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

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SUMMARY STATEMENT
Leatherback turtles feed on salty jellyfish to accumulate blubber that fuels reproduction. They eat 80% body mass per day and secrete 6-9 litres of tears per hour to remove salt.

ABSTRACT
Leatherback turtles (*Dermochelys coriacea*) are capital breeders that accumulate blubber (33 kJ g wet mass$^{-1}$) 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 wet mass$^{-1}$), so leatherbacks must ingest large quantities. Two published estimates of feeding rate (50% body mass d$^{-1}$ (on *Rhizostoma pulmo*), 73% body mass d$^{-1}$ (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 450kg turtle; relatively 3 times the size of salt glands in cheloniid turtles) is measured for the first time by CT scanning. Various published values for leatherback field metabolic rate (FMR), 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 salt gland mass$^{-1}$ h$^{-1}$ (tear osmolality 1800 mOsm kg$^{-1}$). This will permit consumption of 80% body mass d$^{-1}$ of *Cyanea 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.
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 wet mass\(^{-1}\)), 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 wet mass\(^{-1}\) for a range of oceanic fish (Anthony et al., 2000) and about 3.5 kJ g wet mass\(^{-1}\) 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 sea water; 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 a) accessing sufficient water from the environment and/or diet, and b) 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 medusae, but they also feed on pyrosomes
(Davenport and Balazs, 1991) (see also http://www.nhm.ac.uk/resources/visit-us/wnpy/2013/large/57.jpg). They grow rapidly; though there is dispute about age at maturity, recent estimates range from 12-29 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 amongst 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.

Recently, observations using turtle-borne cameras indicated that leatherbacks (mean 455 kg body mass) feeding off Nova Scotia 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 below 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 plentiful 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 wet mass\(^{-1}\), given 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) present satellite-tagging data that show 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) show 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 sea water (1163 mOsm. Kg\(^{-1}\)); the lachrymal fluid is almost pure NaCl solution. After feeding ad lib. 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 per hour, 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 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 resultant 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\(^{++}\) and Mg\(^{++}\) as microcrystalline complexes, so further reducing the osmolarity of the gut fluid, promoting water absorption in the hind gut, and protecting the kidneys against formation of kidney stones (Wilson et al., 2002). The role of the gut of sea turtles in ionic regulation is largely unstudied, but it must function in 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 a) establish the size of adult salt glands of *Dermochelys*, b) to estimate rates of salt gland secretion under two feeding rate scenarios (Duron, 1978; Heaslip et al., 2012), c) 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 N. Atlantic waters.
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. 168cm in standard curved carapace length, it would have weighed about 450 kg (Georges and Fossette, 2006). The head and neck were removed, embalmed and 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. figure 1) were inspected and measurements 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.

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 (Chelonia 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, since the urine is known to be isosmotic with the plasma (Lutz, 1996). It is accepted that the gut wall pumps virtually pure NaCl from lumen to the blood, so that 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 body mass\(^{-1}\) day\(^{-1}\) (Wallace et al., 2005), though there was much variability in this estimate, principally because one individual had an FMR more than 3 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 body mass\(^{-1}\) day\(^{-1}\) (Bradshaw et al., 2007), similar to those measured in two of the individuals studied by Wallace et al. (2005). These published values are both lower than the 46.2 kJ kg body mass\(^{-1}\) 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). Since 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. On the one hand 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 body mass\(^{-1}\) day\(^{-1}\). Here the only currently-available values (‘low’ FMR: 22.24 kJ kg body mass\(^{-1}\) day\(^{-1}\) (Bradshaw et al., 2007), ‘medium’ FMR: 41.4 kJ kg body mass\(^{-1}\) day\(^{-1}\) (Wallace et al., 2005) and ‘high’ FMR: 88.6 kJ kg body mass\(^{-1}\) 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 *Rhizostoma pulmo*, while turtles filmed in Canadian waters (Heaslip et al., 2012) were
mainly eating the lion’s mane jellyfish *Cyanea 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 (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 wet mass\(^{-1}\)), with *Rhizostoma pulmo* having 61% of the mass-specific energy content of *Cyanea capillata*.

**Losses of energy 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 *Cyanea capillata*, 30% for a diet of *Rhizostoma 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 *Dermochelys coriacea*, but data are available for other sea turtles. Immature green turtles (*Chelonia mydas*) fed on an animal diet (fishmeal-based trout pellets: 17.6–21.0 kJ g dry mass\(^{-1}\); 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 content (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; it is also likely that gut function is continuously upregulated. SDA is therefore here judged to be proportionally imperceptible (as found for green turtles, *Chelonia 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 5-17%. A conservative estimate for leatherback blubber energy density used here (33 kJ g wet mass⁻¹) 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 (Georges and Fossette, 2006; James et al., 2005b). 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 hour per day foraging sessions (Heaslip et al., 2012), this means that a net 2,444 kJ h⁻¹ must be acquired, purely for blubber lipid storage. For a 450 kg turtle this equates to 5.43 kJ kg body mass⁻¹ 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 body mass⁻¹ 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 litres, 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 gut and lachrymal glands
Given a turtle of mass 450 kg eating 50% body mass of jellyfish (Duron, 1978) in a 13.5 hour per day foraging session, then intake will be about 16.7 kg jellyfish h⁻¹. At the higher intake rate of 73 % body mass per day (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 it may be calculated that:
Predicted lachrymal secretion production rate = \( \frac{16.7 \times (1000 - 360)}{1800} = 5.94 \text{ litres h}^{-1} \)
(intake 16.7 kg jellyfish h\(^{-1}\))

or:

Predicted lachrymal secretion production rate = \( \frac{24.3 \times (1000 - 360)}{1800} = 8.64 \text{ litres h}^{-1} \)
(intake 24.3 kg jellyfish h\(^{-1}\))

Given a salt gland mass of 0.622 kg these lachrymal secretion production rates correspond to 9.55 and 13.89 ml secretion g salt gland mass\(^{-1} \) 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 salt gland mass\(^{-1} \) h\(^{-1} \) respectively.

**Energetics**

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

A ‘high’ FMR of 88.6 kJ kg body mass\(^{-1} \) day\(^{-1} \) equates to 3.69 kJ kg body mass\(^{-1} \) h\(^{-1} \); this is 1.65 kJ kg body mass\(^{-1} \) h\(^{-1} \) above that gained by eating 50% of its body mass as *Rhizostoma 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 body mass\(^{-1} \) day\(^{-1} \) equates to 1.72 kJ kg body mass\(^{-1} \) h\(^{-1} \), so it would appear that a turtle eating 50% of its body mass per day as *Rhizostoma pulmo* could support its FMR and have 0.32 kJ kg body mass\(^{-1} \) h\(^{-1} \) to spare for blubber accumulation. However, this falls far short of either the 5.43 kJ kg body mass\(^{-1} \) h\(^{-1} \) required to lay down 1 kg blubber d\(^{-1} \), or the 2.72 kJ kg body mass\(^{-1} \) h\(^{-1} \) needed to lay down 0.5 kg blubber d\(^{-1} \). It also implies that a leatherback turtle feeding on *Rhizostoma pulmo* would need to eat about 42% body mass d\(^{-1} \) simply to support a ‘high’ FMR.
A ‘low’ field metabolic rate of 22.24 kJ kg body mass\(^{-1}\) day\(^{-1}\) equates to 0.93 kJ kg body mass\(^{-1}\) h\(^{-1}\) energy intake rate (equivalent to eating about 23% body mass d\(^{-1}\) as *Rhizostoma pulmo*), which would release 1.11 kJ kg body mass\(^{-1}\) h\(^{-1}\) for blubber deposition, still well below a 0.5 or 1kg blubber day\(^{-1}\) accumulation requirement.

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

Given a ‘high’ FMR of 3.69 kJ kg body mass\(^{-1}\) h\(^{-1}\), *Cyanea capillata* would yield an excess of 2.14 kJ kg body mass\(^{-1}\) h\(^{-1}\), 60.6% below that required to deposit 1kg 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 body mass\(^{-1}\) h\(^{-1}\), *Cyanea capillata* would release 4.31 kJ kg body mass\(^{-1}\) h\(^{-1}\) for blubber deposition, 20.6% below that required for a 1kg blubber day\(^{-1}\) requirement, but 58% above that required for an 0.5kg blubber day\(^{-1}\) accumulation rate.

Using a ‘low’ FMR of 0.93 kJ kg body mass\(^{-1}\) h\(^{-1}\), 5.1 kJ kg body mass\(^{-1}\) h\(^{-1}\) would be available for blubber deposition (only 6.7% below that required for a 1kg blubber day\(^{-1}\) deposition rate and 87.5% above the 0.5kg 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 d\(^{-1}\), 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 *Rhizostoma 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). On the other hand *Cyanea capillata* eaten at a rate of about 80% body mass per day would support adequate blubber deposition at 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 salt gland mass\(^{-1}\) h\(^{-1}\) (corresponding to reported adult leatherback jellyfish intake rates of 50% and 73% body mass d\(^{-1}\) respectively) realistic? Salt-loaded hatchling leatherbacks (body mass about 38g, salt gland mass about 0.109 g) produced lachrymal secretions at about 1.7 ml secretion g salt gland\(^{-1}\) 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 (Chelonia mydas) hatchlings, which could apparently reach rates of about 18.6 ml secretion g salt gland\(^{-1}\) 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 body mass and can produce about 36 ml secretion g salt gland mass\(^{-1}\) 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 salt gland mass\(^{-1}\) 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 d\(^{-1}\) (see Table 2).

Energetics

Leatherback turtles are capital breeders (Plot et al., 2013) that utilize 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 study has 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 is the energy-demand of blubber deposition. From the calculations
presented here (Table 2), it is evident that the 1978 estimate of consumption of *Rhizostoma pulmo* (50% body mass d\(^{-1}\)) 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 *Rhizostoma pulmo* has a relatively low energy density by comparison with *Cyanea capillata* (Doyle et al., 2007). In contrast, the recent video-based estimate of a mean ingestion rate of 73% body mass d\(^{-1}\) (mainly *Cyanea 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 *Rhizostoma pulmo* if they are to accumulate adequate levels of blubber. There is no doubt that they often do so, since 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 (viz: *Pelagia noctiluca*, *Chrysaora hysoscella*, *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* (Den Hartog and Van Nierop 1984)). An alternative possibility is that leatherbacks can forage selectively on different parts of *Rhizostoma 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 *Rhizostoma 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 metres. 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 vascularized, 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 sea water via the pharynx. The stomach is also relatively very long (ca. 2 metres 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 metres). It is likely the major site of NaCl uptake and HCO₃⁻ 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 *Chelonia 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 are 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 *Cyanea capillata*: 18.19 kJ g organic dry mass⁻¹; 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 dry mass⁻¹; 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 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 near-continually too. A 450kg leatherback ingesting 73% of its body mass per day during a 13.5 h foraging day takes in about 24 litres of jellyfish h⁻¹ (roughly 5% body volume h⁻¹). Salt gland secretion is calculated here to be 8.64 litres h⁻¹, leaving about 15.4 litres 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 d⁻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). DWL accuracy relies on the rate of production of CO₂ 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%. On the other hand, 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 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 gelatinous species 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 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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AUTHOR CONTRIBUTION
The work is wholly the responsibility of the single author.

COMPETING INTERESTS
The author declares no competing interests.
REFERENCES


Table 1. Composition of whole jellyfish prey (*Cyanea capillata*, *Rhizostoma pulmo*) of *Dermochelys coriacea*. Extracted and calculated from Doyle et al. (2007).

<table>
<thead>
<tr>
<th></th>
<th><em>Cyanea capillata</em></th>
<th><em>Rhizostoma pulmo</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean water content (%)</td>
<td>95.8</td>
<td>96.1</td>
</tr>
<tr>
<td>Ash content (% dry mass)</td>
<td>76.8</td>
<td>83.4</td>
</tr>
<tr>
<td>Organic content (% dry mass)</td>
<td>23.2</td>
<td>16.6</td>
</tr>
<tr>
<td>Energetic content (kJ g wet mass⁻¹)</td>
<td>0.18</td>
<td>0.11</td>
</tr>
<tr>
<td>Energetic content (kJ g dry mass⁻¹)</td>
<td>4.22</td>
<td>2.80</td>
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<tr>
<td>Energetic content (kJ g organic dry mass⁻¹)</td>
<td>18.19</td>
<td>16.86</td>
</tr>
<tr>
<td>Protein content (% organic dry mass)</td>
<td>71.1</td>
<td>77.1</td>
</tr>
<tr>
<td>Lipid content (% organic dry mass)</td>
<td>2.2</td>
<td>1.9</td>
</tr>
<tr>
<td>Carbohydrate (% organic dry mass)</td>
<td>3.8</td>
<td>5.0</td>
</tr>
<tr>
<td>Unknown matter (% organic dry mass)</td>
<td>22.9</td>
<td>16.0</td>
</tr>
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</table>
Table 2 Predicted jellyfish ingestion rates required for leatherback turtles consuming different jellyfish species to lay down blubber, given ‘low’ (22.24 kJ kg body mass\(^{-1}\) day\(^{-1}\) (Bradshaw et al., 2007)), ‘medium’ (41.4 kJ kg body mass\(^{-1}\) day\(^{-1}\) (Wallace et al., 2005)), or ‘high’ (88.6 kJ kg body mass\(^{-1}\) day\(^{-1}\) (Casey et al., 2014) estimates of field metabolic rate (FMR). 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 salt gland mass\(^{-1}\) h\(^{-1}\) (see Discussion for details).

<table>
<thead>
<tr>
<th>Prey species</th>
<th>FMR</th>
<th>Blubber accumulation rate (kg blubber d(^{-1}))</th>
<th>Required ingestion rates (% body mass d(^{-1}))</th>
<th>Required lachrymal secretion rates (litres h(^{-1}))</th>
<th>Required mass-specific lachrymal secretion rates (ml secretion g salt gland mass(^{-1}) h(^{-1}))</th>
</tr>
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<tbody>
<tr>
<td><em>Rhizostoma pulmo</em></td>
<td>Low</td>
<td>1.0</td>
<td>155</td>
<td>18.3</td>
<td>29.5</td>
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<td></td>
<td>0.5</td>
<td></td>
<td>89</td>
<td>10.6</td>
<td>17.1</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>1.0</td>
<td>175</td>
<td>20.7</td>
<td>33.3</td>
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<tr>
<td></td>
<td>0.5</td>
<td></td>
<td>109</td>
<td>12.9</td>
<td>20.8</td>
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<tr>
<td></td>
<td>High</td>
<td>1.0</td>
<td>224</td>
<td>26.6</td>
<td>42.8</td>
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<td></td>
<td>0.5</td>
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<td>157</td>
<td>18.7</td>
<td>30.0</td>
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<tr>
<td><em>Cyanea capillata</em></td>
<td>Low</td>
<td>1.0</td>
<td>77</td>
<td>9.1</td>
<td>14.6</td>
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<td></td>
<td>0.5</td>
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<td>54</td>
<td>6.4</td>
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<tr>
<td></td>
<td>Medium</td>
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<td>86</td>
<td>10.2</td>
<td>16.4</td>
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<td></td>
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<td>44</td>
<td>5.2</td>
<td>8.4</td>
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<tr>
<td></td>
<td>High</td>
<td>1.0</td>
<td>110</td>
<td>13.1</td>
<td>20.9</td>
</tr>
<tr>
<td></td>
<td>0.5</td>
<td></td>
<td>78</td>
<td>9.2</td>
<td>14.8</td>
</tr>
</tbody>
</table>
Table 3 Relative gut lengths of sea turtle species (calculated from Magalhães et al., 2012)

<table>
<thead>
<tr>
<th></th>
<th>Leatherback turtle</th>
<th>Green turtle</th>
<th>Loggerhead turtle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Dermochelys coriacea</em> (gelativore)</td>
<td><em>Chelonia mydas</em> (herbivore)</td>
<td><em>Caretta caretta</em> (carnivore)</td>
</tr>
<tr>
<td>1. Gut length as % curved carapace length</td>
<td>800</td>
<td>1152</td>
<td>754</td>
</tr>
<tr>
<td>2. Oesophagus length as % total gut length</td>
<td>15.5</td>
<td>4.5</td>
<td>3.6</td>
</tr>
<tr>
<td>3. Stomach length as % total gut length</td>
<td>15.0</td>
<td>5.3</td>
<td>6.3</td>
</tr>
<tr>
<td>4. Small intestine length as % total gut length</td>
<td>54.8</td>
<td>34.1</td>
<td>51.2</td>
</tr>
<tr>
<td>5. Large intestine length as % total gut length</td>
<td>14.6</td>
<td>56.1</td>
<td>38.9</td>
</tr>
</tbody>
</table>
Fig. 1. Labelled tranverse CT image of head of adult *Dermochelys coriacea*. Left-hand scale = 10×1cm.