

# SUSTAINING ENDOTHERMY ON A DIET OF COLD JELLY: ENERGETICS OF THE LEATHERBACK TURTLE *DERMOCHELYS CORIACEA*

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## INTRODUCTION

The Leatherback Turtle *Dermochelys coriacea* (Vandelli, 1761) is geographically the most widely distributed living reptile species, being found from the tropics to beyond the Arctic Circle in the north and to the waters around New Zealand in the South (Nishimura, 1964; Bleakney, 1965; Davenport, 1991). It has been reported from all oceans except the Southern Ocean. Leatherbacks dive to 1000+m where they also encounter low temperatures (Eckert *et. al.*, 1984, 1986; Mrosovsky, 1987). There is much direct and indirect evidence to show that Leatherback Turtles are endothermic, being able to sustain a core temperature of around 25°C in water temperatures of about 5-15°C (Pritchard, 1969; Frair, Ackman & Mrosovsky, 1972; Greer, Lazell & Wright, 1973; Mrosovsky, 1980; Davenport, Holland & East, 1990). Whether they are facultative endotherms, reverting to ectothermy in tropical waters is unclear (Sapsford & Hughes, 1978; Davenport, 1991). Paladino, O'Connor & Spotila (1990) derived a model from Leatherback data to support the concept of 'gigantothermy' (endothermy without the enhanced metabolic rate of birds and mammals), calculating that Leatherbacks could sustain resting metabolic rates (RMR) when in cold water solely because of the species' large size (>900 kg), good insulation and control of peripheral circulation. They also stated that actively swimming Leatherbacks could sustain a 10°C difference between core and ambient temperatures on a metabolic rate of 0.8 W Kg<sup>-1</sup>. Calculations are presented here to show that this model substantially underestimates the cost of life for *Dermochelys* in cold sea water, because of the wholly gelatinous diet of Leatherbacks. They also indicate why a gelatinous diet is unusual in endothermic vertebrates, though commonplace amongst ectothermic fish.

## CALCULATIONS AND DISCUSSION

It is well established that Leatherbacks are specialised medusivores when foraging in cool surface waters of the north Atlantic (Bleakney, 1965; Brongersma, 1969; Hartog & van Nierop, 1984); particular prey items are *Rhizostoma*, *Cyanea*, *Aurelia* and *Chrysaora*. Individual jelly fish can be very large, with *Rhizostoma* reaching masses exceeding 30 kg. In UK, Irish and French waters, summers when large numbers of Leatherbacks are seen coincide with years when swarms of jellyfish are numerous. Leatherbacks also eat large pyrosomas (Davenport & Balazs, 1991) both in shallow and deep water, and the fatty acid signature of the blubber of Leatherbacks is consistent with a wholly gelatinous diet (Holland, Davenport & East, 1990; Davenport & Balazs, 1991). Leatherbacks are specialists on gelatinous organisms throughout their life; Lutcavage & Lutz (1986) noted that recently-hatched Leatherbacks (almost certainly too small for endothermy) consumed jellyfish equivalent to their body weight each day, simply to

support routine metabolism. Bjorndal (1996) has recently summarized findings for the species' foraging ecology, and extends the list of gelatinous prey to include salps and siphonophores, often eaten at great depth (where ambient temperatures, and hence prey temperatures, are below 5°C throughout the world; Raymont, 1963). Other endothermic marine carnivores (e.g. lamnid sharks, seabirds, marine mammals) eat high-quality, lipid/protein rich diets; *Dermochelys* is unique in consuming food with an extremely low lipid and energy content, more than an order of magnitude less than the content of an equivalent mass of fish flesh (Table 1). The small amount of organic material in gelatinous prey is also of poor nutritional quality; 70% carbohydrate, 27% protein and 3% lipid (Davenport & Balazs, 1991); a typical diet of fish or molluscan flesh contains about 47% carbohydrate, 45% protein and 8% lipid. The caloric content (about 12 joules mg dry organic wt<sup>-1</sup>) is also very low, lower than that of all organisms listed by Crisp (1971).

Turtles (*Chelonia mydas*) eating high quality diets exhibit high assimilation rates (87%) for energy, but show significantly lower assimilation rates (68%) on poor quality diets (Davenport, Antipas & Blake, 1989). It is probable that high prey water content, poor nutritional quality and low assimilation efficiency will act synergistically in *Dermochelys* so that very little energy and nutrient is extracted from a given mass of prey.

Leatherbacks consequently have to consume great quantities of food for such large carnivores, at least 50% body mass d<sup>-1</sup> (equivalent in energetic [but not protein/lipid] terms to eating only 4% body mass d<sup>-1</sup> of fish). Seals and birds eat 10-20% body weight per day of fish - but sustain higher body temperatures and levels of activity. Duron (1978) confirmed that large Leatherbacks (ca 400 kg body mass) foraging off the coast of France each ate about 200 kg *Rhizostoma* d<sup>-1</sup>. This was a conservative estimate since observation was limited to daylight hours. Leatherbacks browse almost continually when in jellyfish swarms; recent kinematic study (Bels, Davenport & Renous, in press) shows that Leatherbacks can capture additional prey whilst continuing to transport food to the oesophagus, a conveyor-belt-like process not found in other sea turtles.

Eating large quantities of ectothermic gelatinous animals poses a thermal problem for a Leatherback. Part of the oesophagus, the whole of the stomach and most of the intestine are inside the blubber capsule of the body, so are presumably within the warm core. The throat of the Leatherback is covered by a thick adipose pad, which insulates the great vessels, trachea and oesophagus in the neck region. Food must therefore be heated from ambient (t<sub>a</sub>) to core (t<sub>c</sub>) temperature. Gelatinous animals are mostly water (Table 1), so can be considered to have a heat capacity of 4.2 x 10<sup>3</sup> J Kg<sup>-1</sup> °C<sup>-1</sup>. Assuming that a 400 Kg turtle eats 200 Kg food d<sup>-1</sup>, then the energetic cost of heating the food will be 8.4 x 10<sup>6</sup> J d<sup>-1</sup> where t<sub>c</sub> - t<sub>a</sub> = 10°C or 16.8 x 10<sup>6</sup> J d<sup>-1</sup> where t<sub>c</sub> - t<sub>a</sub> = 20°C. How significant are these costs in terms of the metabolism of adult *Dermochelys*? Paladino *et al.* (1990), working on tropical beaches, measured RMR at a mean of 0.39 W Kg<sup>-1</sup>, minimum active metabolism at about 0.8 W Kg<sup>-1</sup> and maximum active metabolism at around 1.8 W Kg<sup>-1</sup>. For a 400 Kg turtle these values translate to 13.5 x 10<sup>6</sup> J d<sup>-1</sup>, 27.6 x 10<sup>6</sup> J d<sup>-1</sup> and 62.2 x 10<sup>6</sup> J d<sup>-1</sup> respectively. Evidently the cost of heating up food to core temperature can be a large fraction of metabolic rate. If a turtle eats 200 Kg of medusae per day where t<sub>c</sub> - t<sub>a</sub> = 20°C, then the cost of heating exceeds RMR and a combination of RMR and heating costs would be greater than the minimum active metabolism recorded by Paladino *et al.* (1990).

In addition, Leatherbacks feeding in cold water will use much of the energy gained from eating medusae or pyrosomas simply in heating them before digestion. 200 kg *Pyrosoma*

*atlantica* (Davenport & Balazs, 1991) contains 5 kg dry organic matter with an energy content of about  $62 \times 10^6$  J. Heating such pyrosomas by 10°C or 20°C will use up 13.5% or 27% (respectively) of the available energy (much of which may not be readily available, being derived from indigestible mucopolysaccharides). Heating costs for a fish diet would be trivial by comparison.

There are other possible sources of heat loss beyond simple loss across the body surface in cold water; the above analysis takes no account of faecal heat losses (unknown), or of the costs involved in warming and humidifying inspired air (insufficient environmental data are available to permit calculation). Leatherbacks also incur a substantial salt and water regulation problem by eating a diet so rich in both salts (cnidarians and tunicates are osmoconformers) and water. Other than their known ability to secrete salts from the lachrymal glands (Hudson & Lutz, 1986), Leatherback osmotic physiology is unstudied, so the means by which they remove the enormous salt/water load associated with a gelatinous diet are obscure; mechanisms to strip heat from that water before release might be predicted. However, even if these extra potential routes of heat loss are ignored, the information presented here indicates that Leatherbacks foraging in cold waters must have a much higher routine metabolic rate (requiring consumption of even more jellyfish) than that recorded in the tropics by Paladina *et al.* (1990). In addition, the poor quality diet suggests that Leatherbacks will not be able to sustain vigorous activity in cold water for long; 200 Kg of gelatinous material contains about the same amount of energy that a turtle would expend in maintaining the maximum metabolism recorded by Paladino *et al.* (1990) for 24 h (not allowing for warming, losses during assimilation, etc.). Relying on a cold, energy-poor diet must result in a greatly limited scope for activity, particularly if it is assumed that high-latitude foraging is adaptive, and should result in capture of surplus energy for somatic growth or gonadal development. Fortunately, gelatinous prey are themselves slow-moving, so prey capture near the sea surface should involve minimal activity.

The interplay of endothermy and a gelatinous diet may involve the unusual anatomy of the oesophagus of the leatherback. I took part in the dissection of the largest Leatherback so far reported (Eckert & Luginbuhl, 1988). The animal, mass 916 kg, was about 2.5 m long and 2.5 m in flipper span. The capacious oesophagus (muscular, well vascularized and lined with hundreds of semirigid cornified conical processes that probably shred the prey (Davenport & Balazs, 1991), was more than 2m long and ran not from the back of the throat directly to the stomach as in other sea turtle species, but to the centre of the visceral cavity (i.e. posterior to the midpoint of the turtle), before looping anteriorly and leftwards to join the stomach. The exceptional length and volume of the oesophagus is probably primarily required to allow Leatherbacks to take up and store more food than could be stored in the stomach alone, but should also provide the opportunity for food to warm and break up relatively slowly before reaching the stomach; slow movement of food through the oesophagus is known from other sea turtle species with much shorter gullets (Birse & Davenport, 1987; Davenport & Kjørsvik, 1985; Davenport *et al.*, 1989).

In all of the above analysis, the author has only considered Leatherbacks foraging at the surface in cool temperate waters where they cannot afford to allow the core temperature to fall. In the tropics, Leatherbacks forage at great depth (see Bjørndal, 1996 for review) in cold water, but return to warm surface waters (25+°C) at the end of a dive. It is not known whether Leatherbacks forage at depth when in temperate waters, nor are data yet available concerning the thermal biology of diving Leatherbacks in the tropics – if they allow the core temperature to drop during such excursions, then they may subsequently allow themselves and their prey to re-warm with environmental heat.

**Table 1.**  
Comparison of composition of fish and gelatinous animals

	Water as % wet mass	Organic mass as % wet mass	Energy content (J x 10 <sup>3</sup> Kg wet mass <sup>-1</sup> )	Lipid content (g lipid mass Kg wet mass <sup>-1</sup> )
Medusae	9-97	0.5-2.5	—	0.3-1.2
Pyrosomas	94	2.5	313	0.7
Fish (plaice)	82	15.8	3890	14.0

Data sources: Tessier, 1926; Davenport & Kjørsvik, 1986; Holland *et al.*, 1990; Davenport & Balazs, 1991;

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