Exercise warms adult leatherback turtles ☆

Brian L. Bostrom *, David R. Jones

Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

Abstract

Leatherback sea turtles (*Dermochelys coriacea*) can maintain body temperature (T_B) up to 18 °C above that of the surrounding sea water (T_W) which allows leatherbacks to enter cold temperate waters and have the largest global range of any reptile. Using a cylindrical model of a leatherback we investigated the extent to which heat production through variation of swim speed could be used in a leatherback's thermal strategy. Drag force of a full scale cast of a leatherback was measured in a low velocity wind tunnel to obtain an estimate of the metabolic cost needed to offset drag. Heat released in the core of a turtle as a byproduct of the metabolic cost of locomotion is conducted from the core of the turtle to the surrounding water through its insulation layer. By keeping insulation thickness constant, we highlight the effectiveness of swim speed in maintaining $T_B - T_W$. Our model, when tested against published data at a given T_W, showed a close correlation between predicted and measured swimming speed at a given T_B. We conclude that the ability to maintain a large $T_B - T_W$ is an interplay between mass, insulation thickness and water temperature selection but behavioural control of swimming speed predominates.
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1. Introduction

Leatherback sea turtles (*Dermochelys coriacea*) have the greatest global distribution of all sea turtles. Not only are they the deepest diving, having been recorded diving to depths over 1200 m (Hays et al., 2004), but also have the largest global range. Leatherbacks migrate thousands of kilometers from tropical nesting beaches to distant foraging grounds (Morreale et al., 1996; Hughes et al., 1998). As a result, leatherbacks experience ambient water temperatures (T_W) ranging from 0 °C in the high latitudes to 30 °C in the tropics (Goff and Lien, 1988). Impressively, they do not cool down to the point of becoming lethargic when foraging on gelatinous zooplankton in temperate waters, or overheat when venturing into warm tropical waters. Obviously, leatherbacks' thermal biology is an integral part of their ability to venture into regions that are out of reach of other marine turtles.

In the tropics, female leatherbacks maintain body temperatures (T_B) 1.2 to 4.3 °C higher than T_W (Southwood et al., 2005). Recently, foraging leatherbacks captured off the coast of Nova Scotia, Canada, had an average T_B 8.2 °C above surface water that was at 15 °C (James and Mrosovsky, 2004). This is an amazing feat considering the leatherback may spend up to 40% of the time foraging at depth in water much colder than at the surface. Ingestion of large volumes of prey offers a substantial thermal challenge due to the high heat capacity and cold temperature of gelatinous zooplankton (Davenport, 1998).

Many reptiles use behavioural means to regulate T_B. When faced with changes in ambient temperature they vary body position and/or move between thermal environments to keep T_B in an optimum range (Avery, 1982). Crocodiles, when faced with seasonal or daily changes in ambient temperature, vary the time spent on land and in water to regulate a high and stable T_B (Seebacher et al., 1999). Marine iguanas (*Amblyrhynchus cristatus*) spend a large percentage of time basking on shore to counteract the heat they lose to the ocean during foraging excursions (Trillmich and Trillmich, 1986).

Such behavioral strategies, however, are not feasible for ectotherms continually roaming a marine environment. They are unable to escape the high convective heat loss of water and, in

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higher latitudes, large thermal gradients. In addition, relying on solar energy for heat is not a viable option due to the rapid absorption of infrared radiation by sea water and possible cloudy conditions. Metabolic heat is thus particularly important in a marine animal's thermal biology. Loggerhead turtles maintain T_B above T_W without staying near the surface and basking (Sato et al., 1995). Sato et al. (1995) found no correlation between T_B and light intensity. This suggests the loggerheads' elevated T_B came purely from metabolic processes. A thermal gradient of up to 8 °C has been measured between T_W and the pectoral muscles of a vigorously swimming green turtle (Chelonia mydas) compared with only 1–2 °C when at rest (Standora et al., 1982). In the tropics, leatherbacks do not spend time near the surface basking, again suggesting that heat production is purely metabolic (Eckert, 2002).

For marine animals to maintain large temperature gradients retaining metabolic heat is essential. Some tunas are able to maintain regions in their body 10 °C above T_W by using counter-current heat exchangers to control heat loss (Brill et al., 1994). Another important physical attribute for heat retention is large size. Larger animals have a lower surface area to volume ratio than smaller animals. Since heat energy is lost through an animal's surface there is an effective dampening effect on changes in T_B in large animals. This phenomenon is referred to as thermal inertia. The amplitude of fluctuations in crocodile T_B as a result of changing ambient temperatures decreases with an increase in body mass (M_B) (Seebacher et al., 1999).

Due to large thermal gradients (T_B-T_W) in cold water leatherbacks must be particularly efficient at retaining metabolic heat. They are the largest sea turtle (nesting adults typically weigh 300–500 kg), which gives them a large thermal inertia. They also have heat exchangers which enable them to maintain their flippers at T_W to further aid in heat retention (Greer et al., 1973). Currently a thermal strategy termed "gigantothermy" is thought to be employed where large body size, peripheral tissues as insulation, and circulatory changes enable leatherbacks to regulate T_B in the face of low metabolic rates (Paladino et al., 1990). Paladino et al. (1990) suggested that a leatherbacks large size sets it apart from other marine turtles in the latitude ranges it can explore although effects of M_B we not explicitly explored in their model. By varying the rate of heat loss through circulatory changes they suggested a leatherback could theoretically thermoregulate. However, gigantothermy considers physiological mechanisms solely for thermal regulation despite the fact that many other reptiles use behavioural means.

Since reptiles commonly use behavioral adjustments to maintain high and stable T_B's, Southwood et al. (2005) hypothesized that behavioral control in leatherbacks may be important in their thermoregulatory technique i.e. depth and T_W selecting could be a way to control T_B. Furthermore, there also appears to be a correlation between swim speed (U) and T_B, with low average U's corresponding to a decrease in T_B, and T_B increasing as U rises (see Fig. 7B from Southwood et al., 2005). These data suggest that the rate of production of metabolic heat in a leatherback directly affects its achievable T_B-T_W.

In this paper we attempt to further the understanding of leatherback thermal biology by looking at the rate metabolic heat is produced as a result of overcoming hydrodynamic drag. Moreover, by estimating heat loss we can predict a leatherbacks' achievable temperature gradient at different metabolic costs, i.e. swim speeds. In a heat flow model it is important to estimate where heat is produced and from where it is lost. We assume that in a leatherback heat production is the byproduct of resting metabolic rate (Γ_o) and the metabolic cost of locomotion (Γ_{Loco}). Heat loss depends on T_B-T_W, insulation thickness, thermal conductivity of the insulation (k) and the convection coefficient.

For a leatherback to maintain a certain T_B-T_W the rate at which heat is produced must be equal to the rate at which heat is lost to the surrounding water. With this assumption we can quantitatively predict the extent to which behavioral control of U could be used in a leatherback's thermoregulatory strategy. We propose that metabolic heat produced as a byproduct of locomotion is crucial in maintaining a high T_B. By keeping insulation thickness constant in this model we highlight the effect that the behavioral control of swim speed has on generating a large thermal gradient. Overall, we hypothesize that behaviourally controlling the rate of heat production, through variation of swim speed, could be an equally effective way for a leatherback to thermoregulate as controlling the rate of heat loss, through circulatory adjustments and T_W selecting.

2. Materials and methods

2.1. Heat production

Any metabolic energy that does not perform a function or perform work external to the body must be released as heat energy. The portion of metabolic energy produced for locomotion that performs external work is the aerobic efficiency of the muscle, the rest is then released as heat. This can be summarized in the following equation, $(1-\eta_a)\Gamma_{Loco}$=heat production rate; where η_a is the aerobic efficiency of muscle and Γ_{Loco} is the metabolic cost of locomotion. Resting metabolic rate Γ_o has been measured in leatherbacks (Lutcavage et al., 1990; Paladino et al., 1990; Lutcavage et al., 1992) and Γ_{Loco} can be estimated from the work a turtle expends in overcoming hydrodynamic drag forces (F_{drag}).

For a turtle to swim at a constant speed the propulsive force the turtle produces must exactly balance the drag force on its body. The F_{drag} (N) on an object with surface area S (m^2) moving through a fluid of density ρ (kg m^{-3}) at a speed U (m s^{-1}) is:

$$F_{drag} = \rho C_D S U^2/2 \qquad (1)$$

where C_D is the drag coefficient which accounts for the shape and boundary flow characteristics around the turtle. The work a turtle does while swimming is the product of F_{drag} and U. Γ_{Loco} is the quotient of work and the efficiency at which the turtle converts biochemical energy into forward thrust. Efficiency includes converting chemical energy into muscular energy (η_a), and the propeller efficiency (η_p) of the flippers. Hence, the heat production rate by a swimming turtle can be written as,

$$\dot{Q}_{prod} = \Gamma_o + \frac{(1-\eta_a)\rho C_D S U^3}{2\eta_p\eta_a} \qquad (2)$$

with whole animal metabolic rate (Γ_{Tot}) estimated as:

$$\Gamma_{\text{Tot}} = \Gamma_{\text{o}} + \frac{\rho C_{\text{D}} S U^3}{2\eta_{\text{p}}\eta_{\text{a}}} \tag{3}$$

2.1.1. Parameters and variables of the heat gain equation

2.1.1.1. Resting metabolic rate. The metabolic rate of three undisturbed nesting female leatherbacks (average mass 305 kg) was 0.083 W kg^{-1} (Lutcavage et al., 1990). The leatherbacks were quiescent so this value is a good approximation of Γ_{o}. Scaling allometrically with body mass (M_{B}) to the 0.83 power (Prange and Jackson, 1976) gives Γ_{o} for leatherbacks as:

$$\Gamma_{\text{o}} = 0.22 M_{\text{B}}^{0.83} \tag{4}$$

2.1.1.2. Aerobic efficiency. The best estimates of η_{a} come from the efficiency of excised muscle performing a complete contraction cycle. This is 25% in frogs (Heglund and Cavagna, 1987) and 35% in tortoises (Woledge, 1968). Leatherback muscle η_{a} has not been measured so we used 30% for η_{a}, midway between that of a frog and tortoise.

2.1.1.3. Drag force. Drag force was measured on a full scale leatherback turtle model borrowed from the Vancouver Aquarium and Marine Science Centre (Vancouver, B.C., Canada). This model was cast from a 340 kg leatherback that died around 30 years ago (Carla Sbrocchi, personal communication), and is very realistic, having most of the surface elements of the skin such as folds and wrinkles. The leatherback is fixed with its fore-arms pulled back in a gliding position.

The cast was tested in an open circuit, low velocity, wind tunnel in the Mechanical Engineering Department at the University of British Columbia. The working section of the tunnel is 1.6 m × 2.5 m in cross section and 23 m long. The leatherback cast was fixed to a force balance projecting through the floor of the wind tunnel. The leatherback cast was mounted upside down on the force balance by brackets on its dorsal carapace. The cast was positioned 30 cm above the floor to reduce boundary effects, and faced directly into the wind. The force balance measured drag force parallel to the wind direction.

A drag test was performed on the mount, before the turtle was attached, to determine its drag. The drag was tested on the mounting bracket at speeds ranging from 5.89 m s^{-1} to 17.0 m s^{-1}, sampling 24 times in this range. Drag was then tested on the turtle at 24 speeds in a range of 6.63 to 17.1 m s^{-1} with each test speed close to speeds used for the mount drag test. The mount drag was subtracted from the drag of the mount and turtle together to estimate F_{drag}.

Fluids at the same Reynolds number (Re) have similar flow patterns so wind speed was converted to water velocity by equating Re for each fluid. Re is expressed as LU/v where v is the kinematic viscosity of the fluid. Equating Re at v for air and water at 25 °C ($1.56 * 10^{-5}$ m^2 s^{-1} and $1.004 * 10^{-6}$ m^2 s^{-1}) showed an air speed of 15.5 m s^{-1} to be equal to water flowing at 1 m s^{-1}. Consequently, F_{drag} was measured over a range of Re that turtles might experience in the ocean by measuring over

a wind speed of 6–17 m s^{-1}. 24 data points were taken over that range to ensure an accurate representation of the drag trend with each data point consisting of an average of 100 samples at a given wind speed.

2.1.1.4. Propeller efficiency. Propeller efficiency accounts for inefficient paddling techniques stemming largely from the added drag of the fins being moved through the water. The flippers were in place on the turtle cast in the wind tunnel so the measured F_{drag} was greater than that required for propulsion. We assumed that the extra drag of the flippers accounted for η_{p}.

2.2. Heat loss

We model a leatherback turtle as a cylinder, with a constant insulation thickness. We consider a turtle as two concentric cylinders. The inner cylinder represents the core of the turtle, where metabolic heat is produced. The core has radius r_{C} and a constant temperature due to blood flow (Paladino et al., 1990; Hind and Gurney, 1997). The outer cylinder has radius r_{T}. The volume of the larger cylinder that lies outside the inner cylinder is the insulation layer of the turtle. No heat is produced in the insulation. Heat will be conducted from the warm core (T_{B}) to the cool surface (T_{S}) across the insulation layer. Heat conduction rate from the core to the surface of a cylinder (Kreith and Black, 1980) is given by:

$$\dot{Q}_{\text{cond}} = \frac{2\pi k L (T_{\text{B}} - T_{\text{S}})}{\ln r_{\text{T}}/r_{\text{C}}} \tag{5}$$

where k is thermal conductivity of the insulation (W °C^{-1}) and L is the length of the cylinder (m). The heat conducted to the surface of the cylinder will then be carried away by movement of the surrounding fluid with temperature T_{W}, through convection. For simplicity, we assume that the convection coefficient is high enough that skin temperature equals T_{W}.

2.2.1. Parameters and variables of the heat loss equation

2.2.1.1. Surface area. Surface area, S, was measured by covering the head, neck, tail, and carapace of the cast with small pieces of paper of known area, and then counting the pieces of paper to give the area. We assumed that heat exchangers kept the flippers at T_{W} (Greer et al., 1973) so they did not contribute to heat loss or the surface area for heat exchange.

2.2.1.2. Insulation. The insulative layer is represented in our model as the ratio of the heated core radius (r_{C}) to the whole body radius (r_{T}) and was held constant at $r_{\text{C}}/r_{\text{T}} = 0.85$. In the cylinder that we use to describe a 300 kg turtle, this ratio is equivalent to an average thickness of insulation of 3.6 cm which makes up 28% of the volume of the cylinder.

2.2.1.3. Cost of ingesting gelatinous prey. As ingested gelatinous zooplankton works its way through a leatherback's digestive system it will warm from T_{W} to the core temperature of the turtle (T_{B}). In doing so, energy is transferred from the

turtle to the ingested prey. The amount of energy required to warm up a mass of zooplankton from T_W to T_B can be written as, $M_G C_G (T_B - T_W)$; where M_G is the mass and C_G is the specific heat capacity of the prey consumed. Therefore, the turtle gains less energy from a mass of cold than from an equivalent mass of warmer jellyfish. The overall energy gained by a leatherback per mass of jelly eaten can be expressed as, $E_G = (134 - 4.186(T_B - T_w))$; where 134 kJ kg^{-1} is the total energy derived per mass of ingested jelly (Lutcavage and Lutz, 1986) and assuming gelatinous zooplankton has a similar specific heat capacity to that of water (4.186 kJ kg^{-1} K^{-1}). Due to the added cost of warming ingested prey, the metabolic rate of an actively foraging leatherback ($\Gamma_{Tot,G}$) can be expressed as, $\Gamma_{Tot,G} = 4.186(T_B - T_W)M_G + \Gamma_{Tot}$. The mass of jellyfish that is needed to be consumed per second to cover Γ_{Tot} can be calculated as, $M_G = \Gamma_{Tot}/E_G$.

2.3. Results

2.3.1. Turtle drag

Drag force (turtle plus mount drag minus mount drag) against wind speed is shown in Fig. 1a. Drag force was converted to $C_D S$ using Eq. (1) (Fig. 1b). In laminar flow C_D varies significantly with Re. However, when flow becomes turbulent dependence of Re on C_D becomes weak (Tritton, 1988). At Re greater than $1.85*10^6$ ($U_{air} = 13.5$ m s^{-1}) C_D is
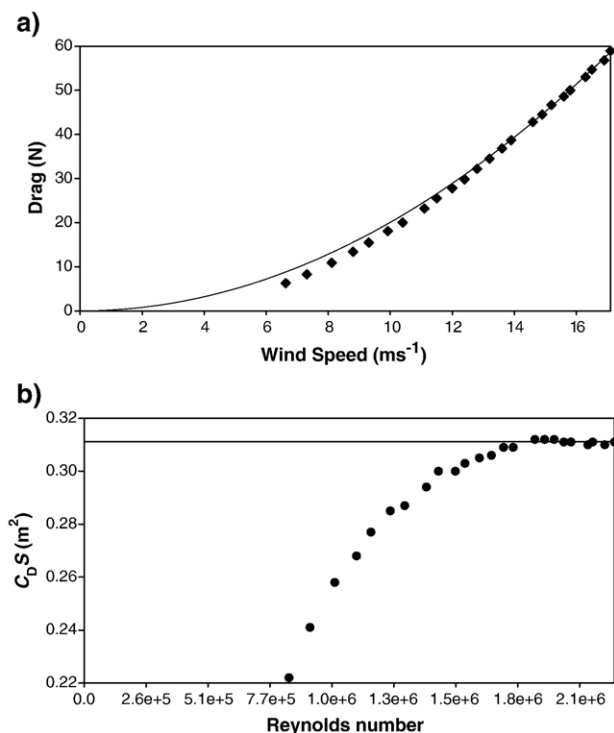

Fig. 1. The results of a drag test performed in a wind tunnel on a full scale cast of a 340 kg leatherback. (a) The measured drag force and the line derived from $C_D S$ and Eq. (1) are plotted against wind speed. (b) $C_D S$ is calculated from drag and is plotted against Reynolds number (Re). Past a Re of $1.85*10^6$ or a wind speed of 13.5 m s^{-1} the air flow around the cast is turbulent and drag scales quadratically with wind speed. This turbulent region is represented in (b) by a constant $C_D S$ and in (a) by the measured data closely matching our fit.
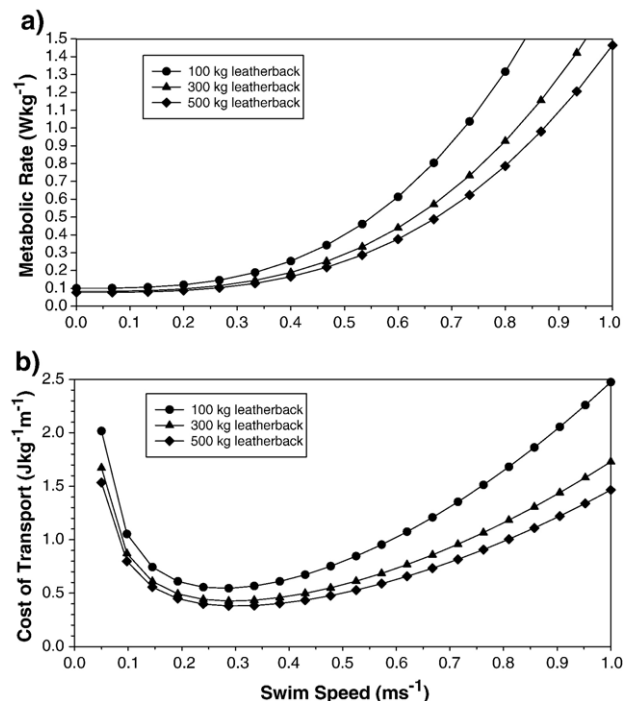

Fig. 2. Metabolic rate predictions from the model. (a) Metabolic rate for a fasting leatherback is plotted against swim speed. Metabolic rate is initially resting metabolic rate and it then increases cubically with swim speed mirroring the work a turtle expends to overcome drag while swimming. (b) The cost of transport (COT) is plotted for leatherbacks against swim speed. The minimum COT occurs at 0.3 m s^{-1}.

constant and flow is turbulent. We assume that flow around a turtle is turbulent and therefore that C_D in the turbulent region (Fig. 1b) accurately represents turtle F_{drag}. Hence C_D of a turtle is invariant and is unaffected by the size of the turtle or density of the fluid so that drag force can be scaled from air to water.
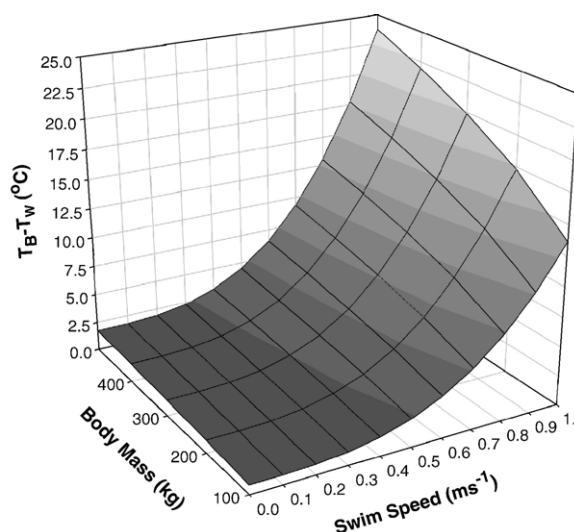

Fig. 3. The predicted achievable temperature gradient ($T_B - T_W$) that a leatherback can maintain above ambient is plotted against swim speed for turtles varying in size from 100 to 500 kg. At a swim speed of 0 m s^{-1} all internally generated heat comes from standard metabolic rate and leatherbacks can only maintain a $T_B - T_W$ of <2 °C regardless of mass. As swim speed increases so does internally generated heat and $T_B - T_W$ rises.
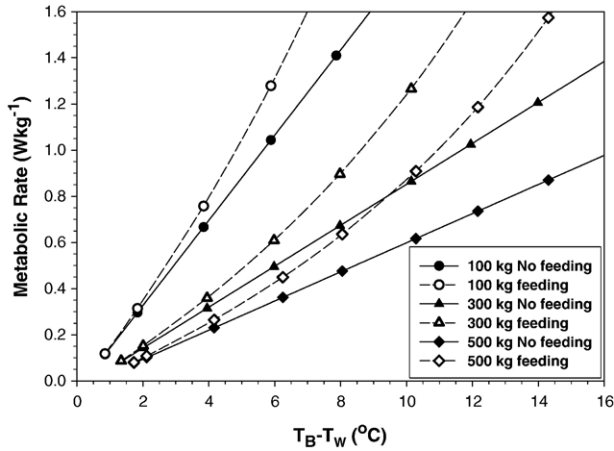
Fig. 4. Metabolic rates (both fasting and feeding) are plotted against $T_B - T_W$ for 100, 300 and 500 kg leatherbacks. In fasting leatherbacks metabolic rate is directly proportional to $T_B - T_W$. Feeding leatherbacks have a lower $T_B - T_W$ than fasting ones because some metabolic energy is used to warm ingested food.

We fit Eq. (1) to our drag data at wind speeds greater than 13.5 m s^{-1}. This produced an average value of $C_D S$ equaling 0.31 m^2. Since C_D depends on the shape of leatherback and is a constant while drag scales proportionally to S, we can use $C_D S$ to scale drag between turtles of different M_B. Assuming that S scales to the 2/3 power with M_B,

$$C_D S = 6.39 \cdot 10^{-3} M_B^{2/3} \qquad (6)$$

2.3.2. Surface area

The 340 kg turtle cast had a surface area (S) of 3.2 m^2. Aquatic animals follow a certain aspect ratio that minimizes total drag (McMahon and Bonner, 1983) which approximates as length/width=4. Since S scales to the 2/3 power with M_B then a cylinder that matches the surface area of a turtle has dimensions described by $8r_T = L$ where $r_T = 0.036 M_B^{1/3}$.

S across which heat is lost is of primary importance. A cylindrical model of a leatherback with $S=3.2$ m^2 and having tissue the density of water, would weigh 390 kg. Therefore, a cylinder matching M_B of a turtle actually underestimates S from which heat is lost. Consequently, we matched the dimensions of the cylinders used in our model to S and not M_B.

2.4. Predictions from the model

2.4.1. Metabolic rate

The metabolic rate (Γ_{Tot}) is plotted against U in Fig. 2a for 100, 300, and 500 kg turtles. As U increases, Γ_{Tot} increases cubically with it. The metabolic rate of a 300 kg turtle swimming at 0.7 m s^{-1} is 0.65 W kg^{-1}.

The cost of transport (COT) is Γ_{Tot} per unit mass divided by the swimming velocity:

$$COT = \Gamma_{Tot} / U M_B \qquad (7)$$

COT gives the energy requirements for a leatherback to swim a given distance. Fig. 2b is a graph of COT as a function of velocity for 100, 300, 500 kg turtles. At very low swim speeds

the COT is high due to the dominance of Γ_o per meter traveled. As U increases, the influence of Γ_o falls but F_{drag} increases, elevating Γ_{Loco}. These two factors combine to give a minimum near 0.3 m s^{-1} for all sizes of leatherback.

2.4.2. Temperature gradient

For a leatherback to maintain a constant temperature gradient the rate that heat is lost must equal the rate heat is produced. By equating Eqs. (2) and (5), $T_B - T_W$ can be solved as a function of swim speed. This relationship is graphed in Fig. 3. This model predicts that leatherbacks up to 500 kg can maintain a $T_B - T_W$ gradient of <2 °C while at rest. At a U of 0.7 m s^{-1}, 100, 300, and 500 kg leatherbacks can maintain a $T_B - T_W$ of 5.2, 7.7 and 9.3 °C, respectively.

The metabolic rate for fasting (Γ_{Tot}) and feeding ($\Gamma_{Tot,G}$) 100, 300 and 500 kg leatherbacks is plotted in Fig. 4 against $T_B - T_W$. Γ_{Tot} is proportional to heat production and is thus directly related to $T_B - T_W$. $\Gamma_{Tot,G}$ is Γ_{Tot} with an added cost of warming the ingested mass of prey from T_W to T_B. Due to this added cost a lower $T_B - T_W$ is achievable at a given metabolic rate for a feeding turtle than for one which is fasting. At a U of 0.5 m s^{-1} ($\Gamma_{Tot}=0.29$ W kg^{-1}, $\Gamma_{Tot,G}=0.33$ W kg^{-1}, $T_B - T_W=3.7$ °C) a 300 kg leatherback would have to eat 63 kg day^{-1} of gelatinous prey, and at 0.7 m s^{-1} ($\Gamma_{Tot}=0.65$ W kg^{-1}, $\Gamma_{Tot,G}=0.85$ W kg^{-1}, $T_B - T_W=7.7$ °C) the animal would have to eat 165 kg day^{-1} to provide for $\Gamma_{Tot,G}$ if it was to remain in energy balance.

3. Discussion

We suggest that heat produced as a metabolic by-product of overcoming F_{drag} while swimming is a crucial aspect of an adult leatherback's ability to maintain a high and stable $T_B - T_W$ gradient. Insulation was held constant in our model which provided evidence that large, stable $T_B - T_W$'s recorded in leatherbacks may be due to this behavioral temperature control mechanism. In conjunction with the ability of a leatherback to spend time at different T_W's, this could be a very effective way to control T_B. We conclude that leatherback thermoregulation does not have to be achieved completely through physiological changes that vary the rate at which the turtle loses heat. In fact, our model provides quantitative evidence that leatherback T_B could largely be behaviorally controlled through T_W selection and by varying the rate of heat production through swim speed selection.

The achievable $T_B - T_W$ for a leatherback scales cubically with swim speed (U) and with M_B to approximately the 1/3 power. Fig. 3 shows that the same thermal gradient in a 500 kg animal swimming at 0.6 m s^{-1} can be achieved by a 300 kg animal with as little as an 8% increase in U. If a leatherback is behaviorally thermoregulating through variation of U and T_W selection, it would be expected that a stronger correlation between U and T_W would be seen than between U and M_B. In fact, studies by Eckert (2002) and Southwood et al. (2005) found no correlation between curved carapace length (thus M_B) and U.

As expected, leatherbacks encountered in northern waters are often larger animals (Eckert, 2002). Our model predicts that to maintain a $T_B - T_W$ of 10 °C in northern waters a leatherback

must be fasting and at least 130 kg if maximum metabolic rate is 1.5 W kg^{-1}. If a leatherback is constantly feeding our model predicts a minimum size limit of 226 kg. In fact, the smallest of 4 leatherbacks captured in Nova Scotia (T_W = 15 °C) was 315 kg (Eckert, 2002).

Dive depth and duration and surface T_W have been monitored for female leatherbacks foraging in northern waters by use of satellite telemetry devices (McMahon and Hays, 2006). As surface T_W cooled both dive depth and duration decreased. This was suggested to be a result of prey availability. However, since leatherbacks need to surface to breathe they are limited by their aerobic dive limit (*ADL*). Our model suggests that turtles could be offsetting the high heat loss of the cold waters by increasing activity. Therefore, to maintain a constant T_B, as T_W drops, a leatherback must increase its metabolic rate which would shorten its *ADL*.

Heat loss in marine animals has been investigated on a number of occasions (Yasui and Gaskin, 1986; Kshatriya and Blake, 1988; Hokkanen, 1990; Paladino et al., 1990; Worthy, 1991; Watts et al., 1993; Kvadsheim et al., 1996; Hind and Gurney, 1997; Ahlborn and Blake, 1999) and, unfortunately, many models are flawed because of inaccurate values for insulation thickness and distribution (Kvadsheim et al., 1997). Due to a lack of detailed data on blood flow and insulation thickness we chose an evenly distributed insulation layer in our model which therefore could be flawed. Fortunately, there is unpublished data from Southwood and colleagues which allows us to test our choice of r_C/r_T at least for tropical waters (Fig. 5). T_B of a 244 kg turtle, resting on the shallow ocean floor at 22 °C, dropped from 30.2 to 29.1 °C over a period of 67 min. This cooling curve can be used to estimate the relative insulation thickness (r_C/r_T). Owing to blood flow, we assume that the whole core of the turtle (approximately half the turtle's

mass) dropped by 1.1 °C. Specific heat capacity of various human tissues varies from 3.6 to 3.9 kJ kg^{-1} K^{-1} (Giering et al., 1995) and assuming that human tissue has a similar heat capacity to that of turtles we use a value that falls in the middle of the range (3.75 kJ kg^{-1} K^{-1}). While resting on the bottom the turtle lost 503 kJ of stored heat energy representing an average of 125 W over 67 min. Total heat lost to the water is from stores plus heat produced internally and for a resting turtle heat produced comes solely from resting metabolic rate (Γ_o). Γ_o for a 244 kg turtle is 21 W from Eq. (4), giving a power loss of 146 W. Assuming that k for leatherback insulation is the same as whale blubber (0.25 J s^{-1} K^{-1}, Kvadsheim et al., 1996) and solving Eq. (5) gives r_C/r_T = 0.86 which is close to the value we used in our model (r_C/r_T = 0.85).

We assumed insulation thickness was constant in our model to highlight the effect U has on a leatherback's achievable temperature gradient. It should be noted that insulation thickness will vary from turtle to turtle and even vary in a single turtle over time. Leatherbacks have been found to be fatter in northern foraging grounds than when on nesting beaches (James et al., 2005). If a leatherback's insulation is thicker than the value used in our model, the rate of heat loss to the surrounding water will be less than predicted. Consequently, less metabolic heat will be needed to achieve a given temperature gradient and leatherbacks could swim at a slower rate.

The wind tunnel experiment gave $C_D S$ as 0.31 m^2 with S being a constant to account for scaling with M_B. Watson and Granger (1998) calculated C_D = 0.339 for a green turtle cast using frontal area to scale with M_B. The frontal area of our turtle cast, not including flippers (Watson and Granger, 1998), was approximately 0.4 m^2 giving a C_D of 0.78. This is not unreasonable because our cast still had the flippers attached. The increase in F_{drag} in our cast was accounted for in our calculations by assuming η_p was 100%. Muscle η_a in the model presented in this paper is 30% which is the average value between η_a of frog and tortoise muscle. If η_p actually accounts for a 50% loss then overall metabolic efficiency is 15% which is slightly higher than the 10% estimated for green turtles (Prange, 1976).

Leatherbacks appear to have a large thermal tolerance as they have been found in T_W above 30 °C in the tropics (Southwood et al., 2005) and near 0 °C off of Nova Scotia (Goff and Lien, 1988; James and Mrosovsky, 2004). In this study we predict the largest internal heat gain comes from metabolic heat as a result of locomotion. We assume η_a will be unchanged at any given T_B because the metabolic rate of leatherback pectoral muscles was found to be thermally independent from 5 to 38 °C (Penick et al., 1998). Therefore our model predicts heat produced at all T_B's a leatherback experiences in the wild.

Other behavioural modifications may play a part in maintaining thermal balance in cold waters. In waters off of Nova Scotia leatherbacks often appear to bring prey from depth to the surface before eating it (James and Mrosovsky, 2004). By surfacing with gelatinous prey before ingesting it, the prey can warm to surface T_W. A leatherback, maintaining T_B 8 °C above surface T_W of 15 °C and capturing prey in water at 10 °C by
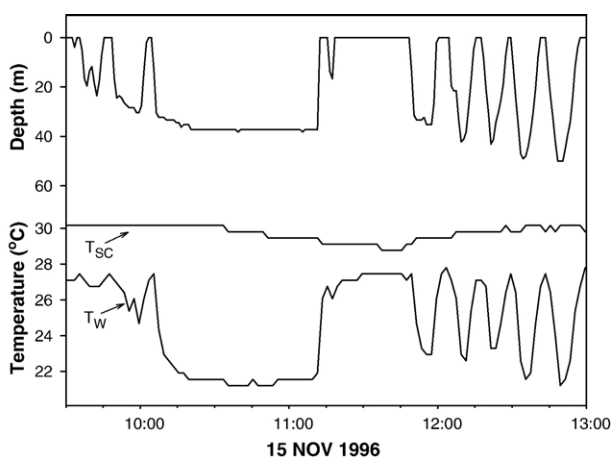

Fig. 5. An unpublished figure from Southwood and colleagues that shows the water temperature (T_W), sub-carapace temperature (T_{SC}) and depth experienced by a leatherback in the tropics during a long dive. The leatherback stayed at a depth near 40 m for 67 min returning to the surface for 30 min before resuming an active dive cycle. The leatherback's T_B decreased throughout the whole dive and continued decreasing during the surface interval despite a $T_B - T_W$ of only a couple degrees. T_B only started climbing once an active dive bout started suggesting metabolic heat from muscle activity is crucial in maintaining a high $T_B - T_W$.

bringing it to the surface would realize a 25% gain in energy per mass of jellyfish consumed.

There is no doubt that physiological and/or behavioural strategies may be required in some situations to prevent overheating. Redistribution of blood flow to the body surface will bypass the insulative layer and greatly enhance heat loss. Also, we assumed that heat exchangers enabled leatherbacks to maintain their flippers at T_W (Greer et al., 1973) and thus they did not contribute to heat loss. However, the heat exchangers are likely not 100% efficient and the possibility exists to greatly increase heat loss by pumping warm blood through the flippers and using them as cooling fins. Green and Loggerhead turtles have been found to vary circulation through their front flippers to control heat exchange (Hochscheid et al., 2002). We did not vary the leatherbacks' insulation thickness or the efficiency of its heat exchangers in this model since we were interested in how different rates of heat production affect T_B.

It has been suggested that in the tropics leatherbacks dive to cold deep waters in order to use the water as a heat sink and cool off (Eckert et al., 1986; Wallace et al., 2005). Wallace et al. (2005) found that high metabolic rates positively correlated with the percentage of time spent in waters colder than 24 °C. They suggested that leatherbacks were actively diving to deep cold waters in order to use the water as a heat sink and cool off. In contrast, our model predicts that in order to dump heat a leatherback is better off to rest and minimize metabolic heat production.

3.1. Test of the model

Southwood et al. (2005) showed temperature data for two turtles of 329 and 251 kg, respectively, in tropical waters. These data sets contain values for gastro-intestinal tract temperature, swim speed, and dive depth. T_W and depth were measured on another turtle in the same area at the same time (Fig. 1 of Southwood et al., 2005), and the data were used to estimate water temperature as a function of depth in Southwood et al.'s Fig. 7 A and B.

In Fig. 7A, from 0:00 to 6:00 and from 18:00 to 21:00, the 329 kg leatherback was swimming in 26 °C water and maintaining T_B of 32.8 °C. To maintain this $T_B - T_W$ our model predicts that a leatherback must maintain a swim speed of $U = 0.66$ m s^{-1}. The measured swim speed varies between 0.6 and 0.7 m s^{-1} during this time which supports results from our model. In Fig. 7B, from 0:00 to 4:00, the 251 kg turtle was swimming to a depth of around 20 m ($T_W = 26$ °C) and T_B is stable at 31 °C. Our model indicates an average U of 0.60 m s^{-1} is necessary to maintain this $T_B - T_W$. Actually, the turtle spent the majority of time at swim speeds oscillating between 0.4 and 0.7 m s^{-1}, which would be close to our prediction. After 16:00 there are similar T_W and T_B and a similar U is predicted to produce this $T_B - T_W$, which is again supported by the data. Between 12:30 and 15:30 there is a T_B gain of approximately 1 °C over 3 h corresponding to an internal heat gain of 44 W. During this dive bout the turtle spent the majority of the time at depths of 30 m ($T_W = 22$ °C). From our model, a U of 0.83 m s^{-1} is needed to achieve a 44 W surplus over heat being lost to the

water. The data shows a swim speed between 0.8 and 0.9 m s^{-1}. From 8:00 to 12:00 the leatherback spent the majority of the time not swimming and T_B dropped over this period. These data provide evidence that T_B is a direct result of the heat produced as a byproduct of the metabolic cost of swimming.

Fig. 5 shows a 244 kg turtle's T_B falling while sitting on bottom (Southwood, personal communication). This is expected since there was a large $T_B - T_W$ (8 °C). However, when the turtle rose to the surface after the dive, T_B continued to fall although $T_B - T_W$ at the surface was only a couple degrees. Our model predicts a $T_B - T_W$ of around 1.2 °C at resting metabolic rate so the animal continued to lose heat. After 11:45 the turtle returned to an active dive cycle and T_B immediately began rising. This confirms that leatherbacks are not able to maintain more than a small thermal gradient in the absence of activity. A large thermal inertia will be useful in dampening out quick changes in ambient temperature but a continuously low T_W will cause T_B to fall. This agrees with research that suggests a crocodile needs to be 10,000 kg before it becomes thermally isolated from its environment (Seebacher et al., 1999). Furthermore, Eckert (2002) reported that leatherbacks swam constantly, day and night, while migrating. They swam about two meters under the surface suggesting they were selecting depth for drag reduction and were not basking. Our model predicts that it is not possible for a leatherback to maintain an elevated $T_B - T_W$ if it stops and rests while in cold water.

Leatherbacks captured off the coast of Nova Scotia had an average T_B of 8 °C above surface T_W (James and Mrosovsky, 2004). To maintain this $T_B - T_W$ we predict a 300 kg leatherback would need to maintain a U of 0.71 m s^{-1} and metabolic rate of 0.90 W kg^{-1} when ingesting food. This metabolic rate is higher than the maximum field metabolic rate of 0.74 W kg^{-1} recorded during the internesting interval (Wallace et al., 2005) but is not unexpected due to the added metabolic cost of a maintaining a large $T_B - T_W$ and warming ingested prey in cold water.

Field metabolic rate (*FMR*) of leatherbacks during the internesting interval in Costa Rica ranged from 0.2 to 0.74 W kg^{-1} (Wallace et al., 2005). Wallace et al. (2005) suggested that leatherbacks were unlikely to be feeding during this time. For 300 kg leatherbacks, measured *FMR* represents a range in U of 0.41–0.74 m s^{-1} and achievable fasting $T_B - T_W$ of 2.7–8.7 °C. If they did happen to be feeding the model predicts ranges of 0.40–0.67 m s^{-1} and 2.5–7.0 °C. These are certainly reasonable ranges for U and $T_B - T_W$ (Southwood et al., 2005).

During the internesting interval, female leatherbacks outfitted with velocity data loggers had an average U of 0.7 m s^{-1} (Southwood et al., 2005). The turtles averaged 282 kg so this swimming velocity corresponds to a metabolic rate of 0.66 W kg^{-1} in a non feeding animal and 0.86 W kg^{-1} in one that is feeding. The *FMR* predicted here for a non feeding turtle is within the range measured by Wallace et al. (2005). Our predicted metabolic rate for a feeding turtle is slightly greater than measured, but as noted by Reina et al. (2005) and suggested by Wallace et al. (2005) these leatherbacks may not be actively foraging during the internesting interval.

In conclusion, we created a quantitative model to predict the thermal gradient that a leatherback can sustain for a given level

of activity. Using this model we were able to accurately replicate published T_B, swim speed and metabolic rate data. We believe these data show the strong predictive power of the model and support the hypothesis that leatherbacks can behaviourally regulate their body temperature through variation in swim speed.

4. Dedication

Our paper is dedicated to the memory of Peter Lutz, a friend and colleague, for the many insights which transformed our field and to his ready wit, which transformed professional and social occasions.

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