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A killer appetite: metabolic consequences of carnivory in marine mammals[☆]

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Abstract

Among terrestrial mammals, the morphology of the gastrointestinal tract reflects the metabolic demands of the animal and individual requirements for processing, distributing, and absorbing nutrients. To determine if gastrointestinal tract morphology is similarly correlated with metabolic requirements in marine mammals, we examined the relationship between basal metabolic rate (BMR) and small intestinal length in pinnipeds and cetaceans. Oxygen consumption was measured for resting bottlenose dolphins and Weddell seals, and the results combined with data for four additional species of carnivorous marine mammal. Data for small intestinal length were obtained from previously published reports. Similar analyses were conducted for five species of carnivorous terrestrial mammal, for which BMR and intestinal length were known. The results indicate that the BMRs of Weddell seals and dolphins resting on the water surface are 1.6 and 2.3 times the predicted levels for similarly sized domestic terrestrial mammals, respectively. Small intestinal lengths for carnivorous marine mammals depend on body size and are comparatively longer than those of terrestrial carnivores. The relationship between basal metabolic rate (kcal day^{-1}) and small intestinal length (m) for both marine and terrestrial carnivores was, BMR = 142.5 intestinal length$^{1.20}$ ($r^2 = 0.83$). We suggest that elevated metabolic rates among marine mammal carnivores are associated with comparatively large alimentary tracts that are presumably required for supporting the energetic demands of an aquatic lifestyle and for feeding on vertebrate and invertebrate prey. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Basal metabolic rate; Carnivore; Dolphin; Marine mammal; Small intestine; Weddell seal; Herbivore

1. Introduction

Diving marine mammals spend considerable time and energy in locating, pursuing, capturing and processing prey. For these activities to be energetically profitable, two physiological requirements must be met. First, more energy must be acquired from the intake of prey than is spent in obtaining and processing them. Second, marine mammals that forage while submerged must be capable of hunting under a constraint of limited oxygen availability (Dunstone and O'Connor, 1979).

Based on these requirements, there is considerable selective pressure for energetic efficiency during underwater hunting by marine mammals. In conventional foraging models, energetic profitability of specific prey and the efficiency of the predator are often expressed in terms of cost/benefit ratios calculated from the ratio of energy gained to energy expended during foraging (Stephens and Krebs, 1986). The duration of hunting by marine mammal predators is also defined by energy expenditure, as oxygen reserves in the blood, muscles and lungs are consumed during a dive (Kooyman, 1989).

Despite the importance of energy expenditure in evaluating foraging costs and overall energetic efficiency of a predator, there is much confusion regarding the metabolic rates of marine mammals. Even the relatively simple measure of basal metabolic rate (BMR) has not been clearly defined for this group. Currently, a question remains regarding whether or not the basal metabolic rates of marine mammals are higher (Irving, 1973; Liao, 1990), lower, or identical (Lavigne et al., 1986; Innes and Lavigne, 1991) to predictions for terrestrial mammals of comparable size. The confusion is due, in part, to a poor understanding of the underlying factors that set metabolic rates in marine mammals, and the impact of diving responses on these factors.

Recent studies on a variety of small vertebrates, including rodents (Konarzewski and Diamond, 1995; Koteja, 1996), birds (Piersma et al., 1996; Burness et al., 1998) and lizards (Garland, 1984), indicate that the organs associated with the processing and distribution of nutrients are coupled to the metabolic rate of the animal. Among a wide variety of terrestrial animals, metabolic rates are influenced by the quality of the diet, as well as digestive tract design and function. Sus-

tained metabolic rates and metabolic ceilings, which ultimately set the limits for foraging behavior, reproductive output and geographic distribution, are linked to the digestive tract's ability to process food (Peterson et al., 1990). As a consequence, the size of the organs comprising the gastrointestinal tract often reflects the immediate metabolic demands of the animal. For example, cold exposure (Koteja, 1996), food habits (McNab, 1986), foraging methods (Jackson, 1992) and ecological conditions (Piersma et al., 1996) that lead to variability in basal metabolic rate have been associated with alterations in the size of the alimentary tract.

To provide a better understanding of the metabolic demands of marine mammals and the organs that must support these demands, we examined the relationship between BMR and gastrointestinal length in cetaceans and pinnipeds. Metabolic measurements were conducted on two species: an odontocete, the bottlenose dolphin (*Tursiops truncatus*) and a phocid, the Weddell seal (*Leptonychotes weddelli*). These data were combined with basal metabolic rates reported for other carnivorous marine mammals measured under comparable conditions. The relationship between gastrointestinal tract morphology and metabolic demand was determined using data for six species of marine mammal, in which both BMR and small intestinal length were measured or known. Similar analyses were conducted for five species of carnivorous terrestrial mammal. The results of this study indicate that the BMR of marine mammals resting on the water surface is higher than predicted for terrestrial mammals. This elevated metabolism is associated with a comparatively large alimentary tract that is presumably required for supporting an aquatic lifestyle and for feeding on vertebrate and invertebrate prey.

2. Materials and methods

2.1. Animals

Three mature, male bottlenose dolphins (mean body mass = 148.6 kg) were used in the metabolic studies. The animals were maintained in floating net pens at the US Navy Marine Mammal Program (SPAWAR, San Diego, CA), and had been at the facility for over 2 years before the mea-

surements were conducted. All animals were fed daily on a diet of mackerel, herring, and smelt supplemented with vitamins. Water temperature in the pens reflected seasonal ambient conditions in the ocean. Average water temperature in the pens during the experimental period was 15.4°C. T_{air} was 15.5°C. The dolphins were trained for 2–3 weeks prior to experimentation to rest quietly in a water-filled metabolic box

Seven mature, male Weddell seals (mean body mass = 388.5 kg) were captured on the sea ice near McMurdo Station, Antarctica. The animals were transported approximately 7 miles from the point of capture to an isolated ice hole (2.4-m-long × 1.1-m-wide shelf with a 1.0-m-diameter hole) that had been cut into the sea ice. All seals were held for 24–48 h and fitted with dive recorders and video instrumentation packs (Davis et al., 1999) before release into the isolated hole. A video recording system and camera mounted on the animals continuously monitored hunting behavior to ensure that the animals were post-absorptive prior to the metabolic measurements. Water temperature in the ice hole was −1.4 to −0.8°C during the experimental period. T_{air} was 1.7–3.6°C.

2.2. Basal metabolic rate

2.2.1. Dolphins

Metabolic measurements were carried out during March–April. Each animal was fasted overnight and placed in an insulated metabolic box the following morning. Water temperature in the box was controlled by a saltwater heat exchanger and ranged from 3.7 to 28.9°C. Only one water temperature was tested on each experimental day. Depending on the animal and the experimental water temperature, metabolic measurements were carried out continuously over 2–3 h. Experiments were conducted on sedentary animals and were terminated if the animal became active. Core body temperature was determined continuously during the experiments with a digital thermometer and flexible rectal probe (Physitemp Inc, Clifton, NJ).

2.2.2. Weddell seals

All metabolic measurements were carried out during the Antarctic austral summer (October–December) and followed the protocols of Castellini et al. (1992). Instrumented seals were

released into the ice hole and were free to dive and rest. Resting metabolic measurements were made on sedentary animals as they floated on the water surface. Only resting periods lasting at least 2 h were used in the analyses. Respiratory rate and apneic periods were recorded visually and acoustically on videotape.

2.2.3. Oxygen consumption

Oxygen consumption was determined using open-flow respirometry systems. Breathing by the animals was restricted to a Plexiglas dome (1.1 m long × 0.8 m wide × 0.8 m high for dolphins; 2.4 m long × 1.1 m wide × 0. 4 m high for seals) mounted at the water level of the metabolic box or ice hole. Air was drawn through the chamber with a vacuum pump (Sears 2.0 Hp Wet/Dry Vac). Flow rate was monitored with a calibrated, dry gas-flow meter (American Meter Co Inc, DTM-325, San Leandro, CA) and was maintained at 45–65 l min^{-1} for the dolphins and 510–550 l min^{-1} for the seals. At these flow rates, the fractional concentration of oxygen in the domes remained above 0.2000. Samples of air from the exhaust port of the domes were dried (Drierite) and scrubbed of CO_2 (Sodasorb) before entering the oxygen analyzer (AEI Technologies S3-A, Pittsburgh, PA). The percentage of oxygen in the exhaust air was monitored continuously during the experiments, and recorded with a personal computer using Sable Systems software (Salt Lake City, UT). The output from the oxygen analyzer was monitored every second and averaged for each minute. These values were converted to oxygen consumption ($\dot{V}_{O_2}$) using equations from Fedak et al. (1981) and an assumed respiratory quotient of 0.77. The lowest value for oxygen consumption averaged over 10–30 min during each 2–3-h experimental session was used in the analyses of basal metabolic rate. All values were corrected to STPD.

The entire system was calibrated daily (dolphins) or immediately before and after measurements (seals) with dry ambient air (20.94% O_2) and 100% nitrogen gas according to Fedak et al. (1981). The theoretical fraction of O_2 leaving the dome was calculated (Davis et al., 1985) and compared to the measured values from the oxygen analyzer. The flow of calibration gases into the dome was controlled and monitored by an electronic flowmeter (Omega, Model #FMA-772V) that was accurate to within 1%. Calibra-

tions of the flow meter were conducted with nitrogen gas and a rotameter (Cole-Palmer Instruments) before and after the studies.

2.3. Length of the small intestine

The length of the small intestine for a wide variety of terrestrial and marine mammals was compiled from published literature. Because diet influences gastrointestinal morphology, including intestinal length in mammals (Stevens and Hume, 1995), the published data used in the present study were limited to carnivorous species, except for comparisons with herbivores. Care was also taken to limit the data to adult, non-pregnant, non-lactating animals. Values for post-prandial animals were excluded whenever the presence of food in the intestinal tract was indicated.

2.4. Statistics

The lower critical temperature for the dolphins was determined from the intersection of multiple regressions using Yeager and Ultsch (1989). Because warm water tests were terminated if core temperature of the dolphins fluctuated $> 0.1°C$,

it was not possible to conduct a similar analysis for the upper critical temperature. Instead, upper critical temperature for the dolphins was based on fluctuations in core body temperature and t-tests conducted for metabolic rates determined at 16, 23 and 29°C.

Differences in the means for the metabolic rates of resting and intermittently breathing seals were determined from t-tests using statistical software (Jandel Scientific Software, 1995). Allometric regressions for basal metabolic rate in relation to body mass, and relationships for basal metabolic rate vs. intestinal length, and intestinal length ratio vs. body length, were determined using least squares methods (Jandel Scientific Software, 1995). Data are reported as means $\pm$ S.E.M., unless otherwise indicated.

3. Results

3.1. Basal metabolic rate

The metabolic rate of dolphins resting on the water surface was dependent on water temperature (Fig. 1). Metabolic rates recorded in this
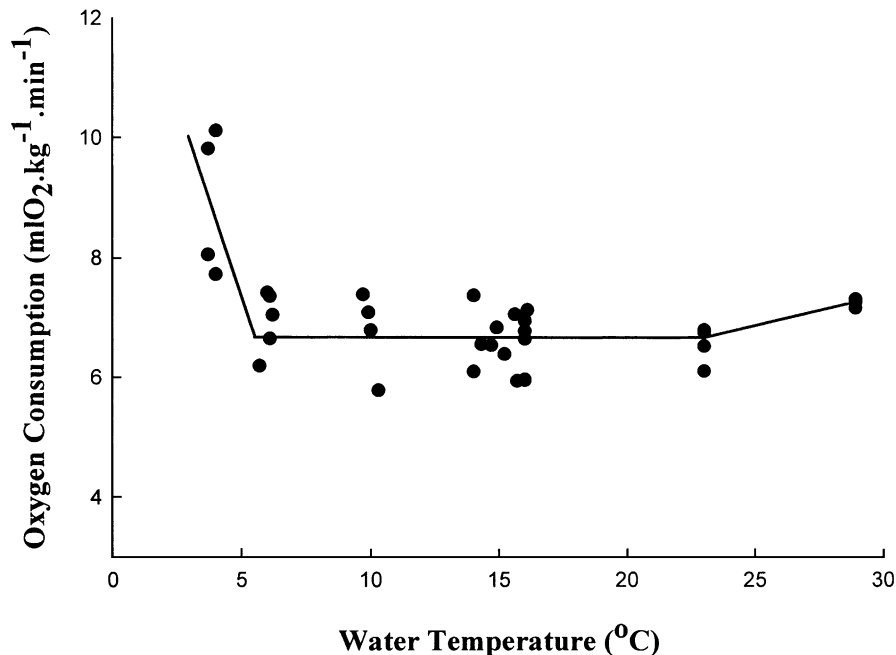

Fig. 1. Resting metabolic rate of three adult, post-absorptive bottlenose dolphins in relation to water temperature. Acclimatization temperature for the dolphins was $T_{water} = 15.4°C$. Each point represents a single metabolic measurement for an individual dolphin. The horizontal line represents the average metabolic rate within the thermal neutral zone (defined in text).

experiment ranged from 5.78 to 10.12 ml O_2 kg^{-1} min^{-1}, with higher metabolic rates occurring at both the high and low water-temperature extremes. The mean minimum metabolic rate for the three dolphins resting on the water surface was 6.53 ± 0.16 ml O_2 kg^{-1} min^{-1} ($n = 9$) at $T_{water} = 15.4°C$ (acclimatization temperature), and was within 8% of that reported by Ridgway and Patton (1971) for a 128-kg dolphin at $T_{water} = 17°C$. Metabolic rate of the dolphins remained at this level until T_{water} was lower than 5.9 or higher than 23.0°C. These water temperatures were considered the lower and upper critical temperatures, respectively, for bottlenose dolphins acclimatized to 15.4°C, as defined by a significant increase in metabolic rate at 3.9 ($n = 4$, $P = 0.029$) and 29.0°C ($n = 4$, $P = 0.004$).

Weddell seals rested on the water surface for periods of up to 6 h. Respiratory cycles alternated between eupnea during quiescent, alert periods and intermittent breathing patterns during sleep. The metabolic rate of alert Weddell seals resting at $T_{water} = -1.4$ to $-0.8°C$ was 3.58 ± 0.24 ml O_2 kg^{-1} min^{-1} (Fig. 2). This decreased to 3.20 ± 0.06 ml O_2 kg^{-1} min^{-1} when the seal was sleeping and breathing intermittently. However, the difference in metabolic rates between the two conditions was not statistically significant ($n = 7$ seals, $t = 1.892$, $P = 0.09$). These results are within 14%
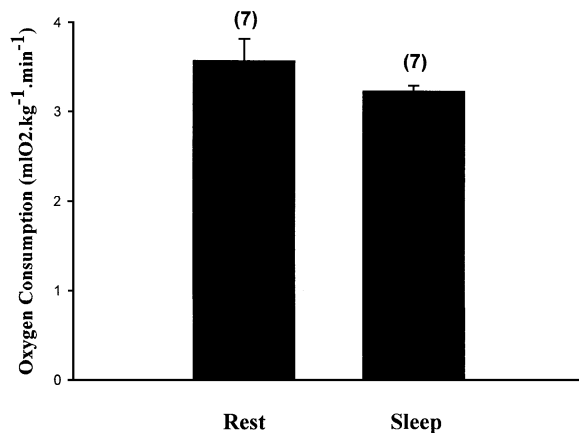

Fig. 2. Metabolic rate of seven adult, post-absorptive Weddell seals resting or sleeping on the water surface. Resting values are for alert, inactive animals breathing continuously. These data are compared to values for the same seals breathing intermittently during sleep. Height of the columns and lines represent means + S.E.M. Numbers in parentheses indicate the number of seals.

of metabolic rates previously reported for resting and sleeping Weddell seals by Castellini et al. (1992), measured under identical conditions.

3.2. Length of the small intestine

Intestinal length for marine carnivores correlated with body size and ranged from 11.4 m in the smallest species, the sea otter (*Enhydra lutris*; Kenyon, 1969), to 100 m in the largest species, the fin whale (*Balaenoptera physalus*; Stevens and Hume, 1995). Values for similarly sized otariids and phocids ranged from 14.5 to 38.0 m in adult animals (Burns, 1981a,b; King, 1983; Stevens and Hume, 1995; Martensson et al., 1998). Owing to their comparatively large body size, small intestinal length was greater for mysticete whales (range 61.2−100.0 m) than for odontocetes (range 30.0−66.0 m) (Stevens and Hume, 1995). The ratio of small intestinal length to total body length correlated negatively with body length in marine mammals (Fig. 3a), and was described by the regression

Intestinal length / body length ratio

$$= 17.6 \, \text{body length}^{-0.41}$$

$$(n = 25 \text{ species}, r^2 = 0.49)$$

where body length is in m. In comparison, small intestinal length increased with body length in these marine mammals (Fig. 3b) and was described by:

Intestinal length $= 16.7 \, \text{body length}^{0.60}$

$$(n = 25 \text{ species}, r^2 = 0.77)$$

where lengths are in m.

Comparable measurements for carnivorous terrestrial mammals ranging in mass from 1.0 to 190.0 kg showed relatively smaller intestinal lengths than for marine species (Fig. 3a,b). Like marine mammals, the length of the small intestines depended on body size, and ranged from 1.2 m for the domestic cat (*Felis catus*; Stevens and Hume, 1995) to 8.7 m for a male African lion (*Panthera leo*; Davis, 1962). The ratio of intestinal length to body length was 2.4−4.9 and did not change with body length for the range of terrestrial species examined in this study (Davis, 1962; Stevens and Hume, 1995).

4. Discussion

4.1. Interrelationships between resting metabolic rate and the alimentary tract of carnivorous marine mammals

In a review of studies reporting basal metabolic rates for marine mammals, Lavigne et al. (1986) recognized that, in many cases, the defined conditions for assessing basal metabolism had not been met. These conditions specify mature, post-absorptive animals resting in a thermally neutral environment. Consequently, the authors suggested that the elevated BMRs reported for many
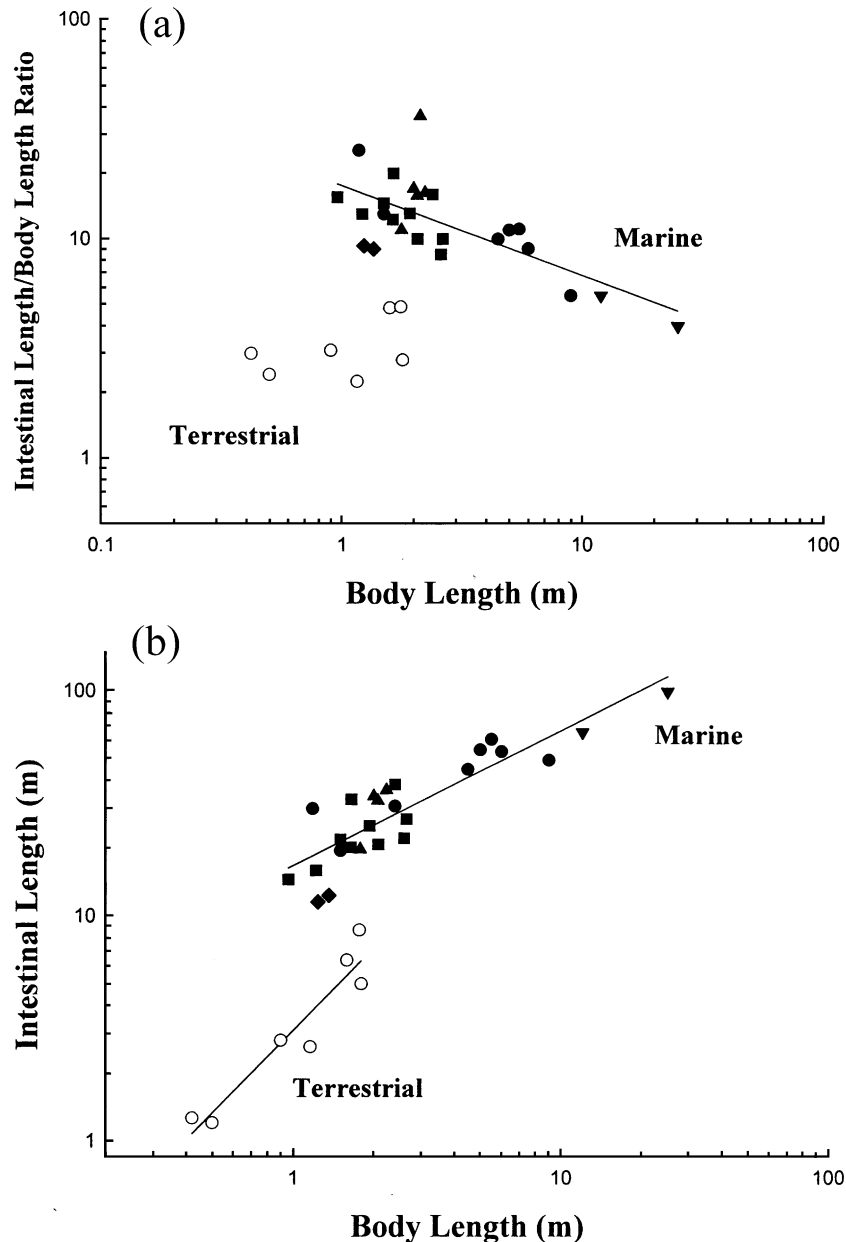

Fig. 3. The ratio of small intestinal length to total body length (a) and intestinal length (b) in relation to body length for carnivorous mammals. Data for marine mammals are denoted by the closed symbols and include sea otters (diamonds), odontocetes (circles), phocid seals (squares), otariids (triangles), and mysticete whales (down-pointed triangles). Terrestrial carnivores are shown by the open circles and include mink, human, cat, dog, leopard, and African lions. The solid lines denote the least squares regressions through the data points and are presented in the text for marine mammals. The regression for terrestrial mammals in (b) is intestinal length = 3.1 body length$^{1.22}$ ($n = 6$ species, $r^2 = 0.90$).

marine mammals were an artifact due to inappropriate comparisons with terrestrial mammals. Results from the present study, in which these conditions were met (assuming acclimatization temperature and minimum oxygen consumption occur within the thermal neutral zone; Bartholomew, 1977), indicate that other factors may also be involved.

In general, we find that the metabolic rates of marine mammals resting on the water surface are higher than those of terrestrial mammals resting in air (Fig. 4). Basal metabolic rates of the bottlenose dolphins and Weddell seals measured here were 2.3- and 1.6-fold the predicted levels for domestic terrestrial mammals (Kleiber, 1975), respectively. When measured under similar conditions, the metabolic rates of other species of resting marine mammal follow a similar pattern. Killer whales trained to breathe into a respiratory balloon (Kriete, 1995) showed metabolic rates that were 1.6-fold those predicted by Kleiber for a 3750-kg adult male, and 1.4-fold those predicted for a 2692-kg adult female. A 73-kg adult female California sea lion resting in a water-filled metabolic chamber had a minimum resting

metabolic rate that was 2.1-fold that predicted (Liao, 1990). Sea otters, with an admittedly elevated mustelid metabolism (Iverson, 1972), show resting rates that are 2.8-fold the predictions when resting quietly on the water surface in a metabolic hood at $T_{water} = 20.0°C$ (Williams, 1989).

A better predictor of the basal metabolic rates for these species of marine mammal can be found in the scaling equation for vertebrate-eaters presented in McNab (1988) (Fig. 4). This agreement may not be surprising, since the species represented in this equation include marine, terrestrial and semi-aquatic mammals. When only terrestrial carnivorous mammals are considered, the differences in BMR between marine and terrestrial groups remain, despite similar food habits. For example, the BMR of a 73-kg California sea lion (Liao, 1990) is 2.3-fold that of a 59-kg cougar (Corts, 1984); a 20-kg sea otter (Williams, 1989) maintains a BMR that is 3.5-fold that of a 14.1-kg dog (Kleiber, 1975). In general, the BMRs reported for many carnivorous terrestrial mammals, including cats, dogs, arctic foxes, red foxes and cougars (reviewed by McNab, 1988), are within 4–23% of the predictions of Kleiber (1975). In
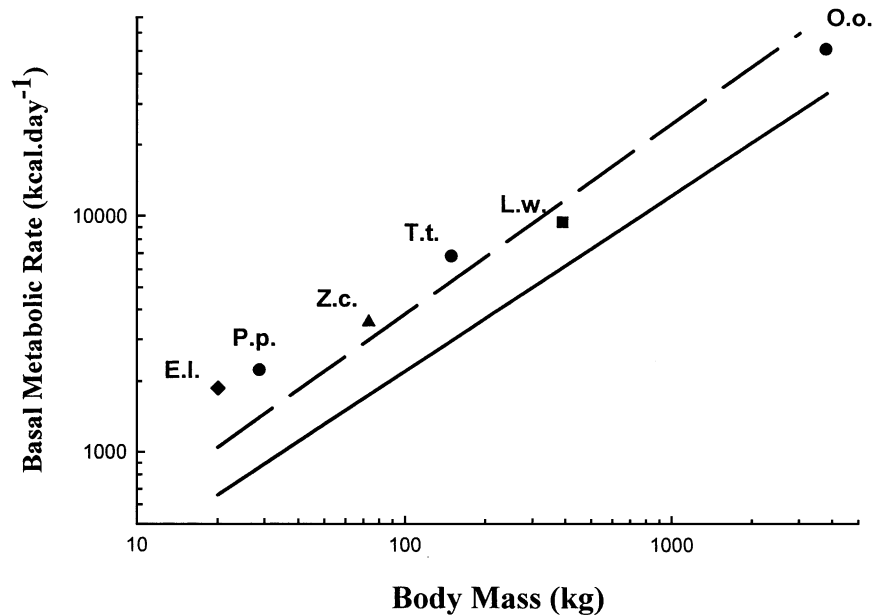

Fig. 4. Basal metabolic rate for marine mammals resting on the water surface in relation to body mass. Each point represents the mean values for sea otters (E.l. diamond; Williams, 1989), harbor porpoise (P.p. circle; Kanwisher and Sundnes, 1965), California sea lions (Z.c. triangle; Liao, 1990), bottlenose dolphins (T.t. circle; present study), Weddell seals (L.w. square, present study), and killer whales (O.o. circle; Kriete, 1995). The solid line is the predicted regression for basal metabolic rate in domestic terrestrial mammals according to Kleiber (1975). The dashed line is the regression for vertebrate eaters, which includes marine, semi-aquatic and terrestrial mammals from McNab (1988).

comparison, the BMR of carnivorous marine mammals ranges from 1.4- to 2.8-fold that predicted.

One confounding factor for marine mammals is the physiological adjustment that occurs with the dive response. In a study using adult California sea lions trained to submerge in a pool, Hurley (1996) found a graded resting metabolic response that correlated with the duration of submergence. Metabolic rates measured on the water surface were 2–3-fold those predicted for domestic terrestrial mammals by Kleiber (1975). These rates were reduced and approached the predicted levels when the measurement period included prolonged submergence. Undoubtedly, the variation in measured BMR for these sea lions can be attributed in part to changes in metabolic demands of specific tissues during submergence. This may also explain the variability in basal metabolic rate reported for marine mammals in comparison to terrestrial mammals.

Several studies have provided explanations to account for the comparatively high metabolic rates of resting marine mammals, regardless of their surface or submerged position (reviewed in Lavigne et al., 1986). These include elevated food consumption of captive subjects, cold acclimatization leading to high thermoregulatory energetic costs, body composition, and high protein diets. Certainly, the high thermal conductivity of water in comparison to air at the same temperature can result in elevated levels of heat loss and increased metabolic demands for mammals resting in water (Dejours, 1987). In addition, the maintenance of metabolically active tissues will influence overall metabolic rate, which in turn could limit dive duration in marine mammals (Ridgway, 1985).

An especially relevant factor in setting the metabolic rate of an animal is the capacity of the body to deliver nutrients to active tissues (Armstrong, 1983). Consequently, the high energetic requirements of marine mammals may place a correspondingly high demand on the gastrointestinal tract. Previous studies examining diverse vertebrate species with different food habits have demonstrated that the metabolic demands faced by an animal have an important bearing on the design and function of the gastrointestinal tract (Stevens and Hume, 1995). Both inter- (Daan et al., 1990) and intraspecific (Konarzewski and Diamond, 1995) variation in basal metabolic rate among terrestrial mammals may be explained by variation in the mass of metabolically active organs that support the processing and delivery of nutrients. Thus, the small intestines, as well as the heart, kidney, and liver, comprise a small proportion ($< 17\%$) of the total body mass of mice, but account for nearly 50% of the variation in BMR in this species (Konarzewski and Diamond 1995).

The proposed demand on the gastrointestinal tract of marine mammals is reflected in the length of the small intestines for otariids, phocids, odontocetes, mysticetes and a mustelid, the sea otter (Fig. 3a,b). Many investigators have noted the exceptional length of the small intestines of marine mammals. It remains one of the most striking features of the gastrointestinal tract of both pinnipeds (Eastman and Coalson, 1974; King, 1983) and cetaceans (Slijper, 1976; Stevens and Hume, 1995). Although the length of the small intestine in many terrestrial carnivores approaches six-fold total body length, it ranges from seven- to 40-fold body length in otariids and phocids (King 1983). Among odontocetes and mysticetes, this length ratio ranges from four- to 23-fold body length, depending on the species (Stevens and Hume, 1995).

Currently, the reason for the exceptional length of the small intestines in marine mammals is not known. Thermoregulatory factors, parasitic infestation necessitating a larger gut, and increased time for enzymatic or microbial breakdown and absorption of ingested whole prey have been suggested (Eastman and Coalson, 1974; King, 1983). The linked ancestral history of cetaceans and herbivorous mammals may also explain similarities in alimentary tract length for both of these groups (Stevens and Hume, 1995), but does not apply to other marine mammal lineages. The current study indicates that metabolic demands associated with an aquatic lifestyle and with carnivory may be key factors. The length of the small intestines is a major distinguishing feature between marine and terrestrial carnivores, and is correlated with metabolic rate. A single regression describes the relationship between basal metabolic rate and total length of the small intestine for both mammalian groups (Fig. 5):

Basal metabolic rate = 142.5 intestinal length$^{1.20}$

$$(n = 11 \text{ species}, r^2 = 0.83)$$

where metabolic rate is in kcal day^{-1} and intestinal length is in m. This relationship differs from that of mammalian herbivores, which shows correspondingly lower basal metabolic rates and shorter intestinal lengths (Fig. 5). Based on these differences, there appears to be a cost with carnivory that is associated with an increase in length of the small intestines. For both carnivorous and herbivorous groups, marine-living species represent the upper extremes of these relationships. Thus, an aquatic lifestyle appears to add a second influencing factor on the relationship between basal metabolic rate and intestinal length.

By maintaining a large alimentary tract, marine mammals obtain both the advantages inherent with being able to meet elevated metabolic demands and the disadvantages associated with supporting a metabolically active tissue. A large digestive tract provides an advantage for marine predators that feed on prey that is only intermittently available or patchily distributed in the environment (Gaskin, 1978). In this way, large quantities of prey can be consumed, processed and absorbed when it is suddenly available (Slijper, 1976). The processing of prey items that are high in fat content or possess chitinous exoskeletons will also be facilitated (Stevens and Hume, 1995). By enhancing assimilation efficiency, comparatively high metabolic rates can be supported, with the concomitant advantages of higher rates of sustained activity, independence from environmental temperature fluctuations, faster growth, and higher reproductive output (Konarzewski and Diamond, 1995).

Despite these advantages, there is a metabolic trade-off associated with maintaining a large digestive tract. Because the gastrointestinal tract is a metabolically intense organ in vertebrates, both in terms of protein synthesis and energy utilization, it is expensive to maintain (Stevens and Hume, 1995). Comparative tissue respiration rates and organ masses indicate a disproportionate metabolic demand by the alimentary tract, which ranks fourth in whole-organ oxygen consumption out of 14 organs examined in the rat (Schmidt-Nielsen, 1984).
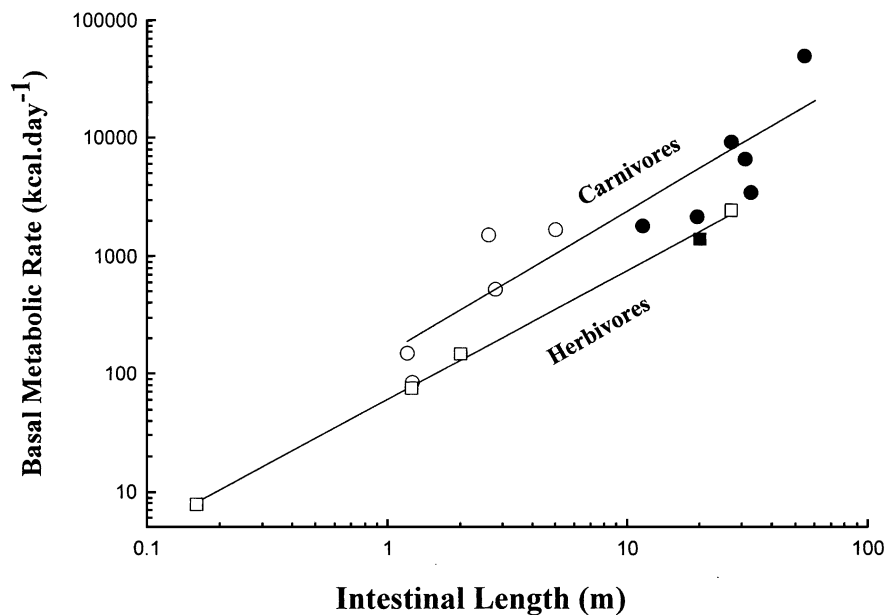

Fig. 5. Basal metabolic rate of carnivorous marine (closed circles) and terrestrial (open circles) mammals in relation to intestinal length. Each point represents the mean value for each species. The solid line for carnivores is the least squares linear regression through the data, as described in the text. Basal metabolic rates for marine mammals are from Fig. 4; intestinal lengths are from Fig. 3. Terrestrial mammal basal rates are from Brody (1945); human), Kleiber (1975); dog, cat), McNab (1986); mink), and Corts (1984, cougar); intestinal lengths are from Fig. 3. Values for representative marine (closed square) and terrestrial (open square) herbivorous mammals are provided for comparison, and include vole, woodchuck, rabbit, sheep and manatee (metabolic rates reviewed in McNab, 1988; intestinal lengths for terrestrial herbivores are from Stevens and Hume, 1995; intestinal length for the manatee is from Reynolds and Rommel, 1996). The least squares regression (solid line) for herbivores is BMR = 61.6 intestinal length$^{1.10}$ ($n = 5$ species, $r^2 = 0.99$).

Interestingly, selective redistribution of blood away from the alimentary tract during diving could reduce these costs in marine mammals, and may explain part of the variability in resting metabolic rates of surface and submerged California sea lions reported by Hurley (1996). Previous studies have demonstrated that the function of splanchnic organs varies with dive duration (Davis et al., 1983), and that blood flow is markedly reduced to the intestines during forced dives in Weddell seals (Zapol et al., 1979). In a study of seven species of polar phocid seals, Martensson et al. (1998) reported no correlation between intestinal length relative to body length and diving capacity. This would be expected if the metabolic demands of maintaining the gastrointestinal tract were reduced during submergence. Crocker et al. (1997) have suggested a trade-off between the metabolic demands of processing food and locomotion in northern elephant seals. Rather than try to simultaneously meet the energetic demands of both, elephant seals may reduce locomotor costs by drifting when increased energy is needed for processing ingested prey. Clearly, further studies examining the function of these tissues will be needed to assess differences in metabolic costs for maintaining gastrointestinal activity for marine and terrestrial predators.

In summary, the present study demonstrates that the metabolic rates of many species of carnivorous marine mammal are elevated when compared to levels for carnivorous terrestrial mammals. These elevated metabolic rates are associated with comparatively large alimentary tracts in marine mammals that are likely required for supporting the energetic demands of an aquatic lifestyle and for feeding on vertebrate and invertebrate prey. Although a large alimentary tract affords several adaptive advantages for marine mammals, it is energetically expensive to maintain. It is possible that physiological changes associated with the dive response may aid in defraying these costs during submergence, and this warrants further investigation of gastrointestinal function in marine predators.

Acknowledgements

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