

## Estimates of Basal Metabolic and Feeding Rates for Marine Mammals from Measurements of Maximum Body Length

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A.M.J. Hunter<sup>1\*</sup>

A.W. Trites<sup>1</sup>

D. Pauly<sup>2</sup>

<sup>1</sup>Marine Mammal Research Unit, Hut B-3, Room 18, 2204 Main Mall, University of British Columbia, Vancouver, B.C., Canada V6T 1Z4; <sup>2</sup>Fisheries Centre, Hut B-8, Room 100, 2204 Main Mall, University of British Columbia, Vancouver, B.C., Canada V6T 1Z4

### Introduction

Compared to terrestrial mammals, marine mammals are generally perceived as having elevated metabolic rates and insatiable appetites, attributable to maintaining their high body core temperatures in a cold aquatic environment. The perception that marine mammals have higher metabolic rates than terrestrial mammals of similar body size is reinforced by a substantial body of literature that dates over half a century (Sergeant, 1973; Lavigne, 1982) and is further supported by reports of captive marine mammals ingesting large quantities of food (Sergeant, 1969, 1973; Bonner, 1982). However, within the past two decades, this convention has been challenged. Lavigne et al. (1986) failed to reject the hypothesis that physically mature phocids (true seals) have similar basal metabolic rates (BMRs) as terrestrial mammals of similar body weight, when measured under standard conditions. Innes et al. (1987) found similar results when comparing feeding rates (FRs) of seals and whales. However, much research has been conducted on the FRs and BMRs of marine mammals since these studies were completed. In our study, we re-investigated whether basal metabolic and feeding rates of marine mammals are similar to those predicted for terrestrial mammals. We also explored relationships between taxa and were able to predict the basal metabolic rates of species of marine mammals not previously studied. These estimates can also be used to assess the amount of prey consumed by species of marine mammals whose metabolisms have never been determined in the field or in the lab.

### Methods

We re-investigated the conclusions of Lavigne et al. (1986) and Innes et al. (1987) by expanding the number of species used in their original analyses, eliminating repeated measures, and implementing maximum body length (L<sub>max</sub>) a more accurate independent variable than body weight. Experimental measurements of BMR of marine mammals with known growth curves were extracted from the literature and expressed as kilocalories per day. Only rates which appeared to meet the conditions defined by Kleiber (1975) were included in our study—the animals must not be growing, thermoneutral, post-absorptive, non-reproductive, and quiescent. Theoretic BMRs (BMR<sub>T,s</sub>) were generated for all species of marine mammals using Kleiber's (1975) interspecific equation for

terrestrial mammal basal metabolism ( $BMR_{(kcal/d)} = 70W_{(kg)}^{0.75}$ ). Mean weights (W) of both males and females of each species at physical maturity were determined from existing growth curves or extrapolated from the literature and substituted into Kleiber's equation to yield  $BMR_T$  for marine mammals. Feeding rates at maintenance (the animals neither gained nor lost weight over the course of the experiment) of adult marine mammals were taken from the literature. Maximum body lengths were obtained from Trites and Pauly (1998). Relationships were constructed with  $L_{max}$  as the independent variable and either BMR or FR as the dependent variable. Simple linear regression analyses were conducted on the relationships to test our hypotheses.

## Results

We were unable to reject the null hypothesis that the BMRs of marine mammals (pinnipeds and cetaceans) were the same as those of terrestrial mammals of similar body size (Figure 1). Feeding rates at maintenance were also compared to BMRs and were found to be reasonably within the limits of those proposed for terrestrial mammals (1.5 to 3.0 times BMR) (Figure 1). Three distinct clusterings emerged from the data when  $BMR_T$ s were used to investigate differences between taxa: pinnipeds (otariids, phocids, and odobenids), toothed whales (odontocetes), and baleen whales (mysticetes) (Figure 2). All relationships between BMRs and FRs of marine mammals in relation to  $L_{max}$  were significant ( $P < 0.05$ ) using least squares regressions.

## Discussion

As noted by Lavigne (1986), past measurements of BMR for marine mammals were not made under standardized conditions as described by Kleiber (1975). This resulted in marine mammals being stereotyped as prolific consumers and having an exaggerated impact on their environment. We conclude that marine mammals have similar BMRs as terrestrial mammals of similar body size. Furthermore, our finding that FRs of marine mammals are within the range stated for terrestrial mammals provides more evidence that the energy consumption of marine mammals is not disproportionate compared to terrestrial mammals of similar body size (Figure 1). Therefore, there is no need to exclude marine mammals from comparative studies on the premise that they have elevated metabolic rates (Millar, 1977; Hennemann, 1983), and published explanations on why marine mammals should have elevated BMRs (e.g., enlarged livers) should be re-evaluated.

The differences among the interspecific relationships between taxa (Figure 2) is due to body morphology. Pinnipeds have a more dense body shape than cetaceans—pinnipeds are stouter with more mass and, thus, have more cells producing metabolic energy per unit of maximum body length. Also, pinnipeds do not have structures, such as rostrums and large tail flukes, that are characteristic of cetaceans and contribute little to metabolic energy use, but greatly increase overall length.

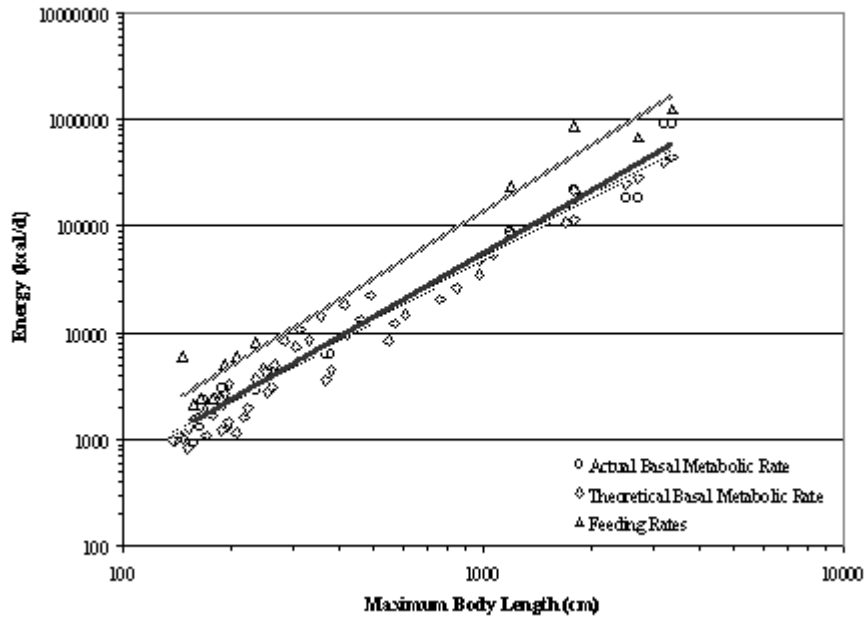
The distinct interspecific relationships between BMR and  $L_{max}$  within taxa (Figure 2) provide a more precise means for estimating metabolic rates of individual species. These estimates can be used to predict the amount of prey consumed by species of marine mammals whose metabolic rates have never been determined in the field or in the lab. These data can be used to assess the extent of direct and indirect competition between marine mammals using ecosystem models.

## Acknowledgments

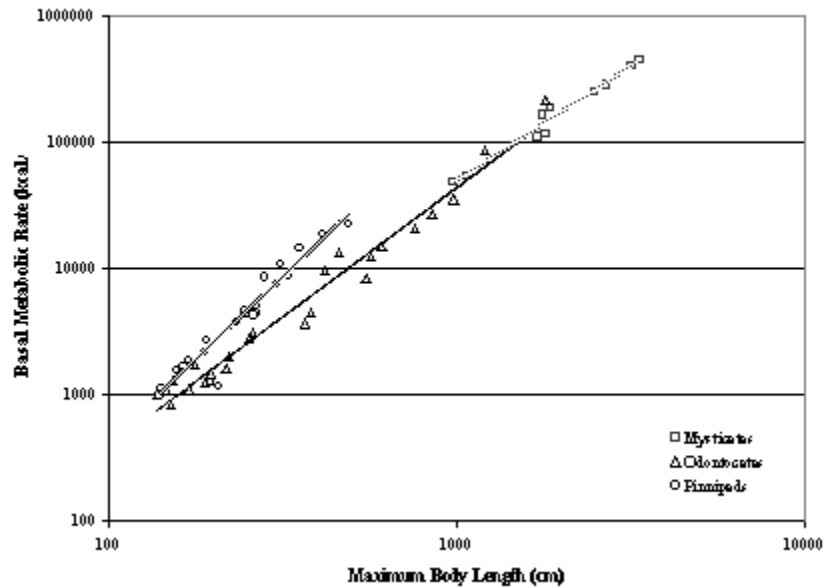
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**Figure 1.** Actual (o) and theoretical (◇) basal metabolic rates, as well as, feeding rates (Δ) for species of marine mammals with known growth curves as allometric functions of maximum body length.



**Figure 2.** Theoretical basal metabolic rates of baleen whales (Mysticetes; □), toothed whales (Odontocetes; Δ), and pinnipeds (Otariids, Phocids and Odobenidae; o) as an allometric function of maximum body length. Separate data for both sexes of each species are represented (sexes were not significantly different). Pinnipeds include female non-dimorphic species, as well as, male dimorphic and non-dimorphic species.