Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada

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Abstract: The leatherback sea turtle, *Dermochelys coriacea* (Vandelli, 1761), has the most extensive range of any reptile, migrating from tropical and subtropical nesting areas to distant foraging habitats, including those in temperate and even boreal waters. This implies flexible thermal functioning. It has been inferred that leatherbacks support active foraging by keeping warm in cold water, rather than becoming lethargic as other marine turtles do. However, data consistent with this view have come from captive turtles in unnatural and stressful conditions. In the present case, foraging leatherbacks were captured at sea off Nova Scotia and their body temperature recorded within 10 min, before such large animals could change their body temperatures appreciably. Mean excess temperature over that of the sea surface (15.0–16.7 °C) averaged 8.2 °C. These results attest to, but underestimate, the capacity of free-swimming leatherbacks to keep warm in northern waters, as data from another turtle that was instrumented to record ocean temperature while diving revealed that leatherbacks foraging in this area at the same time of year may spend 40% of their time diving to waters cooler than the surface.

Résumé : La tortue luth, *Dermochelys coriacea* (Vandelli, 1761), possède l'aire de répartition la plus étendue de tous les reptiles, car elle migre de son aire de nidification tropicale ou subtropicale vers ses habitats lointains de recherche de nourriture qui incluent les eaux tempérées et même les eaux boréales. Un tel comportement suppose un fonctionnement thermique flexible. On en a déduit que les tortues luths maintiennent leur recherche active de nourriture en demeurant chaudes en eau froide, plutôt que léthargiques comme les autres tortues marines. Cependant, les données qui appuient cette hypothèse proviennent de tortues en captivité dans des conditions artificielles et éprouvantes. Dans cette étude, nous avons capturé des tortues en train de se nourrir en mer au large de la Nouvelle-Écosse et nous avons mesuré leur température corporelle dans un délai de moins de 10 min, avant que des animaux de cette taille n'aient le temps de subir une modification de leur température corporelle. Leur température moyenne est de 8,2 °C supérieure en moyenne à celle de la surface de la mer (15,0–16,7 °C). Ces données confirment, tout en la sous-estimant, la capacité des tortues luths en nage libre à se maintenir chaudes dans les eaux nordiques; en effet, des données provenant d'une autre tortue luth porteuse d'un enregistreur de température pendant la plongée indiquent que les tortues luths qui recherchent leur nourriture dans la même région au même moment de l'année peuvent passer 40 % de leur temps à plonger dans des eaux qui sont plus froides que les eaux de surface.

[Traduit par la Rédaction]

Introduction

The leatherback turtle, *Dermochelys coriacea* (Vandelli, 1761), is a giant marine reptile that specializes on a diet of coelenterates. This prey is seasonally abundant in temperate and boreal waters. In 1965, Bleakney collated observations of active leatherbacks that appeared to be in good health in waters off New England and Eastern Canada and suggested that these animals make regular migrations to temperate waters of the northwest Atlantic. How do leatherbacks manage to keep active and feed in temperatures that would induce lethargy, and even death, in most reptiles?

Body temperatures of leatherbacks nesting in the tropics have been found to be about 3 °C above the water from which they emerged (Mrosovsky and Pritchard 1971), and dataloggers attached to implanted thermistors recorded subcarapacial temperatures as high as 3 °C above that of the sea surface during the internesting interval off the Pacific coast of Costa Rica (Southwood et al. 1999). Such findings suggest that leatherbacks might be able to maintain their temperature above ambient levels even in cool waters. Mechanisms consistent with an ability to keep warm in cold water are countercurrent heat exchangers in the flippers, thermal inertia, a high volume to surface area ratio, different compositions of peripheral and central lipids, a thick fibrous lipid-saturated layer, and proposed regulation of blood flow (Frair et al. 1972; Greer et al. 1973; Goff and Stenson 1988; Davenport et al. 1990; Paladino et al. 1990).

However, some cautions are in order about the interpretation of the few data on leatherbacks from cold water. The lo-

Received 12 February 2004. Accepted 27 July 2004. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 29 October 2004.

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 doi: 10.1139/Z04-110

gistics associated with locating and handling these massive animals have hindered field studies of the thermal biology of this species at high latitudes. Deep body temperature data have previously been collected from two live leatherbacks from temperate waters. The first turtle, a male, was housed for 24 h in a tank with circulating 7.5 °C sea water following its capture off Nova Scotia, Canada (Frair et al. 1972). Fifteen minutes after it was removed from the water, the animal's deep body core temperature was 18 °C above that of the tank (Frair et al. 1972). The second turtle, caught off Rhode Island, USA, registered deep body temperatures between 3.4 and 8.3 °C above ambient air temperature (Standora et al. 1984). The differential between deep body temperature and sea temperature was not measured. Although both records attest to the capacity for endothermy, these measurements followed lengthy periods of handling and confinement, and therefore, may be less reliable than those collected immediately after free-swimming leatherbacks are captured at sea.

Northern foraging habitat for the leatherback in the Atlantic includes waters off Eastern Canada (Bleakney 1965; Lazell 1980; Goff and Lien 1988), where the species has been observed in water as cold as 0 °C (Goff and Lien 1988). Leatherbacks are notoriously difficult to locate and capture at sea; however, collaboration with commercial fishers in Eastern Canada has yielded rare opportunities for fieldwork on this species. Here we report on body core temperature data collected from four adult females in waters off Nova Scotia. We relate our findings to ocean temperatures collected by a satellite-linked datalogger attached to a fifth leatherback foraging in the vicinity of three of these animals.

Materials and methods

All turtles were handled in accordance with the principles and guidelines of the Canadian Council on Animal Care. A breakaway hoop-net, operated from a bowsprit attached to a 34-foot (1 foot = 0.3048 m) commercial fishing boat equipped with a stern ramp, was used to capture free-swimming leatherbacks occupying continental shelf waters off Nova Scotia, Canada. This type of net has been used to capture cheloniid sea turtles (Beavers and Cassano 1996), and pinnipeds and small cetacea (Asper 1975). The net was pursed over each turtle when it surfaced. The turtle was quickly brought alongside the boat, where a cargo net constructed of soft 2.5 cm mesh cotton netting was placed under it and secured around it. The turtle was then guided to the stern and moved up the ramp onto a raised platform built flush with the sides of the vessel. Next, a 46 cm long, 0.6 cm diameter, type "T" thermocouple, stainless steel probe (model TJ36-CPSS; Omega Engineering, Inc., Stamford, Connecticut) was inserted into the cloacal opening. The probe was connected to a microprocessor-based handheld thermometer (model HH-21; Omega Engineering, Inc.). Temperature could be read to the nearest 0.1 °C. Calibration was checked by placing the probe in melting ice and readings were always within 0.1 °C of zero. Previous work (Mrosovsky 1980) suggested that it may be necessary to insert cloacal probes a minimum of 24 cm to measure core temperature of nesting leatherbacks. Therefore, the probe was slowly guided beyond this depth until any resistance was encountered. The probe was inserted beyond the tail and into the main body of the animal, and in all cases, probe depth exceeded the point at which temperature readings did not increase further. The immersion depth of the probe was recorded along with the temperature. To minimize potential error related to the use of cloacal probes in the much longer tails of male leatherbacks (Frair et al. 1972), only females were studied (turtles A–D).

A bucket attached to a rope was then tossed over the side of the boat to retrieve a sample of sea water. The same probe was then promptly used to measure sea surface temperature. A second sample of water was then collected to confirm sea surface temperature.

Measurements occurred <10 min after capture, and all turtles were repeatedly doused with buckets of sea water while aboard. Following the collection of temperature measurements, curved carapace length (CCL) and curved carapace width (CCW) were recorded. Monel tags (style #49; National Band and Tag Company, Newport, Kentucky) were applied to the rear flippers and a passive integrated transponder (Avid™ brand) was implanted in the right shoulder muscle. Two turtles were also weighed with a digital hanging scale by raising them off the platform in the cargo net using a lever puller suspended from a tubular aluminum structure.

To better understand the range of temperature experienced by leatherbacks foraging in the vicinity, we considered ocean temperature data collected by a satellite-linked time–depth recorder (SLTDR) (model SSC3; Wildlife Computers, Inc., Redmond, Washington) incorporating a thermistor accurate to 0.15 °C, with a resolution of 0.13 °C, that was attached to an additional female turtle (turtle E). The instrument was deployed earlier in the summer off mainland Nova Scotia (44.273°N, 63.677°W); however, turtle E later moved ~400 km northeast to forage off Cape Breton Island. This leatherback actively foraged in shelf waters (<200 m deep) within a 30-km radius of the capture location of one of three leatherbacks studied in 2003 and captured within this radius (Fig. 1). Temperature data were recorded as the proportion of each of four 6-h periods in a day spent in 2 °C bins from 8–10 °C to 30–32 °C. The instrument collected data for all four periods every day. To evaluate the range of temperature associated with leatherback foraging behaviour in this particular area, we only considered temperature data collected during those days when ARGOS positions with assigned location qualities of 3, 2, and 1 (calculated to lie within 150, 150–350, and 350–1000 m, respectively, of the animal's true position) placed turtle E within the 30-km radius. Recognizing that the temperature of the water column changes with time, we limited our analysis to 3 days (i.e., 2, 3, and 6 September), including the day before the first two turtles were captured and the day the last turtle was captured. Corresponding temperature data from the SLTDR on turtle E were combined over this period to show the percentage of time that the animal spent at different temperatures.

Results

One leatherback was captured in September 2002, and three leatherbacks were captured in September 2003 (Table 1). Curved carapace length ranged from 143 to 163 cm,

Fig. 1. Locations of four female leatherback turtles (*Dermochelys coriacea*) captured off Cape Breton Island, Nova Scotia. The solid square indicates the turtle that was caught in 2002 (turtle A). Solid triangles indicate turtles that were captured in 2003 (turtles B–D). Solid circles indicate ARGOS positions from an additional female leatherback (turtle E) equipped with a satellite-linked sea temperature data recorder. Numbers besides the solid circles represent dates in September 2003.

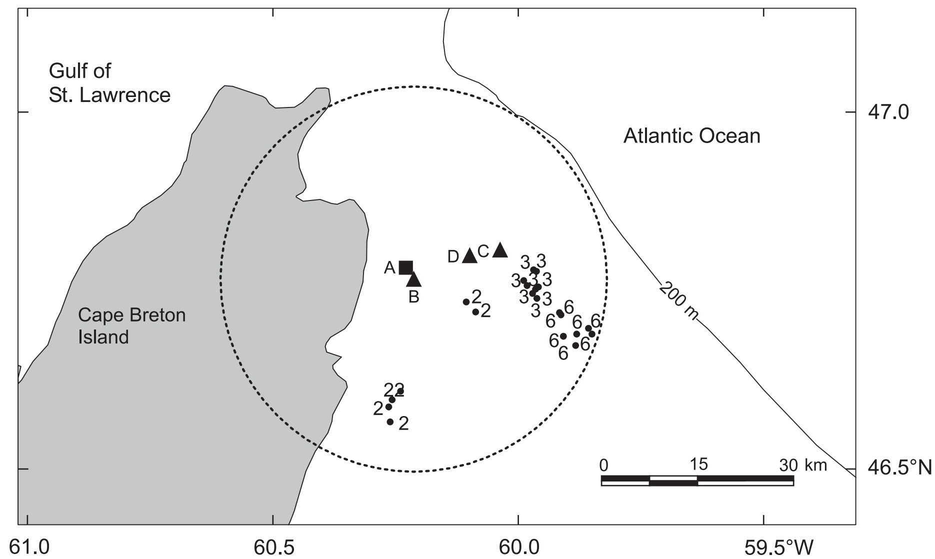


Table 1. Morphometrics and capture locations of four female leatherback turtles, *Dermochelys coriacea*, off Nova Scotia, Canada.

Turtle ID	Passive integrated transponder ID#	Date (dd/mm/yyyy)	Curved carapace length (cm)	Curved carapace width (cm)	Mass (kg)
A	017618055	16/09/2002	152.5	106.5	380
B	017069036	03/09/2003	151.3	105.1	
C	132337156	03/09/2003	143.0	105.0	315
D	032010096	06/09/2003	162.8	113.6	

Table 2. Core temperature and sea surface temperature measurements for four female leatherback turtles in waters off Nova Scotia, Canada.

Turtle ID	Probe depth (cm)	Core temperature (°C)	Sea surface temperature (°C)	Differential temperature (°C)
A	38.5	25.8	15.0	10.8
B	42.0	21.6	16.5	5.1
C	41.0	24.7	16.7	8.0
D	45.0	25.2	16.4	8.8
Mean ± SD	41.63±2.69	24.33±1.87	16.15±0.78	8.18±2.36

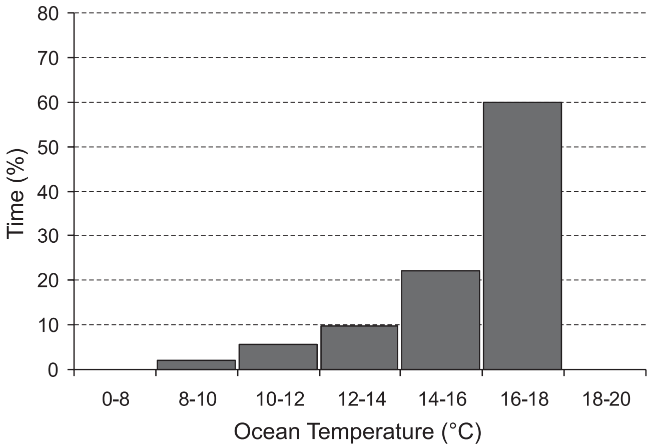
indicating that all turtles were of breeding size, and one (turtle D) was confirmed to have previously nested on Matura Beach, Trinidad, after a microchip was detected in the right shoulder and a metal flipper tag was found on the left rear flipper (Table 1). The smallest turtle (turtle C) had a CCL of 143 cm and weighed 315 kg, and a second turtle (turtle A) had a CCL that was 9.5 cm longer and weighed 380 kg; therefore, each of the other two animals likely weighed a minimum of 315 kg. Body core temperatures ranged from 5.1 to 10.8 °C above ambient temperature (Table 2).

Turtle E foraged within a 30-km radius of turtle A for 3 of the 5 days considered (i.e., 2, 3, and 6 September; Fig. 1) and experienced a wide range of temperature during this time (Fig. 2). Although turtle E spent 60% of the 72-h sampling period in waters 16–18 °C, which corresponded to the point sea surface temperatures associated with three of the captured turtles, she spent 40% of her time at temperatures below 16 °C, including 15% at 12–16 °C and 2% at 10–12 °C.

Discussion

The data reported here were derived from more natural conditions than those published previously, because measurements were taken from wild animals captured for this purpose and handled briefly rather than from leatherbacks

Fig. 2. Percent time at temperature for turtle E in waters off Cape Breton Island, Nova Scotia, during 3 days (2, 3, and 6 September 2003).



that were found entangled in fishing gear for unknown periods and were transported to shore for study where they experienced confinement and additional handling. Despite the differences in procedures, the results support the conclusion of Frair et al. (1972) that leatherbacks can maintain temperature well above ambient levels.

However, our new data do not completely resolve the question of whether leatherbacks in cold water regulate their temperature at a more or less constant value. The temperature of the leatherback studied by Frair et al. (1972) was 25.5 °C; this was 18 °C above the temperature of the water in which it had been kept. The mean temperature of the four leatherbacks studied here was 24.3 °C; this was about 8 °C above the sea surface temperatures of 15–17 °C. In both cases the actual body temperatures were similar, but the cooler the water, the greater the excess of body temperature above ambient levels. This is consistent with regulation, but the point cannot be made with great precision because leatherbacks often dive below the surface to cooler waters (Fig. 2).

If we assume the warmest water temperatures are at or near the surface, then the data from the leatherback instrumented to record temperature external to the body suggest that foraging leatherbacks spend considerable amounts of time below the surface, where temperatures are generally a few degrees cooler. This is consistent with our observations of leatherbacks off the coast of Nova Scotia. Although animals are regularly found in areas where jellyfish are abundant at the surface (James and Herman 2001), we have also observed leatherbacks consuming jellyfish at the surface when such prey are not visible there. Therefore, in these instances, leatherbacks are likely capturing jellyfish at depth and returning to the surface to ingest their prey.

More information is needed to establish the existence of a regulated temperature level in leatherbacks. However, the more time the four animals studied here spent diving to water cooler than that recorded at the surface, the stronger the demonstration that, by whatever means, these turtles can maintain body temperature in cool water. As the turtle with the temperature recorder revealed, leatherbacks foraging in this area off Cape Breton Island may spend 40% of their time diving to cooler water. In addition, ingestion of cold prey could contribute to thermal challenges in foraging areas (Davenport 1998).

All of the leatherbacks considered here were similar in size and were adults. There are potentially large differences in the thermal biology of large and small leatherbacks, with larger animals being better able than small ones to keep warm in cold water. Paladino et al. (1990) considered the thermoregulatory capabilities of leatherbacks of different sizes by modelling heat exchange within a leatherback and between the leatherback and the environment, and concluded that bigger leatherbacks can maintain larger core–skin temperature differences. Moreover, the cloacal temperature (20-cm depth) of a captive immature leatherback weighing 23–26 kg was not appreciably warmer than that of a Kemp's ridley sea turtle, *Lepidochelys kempii* (Garman, 1880), and a green turtle, *Chelonia mydas* (L., 1758), of similar mass, and in 20 °C water the leatherback was only about 1 °C warmer than ambient temperature (Mrosovsky 1980). Eckert (2002) has suggested that differences in the thermoregulatory abilities of large versus small leatherbacks may help explain the apparent absence of small leatherbacks (<100 cm CCL) in high-latitude foraging populations.

Once leatherbacks are large, they may use multiple mechanisms to help them keep warm in cold water. These include an insulating oily layer, high physical activity generating heat, and countercurrent heat exchange. Such adaptations raise the possibility that the greatest thermal challenges faced by this species might arise when it is in warm waters. The leatherback has the greatest distribution of any reptile, ranging from tropical to arctic waters. Body temperatures of leatherbacks that have emerged for nesting (Mrosovsky 1980) and those swimming offshore during their internesting interval (Southwood et al. 1999) have revealed that temperatures as high as 30 °C or even greater can be reached. In these studies a variety of methods were used, including recording the temperature of eggs immediately after they were extruded, cloacal temperature, and subcarapacial implants of thermistors. It seems unlikely that the differences of 5 °C or more between leatherbacks in the tropics and those in cold waters stem only from methodological differences in these studies.

For further understanding of the thermal biology of leatherbacks, it would be instructive to have simultaneous recording of body temperature and surrounding ocean temperature for the same individual over periods long enough to include sojourns off tropical nesting beaches and in temperate foraging areas. With recent technological advances in wildlife satellite-telemetry instrumentation, this goal may not be out of reach much longer. Leatherbacks captured off Nova Scotia may prove ideal candidates for future studies of this nature, as these animals have a predictable migration to tropical waters following their high-latitude foraging period.

Acknowledgements

We thank H. Fricker, B. Fricker, B. Mitchell, R. Myers, and K. Martin for field assistance. Thanks are also extended to S. Eckert for telemetry expertise and C. Harvey-Clark for veterinary advice. Research funding was provided by Fisheries and Oceans Canada, National Marine Fisheries Service, Canadian Wildlife Federation, World Wildlife Fund Canada, Environment Canada, and the Natural Sciences and Engineering Council of Canada (scholarship to M.C.J. and grant to N.M.). This research was conducted under Fisheries and Oceans Canada license Nos. 2002-550 and 2003-534 and Dalhousie University Animal Care permit Nos. 00-008 and 02-053.

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