

Expanded thermal niche for a diving vertebrate: A leatherback turtle diving into near-freezing water

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Abstract

The global distribution of extant reptiles is more limited than that of mammals or birds, with low reptilian species diversity at high latitudes. Central to this limited geographical distribution is the ectothermic nature of reptiles, which means that they generally become torpid at cold temperatures. However, here we report the first detailed telemetry from a leatherback turtle (*Dermochelys coriacea*) diving in cold water at high latitude. An individual equipped with a satellite tag that relayed temperature–depth profiles dived continuously for many weeks into sub-surface waters as cold as 0.4 °C. Global warming will likely increase the foraging range of leatherback turtles further into temperate and boreal waters.

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1. Introduction

The ectothermic nature of reptiles has huge implications for species distributions and activity patterns, with this group often dependent on warming themselves in the sun in order to remain active, especially at high latitudes (Pough et al., 2001). In both temperate terrestrial and aquatic systems, reptiles often enter a dormant state when ambient temperatures drop markedly in late fall and winter (Pough et al., 2001). However, even in cool water, leatherback turtles (*Dermochelys coriacea*) are able to maintain a warm

core (Frair et al., 1972; James and Mrosovsky, 2004) likely due to their large body size (several hundred kilograms) and the resulting thermal inertia, combined with counter-current heat exchangers limiting heat loss from their periphery and thick fat deposits providing insulation (Frair et al., 1972; Greer et al., 1973; Paladino et al., 1990; Davenport et al., 1990). Consequently, although leatherback nesting is limited to tropical and sub-tropical regions due to the thermal dependence of egg development, outside of the nesting season adults may travel widely across ocean basins to reach high latitude foraging areas where they feed on jellyfish and other gelatinous zooplankton. For example, in the Atlantic, leatherbacks are summer and autumn visitors to northern Europe (e.g., France, UK, Ireland) (Brongersma, 1972) and Canada (Bleakney, 1965).

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While a large number of leatherbacks have now been satellite-tracked as they travel extensively across ocean basins (Ferrari et al., 2004; Hays et al., 2004a; James et al., 2005a; Luschi et al., 2003; Sale et al., 2006), most studies have tended to focus on tracking turtles away from their nesting beaches. We set out to deploy satellite transmitters on leatherbacks at the start of their foraging period at temperate latitudes in the boreal summer, in order to identify the range of thermal environments they experience. While satellite tags have been deployed on leatherback turtles at high latitudes off the Canadian coast (James et al., 2005a), these instruments have provided limited information on water temperature (James et al., 2005b). Here we describe the first deployment of a satellite relayed data-logger (SRDL), capable of recording the thermal environment of wide-ranging diving animals in great detail, on a leatherback turtle at high latitude. This instrument provides not only location data but also high-resolution temperature–depth profiles as the animal dives (McMahon et al., 2005), remotely relaying the type of data that could previously only be obtained with archival data-loggers (Metcalf and Arnold, 1997).

2. Materials and methods

On 16 July 2005 a Series 9000 SRDL (Sea Mammal Research Unit, St. Andrews, Scotland) was attached to a female leatherback turtle (curved carapace length 148 cm) captured at sea off Halifax, Nova Scotia, Canada. The turtle was captured using established techniques and the SRDL was attached using a flexible harness (James et al., 2005a). The SRDL was located using the Argos satellite data collecting system (<http://www.argosinc.com>). Here we consider movements of this turtle up to 9 October 2005 at which time the SRDL was still functioning well. To reconstruct the turtle's movements we only used locations of Argos classes A, 1, 2 and 3, which have been shown to be the most accurate (Hays et al., 2001). To improve the track reconstruction, we discarded locations that necessitated speeds of travel more than 5 km h^{-1} and were at least 25 km from the previous location. This filter helped to remove locations that were probably erroneous as they necessitated unrealistically fast speeds of travel (James et al., 2005a). The filter removed 22 of 478 locations. We then calculated the mean daily position of the turtle. The track was plotted together with overlays of surface chlorophyll using the Maptool program (<http://www.seaturtle.org/maptool/>). Chlorophyll values used in the overlays were derived from

MODIS (Moderate-resolution Imaging Spectroradiometer, see: <http://oceancolor.gsfc.nasa.gov/>).

In addition to providing location data, the SRDL was also programmed to relay water temperature and dive information. Temperature data transmitted by this model of SRDL has been shown to successfully capture the thermal properties of oceans over extended space and time scales (McMahon et al., 2005). The SRDL included a pressure sensor, which was used to measure depth to an accuracy of 0.33 m every 4 s. These depth values were analysed onboard the SRDL, and individual dive profiles were then relayed via the Argos system (Hays et al., 2004b). Dive profiles were recorded when the dive depth exceeded 10 m. Profiles were numbered so that we could determine successive profiles and, hence, the post-dive surface interval. The SRDL also relayed the proportion of total time spent on dives > 10 m. Temperature–depth profiles were relayed for the deepest dive conducted every 4 h (provided the dive was over 20 m), with 12 temperature–depth points selected on the upcast (ascent) by a broken-stick algorithm (McMahon et al., 2005). Temperature was recorded with a precision of 0.01 °C and accuracy of 0.1 °C. Due to limited bandwidth within the Argos system, not every available dive profile or temperature–depth profile was obtained, so we collected a random sample of these profiles.

In addition to the detailed information for the turtle equipped with an SRDL in 2005, we also obtained location data from the same area for four additional turtles (two mature males and two mature females) equipped with Argos tags off Nova Scotia (Kiwisat 101, Sirtrack Ltd., Havelock North, NZ, $n=1$; Spot 4, Wildlife Computers, Redmond, WA, USA, $n=1$; SSC3, Wildlife Computers, Redmond, WA, USA, $n=2$). One turtle was tagged in 2000, and three turtles were tagged in 2003. All four satellite tags were programmed with a duty cycle of 24 h on and 24 h off. Due to this duty cycling, we did not examine mean daily positions, but instead used Argos location classes A, 1, 2 and 3 to reconstruct the turtles' movements. We removed positions at least 2 h apart which yielded rates of travel more than 5 km h^{-1} (after James et al., 2005a). These tags did not provide temperature–depth profiles.

3. Results

The turtle equipped with an SRDL travelled northeast along the coast of Nova Scotia to the northeast shore of Cape Breton Island before travelling northwest into the Gulf of St. Lawrence on 10 August 2005. She then travelled around the southern half of the Gulf of St.

Lawrence, before eventually travelling east along the north shore of Cape Breton Island, arriving at the most northerly tip on 22 September. She then proceeded south into the open waters of the North Atlantic (Fig. 1a). Evidence from leatherback turtles tracked in previous years suggests that their entry and prolonged seasonal residence in the southern Gulf of St. Lawrence is not unusual (Fig. 1b).

During her 44 day sojourn in the Gulf of St. Lawrence, the turtle equipped with an SRDL utilised relatively near-surface waters. 53% of the total time was spent on dives to deeper than 10 m. These dives had a mean duration of 6.0 min ($n=1312$, $SD=1.7$ min) (Fig. 2a). The maximum dive depth during this period occurred on 21 September with a dive to 96 m. The modal dive depth was around 20–25 m (Fig. 2b), although dives to over 40 m occurred throughout her residence period in the Gulf of St. Lawrence (Fig. 2c). Water depth was generally between 50 and 100 m. This turtle encountered very cold ambient temperatures, routinely diving into water less than 2.5 °C, with the minimum temperature experienced being 0.4 °C on

dives to 49 and 61 m on 5 and 6 September respectively (Fig. 2d). The modal surface interval between successive dives was 3 min (median 2.7 min, $n=902$ surface intervals relayed).

A clear pattern of temperature variation with depth was recorded during individual dives. Surface waters were about 17.5 °C (range 15.6–19.1 °C), and a thermocline existed between 15 and 30 m (Fig. 3a). Waters deeper than 40 m were uniformly cold: mean temperature at 20 m was 13.3 °C; at 30 m, 5.7 °C; at 40 m, 2.6 °C; and below 40 m, 1.6 °C (Fig. 3b). Dive duration increased with dive depth, suggesting that deep dives were not terminated prematurely due to cold water (Fig. 3b), a conclusion corroborated by examination of individual dive profiles to beneath the thermocline (Fig. 3c). Diving occurred throughout the day and night with no diel pattern (Fig. 3d).

4. Discussion

We have shown here that a leatherback turtle foraging at high latitude repeatedly dived into near-

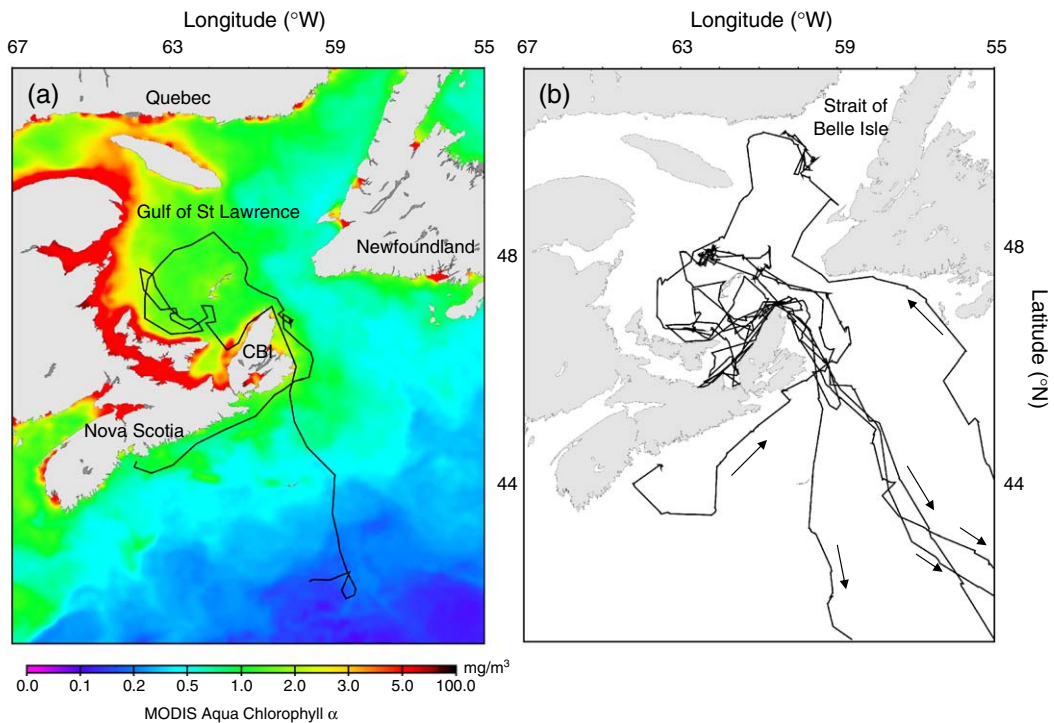


Fig. 1. (a) The track of a leatherback turtle, 16 July to 9 October 2005. Track is overlaid with the mean chlorophyll levels during August 2005 to indicate the higher productivity in coastal waters compared to the oceanic Atlantic. CBI = Cape Breton Island. (b) The tracks of four leatherback turtles equipped with Argos tags off Nova Scotia that utilised waters of the Gulf of St. Lawrence in 2000 ($n=1$), 2003 ($n=2$), and 2004 ($n=1$). Most northerly track represents movement of a turtle tagged in 2003 that returned to Canadian waters in summer 2004, venturing to an area heavily influenced by the cold Labrador current, which flows southwest into the Gulf of St. Lawrence through the Strait of Belle Isle. Arrows indicate direction of travel.

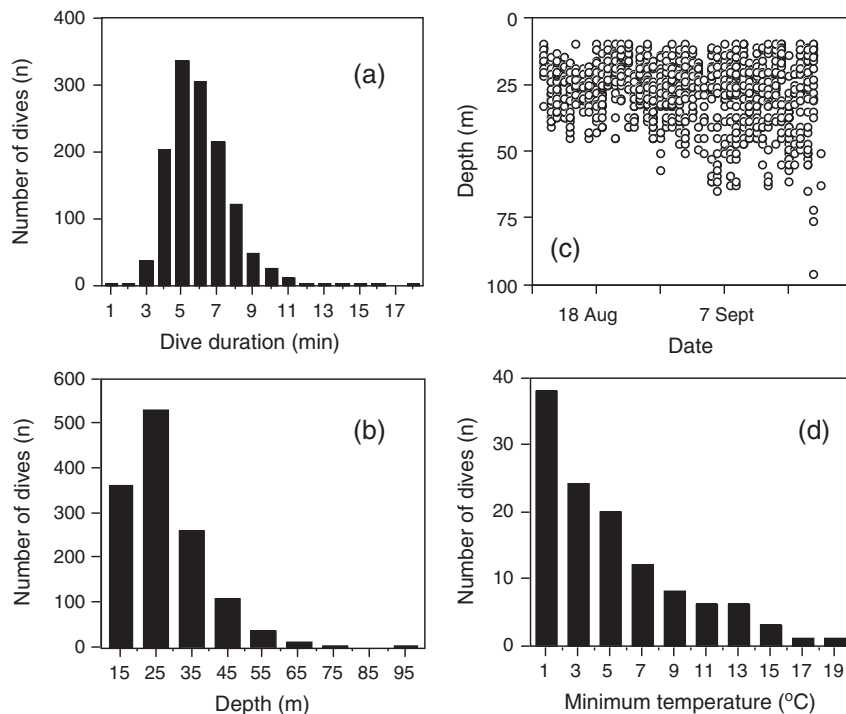


Fig. 2. Dive parameters for a leatherback turtle equipped with an SRDL in 2005. (a and b) Frequency histograms of dive durations and depths for dives to over 10 m ($n=1312$). (c) The depth of dives versus date. (d) Minimum temperatures recorded on individual dives to over 20 m.

freezing water for several weeks. Turtles in the Gulf of St. Lawrence will experience very cold water in all years, even with a pattern of relatively shallow diving. There have been extensive oceanographic studies in this region and it is well known that even in summer months, relatively warm surface water overlays very cold, near-freezing waters at a few tens of metres (Plourde and Theriault, 2004). Indeed, the region provides habitat for cold water species such as the Greenland shark (Stokesbury et al., 2005). While leatherback turtles in Canada are migrants from warm tropical waters, our results suggest that dives into cold sub-surface waters constitute normal behaviour, presumably associated with their search for jellyfish prey. Dives were relatively shallow compared to previous measurements in warmer waters (Hays et al., 2004a,b; James et al., 2005b). This finding is consistent with a shallower distribution of gelatinous zooplankton in colder water (Sparks et al., 2005). Furthermore in warmer waters at low latitude, leatherback turtles often show a diel periodicity in their diving with more diving at night (Hays et al., 2004a; James et al., in press), probably as a result of the vertical migration of their gelatinous zooplankton prey. The lack of a diel pattern in diving that we recorded in cold water, is consistent with other leatherback diving data from high latitudes (James et al., in press) and suggests that,

not only are gelatinous zooplankton found at shallower depths in cold water, but also that they do not exhibit marked vertical migration. However, more data on the vertical distribution of gelatinous zooplankton is needed to explore this hypothesis further.

Hard-shelled sea turtles (e.g. loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*) found in waters less than 8 °C are likely to be “cold stunned” (hypothermic and inactive), and will die after prolonged exposure (Spotila et al., 1997). While such species may survive seasonal temperatures below 20 °C in certain areas (such as the Mediterranean), at such temperatures they enter a quiescent state, resting on the seabed and conducting very long dives, sometimes more than 5 h in duration (Hochscheid et al., 2005). In contrast, our results suggest that leatherback turtles can remain active even in very cold water, down to at least 0.4 °C. Presumably leatherbacks move into cold regions to look for their jellyfish prey which may be abundant at high latitudes (Brodeur et al., 2002; James and Herman, 2001).

The gelatinous diet of leatherbacks poses energetic challenges in the context of cold water foraging (Davenport, 1998). *Dermochelys* is unique amongst endothermic/gigantothermic marine carnivores in consuming food with an extremely low lipid and energy

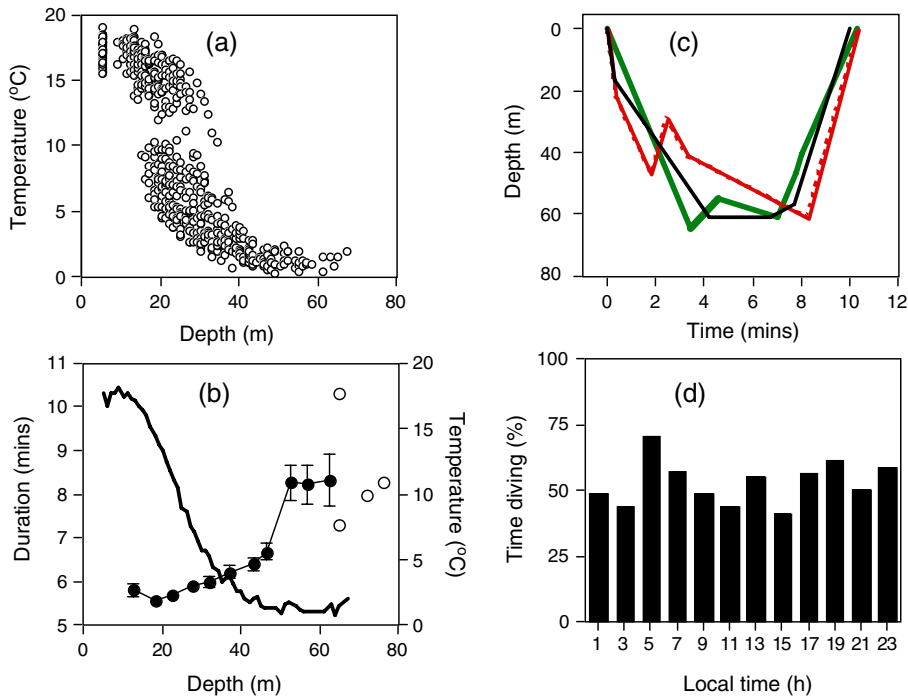


Fig. 3. Dive parameters for a leatherback turtle equipped with an SRDL in 2005. (a) Temperature and depth values relayed from a subset of 47 dives in which the minimum temperature was less than 2.5 °C illustrate the consistent decline in temperature with depth. (b) The relationships between dive depth, dive duration and water temperature. Dive duration: filled symbols show mean values (± 1 SE) for 5 m increments down to 65 m. Open symbols show individual dives deeper than 65 m. One dive (15.5 min to 96 m) is omitted for clarity. Temperature: solid line shows average temperatures for each 1 m increment in depth from 119 temperature–depth profiles. (c) Profiles of the three dives to around 60 m illustrate that dives were not terminated immediately upon entry into cold water beneath the thermocline. (d) The percentage of time spent diving in each 2-h period of the 24-h cycle indicates the lack of any strong diel variation in diving behaviour.

content, forcing the animals to consume large volumes of prey, potentially as high as 50% body mass d^{-1} or more (Davenport, 1998; Duron, 1978). Furthermore, feeding inevitably results in an intake of sea water along with jellyfish prey (Bels et al., 1998). Consequently, eating cold jellyfish could impose significant energetic costs upon leatherbacks, which would lose much of the meagre energetic benefits of their low-quality food in warming the jellyfish (and entrained water) to core body temperature (Davenport, 1998). In addition to their large size, insulation and counter-current heat exchangers, it is also possible that behavioural adaptations might help leatherback turtles stay warm while foraging in cold water. For example, carrying out short dives from warm surface waters into very cold (but relatively shallow) water to catch prey items that are not ingested until returning to the surface would not only minimise heat loss from the body surfaces, but would also allow leatherbacks to eat food that will be at least partially warmed. Future studies might test this possibility of behavioural mitigation of heat loss, building on previous work that has shown leatherback turtles consuming

large jellyfish at the surface in Canadian waters (James and Herman, 2001).

Leatherbacks are already known to be the most widely distributed reptiles in the world, occurring from the Barents Sea in the northern hemisphere, to the seas around South Island (New Zealand) (Gill, 1997). Our results reveal the existence of an even broader thermal niche resulting from the ability to dive into cold water. Any increases in surface water temperatures at high latitudes, for example, as a result of global warming, will most likely extend the foraging range of this species even further.

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