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RESEARCH ARTICLE

Behavioral and metabolic contributions to thermoregulation in freely swimming leatherback turtles at high latitudes

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ABSTRACT

Leatherback turtles in the Northwest Atlantic Ocean have a broad geographic range that extends from nesting beaches near the equator to seasonal foraging grounds as far north as Canada. The ability of leatherbacks to maintain core body temperature (T_b) higher than that of the surrounding water is thought to be a key element of their biology that permits them to exploit productive waters at high latitudes. We provide the first recordings of T_b from freely swimming leatherbacks at a northern foraging ground, and use these data to assess the importance of behavioral adjustments and metabolic sources of heat for maintenance of the thermal gradient (T_g). The mean T_b for individual leatherbacks ranged from 25.4±1.7 to 27.3±0.3°C, and T_g ranged from 10.7±2.4 to 12.1±1.7°C. Variation in mean T_b was best explained by the amount of time that turtles spent in the relatively warm surface waters. A diel trend in T_b was apparent, with daytime cooling suggestive of prey ingestion and night-time warming attributable to endogenous heat production. We estimate that metabolic rates necessary to support the observed T_g are ~3 times higher than resting metabolic rate, and that specific dynamic action is an important source of heat for foraging leatherbacks.

KEY WORDS: Endothermy, *Dermochelys coriacea*, Jellyfish, Diving, Reptile, Specific dynamic action

INTRODUCTION

Leatherback turtles, *Dermochelys coriacea* (Vandelli 1761), forage on gelatinous zooplankton in temperate waters of the North Atlantic Ocean during the summer and autumn (James et al., 2006; Heaslip et al., 2012). The ability of leatherbacks to tolerate cold water temperatures experienced at high latitude is attributed to morphological features and physiological and behavioral adjustments that permit maintenance of a thermal gradient (T_g) between core body temperature (T_b) and ambient water temperature (T_a). Point measurements of T_b obtained from leatherbacks captured off Cape Breton, NS, Canada, indicate a T_g of 5.1–10.8°C is achievable in waters with an average sea surface temperature of 16.2°C (James and Mrosovsky, 2004).

Adult leatherbacks typically weigh 250–600 kg, and a small surface area-to-volume ratio combined with extensive fat deposits beneath the shell and throughout the head and neck region predisposes them to heat retention (Davenport et al., 2009a; Davenport et al., 2011). Vascular heat exchangers at the base of the flippers (Greer et al., 1973) and blood flow adjustments (Bostrom et al., 2010) permit tight control of heat loss at the extremities, and a vascular plexus lining the trachea minimizes respiratory heat loss (Davenport et al., 2009b). In order to maintain a steady T_b in cold water, the rate at which heat is lost to the environment must be matched by the rate of heat gain. The evidence to date suggests that metabolic heat production serves as the primary source of heat gain in leatherbacks (Paladino et al., 1990; Bostrom and Jones, 2007; Bostrom et al., 2010), and models indicate that the T_g observed in adult leatherbacks necessitates metabolic rates substantially higher than resting levels (Bostrom et al., 2010). Previous studies have demonstrated that juvenile leatherbacks (16–37 kg) increase swimming activity in response to a decrease in water temperature, resulting in a larger T_g in cool water compared with warm water (Bostrom et al., 2010). The relative importance of skeletal muscle heat production versus heat produced by other vital organs for thermoregulation in adult leatherbacks is less clear. Given high rates of prey intake (Heaslip et al., 2012), specific dynamic action (SDA, i.e. heat produced from ingestion, digestion, absorption and assimilation of a meal) (Secor, 2009) may be an important source of heat gain for adult leatherbacks at high latitude foraging grounds. Metabolic rate can increase by 1.6–2.1 times following meal ingestion in captive sea turtles (Jones and Seminoff, 2013).

Leatherbacks can use behavioral means to alter both sides of the heat gain=heat loss equation. Adjustments in swimming behavior allow leatherbacks to modulate rates of heat production (Bostrom and Jones, 2007; Bostrom et al., 2010), and adjustments in dive patterns allow leatherbacks to modulate rates of heat loss. For example, leatherbacks in tropical waters exhibit a significant negative correlation between dive depth and T_b (Southwood et al., 2005). Behavioral selection of cooler T_a at depth may act in conjunction with circulatory adjustments to permit effective heat transfer and prevent overheating while in tropical waters (Southwood et al., 2005; Wallace et al., 2005). Conversely, utilization of warmer surface waters while resident at high latitude foraging grounds may facilitate heat retention and maintenance of elevated T_b. Increased time at the surface would also allow for basking if environmental conditions were appropriate (James et al., 2005).

In this study, we document for the first time T_b of freely swimming adult leatherbacks during the resident foraging period and post-resident migration at high latitudes. Our primary goal was to investigate the behavioral and metabolic factors that contribute to the maintenance of elevated T_b under natural conditions. We deployed a combination of stomach temperature pills (STPs) and satellite-linked data recorders on leatherback turtles offshore Eastern Canada. The instrumentation provided data on dive patterns, T_b within the gastrointestinal tract, T_a, and location via the Argos Satellite System. Linear mixed models were used to explore the effects of dive behavior, diel status and residency status on T_b and the maximum change in T_b (ΔT_b). We used our calculated values for mean T_g, a range of values for insulation thickness of the shell (L), and data and equations from the published literature to estimate rates

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List of symbols and abbreviations

A	surface area of shell
CCL	curved carapace length
C_P	specific heat capacity of prey
k	thermal conductivity of shell
L	insulation thickness
M_P	mass of ingested prey
ME	meal energy
MR	metabolic rate
PTT	platform transmitter terminal
$\dot{q}_F$	heat transferred across flippers
$\dot{q}_P$	heat transferred to ingested prey
$\dot{q}_S$	heat transferred across the shell
$\dot{q}_T$	heat loss
SDA	specific dynamic action
SSM	state space model
STP	stomach temperature pill
T_a	ambient temperature
TAT	time-at-temperature
T_b	body temperature
T_g	thermal gradient
ΔT_b	change in body temperature

of heat transfer to ingested prey ($\dot{q}_P$) and heat transfer to the external environment across the shell ($\dot{q}_S$) and flippers ($\dot{q}_F$). Assuming that the mean T_g reflects maintenance of an internal thermal steady state, heat production (i.e. metabolic rate, MR) is equivalent to total heat transfer, $\dot{q}_T$ ($=\dot{q}_P+\dot{q}_S+\dot{q}_F$) (Bostrom et al., 2010). We evaluate the contribution of SDA to heat production in foraging leatherbacks, and consider the energetic cost associated with thermoregulation.

RESULTS

Satellite track durations ranged from 56 to 131 days, but for this study we focused only on data during the T_b monitoring period north of 42°N (range 12–60 days, Table 1). Turtles with T_b monitoring periods <45 days were assumed to have excreted the STP; cessation of T_b transmissions in all other turtles was assumed to reflect battery failure of the pill. The T_b transmissions for two turtles ceased during the resident period; T_b transmissions for five turtles extended into the post-resident period (Fig. 1). The mean rate of travel was 1.8 times higher during the post-resident period (2.7±0.7 km h^{-1}) compared with the resident period (1.5±0.3 km h^{-1}). Leatherbacks maintained a consistent dive pattern over the course of the entire monitoring period, with the same mean dive depth (20±6 m) during the resident and post-resident periods (Table 2). The mean percentage time at the surface was similar for the resident (41±8%) and post-resident (36±13%) periods (Table 2).

Mean T_b for individual turtles for the entire monitoring period ranged from 25.4±1.7 to 27.3±0.3°C. Mean T_a experienced by turtles over the course of the entire monitoring period ranged from 13.6±6.4 to 15.9±2.0°C, and mean T_g ranged from 10.7±2.4 to 12.1±1.7°C. Table 1 provides data on mean T_b, T_a and T_g for the resident and post-resident periods separately for each turtle. Fig. 2 provides an illustration of the daily variation in T_b for a female leatherback turtle (519 kg), and shows the stability of mean daily T_b in relation to T_a. The average mass of turtles was 467±76 kg (N=5). There was no significant correlation between mass and T_b (d.f.=3, r=0.809, P=0.097).

Results of the linear mixed models showed that the percentage time at the surface and diel status were the best predictors of mean T_b (Table 3). The 95% confidence intervals for the model estimates of percentage time at the surface (0.0326, 0.0902) and diel status (0.0014, 0.9888) excluded zero, which indicates a strong effect for both of these factors. The mean T_b increased with increased time at the surface, and mean night-time T_b tended to be higher than mean daytime T_b (Fig. 3). A strong diel effect was also observed for mean ΔT_b. The 95% confidence interval for the model estimate of diel status (1.3365, 3.1808) excluded zero. Negative values for ΔT_b (−1.2±1.1°C), indicative of cooling, occurred during the day and positive values for ΔT_b (1.5±1.2°C), indicative of warming, occurred at night (Fig. 2B).

Fig. 4A illustrates estimated $\dot{q}_T$ during the resident period of leatherbacks for which mass was measured. The mean $\dot{q}_T$ decreases as insulation thickness (L) increases: 698±123 W at L=2 cm, 478±87 W at L=3.5 cm, 390±73 W at L=5 cm. The estimated mass-specific MR based on $\dot{q}_T$ decreases accordingly as L increases (Fig. 4B): 1.498±0.122 W kg^{-1} at L=2 cm, 1.026±0.082 W kg^{-1} at

Table 1. Morphometric data, body temperature (T_b), ambient temperature (T_a) and thermal gradient (T_g) for leatherback turtles monitored while freely swimming in Canadian waters north of 42°N in 2009

						T_b (°C)		T_a (°C)*		T_g (°C)	
Turtle ID	Sex	CCL (cm)	Mass (kg)	Resident period (N=7)	Post-resident period (N=5)	Resident	Post-resident	Resident	Post-resident	Resident	Post-resident
DCTM	M	141.1	NA	21/8/2009–9/9/2009	9/9/2009–20/10/2009	26.3±1.3	24.5±1.1	15.3±2.1	11.1±1.4	11.0±2.8	13.3±1.5
DCUF	F	150.2	391	22/8/2009–3/9/2009	na	25.4±1.7	na	13.6±6.4	na	11.9±5.3	na
DCVM	M	147.6	403	22/8/2009–27/9/2009	na	25.9±1.3	na	15.4±2.2	na	10.7±2.4	na
DCWF	F	142.6	433	22/8/2009–20/9/2009	20/9/2009–8/10/2009	26.7±0.9	26.8±0.4	16.8±1.5	13.0±0	10.0±1.6	14.1±0.2
DCXF	F	151.0	519	25/8/2009–24/9/2009	24/9/2009–5/10/2009	27.2±0.6	27.6±0.4	15.1±1.4	15.7±2.5	12.2±1.6	11.9±2.5
DCYM	M	163.9	NA	26/8/2009–28/9/2009	28/9/2009–23/10/2009	26.2±1.1	25.3±1.2	15.2±1.8	13.1±0.9	10.9±1.8	12.1±0.9
DCZF	F	161.8	589	26/8/2009–14/9/2009	14/9/2009–20/9/2009	26.9±0.8	27.1±0.4	15.7±2.1	17.0±1.4	11.2±2	10.2±1.6
Grand mean ± s.d.		151.1±8.1	467±76			26.4±0.6	26.3±1.2	15.3±0.9	14.0±2.1	11.1±0.7	12.3±1.3

Resident and post-resident periods are given as day/month/year. N, number of turtles; CCL, curved carapace length.
*Based on the number of 6 h time-at-temperature (TAT) blocks for T_a that corresponded with core body temperature T_b data and were suitable for analysis. The number of TAT blocks used ranged from 3 to 70 during the resident period, and from 2 to 9 during the post-resident period.

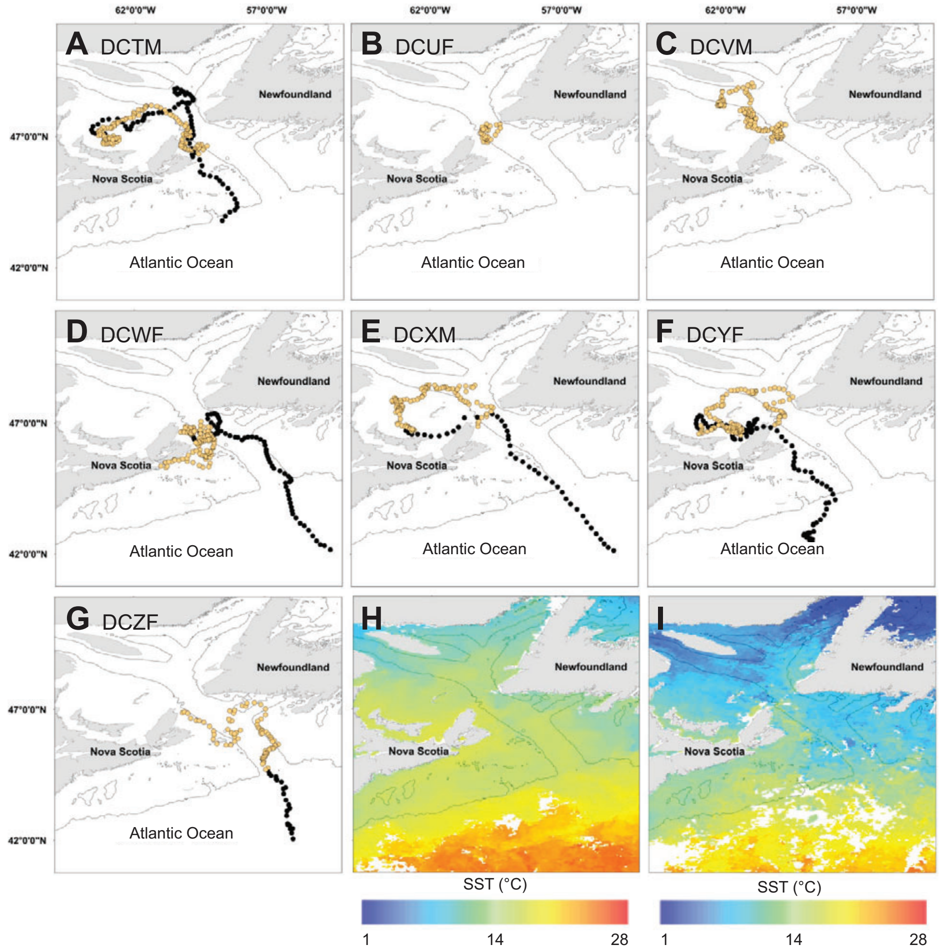

Fig. 1. State space model (SSM) tracks of leatherback sea turtles tracked offshore Eastern Canada. (A–G) Tracks show resident (yellow circles) and post-resident (black circles) periods of leatherback turtles in Canadian waters north of 42°N. Monthly mean sea surface temperature (SST) data for September (H) and October (I) of 2009 were recorded by Advanced Very High Resolution Radiometer (AVHRR) onboard NOAA Polar-orbiting Operational Environmental Spacecraft (Pathfinder Version 5, 4.4 km resolution). DC identifiers correspond to different turtles.

L=3.5 cm and 0.837±0.066 W kg^{-1} at L=5 cm. As L increases, the proportion of $\dot{q}_{\mathrm{T}}$ attributable to heat loss across the body surface ($\dot{q}_{\mathrm{S}}$ and $\dot{q}_{\mathrm{F}}$) decreases and the proportion due to $\dot{q}_{\mathrm{P}}$ increases (Fig. 4A). Mean $\dot{q}_{\mathrm{P}}$ is 186 W, or 0.397 W kg^{-1}. The calculated rate of heat production due to SDA was 0.439 W kg^{-1}.

DISCUSSION

Our results indicate that leatherbacks maintained T_{g}≥10°C in Canadian waters through a combination of both behavioral and physiological means. The amount of time that turtles spent in relatively warm (~15–17°C) surface waters had a strong influence on mean T_{b} (Table 3, Fig. 3). Individual leatherbacks spent 16–54% of time at the surface while north of 42°N. These results align with previous research at our study site, which documented surface times up to 41% for leatherbacks (James et al., 2005). Factors related to both foraging and thermoregulation are likely to contribute to the large amount of time spent at the surface. Leatherbacks have been observed to float at the surface to process large prey items (James and Mrosovsky, 2004; James et al., 2005), although video documentation from turtle-borne cameras suggests that the majority of prey can be manipulated and ingested in under 5 min (Heaslip et al., 2012). Modification of dive patterns to exploit warmer water at the surface and reduce rates of heat loss may be an important component of the leatherback's thermoregulatory strategy at high latitudes. Sightings of leatherbacks passively floating at the surface, flippers extended, during daylight hours at northern foraging grounds provide evidence that turtles may also bask to absorb solar radiation (James et al., 2005; Lindgren et al., 2014).

While basking may augment heat gain under suitable environmental conditions, the primary source of heat gain for

Table 2. Dive behavior and rate of travel for leatherback turtles monitored while freely swimming in Canadian waters north of 42°N

	Depth (m)		% Time at surface		Rate of travel (km h^{-1})	
Turtle ID	Resident	Post-resident	Resident	Post-resident	Resident	Post-resident
DCTM	29±13	28±16	29±13	16±13	1.3±0.6	2.5±1.1
DCUF	22±8	na	41±15	na	1.4±1.3	na
DCVM	16±6	na	45±16	na	1.3±1.0	na
DCWF	10±11	14±34	43±27	34±28	1.4±1.0	2.2±1.1
DCXF	18±10	20±19	49±18	46±16	1.5±0.9	3.8±1.3
DCYM	22±11	14±14	30±20	31±26	1.4±0.8	2.2±1.0
DCZF	21±11	23±23	50±22	54±26	2.2±1.3	2.8±1.3
Grand mean ± s.d.	20±5	20±5	41±8	36±13	1.5±0.3	2.7±0.7

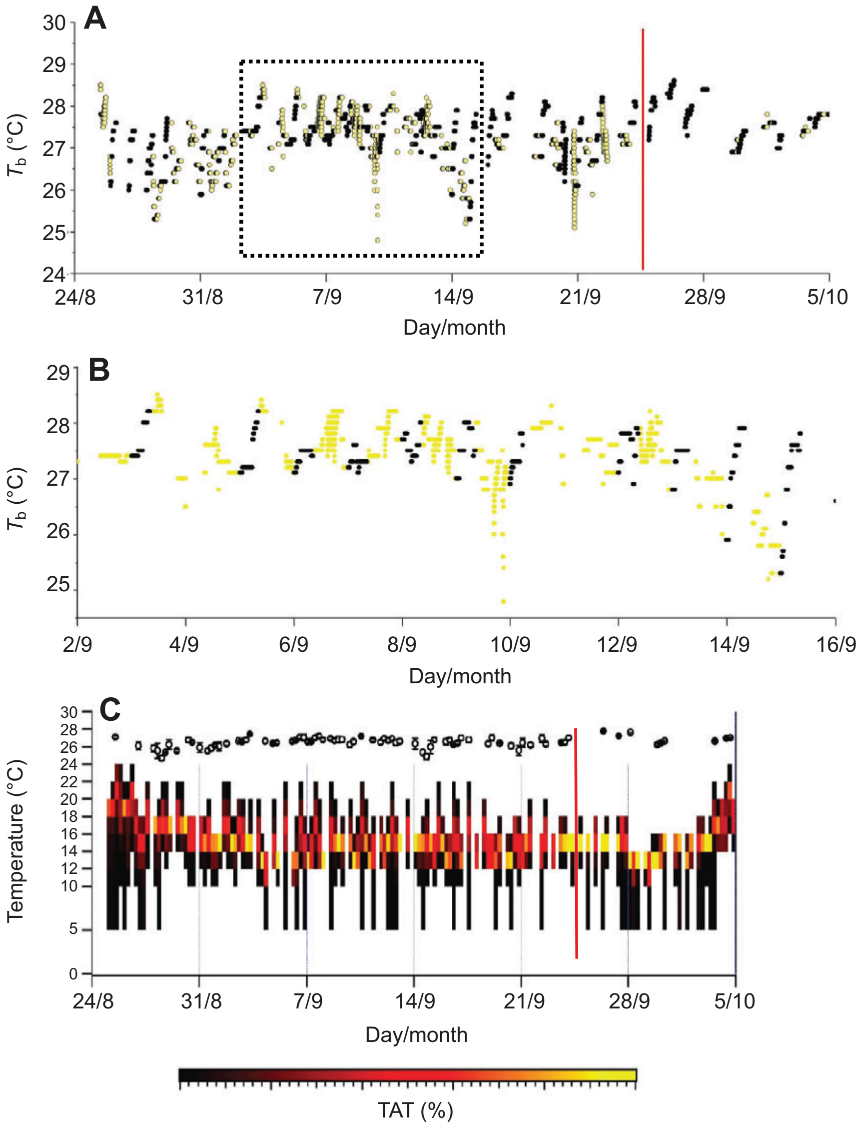

Fig. 2. Body temperature of a female leatherback sea turtle tracked offshore Eastern Canada between 25 August 2009 and 5 October 2009. (A) Filtered core body temperature (T_b) data for turtle DCXF over a 41.5 day monitoring period. The solid vertical line divides resident and post-resident periods and the area outlined by the dotted rectangle is expanded in B to demonstrate the trend of daytime cooling (yellow circles) and night-time warming (black circles). (C) Mean (±1 s.d.) T_b (open circles) plotted with ambient ocean temperature (T_a) data from 6 h time-at-temperature (TAT) blocks (shaded bars) illustrates the magnitude of the thermal gradient maintained by leatherbacks at high latitude.

leatherbacks derives from metabolic processes. Compelling evidence to support this assertion is found in the diel trends observed for T_b and ΔT_b. It is important to note that we measured T_b from within the gastrointestinal tract; consequently, variation in T_b reflects cooling due to prey ingestion and warming due to SDA and transfer of heat via blood flow. We observed a trend for T_b of daytime cooling, suggestive of diurnal foraging, and night-time warming (Fig. 2). Model results did not show a strong correlation between dive parameters (depth and percentage time at the surface) and diel status, so alterations in dive behavior are unlikely to contribute to the night-time warming trend. We conclude that endogenous heat production warms gastrointestinal tract contents and accounts for the positive ΔT_b observed during the night.

The non-surgical method used for deploying the STPs in this study limited our ability to know the precise location of the pills while monitoring T_b. It is possible that our measurements of T_b

Table 3. Results of linear mixed models to assess the factors contributing to variation in T_b and the maximum change in T_b (ΔT_b)

Model	K*	log(1)	AIC$_c$	Δ_i	w_i
T_b					
% Surface + diel + state + (1|subject)	6	−25.30	67.551	4.5178	0.0474
% Surface + state + (1|subject)	5	−26.85	67.043	4.0100	0.0611
% Surface + diel + (1|subject)	5	–24.85	63.033	0.0000	0.4538
% Surface + (1|subject)	4	–26.53	63.165	0.1319	0.4248
ΔT_b					
Depth + diel + (1|subject)	5	−37.91	89.163	7.7481	0.0200
% Surface + diel + (1|subject)	5	−38.43	90.193	8.7781	0.0119
Diel + (1|subject)	4	–35.66	81.415	0.0000	0.9610

Models that incorporated a diel influence and the percentage time spent at surface provided the best fit to explain variation in T_b. Variation in ΔT_b showed a strong diel influence.

*Parameter count includes intercept and variance.

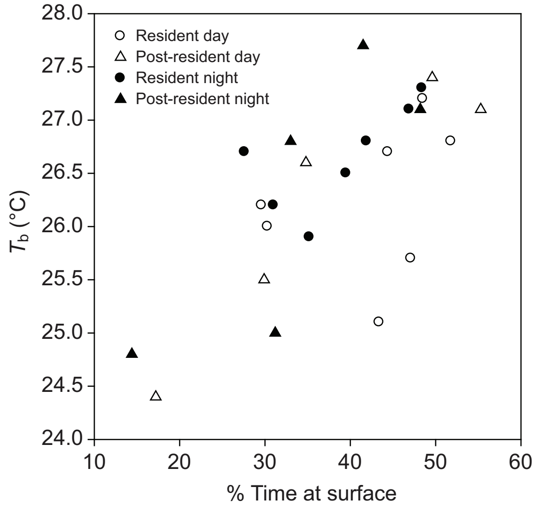

Fig. 3. Mean daytime and night-time T_b of individual leatherback turtles during the resident and post-resident period offshore Eastern Canada plotted against the percentage time spent in surface waters. Results from linear mixed models indicate that variation in T_b is best explained by the percentage of time spent in warmer surface waters. A diel effect was also detected, with a trend towards higher T_b at night.

underestimate the true core temperature, as a result of decreases in T_b with prey ingestion. Alternatively, processes external to the gastrointestinal tract known to be involved in SDA [e.g. amino acid catabolism, anabolic processes and urea production by the liver (McCue, 2006)], as well as the localized effects of SDA within the stomach and small intestine, may result in T_b that is higher than temperatures in other parts of the core. The mean T_b for leatherbacks during the residency period in the current study (26.4±0.6°C, mass 391–589 kg) is 2.1°C higher than the mean cloacal temperature recorded for four leatherbacks captured at our study site and brought on-deck of a research vessel during a 2002–2003 field season (24.3±1.9°C, mass 315–380 kg) (James and Mrosovsky, 2004). Our calculations of T_g assume that T_b recorded in the gastrointestinal tract and averaged over a period of several days to weeks provides a good estimation of temperature throughout the body core.

Metabolic rates necessary to sustain observed T_g depend heavily on the thickness of the insulation layer underlying the shell (L) and rates of prey ingestion. Measurements of L obtained from stranded leatherbacks within our study area fall within the range of 2–5 cm (M.C.J., unpublished data). The mean mass-specific MR required to offset $\dot{q}_T$ and maintain T_g for a foraging leatherback with L=3.5 cm is 1.026 W kg^{-1}, 3.3 times higher than the average resting MR (0.312 W kg^{-1}) (Wallace and Jones, 2008) but still considerably lower than maximal MR recorded for adult leatherbacks on nesting beaches (1.510 W kg^{-1}) (Paladino et al., 1990). Insulation thickness is likely to increase over the course of the foraging season as leatherbacks store energy for migration, and this could result in a substantial decrease in $\dot{q}_T$ and thermoregulatory costs (Fig. 4) (Davenport et al., 2011). Our estimates of MR based on field measurements of T_g are in agreement with outputs from previous models of leatherback thermoregulatory abilities based on laboratory studies (Bostrom and Jones, 2007; Bostrom et al., 2010).

Leatherbacks ingest large quantities of cold jellyfish during the foraging season (Heaslip et al., 2012), and a substantial amount of energy must be allocated to warm prey to core temperature (Davenport, 1998). The metabolic cost of warming food ($\dot{q}_P$) is included in SDA, and can account for a large proportion of the total SDA response in cold environments (Secor, 2009). Based on our estimates for $\dot{q}_P$ (0.397 W kg^{-1}) and SDA (0.439 W kg^{-1}), over 90% of the heat production attributed to SDA goes towards warming prey. Depending on the degree of insulation, SDA may account for ~30–50% of MR for leatherbacks during the foraging period (Fig. 4A). These estimates illustrate that visceral metabolic heat production plays an important role in maintaining stable T_b for leatherbacks foraging in cold water.

Cessation of area-restricted searching and an increase in the rate of travel occur as leatherbacks transition from resident foraging to post-resident migration. Surprisingly, model results indicated that residency status did not have a strong effect on mean T_b, and the pattern for ΔT_b of daytime cooling and night-time warming persisted into the post-residency period, although it was slightly attenuated (Fig. 2). Furthermore, model results did not show a strong correlation between dive parameters (depth and percentage time at the surface) and residency status and there were no obvious shifts in dive behavior (Table 2). Taken together, these results provide evidence that leatherbacks continue to forage in the early stages of migration. The increase in the rate of travel with the onset of southward migration occurs without an appreciable change in dive patterns, which suggests that leatherbacks simply are moving in a more directed manner to cover greater distances in a given time. Under these circumstances, prey encounters may be opportunistic and prey ingestion rates are likely to be lower.

Measurements of T_b in freely swimming leatherbacks provide important insight into the factors that contribute to thermoregulation in this wide-ranging reptile. Our field data validate earlier models to assess leatherback thermoregulatory capacity (Paladino et al., 1990; Bostrom and Jones, 2007; Bostrom et al., 2010) and we provide additional support for endothermy in leatherbacks by illustrating the role of heat produced in visceral organs (SDA) for maintenance of

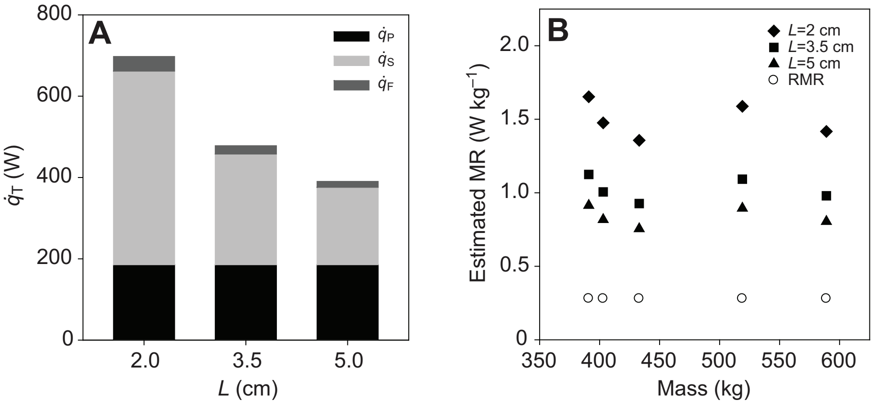

Fig. 4. Estimates for total heat transfer and metabolic rate of leatherback sea turtles at high latitude. (A) Estimates of total heat transfer ($\dot{q}_T$) represented as the sum of heat transferred to ingested prey ($\dot{q}_P$) and heat loss across the shell ($\dot{q}_S$) and flippers ($\dot{q}_F$) at various values for insulation (fat) thickness L. In order to maintain a thermal gradient, rates of metabolic heat production must equal $\dot{q}_T$. (B) Estimated mass-specific metabolic rate (MR) based on $\dot{q}_T$ for five leatherbacks during the resident period assuming an insulation thickness L of 2, 3.5 and 5 cm. Resting metabolic rate (RMR) was calculated as RMR=0.768mass$^{-0.169}$ (Wallace and Jones, 2008).

T_g. As more data become available from remote monitoring studies conducted in both tropical and temperate waters, a clearer picture emerges of the integrative and versatile thermal strategy employed by leatherbacks. Mean T_b values recorded from leatherbacks foraging in Canadian waters (25.4–27.3°C) were remarkably similar to mean T_b recorded using the same techniques with leatherbacks during the nesting season in the Caribbean Sea (28.1–28.7°C) (Casey et al., 2010). The ability of leatherbacks to address thermal challenges and maintain high, stable T_b over a broad range of temperatures is the result of morphology and the orchestration of behavioral and physiological adjustments.

MATERIALS AND METHODS

Instrument deployment

Pre-calibrated stomach temperature pills (STP, 30 g in air, 63×24 mm, battery life 45–65 days, range 0–50°C, resolution 0.1°C; Wildlife Computers, Redmond, WA, USA) and platform transmitter terminals (PTT, 175 g in air, 93×52×26 mm, battery life 100–120 days; Wildlife Computers) were deployed on seven leatherbacks captured off Northern Cape Breton Island, NS, Canada (~47°N, 60°W), during August 2009 (Table 1). Turtles were live-captured at the surface, measured (curved carapace length, CCL), weighed, and equipped with identification tags (James et al., 2005). A PTT was attached using Tygon-coated stainless steel wires passed through drill holes (4 mm diameter) in the medial ridge (Casey et al., 2010). The turtle's mouth was opened using nylon straps and an STP was inserted ~40 cm into the esophagus using a lubricated, flexible tube (Casey et al., 2010). Turtles were released within 30 min of capture. All procedures were conducted in accordance with UNCW IACUC Protocol A0809-018 and Fisheries and Oceans Canada Licenses 323395 and 323398.

Data collection

The ingested STP emitted a pulse-coded acoustic signal that corresponded to the coldest temperature detected by the instrument's thermistors (T_b). The T_b data were transmitted to and archived by the PTT at 1–2 min intervals. The effective range for communication between the STP and PTT was ≤2 m. Each PTT communicated with the Argos satellite system on a 24 h duty cycle for the first 40–44 days, and thereafter on a 48 h duty cycle. The PTT relayed archived time-series T_b data and binned data for T_a (range: −40 to +60°C, resolution 0.05°C) in 6 h blocks starting at 00:00 h (GMT). Data for T_a were transmitted as the total percentage of each 6 h block spent in a given temperature bin (time-at-temperature, TAT; see below). The PTTs also relayed dive behavior messages that included maximum depth (up to 1000 m, resolution 0.5 m), dive duration and post-dive surface time for dives with depths that exceeded 3 m. Turtles were considered to be at the surface at depths <3 m. Percentage time spent at the surface was calculated based on the dive duration and post-dive surface time for individual dives. The Argos satellite system provided Doppler-derived locations for the PTTs and an index of location accuracy from <150 to >1000 m.

Analysis and statistics

A state space model (SSM) interpolated latitude and longitude at 6 h intervals, using raw Argos locations (Jonsen et al., 2007). The SSM assigned a turtle's 'state' as either transiting or foraging based on rate of travel and turning frequency and angles. We interpreted a shift from resident to post-resident status when a turtle was no longer detected foraging north of 44°N. Only post-resident locations north of 42°N were included in our analyses to ensure that resident versus post-resident comparisons of T_b and T_g were made at similar T_a. Twenty rate of travel measurements, calculated as the distance between two consecutive SSM locations divided by the time lag between locations, were randomly sampled from each turtle's resident and post-resident period for descriptive statistics. A daily SSM location closest to 12:00 h (GMT) was used to determine the start/end time for daytime and night-time periods based on nautical twilight (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). A random sample of 200 dive behavior messages from both the resident and post-resident periods were used to calculate descriptive statistics for dive parameters.

Analyses of time-series T_b data were constrained by the sporadic nature of STP transmissions. The T_b data were manually filtered for erroneous records, which occurred because of interrupted STP–PTT communication (OriginLab Corporation, Northampton, MA, USA). We then selected daytime and night-time periods that contained ≥30% of total possible T_b readings for diel analyses of mean T_b and maximum change in T_b (ΔT_b). Random samples of 1500 T_b readings were drawn from the filtered data for the resident and post-resident periods to calculate mean T_b for each period and the entire monitoring period.

The manually filtered T_b data were also partitioned into 6 h blocks to correspond with TAT bin data for T_a. Only 6 h blocks with >40% of total possible T_b readings were analyzed. A single temperature value was assigned to each TAT bin for T_a: 0–5°C=5°C, 5–10°C=10°C, mean value for bins with intervals of 2°C, and >32°C=32°C. A proportional analysis was used to determine a representative T_a for each 6 h block based on the percentage time spent in each TAT bin. For example, if a turtle spent 60% of time in the 16–18°C bin and 40% of time in the 14–16°C bin, a T_a of 16.2°C [(0.6×17)+(0.4×15)] was assigned for that 6 h block. The T_g for each 6 h block was calculated using the mean T_b and T_a.

We used linear mixed models to investigate factors affecting T_b and ΔT_b (lme4 package, R software, http://www.r-project.org). The mean percentage time at the surface, mean dive depth, diel status (day or night) and SSM state (resident or post-resident) were treated as fixed effects in the models, and turtle identity was treated as a random effect. Given the temporal limitations of the TAT data, we did not include T_a in the models. We assumed that T_a varies with depth. Models that exhibited subject variance ≥60% of the total variance were excluded from further analysis. We used second order AIC corrected for small sample size (AIC$_c$), AIC differences (Δ_i) and Akaike weights (w_i) to evaluate models (Akaike, 1974). Confidence intervals calculated using Markov chain Monte Carlo simulations were used to assess the strength of fixed effects in models that exhibited the best fit. We did not include mass in the models, as we had just one measurement taken at the time of capture and could not predict mass change over the course of the foraging season (Davenport et al., 2011). The potential influence of mass on mean T_b for the entire monitoring period was investigated using Pearson's correlation.

To estimate metabolic heat production for leatherbacks, we assumed that (1) blood flow results in continual heat exchange throughout body core (Paladino et al., 1990) and (2) mean T_b reflects maintenance of an internal thermal steady state in relation to T_a. Under these conditions, heat production (i.e. metabolic rate, MR) is equivalent to total heat transfer ($\dot{q}_T$) (Bostrom et al., 2010), i.e. the sum of heat transfer to ingested prey ($\dot{q}_P$) and heat transfer to the external environment (i.e. heat loss) across the shell ($\dot{q}_S$) and flippers ($\dot{q}_F$). Heat loss from the head and neck is assumed to be negligible as a result of extensive insulation (Davenport et al., 2009a). Heat loss due to excretion has not been well characterized for leatherbacks, but is assumed to be small relative to other sources of heat loss:

$$\dot{q}_S = (A\ k\ T_g)\ L^{-1} \tag{1}$$

(Bostrom et al., 2010) where A is the surface area of the shell (m^2), calculated as A=0.049mass$^{0.69}$ (Bostrom et al., 2010); k is the thermal conductivity of the shell, 0.25 W m^{-1} K^{-1} (Bostrom et al., 2010); T_g is the mean thermal gradient (K); and L is insulation thickness (m):

$$\dot{q}_F = (\dot{q}_S\ /\ 0.93) - \dot{q}_S\ , \tag{2}$$

as $\dot{q}_F$ accounts for approximately 7% of total surface heat loss in cold water (Bostrom et al., 2010):

$$\dot{q}_P = M_P\ C_P\ T_g \tag{3}$$

(Bostrom and Jones, 2007) where M_P is prey mass consumed, equivalent to 73% of leatherback mass per day (Heaslip et al., 2012), or mass (8.45×10^{-6}) for units of kg s^{-1}; and C_P is the specific heat capacity of prey (4186 J kg^{-1} K^{1}) (Bostrom and Jones, 2007). We assume our calculated T_g provides a good approximation of the difference between core T_b and prey temperature, and warming of prey prior to ingestion is minimal (Heaslip et al., 2012).

Estimates for rate of heat production due to SDA were obtained by applying a general equation for SDA of reptiles: SDA=0.26ME–10.65, where ME is the meal energy (kJ) ingested per day based on published energy values for jellyfish prey (0.2 kJ g^{-1}) (Doyle et al., 2007) and prey consumption equivalent to 73% of body mass per day (340,910 g of jellyfish for a 467 kg turtle) (Heaslip et al., 2012). The resulting value of SDA (kJ) for an average day's foraging effort was then converted to W kg^{-1}, using our mean mass of 467 kg.

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Competing interests

The authors declare no competing financial interests.

Author contributions

J.P.C., M.C.J. and A.S.W. contributed to the conception and design of the experiment, interpretation of findings, and drafting and revision of the manuscript. J.P.C. and M.C.J. conducted field work, and A.S.W. conducted metabolic analyses.

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