosker (1987) in South Australia. Sea surface temperature in McCosker's study was several degrees warmer than at SFI (18.1 °C versus 13.3–16.1 °C), yet the stomach temperature (24.5 °C) was just slightly lower than the values in this study (Fig. 4). Ingestion of sea water with food appears to be the cause of the lower stomach temperatures in this situation and on days when sharks fed at SFI. The shark in the McCosker study ingested several tuna baits over the course of data collection and its stomach temperature closely resembles the stomach temperature on days the sharks at SFI fed (Fig. 4). Its stomach temperature showed a similar increase and asymptotic stabilization (as in Fig. 1) after ingesting each tuna. Had the shark in the McCosker study been tracked for longer after feeding, its stomach temperature may have shown a closer resemblance to that of the sharks at SFI on non-feeding days (Figs. 2,4).

Control of body core temperature in white sharks may be accomplished through vascular shunts. The suprahepatic rete can be bypassed through a hepatic sinus (Carey et al. 1981). The sinus can be opened and closed, thereby regulating the amount of heat retained within the system. The efficiency of heat exchange by the lamnid retia has been estimated to be 96.5% when the hepatic sinus is closed, and 76.5% when it is open (Carey et al. 1981). There is also speculation as to the presence of other venous shunts and arterial ones (Carey et al. 1981) which would mean that the hepatic sinus is not completely responsible for regulating blood flow around the suprahepatic rete.

White sharks also possess unique features of hematology and cardiac morphology relative to other elasmobranch fishes. Their hemoglobin and hematocrit levels are higher than most birds and mammals, and they have a large heart with a thick muscular ventricle (remarkably similar to the left ventricle in humans). These features indicate a highly active species with a large aerobic scope, a heart design characteristic of endotherms, and suggest a high resting metabolic rate similar to that of birds and mammals (Emery 1985).

White sharks are well adapted for dealing with the difficulties of heat loss (conductive and convective) associated with living in an aquatic environment. In addition to having orbital, muscular, and visceral retia, they transport warm blood from the lateral cutaneous rete to the brain, supplementing the orbital rete (Wolf et al. 1988). Several benefits resulting from their thermal retention ability have been proposed, which are similar to findings in the endothermic tunas and regionally endothermic (warm-brained) billfishes (Carey 1982; Carey et al. 1984; Stevens and McLeese 1984). These include increased rates of neural, digestive, and muscular activity. It would be reasonable to assume that these benefits occur based on the natural operation of physiological systems relative to temperature increases (Schmidt-Nielsen 1990). For example, an increase in the

rate of digestion may allow for the complete digestion and assimilation of large amounts of blubber from pinnipeds, thereby preventing defecation of undigested food material, analogous to the condition in bluefin tuna, *Thunnus thynnus* (Carey et al. 1984).

White sharks are atypical among shark species in that adults prey mostly on marine mammals (pinnipeds) and that they are very active predators in cold water. It is my contention that if white sharks did not possess and regulate an elevated body core temperature, they would not be able to actively search for and successfully prey upon pinnipeds in the cool temperate waters off SFI, and elsewhere. Hence, the evolutionary (primary) benefit to developing a heat retention system is the ability to inhabit colder water and remain active predators of very swift and agile prey (Carey et al. 1985; Goldman et al. 1996). This evolutionary benefit applies to the other members of the Lamnidae (*I. oxyrinchus*, *I. paucus*, *L. nasus*, and *L. ditropis*), which are also apparently endothermic and live in cool waters. They too feed on swift and agile prey such as tunas and salmon (Compagno 1984).

The data presented here support the thermoregulation hypothesis (Goldman et al. 1996) in that white sharks appear to maintain a constant stomach temperature (therefore body core temperature) regardless of the ambient water temperature around SFI. And, when combined with previous studies on thermal physiology and anatomy of white sharks (and other lamnids), it provides evidence that white sharks have evolved as physiological endotherms. White sharks seem to operate in a physiological and ecological manner that is similar to mammals. Considering their possible competitors (e.g. transient *Orcinus orca*), and primary prey (pinnipeds), it can be inferred that they have evolved to compete on the level of mammals and have accomplished this ability through anatomical and physiological mechanisms resulting in thermoregulation and endothermy.

Future research in this area could focus on the suspected arterial shunts around the suprahepatic rete (Carey et al. 1981), examining body core temperature in warmer and colder water temperature regimes, and obtaining nocturnal and crepuscular data that could reveal whether white sharks have a circadian temperature cycle analogous to birds and mammals.

Acknowledgements Thanks go to the Gulf of the Farallones National Marine Sanctuary (GFNMS) for permission to work in the sanctuary, particularly Ed Ueber for his many forms of support. Thanks to the U.S. Fish and Wildlife Service and the Point Reyes Bird Observatory (PRBO) for access to the South Farallon Islands (SFI), and Tom Charkins (vessel "Kumbaya") for transportation to and from the islands on occasion. I am grateful for assistance provided by an anonymous donor (L.V.A.O.), and funding provided by the Samuel S. Johnson Foundation, the California Academy of Sciences, National Geographic Society, and San Francisco State University (SFSU). I thank the Waikiki Aquarium for the use of their hydrophone. Thanks to D. Nelson, S. Gruber, J. Morrissey, T. Tricas, F. Voegeli, J. McKibben, and C. Lowe for their assistance with telemetry ideas and questions. Thanks to I. Gordon, G. Skomal, G. Macleay, P. March, B. Sampson and

M. Blake for their assistance in South Australia. Pinniped bait was obtained through PRBO (NMFS Permit #667). Thanks go to the American Elasmobranch Society for travel funds to present this research at their annual meeting. Several people at SFSU provided various forms of support, including T. Niesen, M. Fountain, E. Gartside, S. Williams, and B. Robbins. Special thanks are extended to R. Larson, A. Arp, G. Cailliet, and J. McCosker for their personal and professional support. Thanks also to the staff at Steinhart Aquarium, especially T. Tucker and J. Rampley. A special acknowledgement goes to S. Anderson and P. Pyle for their undying support and assistance in the field, and to my family for everything over the years. Thanks to R.D. Grubbs and three anonymous reviewers for their helpful comments on the manuscript. This paper is proudly dedicated in the fond memory of Frank Carey.

References

- Ainley DG, Strong CS, Huber HR, Lewis TJ, Morrell SH (1981) Predation by sharks on pinnipeds at the Farallon Islands. *Fishery Bull* 78: 941–945
- Ainley DG, Henderson RP, Huber HR, Boekelheide RJ, Allen SG, McElroy TL (1985) Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *So Calif Acad Sci Mem* 9: 109–122
- Anderson SD, Klimley AP, Pyle P, Henderson RP (1996a) Tidal height and white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. In: Klimley AP, Ainley DG (eds) *Great white sharks: ecology and behavior*. Academic Press, San Diego, CA, pp 275–279
- Anderson SD, Henderson RP, Pyle P, Ainley DG (1996b) Observations of white shark reactions to un-baited decoys. As for Anderson et al. (1996a) Academic Press, San Diego, CA, pp 223–228
- Bone Q, Chubb AD (1983) The retial system of the locomotor muscles in the thresher shark. *J Mar Biol Assoc UK* 63: 239–241
- Block BA, Carey FG (1985) Warm brain and eye temperatures in sharks. *J Comp Physiol B* 156: 229–236
- Burne RH (1923) Some peculiarities of the blood vascular system of the porbeagle shark, *Lamna cornubica*. *Phil Trans R Soc London Ser B* 212: 209–257
- Carey FG (1982) A brain heater in the swordfish. *Science* 216: 1327–1329
- Carey FG, Teal JM (1969) Mako and porbeagle: warm-bodied sharks. *Comp Biochem Physiol* 28: 199–204
- Carey FG, Teal JM, Kanwisher JW (1981) The visceral temperatures of mackerel sharks (Lamnidae). *Physiol Zool* 54: 334–344
- Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HL Jr (1982) Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* 2: 254–260
- Carey FG, Kanwisher JW, Stevens ED (1984) Bluefin tuna warm their viscera during digestion. *J Exp Biol* 109: 1–20
- Carey FG, Casey JG, Pratt HL, Urquhart D, McCosker JE (1985) Temperature, heat production, and heat exchange in lamnid sharks. *So Calif Acad Sci Mem* 9: 92–108
- Compagno LJV (1984) *FAO species catalog: sharks of the world*, part 1. Food and Agriculture Organization of the United Nations 4: 237–249
- Emery SH (1985) Hematology and cardiac morphology in the great white shark, *Carcharodon carcharias*. *So Calif Acad Sci Mem* 9: 73–80
- Goldman KJ, Anderson SD, McCosker JE, Klimley AP (1996) Temperature, swimming depth, and movements of a white shark at the South Farallon Islands, California. In: Klimley AP, Ainley DG (eds) *Great white sharks: ecology and behavior*. Academic Press, San Diego, CA, pp 111–120
- Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatio-temporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* 3: 680–690
- Langley LL, Telford IR, Christensen JB (1980) *Dynamic anatomy and physiology*, 5th edn. McGraw-Hill, New York, NY, pp 70–73
- McCosker JE (1987) The white shark, *Carcharodon carcharias*, has a warm stomach. *Copeia* 1: 195–197
- Schmidt-Nielsen K (1990) *Animal physiology: adaptation and environment*, 4th edn. Cambridge Univ. Press, Cambridge, UK
- Smith RL, Rhodes D (1983) Body temperature of the salmon shark, *Lamna ditropis*. *J Mar Biol Assoc UK* 63: 243–244
- Stevens ED, McLeese JM (1984) Why bluefin tuna have warm tummies: temperature effect on trypsin and chymotrypsin. *Am J Physiol* 246: R487–R494
- Tricas TC, McCosker JE (1984) Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc Calif Acad Sci* 43: 221–238
- Vander AJ, Sherman JH, Luciano DS (1990) *Human physiology: the mechanisms of body function*, 5th edn. McGraw-Hill, New York, NY, pp 588–591
- Wolf NG, Swift PR, Carey FG (1988) Swimming muscle helps warm the brain of lamnid sharks. *J Comp Physiol B* 157: 709–715

Communicated by G. Heldmaier