

Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia

Kevin C. Weng

Barbara A. Block

Tuna Research and Conservation Center
Hopkins Marine Station of Stanford University
120 Oceanview Boulevard
Pacific Grove, California 93950

E-mail address (for K. C. Weng): kevin.cm.weng@stanford.edu

The bigeye thresher shark (*Alopias superciliosus*, Lowe 1841) is one of three sharks in the family Alopiidae, which occupy pelagic, neritic, and shallow coastal waters throughout the tropics and subtropics (Gruber and Compagno, 1981; Castro, 1983). All thresher sharks possess an elongated upper caudal lobe, and the bigeye thresher shark is distinguished from the other alopiid sharks by its large upward-looking eyes and grooves on the top of the head (Bigelow and Schroeder, 1948). Our present understanding of the bigeye thresher shark is primarily based upon data derived from specimens captured in fisheries, including knowledge of its morphological features (Fitch and Craig, 1964; Stillwell and Casey, 1976; Thorpe, 1997), geographic range as far as it overlaps with fisheries (Springer, 1943; Fitch and Craig, 1964; Stillwell and Casey, 1976; Gruber and Compagno, 1981; Thorpe, 1997), age, growth and maturity (Chen et al., 1997; Liu et al., 1998), and aspects of its reproductive biology (Gilmore, 1983; Moreno and Moron, 1992; Chen et al., 1997).

Limited information on the movement patterns of bigeye thresher sharks has been obtained from mark-recapture studies by using conventional tags. The longest straight-line movement of a conventionally tagged bigeye thresher shark to date is 2767 km from waters off New York to the eastern Gulf of Mexico (Kohler and Turner, 2001). The bigeye thresher shark has been captured on longlines set near the surface at night (0 m to 65 m, Fitch and Craig, 1964; Stillwell and

Casey, 1976; Thorpe, 1997; Buencuerpo et al., 1998) and at 400 m to 600 m during the day (Nakamura¹). There is no published information available regarding its habitat and behavior, although Francis Carey tracked a bigeye thresher with an acoustic tag for six hours (Carey²).

Endothermy is a rare trait in fishes and has been demonstrated only in tunas (Thunnini), billfishes (Xiphiidae, Istiophoridae), and lamnid sharks (Lamnidae) (Carey and Teal, 1969; Carey, 1971, 1982a; Block, 1991). In all endothermic fishes, the blood supply to aerobic tissues such as slow-twitch swimming muscle, visceral organs, extraocular muscles, retina, and brain occurs by counter-current heat exchangers known as retia mirabilia. The vascular supply reduces heat loss to the environment and enables heat conservation in metabolically active tissues (Carey, 1971). Lamnid sharks have retia mirabilia in the circulatory anatomy supplying the slow-oxidative swimming muscles, viscera, brain, and eyes (Burne, 1924; Block and Carey, 1985; Tubbesing and Block, 2000). In many lamnid species, tissue temperatures significantly above ambient have been recorded from freshly captured specimens and through telemetry studies of swimming animals (Carey, 1971; Carey et al., 1981, 1982, 1985; McCosker, 1987; Goldman, 1997; Tubbesing and Block, 2000).

The anatomy of alopiid sharks suggests that endothermy may occur in this family. The bigeye thresher and the common thresher (*Alopias vulpinus*) have centrally located slow-oxidative

muscle and primitive retia mirabilia supplying blood to them (Carey, 1982b; Bone and Chubb, 1983). Burne (1924) noted a coiling of the pseudobranchial artery supplying the orbit and cranial regions in the common thresher. No internal tissue temperature measurements have been taken for free-swimming thresher sharks to ascertain whether heat is conserved in oxidative tissues. A freshly caught bigeye thresher shark was found to have a body-core thermal excess of 4°C (Carey, 1971); thus the species may have the ability to conserve metabolic heat.

In this study we present electronic tagging data on the movements, diving behavior, and habitat preferences of the bigeye thresher shark based on two individuals studied with pop-up satellite archival tags. In addition, we provide a brief description of the orbital rete mirabile of the species. The presence of this highly developed rete mirabile within the orbital sinus suggests a physiological mechanism to buffer the eyes and brain from the large temperature changes associated with diel vertical migration, potentially conferring enhanced physiological performance.

Materials and methods

The movements of two bigeye thresher sharks were monitored with pop-up satellite archival tags (PAT tag version 2.00, Wildlife Computers, Redmond, WA; Gunn and Block, 2001; Marcinek et al., 2001). The first shark was captured on a longline set in the Gulf of Mexico at 26.5°N, 91.3°W on 12 April

¹ Nakamura, I. 2002. Personal commun. Institut National des Sciences et Technologies de la Mer, 28 rue 2 Mars 1934, 2025 Salammbou, Tunisia.

² Carey, F. G. (deceased). 1990. Personal commun. Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

Manuscript approved for publication 15 August 2003 by Scientific Editor.

Manuscript received 20 October 2003 at NMFS Scientific Publications Office. Fish. Bull. 102:221–229 (2004).

2000 in waters with a surface temperature of 21.9°C. The longline set contained 184 hooks set at depths between 70 m and 90 m and was made at 06:00 h and retrieved at 09:00 h. Circle hooks (L2045 20/0 circle hook, Eagle Claw, Denver, CO) were used to avoid hooking of the gut, and the shark in this study was hooked in the corner of the jaw. Hooks were baited with squid, and chemical light sticks were attached to every other line. The mass of the shark was visually estimated at 170 kg by an experienced commercial longline fisherman, which corresponds to a fork length of 229 cm, and a total length of 377 cm, based on the weight-length relationship of Kohler et al. (1995). According to this size estimation and the published size-at-maturity data (Chen et al., 1997; Liu et al., 1998), the shark was mature. The sex of the shark was not determined. The second shark was captured by hook-and-line gear near Hawaii at 19.5°N, 156.0°W on 13 May 2003 in waters with a surface temperature of 25.5°C. A baited circle hook set at a depth of 40 m was taken by the shark at 02:00 h. The mass of the shark was estimated at 200 kg by an experienced sportfishing captain, which corresponds to a fork length of 242 cm, and a total length of 400 cm (after Kohler et al., 1995). Given this size, the shark was mature (Chen et al., 1997; Liu et al., 1998), but its sex was not determined.

Each pop-up satellite archival tag was attached to a titanium dart (59 mm × 13 mm) with a 17 cm segment of 136-kg monofilament line (300-lb test extra-hard Hi-Catch, Momo Fishing Net Mfg. Co. Ltd., Ako City, Hyogo prefecture, Japan). The dart was inserted into the dorsal musculature of the shark at the base of the first dorsal fin, such that the tag trailed behind the fin. Following attachment of each tag, the fishing line was cut near the hook and both sharks swam away vigorously. Tagging locations were recorded by using the vessel's global positioning system. After the Gulf of Mexico shark was tagged, a depth-temperature recorder (ABT-1, Alec Electronics, Kobe, Japan) was used to determine the temperature-depth profile of the upper 200 m of the ocean at the release site, at a resolution of 1 m.

The pop-up satellite archival tag deployed in the Gulf of Mexico was programmed to collect pressure and temperature data at two-minute intervals, which the on-board software (PAT software version 1.06, Wildlife Computers, Redmond, WA) summarized into six-hour bins. This version of PAT software did not permit light-based geolocation. The summary data for each time interval comprised percentage distributions of time-at-depth and time-at-temperature, and profiles of temperature-at-depth. Temperature-depth profiles for this generation of software were recorded at intervals by measuring a single temperature at depths of 0, 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, and 400 meters for the deepest dive. A mean temperature-depth profile was obtained by calculating the mean temperature at each specified depth for all profiles taken during the track. The endpoint position of the shark's track was obtained from the tag's radio transmissions to the Argos satellites. The six-hour bins were later combined into 12-hour bins representing day (06:00 to 17:59 h local time) and night (18:00 to 05:59 h local time). At the time and place of tag deployment, sunrise occurred at 05:45 h and sunset at 18:28 h; whereas at the pop-up time and position, sunrise occurred at 05:02 h

and sunset at 18:55 h (U.S. Naval Observatory), such that the day and night bin cutoffs were always within one hour of true sunrise and sunset.

The pop-up satellite archival tag deployed off Hawaii collected data at 30-second intervals and summarized them into four-hour bins (PAT software version 2.08e, Wildlife Computers, Redmond, WA). The data were later combined into day and night bins as for the first tag, and the actual sunrise and sunset times were within one hour of 06:00 h and 18:00 h, respectively (U.S. Naval Observatory). The tag measured the minimum and maximum temperature at the surface, maximum depth, and six intermediate depths, for the deepest dive in each time interval. Temperature-depth profiles for each time interval were later constructed by using the maximum temperature at each depth for all profiles taken during the track, and a curve was fitted by using a LOWESS (locally weighted regression smoothing) function (Cleveland, 1992). Version 2.08e PAT software collected light data for geolocation; however the diel dive pattern of the shark prevented the calculation of accurate positions.

The vascular circulation to the brain and eyes was examined in two bigeye thresher sharks: one common thresher shark and one pelagic thresher shark (*Alopias pelagicus*). A female bigeye thresher (1.5 m fork length) was captured off Cape Hatteras, North Carolina, and a male (1.4 m fork length) was captured in the Gulf of Mexico. The circulatory systems of the bigeye threshers were injected with latex to aid in identifying the blood vessels. A male common thresher (1.3 m fork length) was captured off Cape Hatteras, North Carolina, and was examined without being frozen or preserved. An immature female pelagic thresher shark (1.37 m fork length) was captured in the Indian Ocean. The orbital retia mirabilia were prepared from casts of the vascular circulation that were removed from the orbit.

Results

One bigeye thresher shark was tracked in the Gulf of Mexico for 60 days, and another in the Hawaiian Archipelago for 27 days, by using pop-up satellite archival tags. Both tags released from the sharks as programmed and transmitted summary information to Argos satellites. The tag deployed in the Gulf of Mexico popped up on 10 June 2000 at 27.95°N, 89.54°W (Fig. 1A). The shark moved a straight-line distance of 320 km during the track, starting from the central Gulf in depths exceeding 3000 m and moving to waters 150 km south of the Mississippi Delta where depths were approximately 1000 m. The second shark was tagged off the Kona coast of Hawaii and the tag released on 9 June 2003 at 24.2°N, 165.6°W, northeast of French Frigate Shoals, a straight-line distance of 1125 km from the deployment position (Fig. 1B).

The depth and temperature distributions of the bigeye thresher sharks showed a strong diel movement pattern (Fig. 2). The Gulf of Mexico shark spent the majority of the daytime (84% [$\pm 2.3\%$], mean [± 1 SE]) below the thermocline between 300 m and 500 m and the majority of nighttime (80% [$\pm 4.7\%$], mean [± 1 SE]) in the mixed layer

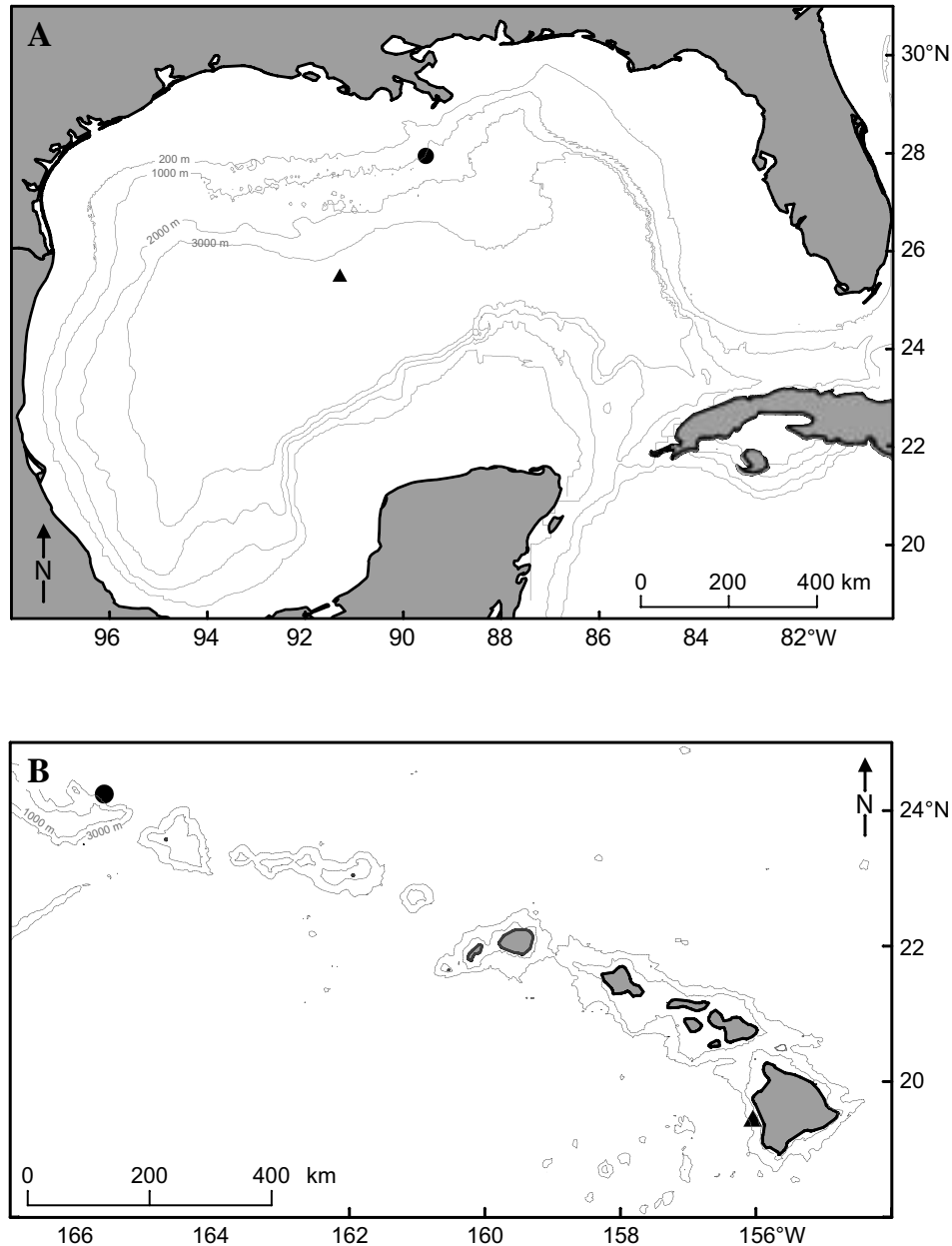


Figure 1

Deployment (▲) and end-point (●) positions for the two pop-up satellite archival tags attached to bigeye thresher sharks. Both tags surfaced on the programmed dates and transmitted data to Argos satellites. Pressure sensors in the tags confirmed that the tags remained attached to the sharks for the duration of the tracks. (A) In the Gulf of Mexico a shark was tagged and released on 12 April 2000 and the tag surfaced on 10 June 2000. The shark moved a straight-line distance of 320 km during the 60-day track. (B) In the Hawaiian Archipelago a shark was tagged on 13 May 2003 off Kona, Hawaii, and the tag surfaced on 9 June 2003 northeast of French Frigate Shoals. The shark moved a straight-line distance of 1125 km during the 27-day track.

and upper thermocline between 10 m and 100 m (Fig. 2A). The shark spent most of the daytime in deeper waters of 6°C to 12°C (70% [$\pm 4.4\%$], mean [± 1 SE]), and most of the nighttime in shallower waters from 20°C to 26°C (70% [$\pm 2.7\%$], mean [± 1 SE]) (Fig. 2B). A temperature-depth

profile taken by the tag during the first day of the shark's track closely matched a profile taken from the vessel with a bathythermograph (Fig. 3A). The mean temperature-depth profile for the 60-day track (Fig. 3B), when compared with the shark's depth preferences (Fig. 2A), indicated that

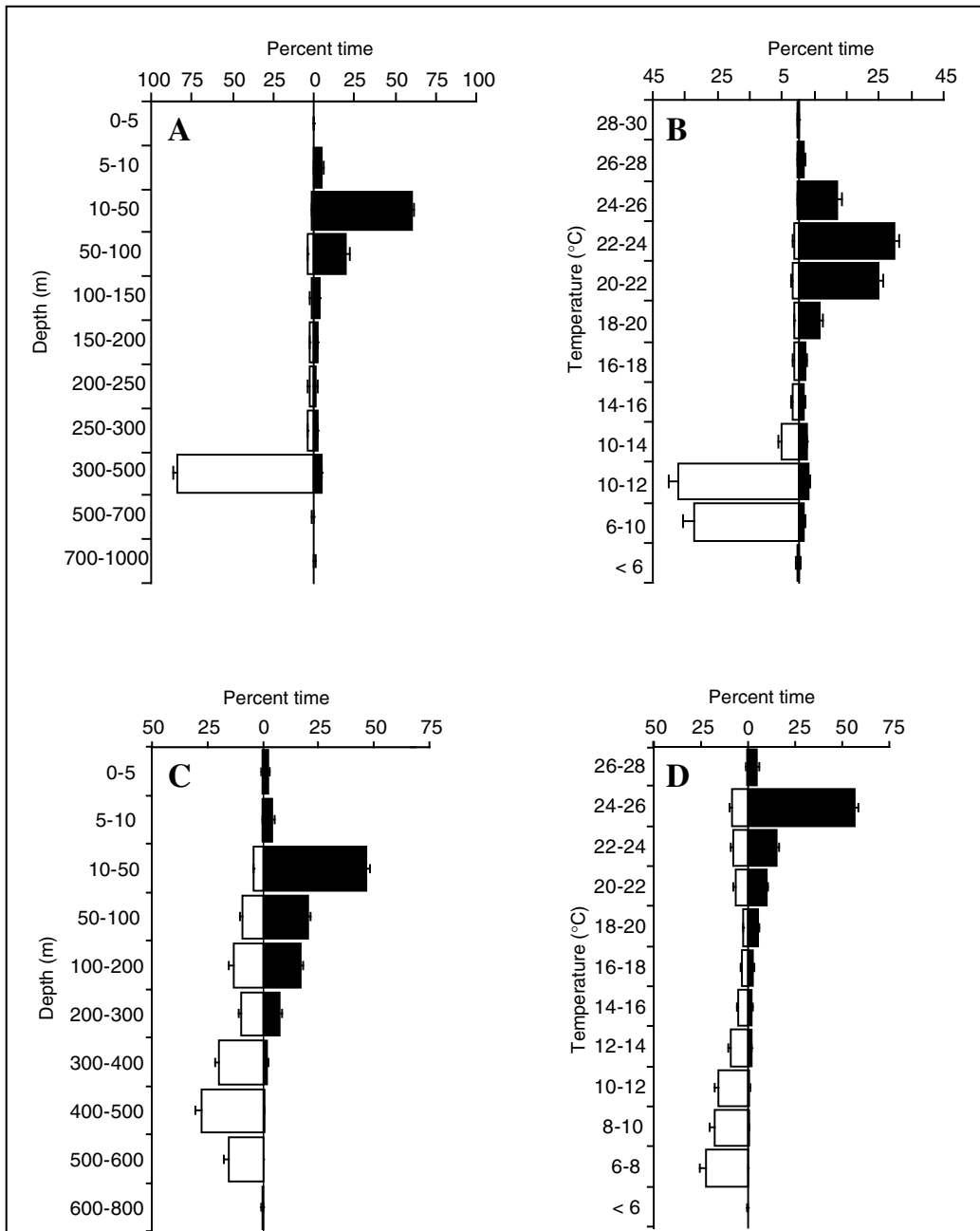
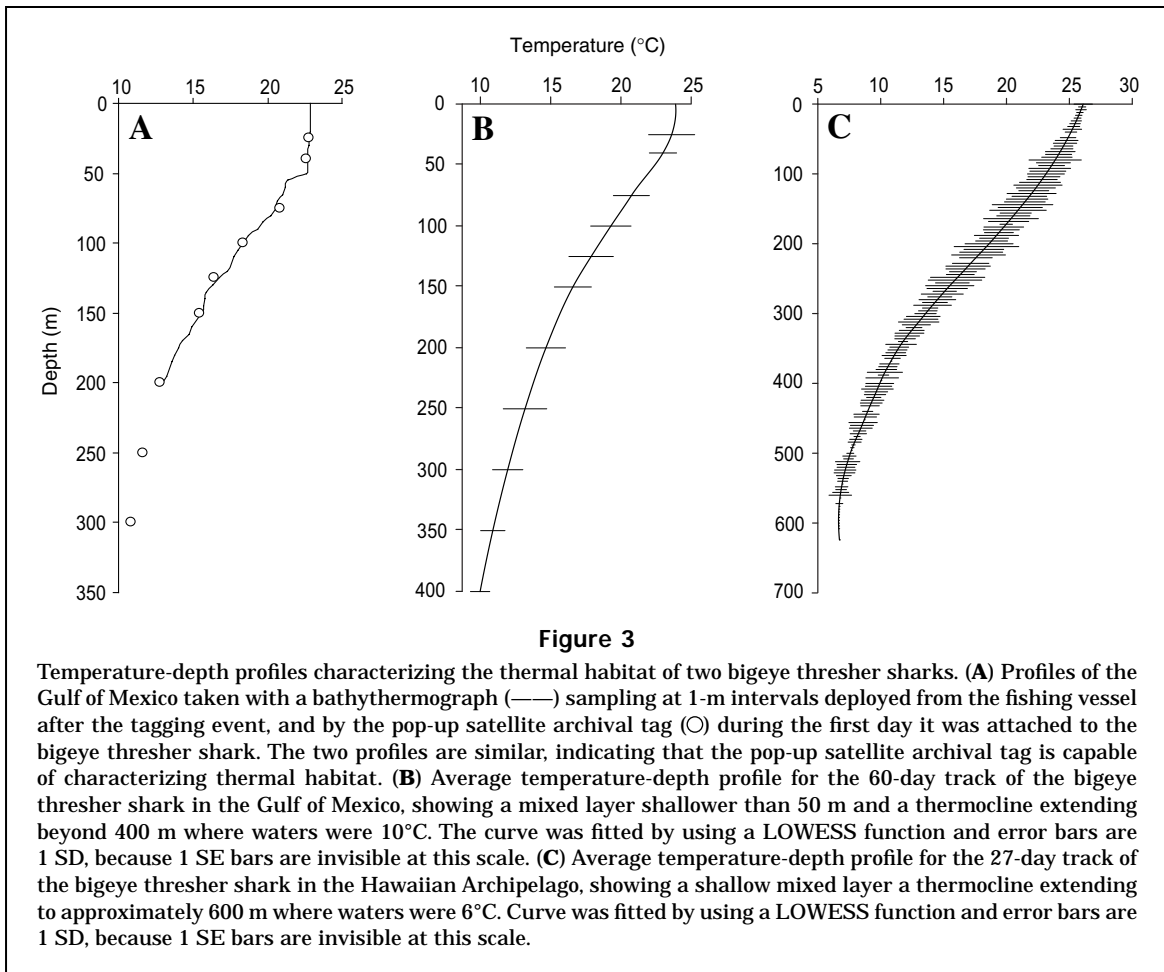


Figure 2

Depth and temperature distributions of two bigeye thresher sharks showing diel vertical migration. The tags recorded depth and temperature at two-minute (A, B) or 30-second (C, D) intervals; data are summarized into a series of bins for the full duration of each track. (A) Depth distribution for the Gulf of Mexico shark is shown as the percentage of day (□) and night (■) spent within depth bins ranging from the surface to 1000 m. Error bars are 1 SE. (B) Temperature distribution for the Gulf of Mexico shark is shown as the percentage of day (□) and night (■) spent within temperature bins ranging from 6°C to 30°C. The shark occupied cool waters during the day and warm waters during the night, a consequence of its deep daytime and shallow nighttime habitats. Error bars are 1 SE. (C) Depth distribution for the Hawaii shark showing diel vertical migration. The shark spent most of the daytime at the base of the thermocline and most of the nighttime in the mixed layer and upper thermocline. (D) Temperature distribution for the Hawaii shark showing cool daytime and warm nighttime water temperatures.



the shark spent most of the daytime below the maximum gradient of the thermocline where temperatures were approximately 10°C. On 25 April and 25 May 2000 the shark spent two hours of the day in waters between 4°C and 6°C. The Hawaii shark showed a similar diel vertical migration, with a lesser contrast between day and night (Fig. 2, C and D). The shark's modal nighttime depth was between 10 m and 50 m, whereas its modal daytime depth was between 400 m and 500 m (Fig. 2C). The temperature-depth profile for the Hawaii shark (Fig. 3C) indicated that it spent nighttime above the thermocline and daytime below it.

The bigeye thresher shark possesses a large arterial plexus between the posterior part of the eye and the wall of the orbital sinus, which appears to be a rete mirabile (Fig. 4). The orbital rete is bathed in venous blood from the orbital sinus and its anterior surface is contoured to the posterior surface of the eye. The sources of venous input to the orbital sinus remain unknown but are most likely within the surrounding extraocular muscles, which are large and comprise numerous aerobic muscle fiber types, and the retina. The rete shown in Figure 4 measures 72 mm by 49 mm by 19 mm. A reduced structure of similar form is also found in the pelagic thresher shark, but is not present in the common thresher. The orbital rete of the bigeye and pelagic threshers is larger in absolute size and

occupies a greater cross sectional proportion of the orbital sinus than the lamnid orbital rete noted by Burne (1924). The arterial vessels form a finer and more orderly meshwork than those in the lamnid sharks (Block and Carey, 1985; Tubbesing and Block, 2000) and appear similar in physical structure to the mammalian carotid rete used for brain cooling (Baker, 1982).

Discussion

Observations of the biological features of the bigeye thresher shark are rare and our knowledge of the species is based primarily on incidental catches in fisheries. Using pop-up satellite archival tags we were able to record behavior for a total of 87 days, and for individual periods up to 60 days without recapturing or following the study animals. We observed a pronounced diel alternation between warm shallow waters and cool deep waters and a rete mirabile that may confer physiological benefits during deep dives by stabilizing brain and eye temperatures.

The depth data obtained for the bigeye thresher shark shows a striking pattern of diel vertical migration. The bigeye thresher shark's vertical movement pattern is distinct from those of most other sharks for which observations

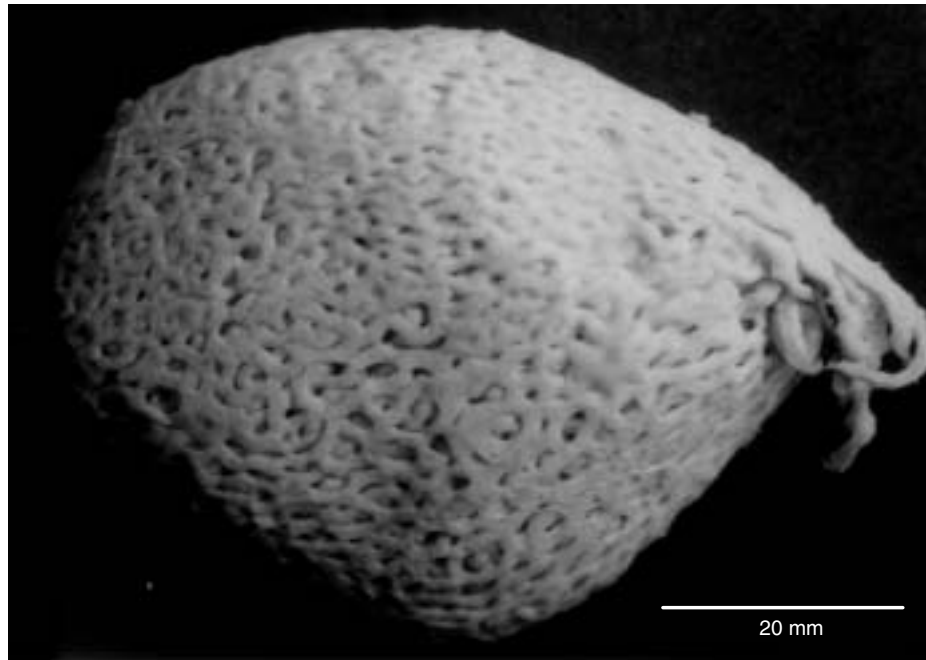


Figure 4

Orbital rete of a bigeye thresher shark, showing the highly developed arterial network. The rete was injected with latex so that the arterial structure (72 mm by 49 mm by 19 mm) could be photographed. The structure of the rete and its position in the orbital sinus suggest that it may be a heat exchanging vascular plexus. Retention of metabolic heat in the eyes and brain would buffer these sensitive organs from the large ambient temperature swings that occur as a result of the bigeye thresher shark's diel vertical migrations. A smaller but similar structure is found in *A. pelagicus* but not in *A. vulpinus*.

exist. In satellite or acoustic tracks, diel vertical migration was not observed for white sharks (*Carcharodon carcharias*; Carey et al., 1982; Goldman and Anderson, 1999; Boustany et al., 2002), salmon sharks (*Lamna ditropis*; Block et al.³), shortfin mako (*Isurus oxyrinchus*; Carey, 1982b; Holts and Bedford, 1993), blue (*Prionace glauca*, Carey, 1982b; Carey and Scharold, 1990), sixgill (*Hexanchus griseus*; Carey and Clark, 1995), tiger (*Galeocerdo cuvier*; Tricas et al., 1981; Holland et al., 1999), Pacific angel (*Squatina californica*; Standora and Nelson, 1977), whale (*Rhincodon typus*; Gunn et al., 1999), or scalloped hammerhead sharks (*Sphyrna lewini*; Klimley, 1993).

Diel vertical migration has been observed in the swordfish (*Xiphias gladius*; Carey and Robison, 1981; Carey⁴), the megamouth shark (*Megachasma pelagios*; Nelson et al., 1997), and the school shark (*Galeorhinus galeus*; West

and Stevens, 2001). Carey and Robison (1981) and Carey⁴ studied swordfish in both the Pacific and Atlantic Oceans, acoustically tracking fish that moved from the surface at night to over 600 m during day. A megamouth shark showed a strong diel vertical migration when tracked acoustically off southern California (Nelson et al., 1997) with shallow nighttime and deep daytime distribution in a vertical range of 20 m to 160 m. West and Stevens (2001) studied school sharks in southern Australia using archival tags and noted that they ascended in the water column at night.

The ambient temperature at the modal day- and nighttime depths of the two bigeye thresher sharks differed by 15° to 16°C, requiring them to be eurythermal. The sharks spent most of the nighttime in shallow waters warmer than 20°C and commonly spent 8 or more hours during the daytime in deep waters cooler than 10°C. The coolest waters occupied had temperatures between 4°C and 6°C. The bigeye thresher sharks tracked in our study spent a higher proportion of their time in waters below 10°C than did white sharks (Carey et al., 1982; Boustany et al., 2002) and mako sharks (Carey and Scharold, 1990; Klimley et al., 2002).

The presence of a rete mirabile in the cranial region may indicate a mechanism for heat conservation. Heat conservation in the brain and eyes would enable the big-

³ Block, B. A., K. G. Goldman, and J. A. Musick. 1999. Unpubl. data. Hopkins Marine Station of Stanford University, 120 Oceanview Boulevard, Pacific Grove, CA 93950.

⁴ Carey, F. G. 1990. Further acoustic telemetry observations of swordfish. In *Planning the future of billfishes; proceedings of the second international billfish symposium, 1–5 August 1988, Kailua-Kona, Hawaii* (R. H. Stroud, ed.), p. 103–122. National Coalition for Marine Conservation, 3 North King St., Leesburg, VA 20176.

eye thresher shark to prolong its foraging time beneath the thermocline, as we observed for both of the sharks tagged in our study. The retina and brain are extremely temperature sensitive in most vertebrates and the large changes in depth and temperature recorded would impose significant effects on the biochemical processes occurring in these tissues (Block and Carey, 1985; Block, 1994). Delayed responses to retinal stimulation can be caused by cooling, whereas increased noise and random firing of neurons can be caused by warming—both responses having adverse effects on sensory function (Konishi and Hickman, 1964; Friedlander et al., 1976; Prosser and Nelson, 1981).

Anatomical and physiological adaptations to warm the brain and eyes have evolved independently in divergent pelagic fish lineages, including the lamnid sharks (Block and Carey, 1985), billfishes of the Xiphiidae and Istiophoridae (Carey, 1982a; Block, 1983) and some scombrid fishes (Linthicum and Carey, 1972). A cranial rete mirabile also has been identified in mobulids (Schweitzer and Notarbartolo di Sciara, 1986) and is thought to be a heat exchanger (Alexander, 1995, 1996). Although it is premature to suggest that the orbital rete of the bigeye thresher shark is a heat exchanger without direct evidence of elevated tissue temperatures in the brain and eyes, the structure is larger than the rete mirabile of lamnid sharks, for which elevated brain and eye temperatures have been demonstrated (Block and Carey, 1985). The anatomical arrangement of an arterial plexus in an orbital sinus is correlated with heat conservation strategies in other vertebrates (Baker, 1982). The phylogenetic relationships of the alopiid and lamnid sharks (Compagno, 1990; Naylor et al., 1997) suggest that endothermic traits evolved independently in the two families.

This note presents new information on the depth and ambient temperature preferences of the bigeye thresher shark based on observations of two individuals, as well as the anatomy of the orbital rete mirabile, which appears to function as a vascular heat exchanger. Behavior of many organisms varies with ontogeny, season and location; therefore the present study should be considered as only the beginning of an understanding of the bigeye thresher shark's physical habitat preferences and adaptations to temperature change. Further studies on individuals of different sizes and in different regions will enhance our understanding of the behavior, and morphological and physiological adaptations, of the bigeye thresher shark to variations in temperature.

Acknowledgments

This research was supported by grants from the National Marine Fisheries Service, the National Fish and Wildlife Federation and the Packard Foundation. The authors wish to thank Captain David Price and crew of the FV *Allison*, and Captain John Bagwell and crew of the FV *Silky*. Shana Beemer provided scientific assistance on the cruise and Captain McGrew Rice assisted in tagging and releasing the Gulf of Mexico shark. This research was conducted under Scientific Research Permit TUNA-SRP-2000-002, issued

by the Office of Sustainable Fisheries, National Marine Fisheries Service, Silver Spring, MD 20910.

Literature cited

- Alexander, R. L.
1995. Evidence of counter-current heat exchanger in the ray, *Mobula tarapacana* (Chondrichthyes: Elasmobranchii: Batoidea: Myliobatiformes). *J. Zool. (Lond)* 237:377–384.
1996. Evidence of brain-warming in the mobulid rays, *Mobula tarapacana* and *Manta birostris* (Chondrichthyes: Elasmobranchii: Batoidea: Myliobatiformes). *Zool. J. Linn. Soc.* 118:151–164.
- Baker, M. A.
1982. Brain cooling in endotherms in heat and exercise. *Annu. Rev. Physiol.* 44:85–96.
- Bigelow, H. B., and W. C. Schroeder.
1948. Sharks. *In* Fishes of the western North Atlantic, part one (A. Parr and Y. Olsen, eds), p. 59–546. Sears Found. Mar. Res., Yale Univ., Mem. 1.
- Block, B. A.
1983. Brain heaters in the billfish. *Am. Zool.* 23:936.
1991. Endothermy in fish: thermogenesis ecology and evolution. *In* Biochemistry and molecular biology of fishes. Volume 1: Phylogenetic and biochemical perspectives (P. Hochachka and T. Mommsen, eds.), p. 269–311. Elsevier, Amsterdam.
1994. Thermogenesis in muscle. *Annu. Rev. Physiol.* 56: 535–577
- Block, B. A., and F. G. Carey.
1985. Warm brain and eye temperatures in sharks. *J. Comp. Physiol. B. Biochem. Syst. Environ. Physiol.* 156: 229–236.
- Bone, Q., and A. D. Chubb.
1983. The retial system of the locomotor muscles in the thresher shark (*Alopias vulpinus*). *J. Mar. Biol. Assoc. U.K.* 63:239–242.
- Boustany, A. M., S. F. Davis, P. Pyle, S. D. Anderson, B. J. Le Boeuf, and B. A. Block.
2002. Satellite tagging: expanded niche for white sharks. *Nature* 415:35–36.
- Buencuerpo, V., S. Rios, and J. Moron.
1998. Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern North Atlantic Ocean and the strait of Gibraltar. *Fish. Bull.* 96:667–685.
- Burne, R. H.
1924. Some peculiarities of the blood vascular system of the porbeagle shark (*Lamna cornubica*). *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 212B:209–257.
- Carey, F. G.
1971. Warm bodied fish. *Am. Zool.* 11:135–143.
1982a. A brain heater in the swordfish (*Xiphias gladius*). *Science* 216:1327–1329.
1982b. Warm fish. *In* A companion to animal physiology: 5th international conference on comparative physiology: Sandbjerg, Denmark, July 22–26, 1980 (C. R. Taylor, K. Johansen and L. Bolis, eds.), p. 216–234. Cambridge Univ. Press, Cambridge, England; New York, NY.
- Carey, F. G., J. G. Casey, H. L. Pratt, D. Urquhart, J. E. McCosker, J. A. Seigel, and C. C. Swift.
1985. Temperature, heat production and heat exchange in lamnid sharks. *In* Biology of the white shark (J. A. Seigel and C. C. Swift, eds.), p. 92–108. Mem. South. Calif. Acad. Sci., vol. 9, Fullerton, CA.

- Carey, F. G., and E. Clark.
1995. Depth telemetry from the sixgill shark, *Hexanchus griseus*, at Bermuda. *Environ. Biol. Fishes* 42:7–14.
- Carey, F. G., J. W. Kanwisher, O. Brazier, G. Gabrielson, J. G. Casey, and H. L. J. Pratt.
1982. Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* 1982:254–260.
- Carey, F. G., and B. H. Robison.
1981. Daily patterns in the activities of wordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish. Bull.* 79: 277–292.
- Carey, F. G., and J. V. Scharold.
1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* 106:329–342.
- Carey, F. G., and J. M. Teal.
1969. Mako and porbeagle: warm-bodied sharks. *Comp. Biochem. Physiol.* 28:199–204.
- Carey, F. G., J. M. Teal, and J. W. Kanwisher.
1981. The visceral temperatures of mackerel sharks (Lamnidae). *Physiol. Zool.* 54:334–344.
- Castro, J. I.
1983. The sharks of North American waters, 180 p. Texas A&M Univ. Press, College Station, TX.
- Chen, C.-T., K.-M. Liu, and Y.-C. Chang.
1997. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839)(Chondrichthyes: Alopiidae), in the northwestern Pacific. *Ichthyol. Res.* 44: 227–235.
- Cleveland, W. S., E. Grosse, and W. M. Shyu.
1992. Local regression models. Chapter 8 in *Statistical models in S* (J. M. Chambers and T. J. Hastie eds.), 608 p. Wadsworth & Brooks/Cole, Pacific Grove, CA.
- Compagno, L. J. V.
1990. Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding behavior. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries* (H. L. J. Pratt, S. H. Gruber, and T. Taniuchi, eds.), p. 357–379. NOAA Technical Report 90.
- Fitch, J. E., and W. L. Craig.
1964. First records for the bigeye thresher (*Alopias superciliosus*) and slender tuna (*Allothunnus fallai*) from California, with notes on eastern Pacific scombrid otoliths. *Calif. Fish Game* 50:195–206.
- Friedlander, M. J., N. Kotchabhakdi, and C. L. Prosser.
1976. Effects of cold and heat on behavior and cerebellar function in goldfish. *J. Comp. Physiol. A Sens. Neural. Behav. Physiol.* 112:19–45.
- Gilmore, R. G.
1983. Observations on the embryos of the longfin mako, *Isurus paucus* and the bigeye thresher, *Alopias superciliosus*. *Copeia* 1983:375–382.
- Goldman, K. J.
1997. Regulation of body temperature in the white shark, *Carcharodon carcharias*. *J. Comp. Physiol. B. Biochem. Syst. Environ. Physiol.* 167:423–429.
- Goldman, K. G., and S. D. Anderson.
1999. Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Environ. Biol. Fishes* 56:351–364.
- Gruber, S. H., and L. J. V. Compagno.
1981. Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus*. *Fish. Bull.* 79:617–640.
- Gunn, J. S., J. D. Stevens, T. L. O. Davis, and B. M. Norman.
1999. Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Mar. Biol.* 135:553–559.
- Gunn, J. S., and B. A. Block.
2001. Advances in acoustic, archival and satellite tagging of tunas. In *Tunas: physiology, ecology and evolution* (B. A. Block and E. D. Stevens, eds.), p. 167–224. Academic Press, San Diego, CA.
- Holland, K. N., B. M. Wetherbee, C. G. Lowe, and C. G. Meyer.
1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Mar. Biol.* 134:665–673.
- Holts, D. B., and D. W. Bedford.
1993. Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the southern California bight. *Aust. J. Mar. Freshw. Res.* 44:901–909.
- Klimley, A. P.
1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Mar. Biol.* 117:1–22.
- Klimley, A. P., S. C. Beavers, T. H. Curtis, and S. J. Jorgensen.
2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Environ. Biol. Fishes* 63:117–135.
- Kohler, N. E., J. G. Casey, and P. A. Turner.
1995. Length-weight relationships for 13 species of sharks from the western North Atlantic. *Fish. Bull.* 93:412–418.
- Kohler, N. E., and P. A. Turner.
2001. Shark tagging: A review of conventional methods and studies. *Environ. Biol. Fishes* 60:191–223.
- Konishi, J., and C. P. Hickman.
1964. Temperature acclimation in the central nervous system of rainbow trout (*Salmo gairdnerii*). *Comp. Biochem. Physiol.* 13:433–442.
- Linthicum, D. S., and F. G. Carey.
1972. Regulation of brain and eye temperatures by the bluefin tuna. *Comp. Biochem. Physiol. A Comp. Physiol.* 43:425–433.
- Liu, K.-M., P.-J. Chiang, and C.-T. Chen.
1998. Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters. *Fish. Bull.* 96:482–491.
- Marcinek, D. J., S. B. Blackwell, H. Dewar, E. V. Freund, C. Farwell, D. Dau, A. C. Seitz, and B. A. Block.
2001. Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. *Mar. Biol.* 138:869–885.
- McCosker, J. E.
1987. The white shark, *Carcharodon carcharias*, has a warm stomach. *Copeia* 1987:195–197.
- Moreno, J. A., and J. Moron.
1992. Reproductive biology of the bigeye thresher shark *Alopias superciliosus* Lowe 1839. *Aust. J. Mar. Freshwat. Res.* 43:77–86.
- Naylor, G. J. P., A. P. Martin, E. G. Mattison, and W. M. Brown.
1997. Interrelationships of lamniform sharks: Testing phylogenetic hypotheses with sequence data. In *Molecular systematics of fishes* (T. D. Kocher and C. A. Stepien, eds.), p. 199–218. Academic Press, San Diego, CA.
- Nelson, D. R., J. N. McKibben, W. R. Strong Jr., C. G. Lowe, J. A. Sisneros, D. M. Schroeder, and R. J. Lavenberg.
1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: A crepuscular vertical migrator. *Environ. Biol. Fishes* 49:389–399.

- Prosser, C. L., and D. O. Nelson.
1981. Role of nervous systems in temperature adaptation of poikilotherms. *Annu. Rev. Physiol.* 43:281–300.
- Schweitzer, J., and G. Notarbartolo di Sciara.
1986. The *rete mirabile cranica* in the genus *Mobula*: a comparative study. *J. Morphol.* 188:167–178.
- Springer, S.
1943. A second species of thresher shark from Florida. *Copeia* 1943:54–55.
- Standora, E. A., and D. R. Nelson.
1977. A telemetric study of the behavior of free swimming Pacific angel sharks *Squatina californica*. *Bull. South. Calif. Acad. Sci.* 76:193–201.
- Stillwell, C. E., and J. G. Casey.
1976. Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic. *Fish. Bull.* 74:221–225.
- Thorpe, T.
1997. First occurrence and new length record for the bigeye thresher shark in the northeast Atlantic. *J. Fish Biol.* 50: 222–224.
- Tricas, T. C., L. R. Taylor, and G. Naftel.
1981. Diel behavior of the tiger shark *Galeocerdo cuvier* at French Frigate Shoals Hawaiian Islands USA. *Copeia* 1981:904–908.
- Tubbesing, V. A., and B. A. Block.
2000. Orbital rete and red muscle vein anatomy indicate a high degree of endothermy in the brain and eye of the salmon shark. *Acta Zool. (Stockh.)* 81:49–56.
- West, G. J., and J. D. Stevens.
2001. Archival tagging of school shark, *Galeorhinus galeus*, in Australia: Initial results. *Environ. Biol. Fishes* 60: 283–298.