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RESEARCH ARTICLE

Crying a river: how much salt-laden jelly can a leatherback turtle really eat?

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ABSTRACT

Leatherback turtles (*Dermochelys coriacea*) are capital breeders that accumulate blubber (33 kJ g^{-1} wet mass) by hyperphagia on a gelatinous diet at high latitudes; they breed in the tropics. A jellyfish diet is energy poor (0.1–0.2 kJ g^{-1} wet mass) so leatherbacks must ingest large quantities. Two published estimates of feeding rate [50% body mass day^{-1} (on *Rhizostoma pulmo*) and 73% body mass day^{-1} (on *Cyanea capillata*)] have been criticised as too high. Jellyfish have high salt and water contents that must be removed to access organic material and energy. Most salt is removed (as NaCl) by paired lachrymal salt glands. Divalent ions are lost via the gut. In this study, the size of adult salt glands (0.622 kg for a 450 kg turtle; relatively three times the size of salt glands in cheloniid turtles) was measured for the first time by computed tomography scanning. Various published values for leatherback field metabolic rate, body fluid composition and likely blubber accumulation rates are combined with known jellyfish salt, water and organic compositions to calculate feasible salt gland secretion rates and feeding rates. The results indicate that leatherbacks can produce about 10–15 ml secretion g^{-1} salt gland mass h^{-1} (tear osmolality 1800 mOsm kg^{-1}). This will permit consumption of 80% body mass day^{-1} of *C. capillata*. Calculations suggest that leatherbacks will find it difficult/impossible to accumulate sufficient blubber for reproduction in a single feeding season. Rapid jellyfish digestion and short gut transit times are essential.

KEY WORDS: Salt glands, Gelatinous diet, Blubber, *Dermochelys coriacea*, Hyperphagia, Osmoregulation

INTRODUCTION

Gelatinous zooplanktonic organisms (cnidarians, ctenophores, pyrosomes, salps, doliolids) are important components of marine ecosystems both as predators and prey (Pauly et al., 2009; Richardson et al., 2009). Gelatinous prey items have very low-energy densities (ca. 0.1–0.2 kJ g^{-1} wet mass), principally because they have extremely high water contents, typically 95–98% (Doyle et al., 2007; Molina-Ramírez et al., 2015). This compares with 2.0–10.8 kJ g^{-1} wet mass for a range of oceanic fish (Anthony et al., 2000) and about 3.5 kJ g^{-1} wet mass for seagrasses of the genus *Thallassia* (Bjorndal, 1980; Prado and Heck, 2011).

Gelatinous marine animals, like most marine invertebrates, have long been known to have body fluid compositions close to that of seawater. The moon jelly *Aurelia aurita* has an overall osmolality of about 980–1000 mOsm kg^{-1}, while sodium and chloride concentrations are virtually identical with seawater; only divalent sulphate ion concentrations exhibit much regulation (Robertson, 1957). In contrast, marine vertebrates (fish, reptiles, birds and mammals) share a basal trait of blood plasma ionic concentrations much lower than seawater; this reflects their freshwater/brackish water remote ancestry.

Typical plasma osmolalities for most marine teleost fish are 250–400 mOsm kg^{-1} (Holmes and Donaldson, 1969), for marine turtles 320–370 mOsm kg^{-1} (Lutz, 1996) and for marine mammals 315–360 mOsm kg^{-1} (Ortiz, 2001). To maintain homeostasis, marine vertebrates must have mechanisms for: (i) accessing sufficient water from the environment and/or diet; and (ii) losing salts. The problems of achieving this are more severe for vertebrates that consume salt-rich marine plants (e.g. pinfish, green turtles and dugongs), or are invertebrate consumers (e.g. herring, some baleen whales, walruses, loggerhead turtles, oystercatchers), than they are for those (e.g. mackerel, orcas, leopard seals) that predominantly eat other vertebrates.

Gelatinous prey items therefore pose a particular problem for potential vertebrate consumers; their low-energy density means that they must be eaten in large quantities (implying voluminous guts and/or rapid processing), while such consumption inevitably involves the intake of large amounts of salts and water. Despite this situation, many marine vertebrates, particularly fish, eat gelatinous prey (Pauly et al., 2009). However, for most of these carnivores, gelatinous prey items do not make up the whole of their diet, especially early in ontogeny when growth is especially fast.

One iconic marine animal has long been identified as an obligate gelativore throughout its life: the giant leatherback turtle *Dermochelys coriacea* Vandelli (Jones et al., 2000; Houghton et al., 2006). Mostly, leatherbacks feed on medusa, but they also feed on pyrosomes (Davenport and Balazs, 1991) (see also http://www.nhm.ac.uk/resources/visit-us/wpy/2013/large/57.jpg). They grow rapidly; though there is dispute about age at maturity, recent estimates range from 12 to 29 years (Jones, 2009; Eckert et al., 2012). Typically, they reach 300–500 kg body mass, though there is considerable change in that mass during their breeding and feeding cycles, especially among females, which lay large numbers of eggs in <11 clutches (Davenport et al., 2011).

To grow so quickly and to sustain their size and great reproductive output, leatherback turtles must eat large quantities of food, perhaps 300 metric tons to reach maturity and 1000 metric tons in their whole life (Jones et al., 2012). Captive neonates eat 100% body mass day^{-1} of jellyfish (Lutcavage and Lutz, 1986). Direct attempts to quantify adult food intake started in 1978 (Duron, 1978) when turtles of around 400 kg body mass were estimated (visually at/near surface) to eat 200 kg medusae day^{-1} in the Bay of Biscay during daylight hours (i.e. about 50% body mass day^{-1}). The jellyfish concerned were *Rhizostoma pulmo*; a large species commonly reaching 20 kg individual wet mass.

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Recently, observations using turtle-borne cameras indicated that leatherbacks (mean 455 kg body mass) feeding off Nova Scotia, Canada, were eating a mean of 73% body mass day^{-1} (maximum 186% body mass day^{-1}), predominantly in the form of lion's mane jellyfish (*Cyanea capillata*) (Heaslip et al., 2012). Filming of prey capture always took place for periods of less than 4 h because of technical limitations, and estimated food consumption rate was scaled up to a 13.5 h foraging day. This has led to criticism that this is an overestimate and that salt secretion mechanisms could not cope (Wallace and Jones, 2015), though there is plenty of evidence of day-long and flexible foraging in Nova Scotian waters (Wallace et al., 2015). However, any estimate must be compatible with separate observations that Nova Scotian female leatherbacks are about 33% heavier (ca. 100 kg) during the summer feeding season (approximately 100 days long) than females from the same population weighed after they had laid the first clutch of the breeding season (Davenport et al., 2011), implying hyperphagia and capital breeding. This difference results from the laying down of blubber (containing about 33 kJ g^{-1} wet mass, given a 90% fat content). However, leatherback females rarely breed every year; usually 2–4 years elapses between breeding seasons. It has been shown that non-breeding females can migrate from the Nova Scotian feeding grounds to the Caribbean Sea and back to forage again within a year (James et al., 2005a), so the accumulation of blubber almost certainly takes more than one year; in any case leatherbacks also forage at low latitudes. Hays et al. (2006) presented satellite-tagging data that showed that post-nesting Caribbean female leatherbacks exhibit flexible foraging strategies (including nocturnal diving) and travel a wide variety of routes around the North Atlantic to access jellyfish resources. Fossette et al. (2010) showed that jellyfish prey are patchily distributed and that leatherback turtles may spend long periods travelling between patches, further suggesting that accumulating blubber is a multi-year process.

Sea turtle osmoregulation has attracted much study. Like other reptiles, their kidneys can only produce urine isosmotic with the blood plasma, so particular interest has focused on salt secretion by the lachrymal salt glands, which can produce copious lachrymal secretions. Leatherbacks have larger salt glands than other sea turtle species (Wyneken, 2001), though quantification of adult salt gland size has not been carried out. Blood plasma osmolality in fasting hatchling leatherbacks has been reported to be 364 mOsm kg^{-1}. They continually produced lachrymal secretions of a higher osmolality than seawater (1163 mOsm kg^{-1}); the lachrymal fluid was almost pure NaCl solution. After feeding *ad libitum* on the jellyfish *Cassiopeia xamachana* the lachrymal secretion concentration rose to a maximum of 1650 mOsm kg^{-1} (Hudson and Lutz, 1986). Lachrymal secretion rates in feeding adult leatherbacks are unknown.

Inter-nesting female leatherbacks have water turnover rates of about 1% body mass h^{-1}, but these turtles may have enhanced drinking rates because of the incorporation of water into egg clutches (Wallace et al., 2005), so water fluxes are probably comparable in magnitude with fish. The role of the gills and gut in osmoregulation has been extensively studied in marine teleosts. Briefly, ingested seawater is desalinated by the transport of almost pure NaCl from the gut lumen (principally that of the oesophagus) into the blood, leaving a divalent-rich fluid behind in the lumen. The resulting blood plasma salt load is removed by active transport of NaCl at the gills. Intestinal secretion of bicarbonate into the lumen raises the pH of the intestinal fluid, precipitating Ca^{2+} and Mg^{2+} as microcrystalline complexes, so further reducing the osmolarity of the gut fluid, promoting water absorption in the hind gut and protecting the kidneys against the formation of kidney stones (Wilson et al., 2002). The role of the gut in sea turtles in ionic regulation is largely unstudied but it must function in a similar fashion to that of teleost fish if the turtles are to remain in salt and water balance. There is direct evidence of HCO_3^- secretion into the intestine of green turtles (*Chelonia mydas*) (Taylor et al., 2007), while there is indirect evidence that the hind gut luminal fluid of *Dermochelys* has an alkaline pH and is rich in divalent ions (Davenport et al., 1993).

The primary objectives of this study were to: (i) establish the size of adult salt glands of *Dermochelys*; (ii) to estimate the rates of salt gland secretion under two feeding rate scenarios (Duron, 1978; Heaslip et al., 2012); and (iii) to calculate whether the feeding and salt secretion rates are compatible with three published estimates of adult metabolic rates, plus possible rates of blubber accumulation during feeding in North Atlantic waters.

MATERIALS AND METHODS

Estimation of adult salt gland size

Material was collected from a freshly stranded adult female leatherback turtle, found close to the shore at Ballycotton, East Cork, Ireland; 168 cm in standard curved carapace length, it would have weighed about 450 kg (Georges and Fossette, 2006). The head and neck were removed and embalmed. They were computed tomography (CT)-scanned (1 mm slice acquisition with a bony reconstruction algorithm) using a Siemens Somatom Plus 4 scanner (Erlangen, Germany). Analysis of tissues and false colour image production was conducted using OsiriX v. 3.21 Software on a Macbook Pro workstation (Cupertino, CA, USA). OsiriX is an open source DICOM image analysis software package (Osirix Foundation, Geneva, Switzerland) (Davenport et al., 2009). The image slices (e.g. Fig. 1) were inspected and measurements were made to allow estimation of the volume of the salt glands. A tissue density of 1.06 g ml^{-1} was used to allow calculation of salt gland mass (published densities of muscle, liver, kidney and heart tissues cluster around this value; Azhari, 2010).

Basis of calculations

Values for parameters are taken from multiple literature sources. They often involve assumptions but reflect the best available information.

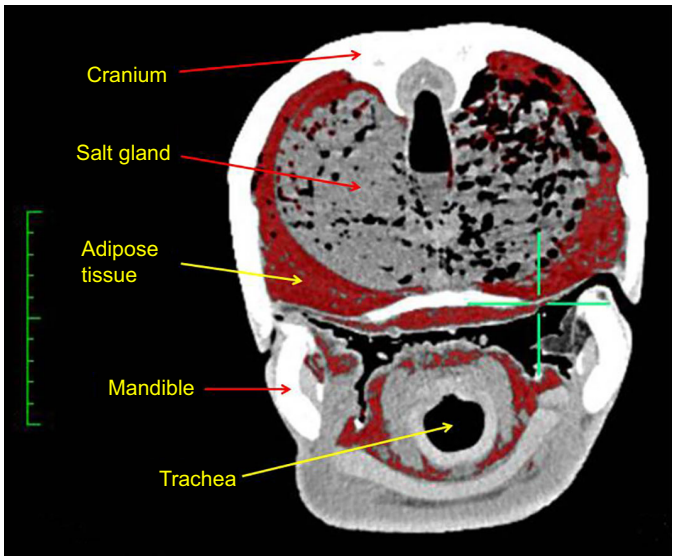

Fig. 1. Labelled tranverse computed tomography image of the head of an adult *Dermochelys coriacea*. Left-hand scale=10×1 cm.

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Body fluid concentrations

Blood plasma osmolarity is 360 mOsm kg^{-1} (Lutz, 1996). Maximum values for lachrymal secretion concentrations in feeding adult leatherbacks are not available. Nesting females climbing the beach produce relatively dilute lachrymal secretions (ca. 570 mOsm kg^{-1}), probably because isosmotic mucus is secreted together with the saline output (Reina et al., 2002), and these turtles are in any case largely non-feeding. However, both adult loggerhead (*Caretta caretta*) and green turtles (*C. mydas*) are capable of secreting lachrymal secretions of close to 2000 mOsm kg^{-1} (Lutz, 1996). Here, the maximum concentration of leatherback tears used is 1800 mOsm kg^{-1}. Lachrymal secretions are taken to be pure NaCl. Most monovalent salt excretion in leatherbacks is via the salt glands, as the urine is known to be isosmotic with the plasma (Lutz, 1996). It is accepted that the gut wall pumps virtually pure NaCl from the lumen to the blood, so that the gut wall and salt glands effectively pump NaCl in series.

Leatherback metabolic rates

No direct measurements of metabolic rates of leatherback turtles foraging in northern temperate waters are available. In the tropics, three inter-nesting females (mean body mass 282 kg) were found (using the double-labelled water technique) to have a mean field metabolic rate (FMR) of about 41.4 kJ kg^{-1} body mass day^{-1} (Wallace et al., 2005), though there was much variability in this estimate, principally because one individual had an FMR more than three times as high as the others. Nine turtles (mean body mass 312 kg) foraging in warm waters after nesting were indirectly estimated to have mean FMRs of 22.24 kJ kg^{-1} body mass day^{-1} (Bradshaw et al., 2007), similar to FMRs measured in two of the individuals studied by Wallace et al. (2005). These published values are both lower than the 46.2 kJ kg^{-1} body mass day^{-1} predicted allometrically for a 455 kg leatherback (Heaslip et al., 2012) from published relationships for reptiles at tropical temperatures (Nagy et al., 1999) but those relationships were derived from terrestrial reptiles.

A complicating factor in choosing a representative metabolic rate is that adult leatherbacks have elevated core temperatures (25–27°C) in cold (10.9–16.7°C) surface seawater (Frair et al., 1972; James and Mrosovsky, 2004; Casey et al., 2014) and regularly dive into near-freezing water when foraging in Canadian waters (James et al., 2006). Current understanding is that an elevated core temperature is maintained by a combination of gigantothermy, insulation, plus muscular and visceral thermogenesis (Casey et al., 2014; Davenport et al., 2015). As leatherbacks swim just as quickly in cold water as they do in the tropics (Davenport et al., 2015), it is likely that their FMRs are elevated at high latitude. However, this may be offset by insulation and peripheral vascular constriction (Casey et al., 2014), but it is accepted that leatherbacks feeding in northern temperate waters are feeding to excess (inevitably involving much use of locomotory and masticatory muscles). Casey et al. (2014) recently used models based on stomach temperature and estimates of heat flow to calculate FMR at 88.6 kJ kg^{-1} body mass day^{-1}. Here, the only currently available values ['low' FMR, 22.24 kJ kg^{-1} body mass day^{-1} (Bradshaw et al., 2007); 'medium' FMR, 41.4 kJ kg^{-1} body mass day^{-1} (Wallace et al., 2005); and 'high' FMR, 88.6 kJ kg^{-1} body mass day^{-1} (Casey et al., 2014)] are used.

Jellyfish composition

The diet of leatherbacks observed in French waters (Duron, 1978) was dominated by the barrel jelly fish *R. pulmo*, while turtles filmed in Canadian waters (Heaslip et al., 2012) were mainly eating the lion's mane jellyfish *C. capillata*. The proximate compositions of these large jellyfish are known (Doyle et al., 2007) and relevant mean values for whole jellyfish are displayed in Table 1. It can be seen that water contents are extremely high (approximately 96%) and that salt makes up a high proportion of the dry mass. The organic content is dominated by protein (71–77%); levels of lipid and carbohydrate are low. Unsurprisingly, the energy contents of whole jellyfish are low (0.11–0.18 kJ g^{-1} wet mass), with *R. pulmo* having 61% of the mass-specific energy content of *C. capillata*.

Energy losses during food intake and nutrient assimilation

Leatherbacks foraging in temperate waters take in food that is colder by several degrees than their core body temperature (Davenport, 1998). A recent study on fine-scale foraging in leatherbacks found that they were feeding in the top 30 m of the water column, and that the mean seawater temperature was 17.2°C (Wallace et al., 2015). This suggests a core-ambient temperature difference of about 8°C. Jellyfish are 96% water (Table 1), so can be regarded as having a heat capacity of 4.2 kJ kg^{-1} $°C^{-1}$. As the food is transported from environment to core, it has to be warmed up and this will 'cost' 0.0336 kJ g^{-1} for an 8°C temperature gradient. Because of the low-energy density of jellyfish, this is a non-trivial energy penalty: 18% for a diet of *C. capillata*, 30% for a diet of *R. pulmo*. Obviously, if the thermal gradient is different from 8°C this will affect the scale of the penalty.

Nutrient assimilation rates have not been recorded in *D. coriacea* but data are available for other sea turtles. Immature green turtles (*C. mydas*) fed on an animal diet (fishmeal-based trout pellets: 17.6–21.0 kJ g^{-1} dry mass; protein 40–50% dry mass) assimilated 76% of energy and 86% of protein (Hadjichristophorou and Grove, 1983). Here, leatherback turtles are taken to assimilate 80% of ingested energy.

No direct estimates of specific dynamic action [SDA, also known as post-prandial increase in metabolic rate: it is the cost of ingesting and processing meals (McCue, 2006)] are available for adult leatherback turtles, and few for any sea turtles. SDA has simply not been measured in gelativores in which organic material in the diet is greatly diluted by water and salts. Broadly speaking, SDA is proportionally greatest in animals eating infrequent meals of high energy, protein and lipid contents (e.g. large snakes and crocodilians) that are followed by physical immobility and substantial gut upregulation (McCue, 2006) and least in animals (such as the leatherback) that are feeding and moving continuously. Casey et al. (2014) suggested that leatherback SDA was dominated (90%) by the cost of warming ingested food (already accounted for in calculations: see above). However, the low-energy density and high volume of the food suggests that metabolic costs of digestion, absorption and processing will be spread evenly over long periods;

Table 1. Composition of whole jellyfish prey (*Cyanea capillata* and *Rhizostoma pulmo*) of *Dermochelys coriacea*

	C. capillata	*R. pulmo*
Mean water content (% wet mass)	95.8	96.1
Ash content (% dry mass)	76.8	83.4
Organic content (% dry mass)	23.2	16.6
Energetic content (kJ g^{-1} wet mass)	0.18	0.11
Energetic content (kJ g^{-1} dry mass)	4.22	2.80
Energetic content (kJ g^{-1} organic dry mass)	18.19	16.86
Protein content (% organic dry mass)	71.1	77.1
Lipid content (% organic dry mass)	2.2	1.9
Carbohydrate (% organic dry mass)	3.8	5.0
Unknown matter (% organic dry mass)	22.9	16.0

Extracted and calculated from Doyle et al. (2007).

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it is also likely that gut function is continuously upregulated. SDA is therefore here judged to be proportionally imperceptible [as found for green turtles, *C. mydas* (Hochscheid, 2003)].

Composition and accumulation rate of leatherback blubber

Some biochemical study of leatherback blubber has been made (Davenport et al., 1990; Holland et al., 1990). Neutral lipid makes up most (ca. 90%) of the lipid content, confirming its energy storage function. The fatty acid makeup differs from that of marine mammals, having rather higher levels of saturated fatty acids. However, the water content of leatherback blubber is not known. Pure lipid has an energy density of 37 kJ g^{-1}. Seal and whale blubbers vary in water content, particularly during lactation, ranging from 5 to 17%. A conservative estimate for leatherback blubber energy density used here (33 kJ g^{-1} wet mass) reflects 90% lipid content and 10% water.

Female leatherback turtles on feeding grounds off Nova Scotia are far heavier (by approximately 33% or 100 kg) for a given carapace length than females after laying their first clutch of eggs on beaches in French Guiana (James et al., 2005b; Georges and Fossette, 2006). Clutches had a mean mass of about 5 kg, most of which was water (Wallace et al., 2007), so this first clutch (of <11) had negligible effect on the 100 kg difference. Body girth and mass increase during the period on the foraging grounds (Davenport et al., 2011). However, it is probable that some of the difference in mass between breeding and foraging areas reflects foraging at lower latitudes and at depth (Hays et al., 2006). Here, the maximum body mass that leatherbacks can possibly accumulate in northern temperate waters is taken to be 100 kg in 100 days (i.e. 1 kg day^{-1}) and that the increase is solely in the form of blubber. This implies that 33,000 kJ has to be stored each day. Given 13.5 h day^{-1} foraging sessions (Heaslip et al., 2012), this means that a net 2444 kJ h^{-1} must be acquired, purely for blubber lipid storage. For a 450 kg turtle this equates to 5.43 kJ^{-1} kg body mass h^{-1}. If half that mass is accumulated in a single foraging season (i.e. that females forage at high latitude for at least 2 years; c.f. Hays et al., 2006), the corresponding accumulation figures are 0.5 kg blubber day^{-1}, 16,500 kJ daily storage and 2.72 kJ kg^{-1} body mass h^{-1}.

Calculations

Values of leatherback body fluid concentrations and metabolic rates, plus jellyfish compositions, losses of energy during turtle food intake and nutrient assimilation are combined with data for the composition and accumulation rate of leatherback blubber to predict likely rates of lachrymal salt gland output (using the measured sizes of salt glands) and maximum feasible food intake levels.

RESULTS

Salt gland size

The combined volume of the two salt glands was estimated to be 0.587 l, some 20 times the volume of the brain. This equates to a mass of 0.622 kg. Given an estimated body mass of 450 kg for the study turtle, this means that the salt glands made up about 0.14% of body mass. This is less than half that recorded for hatchling leatherbacks (0.398%) (Hudson and Lutz, 1986) but about three times the values recorded for adult loggerheads (0.046%) and subadult green turtles (0.05%) (Holmes and McBean, 1964). It is known that hatchling sea turtles in general have proportionately much larger salt glands than adults (Lutz, 1996); this is probably simply an allometric phenomenon; adults have proportionately smaller heads than neonates. Clearly *Dermochelys* has the largest salt glands (relatively and absolutely) of any extant sea turtle species.

Calculations

Desalination of food by the gut and lachrymal glands

Given a turtle of mass 450 kg eating 50% body mass of jellyfish (Duron, 1978) in a 13.5 h day^{-1} foraging session, then intake will be about 16.7 kg jellyfish h^{-1}. At the higher intake rate of 73% body mass day^{-1} (Heaslip et al., 2012), intake will be 24.3 kg jellyfish h^{-1}. Combined gut and salt gland action must reduce gut fluid salt concentration to levels at, or below, those of the blood plasma to permit osmotic uptake of water. Given a jellyfish osmolality of 1000 mOsm kg^{-1}, a turtle plasma osmolality of 360 mOsm kg^{-1}, a lachrymal secretion concentration of 1800 mOsm kg^{-1} and an estimate that 1 kg jellyfish has a volume of 1 litre, then predicted lachrymal secretion production rate (in l h^{-1}) for an intake of 16.7 kg jellyfish h^{-1} may be calculated as:

$$16.7 \times (1000 - 360)/1800 = 5.94, \quad (1)$$

or, for an intake of 24.3 kg jellyfish h^{-1}, the predicted lachrymal secretion production rate (in l h^{-1}) would be:

$$24.3 \times (1000 - 360)/1800 = 8.64. \quad (2)$$

Given a salt gland mass of 0.622 kg these lachrymal secretion production rates correspond to 9.55 and 13.89 ml secretion g^{-1} salt gland mass h^{-1}, respectively. Given a pure NaCl secretion of 1800 mOsm kg^{-1} [and known equivalence between osmolalities and NaCl concentration (Rankin and Davenport, 1981)], these will remove 0.543 g and 0.795 g NaCl g^{-1} salt gland mass h^{-1}, respectively.

Energetics

Scenario 1

Consider a 450 kg turtle eating 50% of its body mass as *R. pulmo* per 13.5 h foraging day. Jellyfish intake rate is 16.7 kg jellyfish h^{-1}. The energy content of *R. pulmo* is 0.11 kJ g^{-1} wet mass, so gross energy intake rate is 4.08 kJ kg^{-1} body mass h^{-1}. Given an 80% energy assimilation rate, the net energy intake rate is 3.26 kJ kg^{-1} body mass h^{-1}. However, there is a 30% loss (1.22 kJ kg^{-1} body mass h^{-1}) of gross energy intake due to warming of the ingested jellyfish before digestion, so the overall energy gain is 2.04 kJ kg^{-1} body mass h^{-1}.

A 'high' FMR of 88.6 kJ kg^{-1} body mass day^{-1} equates to 3.69 kJ kg^{-1} body mass h^{-1}; this is 1.65 kJ kg^{-1} body mass h^{-1} above that gained by eating 50% of its body mass as *R. pulmo* per day, implying that the turtle would be losing significant amounts of energy and have none to spare for blubber accumulation.

A 'medium' FMR of 41.4 kJ kg^{-1} body mass day^{-1} equates to 1.72 kJ kg^{-1} body mass h^{-1}, so it would appear that a turtle eating 50% of its body mass per day as *R. pulmo* could support its FMR and have 0.32 kJ kg^{-1} body mass h^{-1} to spare for blubber accumulation. However, this falls far short of either the 5.43 kJ kg^{-1} body mass h^{-1} required to lay down 1 kg blubber day^{-1} or the 2.72 kJ kg^{-1} body mass h^{-1} needed to lay down 0.5 kg blubber day^{-1}. It also implies that a leatherback turtle feeding on *R. pulmo* would need to eat about 42% body mass day^{-1} simply to support a 'high' FMR.

A 'low' field metabolic rate of 22.24 kJ kg^{-1} body mass day^{-1} equates to 0.93 kJ kg^{-1} body mass h^{-1} energy intake rate (equivalent to eating about 23% body mass day^{-1} as *R. pulmo*), which would release 1.11 kJ kg^{-1} body mass h^{-1} for blubber deposition, still well below a 0.5 or 1 kg blubber day^{-1} accumulation requirement.

Scenario 2

Consider a 450 kg turtle eating 73% of its body mass as *C. capillata* per 13.5 h foraging day. Jellyfish intake is 24.3 kg jellyfish h^{-1}. Energy content of *C. capillata* is 0.18 kJ g^{-1} wet mass, so gross energy intake rate is 9.72 kJ kg^{-1} body mass h^{-1}. Given an 80% energy assimilation rate, the net energy uptake rate is 7.78 kJ kg^{-1} body mass h^{-1}. However, there is an 18% loss (1.75 kJ kg^{-1} body mass h^{-1}) of gross energy intake due to warming of the ingested jellyfish before digestion, so the overall energy gain is 6.03 kJ kg^{-1} body mass h^{-1}.

Given a 'high' FMR of 3.69 kJ kg^{-1} body mass h^{-1}, *C. capillata* would yield an excess of 2.14 kJ kg^{-1} body mass h^{-1} (60.6% below that required to deposit 1 kg blubber day^{-1} and 21.3% below that required to deposit 0.5 kg blubber day^{-1}).

Given a 'medium' FMR of 1.72 kJ kg^{-1} body mass h^{-1}, *C. capillata* would release 4.31 kJ kg^{-1} body mass h^{-1} for blubber deposition (20.6% below that required for a 1 kg blubber day^{-1} requirement but 58% above that required for an 0.5 kg blubber day^{-1} accumulation rate).

Using a 'low' FMR of 0.93 kJ kg^{-1} body mass h^{-1}, 5.1 kJ kg^{-1} body mass h^{-1} would be available for blubber deposition (only 6.7% below that required for a 1 kg blubber day^{-1} deposition rate and 87.5% above the 0.5 kg blubber day^{-1} accumulation rate).

Predicted feeding and lachrymal secretion rates for adequate blubber deposition

Given the calculations above and the requirement for leatherbacks to lay down either 0.5 or 1 kg blubber day^{-1}, it is possible to estimate the corresponding hypothetical feeding rates and lachrymal secretion rates required to achieve this in a 13.5 h foraging bout per day (Table 2). It is apparent that *R. pulmo* does not provide an adequate diet for 100 kg blubber accumulation in 1–2 years, whatever FMR is used (though it is close to a 2 year accumulation). However, *C. capillata* eaten at a rate of about 80% body mass day^{-1} would support adequate blubber deposition at a low FMR within a year (and almost a medium FMR).

DISCUSSION

Salt secretion rates

Are the calculated rates of 9.55 and 13.89 ml secretion g^{-1} salt gland mass h^{-1} (corresponding to reported adult leatherback jellyfish intake rates of 50 and 73% body mass day^{-1}, respectively) realistic? Salt-loaded hatchling leatherbacks (body mass about 38 g; salt gland mass about 0.109 g) produced lachrymal secretions at about 1.7 ml secretion g^{-1} salt gland h^{-1} (calculated from Reina et al., 2002) but this was based on short-term (80 min) experiments on hatchlings in which instantaneous, relatively small salt loads had been injected directly into the body cavity. It is also much lower than values recorded for feeding green turtle (*C. mydas*) hatchlings, which could apparently reach rates of about 18.6 ml secretion g^{-1} salt gland h^{-1} following intraperitoneal injections of NaCl (calculated from Marshall and Cooper, 1988). For technical, logistic and ethical reasons, adult salt gland secretion rates have mostly been measured on birds (whose nasal salt glands have a similar histological structure to sea turtle lachrymal salt glands) but rarely on those exposed to sustained salt loads. An exception was an early study on greater black-backed gulls (*Larus marinus*) (Schmidt-Nielsen, 1960). These gulls have nasal glands that make up 0.1% of their body mass and can produce about 36 ml secretion g^{-1} salt gland mass h^{-1}. However, it has been suggested that avian salt glands produce about three times the amount of tears as those of marine reptiles, simply because of body temperature differences (Q_{10} effects: 25°C gland temperature in reptiles, 38°C in birds; McNab, 2002). Overall, it would appear that a maximum leatherback tear production rate of about 10–15 ml secretion g^{-1} salt gland mass h^{-1} is reasonable, and therefore compatible with eating large quantities of jellyfish throughout a long foraging day. However, it seems probable that salt gland performance will limit adult leatherback consumption of jellyfish to around 80% body mass day^{-1} (see Table 2).

Energetics

Leatherback turtles are capital breeders (Plot et al., 2013) that utilise energy collected and stored as lipid at high latitude to fuel breeding migrations and egg clutches laid in the tropics. Given the energetic calculations laid out in the Results section, it is apparent that leatherbacks need to ingest large quantities of jellyfish if they are to support their FMR and also lay down adequate amounts of blubber. While previous studies have shown that leatherbacks at high latitudes ingest far more gelatinous prey than is needed to support either 'low' or 'medium' estimates of FMR (Heaslip et al., 2012; James et al., 2006) (hyperphagia), it has not previously been appreciated how high the energy demand of blubber deposition is.

Table 2. Predicted jellyfish ingestion rates required for leatherback turtles consuming different jellyfish species to lay down blubber, given 'low', 'medium' or 'high' estimates of field metabolic rate (FMR)

Prey species	FMR	Blubber accumulation rate (kg blubber day^{-1})	Required ingestion rates (% body mass day^{-1})	Required lachrymal secretion rates (l h^{-1})	Required mass-specific lachrymal secretion rates (ml secretion g^{-1} salt gland mass h^{-1})
Rhizostoma pulmo	Low	1.0	155	18.3	29.5
		0.5	89	10.6	17.1
	Medium	1.0	175	20.7	33.3
		0.5	109	12.9	20.8
	High	1.0	224	26.6	42.8
		0.5	157	18.7	30.0
Cyanea capillata	Low	**1.0**	**77**	**9.1**	**14.6**
		0.5	**54**	**6.4**	**10.2**
	Medium	1.0	86	10.2	16.4
		0.5	**44**	**5.2**	**8.4**
	High	1.0	110	13.1	20.9
		0.5	**78**	**9.2**	**14.8**

Low FMR, 22.24 kJ kg^{-1} body mass day^{-1} (Bradshaw et al., 2007); medium FMR, 41.4 kJ kg^{-1} body mass day^{-1} (Wallace et al., 2005); high FMR, 88.6 kJ kg^{-1} body mass day^{-1} (Casey et al., 2014).

Corresponding estimations of necessary lachrymal secretion rates are also displayed. Values in bold are compatible with maximal lachrymal secretion rates of 15 ml secretion g^{-1} salt gland mass h^{-1} (see the Discussion section for details).

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From the calculations presented here (Table 2), it is evident that the 1978 estimate of consumption of *R. pulmo* (50% body mass day^{-1}) in French waters was far too low to support adequate blubber deposition (whether over one or two years), probably because the observer could only detect jellyfish capture at the surface, not below it (Duron, 1978), but also because *R. pulmo* has a relatively low-energy density by comparison with *C. capillata* (Doyle et al., 2007). In contrast, the recent video-based estimate of a mean ingestion rate of 73% body mass day^{-1} (mainly *C. capillata*) for leatherbacks feeding in Nova Scotian waters (Heaslip et al., 2012) is nearly compatible with 100 kg blubber acquisition in a single year, and far exceeds that required for a 50 kg increase (Table 2). It may be concluded from these calculations that leatherbacks foraging in European waters will need to eat some more energy-dense gelatinous prey than whole *R. pulmo* if they are to accumulate adequate levels of blubber. There is no doubt that they often do so because gut contents analysis (based on nematocyst identification) has shown that they also eat all of the other common large medusae available to them in near-surface European waters [i.e. *Pelagia noctiluca*, *Chrysaora hysoscella*, *Aurelia aurita*, *C. capillata* and *Cyanea lamarckii* (Den Hartog and Van Nierop, 1984)]. An alternative possibility is that leatherbacks can forage selectively on different parts of *R. pulmo*. Doyle et al. (2007) showed that the species' bell was energy poor by comparison with the gonads and oral arms. If the turtles selectively ate the oral arms, they would gain around 50% more energy per unit mass of jellyfish than they would if they ate the whole jellyfish. The filming of leatherbacks by Heaslip et al. (2012) suggests that they can feed selectively. It seems likely that selective feeding will be more common in dense patches of prey but more filming would be needed to confirm this hypothesis.

The energetic analysis presented here strongly suggests that leatherbacks will have to eat beyond the requirement to support FMR, either over multiple high latitude foraging seasons or whilst foraging at lower latitudes. Finally, the analysis indicates that the highest currently available estimate of FMR (Casey et al., 2014) is almost certainly far too high [and about twice that predicted allometrically from Nagy et al. (1999)], as there is little compatibility with necessary rates of blubber acquisition (Table 2), and leatherbacks would actually lose much energy if they were feeding on less energy-dense prey such as *R. pulmo*.

Gut anatomy

The gut of an adult leatherback turtle is much longer than in other extant sea turtles (Wyneken, 2001). From data given in Table 3 (Magalhães et al., 2012), and the known relationship between curved carapace length and body mass (Georges and Fossette, 2006), it may be calculated that a 450 kg turtle will have a gut length of about 13.4 m. The oesophagus is proportionally much longer than in other sea turtles, running from the throat to the centre of the body before looping anteriorly to empty into the stomach. Highly muscular and well vascularised, its lumen is lined by a keratin layer (presumably essentially impermeable to salts and water) which features large numbers of posteriorly directed spikes that are believed to direct prey towards the stomach. *In vivo* it is likely that peristalsis of the oesophagus will also cause the spikes to shred the gelatinous prey, as well as squeezing out excess seawater via the pharynx. The stomach is also relatively very long (ca. 2 m in an adult) and much thinner walled than the oesophagus. It is presumably the site of primary proteolytic digestion of prey and the likely site of osmotic flow of water from blood to lumen. The small intestine is the longest part of the gut, relatively and absolutely (54.8% of gut length; ca. 7.3 m). It is likely the major site of NaCl uptake and HCO_3^- secretion, as well as continuing digestion and nutrient absorption. In contrast, the large intestine is relatively extremely short, particularly in comparison with that of the green turtle *C. mydas* in which the large intestine is much involved in the protracted breakdown of a low-quality plant diet (Bjorndal, 1980).

Consequences of hyperphagia

No other large vertebrate species is known to eat such considerable daily quantities of food as adult *Dermochelys* feeding at high latitude to gain and store excess energy (hyperphagia). It has been noted that, in general, hyperphagia is constrained by an interplay between the nature of the diet (e.g. does it lead to indigestible ejecta?), its digestion rate and the storage capacity of the alimentary canal (Barboza and Hume, 2006).

Jellyfish are commonly regarded as providing a poor-quality diet because they have a low organic content in relation to wet mass. However, there is abundant evidence that they are digested extremely quickly [22–50 times as fast as similar masses of crustacean prey (Jackson et al., 1987; Arai, 2005)], principally by proteolytic enzymes. If jellyfish are rapidly stripped of their water and salt content, the remaining organic dry mass is actually a high protein, high energy diet [for *C. capillata*: 18.19 kJ g^{-1} organic dry mass; 71.1% protein (Doyle et al., 2007)], with similar energy content to, and greater protein content than, commercial trout pellets used in aquaculture [17.6–21.0 kJ g^{-1} dry mass; 40–50% protein (Hadjichristophorou and Grove, 1983)]. Digestion of gelatinous prey leads to negligible amounts of indigestible solid material and the gut contents likely remain largely fluid. Certainly, leatherback turtles produce very fluid faeces. Observers in the Gulf of Corinth, Greece reported that 'the animal defaecated (a large yellowish cloud)' (Bearzi et al., 2015); this phenomenon can also be seen in an image taken off Indonesia (http://www.gettyimages.co.uk/detail/photo/leatherback-turtle-defecates-off-of-kei-high-res-stock-photography/547989657), which shows a similar pale diarrhoeal outflow. It is feasible that the pale faecal colour indicates the presence of divalent microcrystalline complexes like those expelled by teleosts (Wilson et al., 2002) but no samples have so far been analysed.

Given plentiful food, most vertebrates, whether carnivorous or herbivorous, feed for a period of time and then cease because some part of the alimentary canal (crop, stomach) is full; they demonstrate maximum appetite and satiation. During hyperphagia at high

Table 3. Relative gut lengths of sea turtle species

	Leatherback turtle *Dermochelys coriacea* (gelativore)	Green turtle *Chelonia mydas* (herbivore)	Loggerhead turtle *Caretta caretta* (carnivore)
Gut length as % curved carapace length	800	1152	754
Oesophagus length as % total gut length	15.5	4.5	3.6
Stomach length as % total gut length	15.0	5.3	6.3
Small intestine length as % total gut length	54.8	34.1	51.2
Large intestine length as % total gut length	14.6	56.1	38.9

Relative gut lengths are calculated from Magalhães et al. (2012).

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latitude, the leatherback turtle appears to adopt a different approach of almost continuous daytime feeding if sufficient prey items are available (Duron, 1978; Heaslip et al., 2012), though it may support routine FMR at low latitudes by browsing on dense jellyfish aggregations for a few hours each day (Fossette et al., 2012).

Near-continuous feeding of bulky jellyfish [a perfect plug-flow reactor mode of feeding and digestion (Penry and Jumars, 1987)] means that they must be digested quickly, and that excess water and salts need to be expelled almost continually too. A 450 kg leatherback ingesting 73% of its body mass per day during a 13.5 h foraging day takes in about 24 l of jellyfish h^{-1} (roughly 5% body volume h^{-1}). Salt gland secretion is calculated here to be 8.64 l h^{-1}, leaving about 15.4 l h^{-1} to be allocated to cutaneous, respiratory, urinary and faecal losses. Insufficient information is available to calculate further but it seems likely that faecal loss is by far the most important route. In turn, this implies that gut transit times for leatherback turtles are low. There is plenty of evidence that total gut clearance times (TGCT) for cheloniid sea turtles are of the order of days–weeks (Jones and Seminoff, 2013), especially in the case of green turtles eating algae or seagrass. However, for adult *Dermochelys*, TGCT must be of the order of a few hours. Although leatherbacks have much more ability than other turtles to vary their body volume (Davenport et al., 2011), it is improbable that they can store more than 4–6 hours' worth (roughly 22–32% body volume given a 73% body mass day^{-1} intake rate) of jellyfish intake. This is consistent with known high rates of digestion of gelatinous prey (Jackson et al., 1987; Arai, 2005) but implies a high rate of peristaltic activity. The high rate of water turnover in leatherbacks also has implications for measurement of FMR by the double-labelled water technique (DLW). DLW accuracy relies on the rate of production of CO_2 being high by comparison with the rate of water turnover (Wallace et al., 2005; Jones, 2009). This is probably not true of leatherbacks, especially when they are feeding.

Costs of osmoregulation

No data are available for the energetic costs of osmoregulation in leatherbacks and this is a deficiency common to other marine vertebrates. Available information is conflicting. In the best-studied group (marine fish, which have large surface areas of highly permeable gills) estimates are below 10% of routine metabolic rate (Evans, 2009), even as low as 0.5%. However, shore birds (dunlin, *Calidris alpina*) showed increases of 17% in basal metabolic rate when their water supply was changed from freshwater to seawater but much of this cost was probably due to an upregulation of osmoregulatory machinery rather than the costs of salt pumping *per se* (Gutierrez et al., 2011). An alternative approach is to estimate feasible metabolic rates of salt gland tissue. The highest tissue metabolic rates (about 77 kJ kg^{-1} h^{-1}) recorded in mammals of comparable size are for heart and kidneys (Elia, 1992). Using a Q_{10} effect as discussed above, and a salt gland mass of 0.622 kg, this suggests that the salt glands of a 450 kg turtle will use about 16 kJ h^{-1}, which equates to 0.036 kJ kg^{-1} body mass h^{-1}, about 4% of the 'low' FMR estimate for leatherbacks (Bradshaw et al., 2007) and much less for the higher FMR estimates (1–2%). The high throughput of salts and water in gelativores makes this an interesting area of future study but *Dermochelys* is unlikely to be a convenient experimental species as far as adults are concerned.

Further study

This investigation reveals several limitations in the current understanding of adult leatherback turtle physiology. Logistic and ethical issues limit progress but technological advances make it likely that video recording of feeding (c.f. Heaslip et al., 2012) will soon become feasible over much longer periods, thereby resolving the criticism of unjustified extrapolation from short-term records. Similarly, long-term (months, years) recording of stomach temperature and jaw movements using satellite telemetry will hopefully refine understanding of the costs of warming food and the frequency/intensity of feeding episodes.

In terms of osmotic and energetic physiology it would be desirable to conduct studies on animals much larger than hatchlings but more tractable than adults. Jones (2009) solved many of the problems of raising *Dermochelys* to juvenile size (<42 kg). Study of such captive turtles could be used to address salt gland secretion rates but also investigate (via isotope studies) the role of the gut in ionic regulation and water turnover. In particular, it would allow determination of whether precipitated carbonates (as microcrystals) are produced as in marine fish (Wilson et al., 2009). Also, in concert with long-established, minimally invasive fish aquaculture techniques, gut transit times and assimilation rates for a variety of nutrients could be established.

If these advances are made, then they may be combined with our increased understanding of movements of adult female leatherbacks to further elucidate the relationships between turtle age, migratory behaviour, breeding frequency and clutch production rate.

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References

Anthony, J. A., Roby, D. D. and Turco, K. R. (2000). Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *J. Exp. Mar. Biol. Ecol.* **248**, 53-78.

Arai, M. N. (2005). Predation on pelagic coelenterates: a review. *J. Mar. Biol. Assoc. UK* **85**, 523-536.

Azhari, M. (2010). *Basics of Biomedical Ultrasound for Engineers*. Hoboken, New Jersey: John Wiley & Sons, Inc.

Barboza, P. S. and Hume, I. D. (2006). Physiology of intermittent feeding: integrating responses of vertebrates to nutritional deficit and excess. *Physiol. Biochem. Zool.* **79**, 250-264.

Bearzi, G., Casale, P., Margaritoulis, D., Bonizzoni, S. and Santostasi, N. S. (2015). Observation of a leatherback sea turtle, *Dermochelys coriacea*, in the Gulf of Corinth, Greece. *Mar. Turtle Newsl.* **146**, 6-9.

Bjorndal, K. A. (1980). Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar. Biol.* **56**, 147-154.

Bradshaw, C. J. A., McMahon, C. R. and Hays, G. C. (2007). Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. *Physiol. Biochem. Zool.* **80**, 209-219.

Casey, J. P., James, M. C. and Williard, A. S. (2014). Behavioral and metabolic contributions to thermoregulation in freely swimming leatherback turtles at high latitudes. *J. Exp. Biol.* **217**, 2331-2337.

Davenport, J. (1998). Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtle *Dermochelys coriacea*. *Br. Herpetol. Soc. Bull.* **62**, 4-5.

Davenport, J. and Balazs, G. H. (1991). 'Fiery bodies' – are pyrosomas an important part of the diet of leatherback turtles? *Br. Herpetol. Soc. Bull.* **37**, 33.

Davenport, J., Holland, D. L. and East, J. (1990). Thermal and biochemical characteristics of the lipids of the leatherback turtle *Dermochelys coriacea*: evidence of endothermy. *J. Mar. Biol. Assoc. UK* **70**, 33-41.

Davenport, J., Balazs, G. H., Faithfull, J. W. and Williamson, D. A. (1993). A struvite faecolith in the leatherback turtle *Dermochelys coriacea* Vandelli. A means of packaging garbage? *Herpetol. J.* **3**, 81-83.

Davenport, J., Fraher, J., Fitzgerald, E., McLaughlin, P., Doyle, T., Harman, L. and Cuffe, T. (2009). Fat head: an analysis of head and neck insulation in the leatherback turtle (*Dermochelys coriacea*). *J. Exp. Biol.* **212**, 2753-2759.

Davenport, J., Plot, V., Georges, J.-Y., Doyle, T. K. and James, M. C. (2011). Pleated turtle escapes the box – shape changes in *Dermochelys coriacea*. *J. Exp. Biol.* **214**, 3474-3479.
Davenport, J., Jones, T. T., Work, T. M. and Balazs, G. H. (2015). Topsy-turvy: turning the counter-current heat exchange of leatherback turtles upside down. *Biol. Lett.* **11**, 20150592.
Den Hartog, J. C. and Van Nierop, M. M. (1984). A study on the gut contents of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zool. Verhandel.* **209**, 1-36.
Doyle, T. K., Houghton, J. D. R., McDevitt, R., Davenport, J. and Hays, G. C. (2007). The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. *J. Exp. Mar. Biol. Ecol.* **343**, 239-252.
Duron, M. (1978). Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. *PhD Thesis*, University of Bordeaux, Talence, France.
Eckert, K. L., Wallace, B. P., Frazier, J. G., Eckert, S. A. and Pritchard, P. C. H. (2012). *Synopsis of the Biological Data on the Leatherback Sea Turtle (Dermochelys coriacea)*. Washington, DC: U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication BTP-R4015-2012.
Elia, M. (1992). Organ and tissue contribution to metabolic rate. In *Energy Metabolism: Tissue Determinants and Cellular Corollaries* (ed. J. M. Kinney and H. N. Tucker), pp. 61-80. New York: Raven Press.
Evans, D. H. (2009). *Osmotic and Ionic Regulation: Cells and Animals*. Boca Raton: CRC Press.
Fossette, S., Hobson, V. J., Girard, C., Calmettes, B., Gaspar, P., Georges, J.-Y. and Hays, G. C. (2010). Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *J. Mar. Syst.* **81**, 225-234.
Fossette, S., Gleiss, A. C., Casey, J. P., Lewis, A. R. and Hays, G. C. (2012). Does prey size matter? Novel observations of feeding in the leatherback turtle (*Dermochelys coriacea*) allow a test of predator–prey size relationships. *Biol. Lett.* **8**, 351-354.
Frair, W., Ackman, R. G. and Mrosovsky, N. (1972). Body temperature of *Dermochelys coriacea*: warm turtle from cold water. *Science* **177**, 791-793.
Georges, J. Y. and Fossette, S. (2006). Estimating body mass in leatherback turtles *Dermochelys coriacea*. *Mar. Ecol. Prog. Ser.* **318**, 255-262.
Gutierrez, J. S., Masero, J. A., Abad-Gomez, J. M., Villegas, A. and Sanchez-Guzman, J. M. (2011). Understanding the energetic costs of living in saline environments: effects of salinity on basal metabolic rate, body mass and daily energy consumption of a long-distance migratory shorebird. *J. Exp. Biol.* **214**, 829-835.
Hadjichristophorou, M. and Grove, D. J. (1983). A study of appetite, digestion and growth in juvenile green turtle (*Chelonia mydas L.*) fed on artificial diets. *Aquaculture* **30**, 191-201.
Hays, G. C., Hobson, V. J., Metcalfe, J. D., Righton, D. and Sims, D. W. (2006). Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* **87**, 2647-2656.
Heaslip, S. G., Iverson, S. J., Bowen, W. D. and James, M. C. (2012). Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PLoS ONE* **7**, e33259.
Hochscheid, S. (2003). Thermoregulation, metabolism and buoyancy regulation in sea turtles. *PhD Thesis*, University of Aberdeen, UK.
Holland, D. L., Davenport, J. and East, J. (1990). The fatty acid composition of the leatherback turtle, *Dermochelys coriacea* L. and its jellyfish prey. *J. Mar. Biol. Assoc. UK* **70**, 761-770.
Holmes, W. N. and Donaldson, E. M. (1969). The body compartments and the distribution of electrolytes. In *Fish Physiology*, Vol. 1 (ed. W. S. Hoar and D. J. Randall), pp. 1-89. New York: Academic Press.
Holmes, W. N. and McBean, R. L. (1964). Some aspects of electrolyte excretion in the green turtle, *Chelonia mydas mydas*. *J. Exp. Biol.* **41**, 81-90.
Houghton, J. D. R., Doyle, T. K., Wilson, M. W., Davenport, J. and Hays, G. C. (2006). Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* **87**, 1967-1972.
Hudson, D. M. and Lutz, P. L. (1986). Salt gland function in the leatherback sea turtle, *Dermochelys coriacea*. *Copeia* **1986**, 247-249.
Jackson, S., Duffy, D. C. and Jenkins, J. F. G. (1987). Gastric digestion in marine vertebrate predators: in vitro standards. *Funct. Ecol.* **1**, 287-291.
James, M. C. and Mrosovsky, N. (2004). Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada. *Can. J. Zool.* **82**, 1302-1306.
James, M. C., Myers, R. A. and Ottensmeyer, C. A. (2005a). Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc. R. Soc. B Biol. Sci.* **272**, 1547-1555.
James, M. C., Ottensmeyer, C. A. and Myers, R. A. (2005b). Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195-201.
James, M. C., Davenport, J. and Hays, G. C. (2006). Expanded thermal niche for a diving vertebrate: a leatherback turtle diving into near-freezing water. *J. Exp. Mar. Biol. Ecol.* **335**, 221-226.
Jones, T. T. (2009). Energetics of the leatherback turtle, *Dermochelys coriacea*. *PhD Thesis*, University of British Columbia.
Jones, T. T. and Seminoff, J. A. (2013). Feeding biology: advances from field-based observations, physiological studies, and molecular techniques. In *The Biology of Sea Turtles, Volume 3. CRC Marine Biology Series* (ed. J. Wyneken, K. J. Lohmann and J. A. Musick), pp. 211-247. Boca Raton: CRC Press.
Jones, T. T., Salmon, M., Wyneken, J. and Johnson, C. (2000). Rearing leatherback hatchlings: protocols, growth and survival *Mar. Turtle Newsl.* **90**, 3-6.
Jones, T. T., Bostrom, B. L., Hastings, M. D., Van Houtan, K. S., Pauly, D. and Jones, D. R. (2012). Resource requirements of the Pacific leatherback turtle population. *PLoS ONE* **7**, e5477.
Lutcavage, M. and Lutz, P. L. (1986). Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*. *Copeia* **1986**, 796-798.
Lutz, P. L. (1996). Salt, water, and pH balance in sea turtles. In *The Biology of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 343-361. Boca Raton: CRC Press.
Magalhães, M. S., Santos, A. J. B., da Silva, N. B. and de Moura, C. E. B. (2012). Anatomy of the digestive tube of sea turtles (Reptilia: Testudines). *Zoologia* **29**, 70-76.
Marshall, A. T. and Cooper, P. D. (1988). Secretory capacity of the lachrymal salt gland of hatchling sea turtles, *Chelonia mydas*. *J. Comp. Physiol. B* **157**, 821-827.
McCue, M. D. (2006). Specific dynamic action: a century of investigation. *Comp. Biochem. Physiol. A* **144**, 381-394.
McNab, B. K. (2002). *The Physiological Ecology of Vertebrates: A View from Energetics*. New York: Comstock Publishing Associates, Cornell University Press, Ithaca.
Molina-Ramírez, A., Cáceres, C., Romero-Romero, S., Bueno, J., González-Gordillo, J. I., Irigoien, X., Sostres, J., Bode, A., Mompeán, C., Puelles, M. F. et al. (2015). Functional differences in the allometry of the water, carbon and nitrogen content of gelatinous organisms. *J. Plankton Res.* **37**, 989-1000.
Nagy, K. A., Girard, I. A. and Brown, T. K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* **19**, 247-277.
Ortiz, R. M. (2001). Osmoregulation in marine mammals. *J. Exp. Biol.* **204**, 1831-1844.
Pauly, D., Graham, W., Libralato, S., Morissette, L. and Deng Palomares, M. L. (2009). Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* **616**, 67-85.
Penry, D. L. and Jumars, P. A. (1987). Modeling animal guts as chemical reactors. *Am. Nat.* **129**, 69-96.
Plot, V., Jenkins, T., Robin, J.-P., Fossette, S. and Georges, J.-Y. (2013). Leatherback turtles are capital breeders: morphometric and physiological evidence from longitudinal monitoring. *Physiol. Biochem. Zool.* **86**, 385-397.
Prado, P. and Heck, K. L.Jr. (2011). Seagrass selection by omnivorous and herbivorous consumers: determining factors. *Mar. Ecol. Prog. Ser.* **429**, 45-55.
Rankin, J. C. and Davenport, J. (1981). *Animal Osmoregulation*. Glasgow: Blackie & Son.
Reina, R. D., Jones, T. T. and Spotila, J. R. (2002). Salt and water regulation by the leatherback sea turtle *Dermochelys coriacea*. *J. Exp. Biol.* **205**, 1853-1860.
Richardson, A. J., Bakun, A., Hays, G. C. and Gibbons, M. J. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* **24**, 312-322.
Robertson, J. D. (1957). Osmotic and ionic regulation in aquatic invertebrates. In *Recent Advances in Invertebrate Physiology* (ed. B. T. Scheer), pp. 229-246. Eugene: University of Oregon.
Schmidt-Nielsen, K. (1960). The salt-secreting gland of marine birds. *Circulation* **21**, 955-967.
Taylor, J., Wilson, J., Jones, T. and Grosell, M. (2007). It all comes out the same in the end: drinking seawater demands intestinal HCO_3^- secretion. *Comp. Biochem. Physiol. A* **146**, S90-S91.
Wallace, B. P. and Jones, T. T. (2015). Leatherback turtle physiological ecology. In *The Leatherback Turtle: Biology and Conservation* (ed. J. R. Spotila and P. S. Tomillo), pp. 149-161. Baltimore: John Hopkins University Press.
Wallace, B. P., Williams, C. L., Paladino, F. V., Morreale, S. J., Lindstrom, R. T. and Spotila, J. R. (2005). Bioenergetics and diving activity of internesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino Las Baulas, Costa Rica. *J. Exp. Biol.* **208**, 3873-3884.
Wallace, B. P., Sotherland, P. R., Tomillo, P. S., Reina, R. D., Spotila, J. R. and Paladino, F. V. (2007). Maternal investment in reproduction and its consequences in leatherback turtles. *Oecologia* **152**, 37-47.
Wallace, B. P., Zolkewitz, M. and James, M. C. (2015). Fine-scale foraging ecology of leatherback turtles. *Front. Ecol. Evol.* **3**, 1-15.
Wilson, R. W., Wilson, J. M. and Grosell, M. (2002). Intestinal bicarbonate secretion by marine teleost fish—why and how? *Biochim. Biophys. Acta* **1566**, 182-193.
Wilson, R. W., Millero, F. J., Taylor, J. R., Walsh, P. J., Christensen, V., Jennings, S. and Grosell, M. (2009). Contribution of fish to the marine inorganic carbon cycle. *Science* **323**, 359-362.
Wyneken, J. (2001). *The Anatomy of Sea Turtles. NOAA Technical Memorandum NMFS-SEFSC-470*. Miami, FL: NOAA Southeast Fisheries Science Center.

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