

Short Note

Metabolic Demands of a Tropical Marine Carnivore, the Hawaiian Monk Seal (*Monachus schauinslandi*): Implications for Fisheries Competition

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One of the primary factors contributing to the endangered status of the Hawaiian monk seal (*Monachus schauinslandi*) is poor survival by the juvenile age class (National Marine Fisheries Service [NMFS], 2007). On French Frigate Shoals, once a major monk seal colony in the outer Hawaiian Islands, survival to age 2 y by weanling pups has declined precipitously from over 80% during the mid-1980s to as low as 8% less than a decade later (Craig & Ragen, 1999). Similarly, juvenile survival remains below historical levels for many other outer island areas. One reason for these trends centers on poor nutritional status in immature Hawaiian monk seals. Evidence includes the overall smaller body size of weaned pups compounded by emaciation and comparatively slow growth rates in juveniles (Craig & Ragen, 1999); all implicate an overall energetic deficit as an underlying factor eventually leading to the decline of the general population.

Despite evidence of inadequate energy intake by immature Hawaiian monk seals and the importance of energetic balance to individual survival and ultimately to population stability (Stephens & Krebs, 1986), little is known about the energetic requirements of monk seals. To date, only one unpublished study (Dunn, 1990) has reported metabolic rates for the Hawaiian monk seal; none have examined changes in metabolic demands for different physiological states. In view of this, we conducted a longitudinal evaluation of the energetic demands of a juvenile Hawaiian monk seal that had been placed in captivity following collection from the wild. Specifically, variability in resting metabolic rate was measured over a 9-mo period as the animal matured and entered pre-molt, molting, and post-molt periods.

We combined longitudinal data collected on this seal with previously reported metabolic rates from Dunn (1990) to evaluate the effect of age and

physiological status on energetic demands in this species. By comparing metabolic values for these tropical seals to those of other marine mammals, including temperate and polar living phocid seals, we examined the role of aquatic adaptation in setting mammalian energetic demands. We find that the Hawaiian monk seal maintains resting metabolic rates lower than those of other marine mammals; and in the adult, this approaches levels predicted for terrestrial mammals. Furthermore, these reduced metabolic demands appear to be associated with morphological structures for food processing that are intermediate to those of highly adapted terrestrial and aquatic mammalian carnivores.

Metabolic rates were determined for the juvenile, male Hawaiian monk seal at 21 to 29 mo of age (body mass range = 70.0 to 94.0 kg during the study). The animal was maintained in a salt water pool at 25°C and fed daily with a mixed fish diet supplemented with vitamins. Body condition was excellent throughout the study.

Two metabolic conditions were examined: (1) during rest in air in a sand filled box (1.8 m long × 1.2 m wide × 0.1 m high) covered with a Plexiglas dome (1.6 m × 1.0 m × 0.6 m), and (2) during rest under a metabolic dome (0.9 m × 0.9 m × 0.2 m) while floating in a salt water pool (1.8 m × 1.2 m × 0.7 m) (Figure 1). We used an open-flow respirometry system to assess metabolic rate from oxygen consumption following the protocols of Williams et al. (2004b). Briefly, ambient air was drawn through the chambers at 200 to 230 l.min⁻¹ with a calibrated vacuum pump (Sable Systems International, Inc., Henderson, NV, USA). At these flow rates, the fractional concentration of oxygen in the chambers remained above 0.2000. Samples of air from the exhaust port of each chamber was dried (Drierite®) and scrubbed of carbon dioxide (Sodasorb®) before entering an oxygen analyzer (F-1B; Sable Systems International,



Figure 1. Metabolic chambers for measuring oxygen consumption of a juvenile Hawaiian monk seal during rest in water (top) and in air (bottom). Target points and the presence of a trainer ensured that the seal remained quiescent beneath each of the domes during the 15- to 30-min measurement sessions.

Inc.). The percentage of oxygen in the expired air was monitored continuously and recorded once per second with a personal computer using Sable Systems *Expedata* software. Oxygen consumption was then calculated using equations from Fedak et al. (1981) and an assumed respiratory quotient of 0.77 based on other phocid seals on a mixed fish diet (Davis et al., 1985; Williams et al., 2004b). All values were corrected to STPD, and the entire system calibrated daily with dry ambient air (20.94% O₂) and every 2 to 4 wks with dry span gases and N₂ gas according to Fedak et al. (1981) and Davis et al. (1985).

The seal was trained over an 8-wk period to rest quietly in the chambers during the measurements. On each experimental day, the seal was fasted overnight and voluntarily introduced to one of the experimental metabolic chambers. Only one metabolic test was conducted per day, with measurements scheduled to prevent tests on sequential days. The lowest metabolic rate maintained for a minimum of 10 min was used from each session. Mean air temperature in the sandbox was 19.5 ± 1.2 SD °C; water temperature ranged from 15.4 to 30.1°C and was within the thermal neutral zone of

the seal as determined in an accompanying study (Williams et al., in prep.). All test temperatures were within the range typically encountered by wild Hawaiian monk seals.

The resting metabolic rate of the juvenile seal resting in water was 5.07 ± 0.07 SE mlO₂.kg⁻¹.min⁻¹ (2,802.0 kcal.day⁻¹ using a conversion factor of 4.8 kcal.lO₂⁻¹). This was similar to the lowest average values reported by Dunn (1990) for an immature (2.8 y old) Hawaiian monk seal resting in air (Figure 2). As reported previously for Weddell seals (Williams et al., 2004b), similar metabolic rates were found for Hawaiian monk seals resting in air and water when these studies were combined. As would be expected due to the effect of age on metabolism in mammals (McNab, 2002), mass specific metabolic rate was 36.1% lower for an older (3.8 y old) Hawaiian monk seal measured in air than for either of the younger seals (Figure 2). The difference in metabolism was significant (ANOVA Tukey Test: $F_{2, 23} = 38.675$, $p < 0.001$) between these age groups.

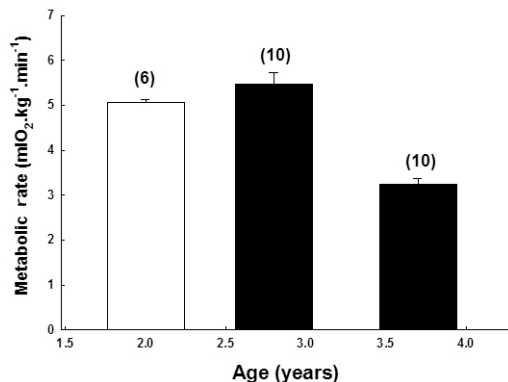


Figure 2. Metabolic rate in relation to age for Hawaiian monk seals; values for the immature seal resting in water in the present study (white bar) are compared to previously reported data for older seals resting in air (black bars) from Dunn (1990). The ten lowest values reported by Dunn for each seal are presented here. Height of the bar and lines represent means + 1 SE for each age. Numbers in parentheses denote the total number of metabolic measurements for each group.

Molting resulted in a marked, prolonged increase in metabolic rate for the immature seal in the present study. At its peak during the catastrophic phase of the molt when the skin and fur is sloughed, metabolic rate increased to 9.55 mlO₂.kg⁻¹.min⁻¹ (6,072.9 kcal.day⁻¹), nearly two times the value for resting during the non-molt period (Figure 3). The effects of molt on metabolic demand were apparent for several weeks before and after this catastrophic molting period.

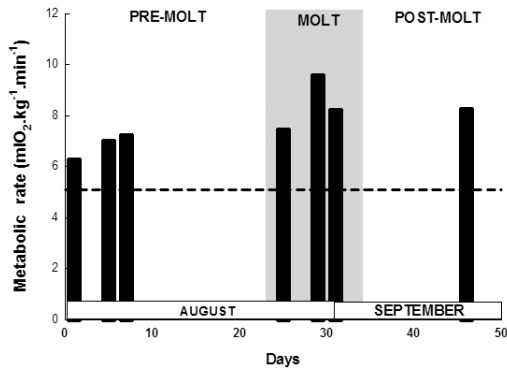


Figure 3. Longitudinal metabolic rates for a juvenile monk seal resting in air during pre-molt, molt, and post-molt periods; height of the bars represents the average value for a single trial on each day. The grey area denotes the period of catastrophic molt for the seal. The horizontal dashed line is the average metabolic value during the non-molt period.

When these results for Hawaiian monk seals are compared to other species of marine mammal, several trends become evident. First, the overall metabolic demands of Hawaiian monk seals appear lower than those of other marine mammal carnivores (Figure 4A). In general, the metabolic rates of adult cetaceans, otariids, and sea otters resting in water average two times predicted basal metabolic rates of terrestrial mammals (based on Kleiber, 1975). Although the metabolism of phocid seals is relatively low compared to the other marine mammal groups, even among phocids, the Hawaiian monk seal is unusual. Compared to temperate and polar seals, the mature Hawaiian monk seal demonstrates one of the lowest resting metabolic rates for a carnivorous marine mammal. The rate, in fact, approaches Kleiber's terrestrial predictions and suggests that tropical living may contribute to an overall reduction in metabolic demands within this group (Figure 4A).

A second trend observed in the present study provides further support for the above suggestion. Previously, we reported that elevated metabolic rates among marine mammal carnivores were associated with comparatively longer alimentary tracts to support the caloric processing demands of an aquatic lifestyle (Williams et al., 2001). By inference, the low metabolic rates of Hawaiian monk seals should be associated with comparatively shorter gastrointestinal tracts. Using allometric regressions for small intestine length in relation to body length for Hawaiian monk seals (Goodman-Lowe et al., 2001), we find that the predicted length of the small intestine is 10.9 m for a juvenile monk seal or 7.23 times its body length. This places Hawaiian monk seals on the low end

of a continuum relating small intestinal length to metabolism in marine mammals (Figure 4B). Once again, this species, by virtue of tropical living or its distinction as the most evolutionarily primitive phocid seal (Repenning & Ray, 1977), shows comparatively moderate adaptations for aquatic living that are intermediate to highly adapted terrestrial and aquatic mammalian carnivores.

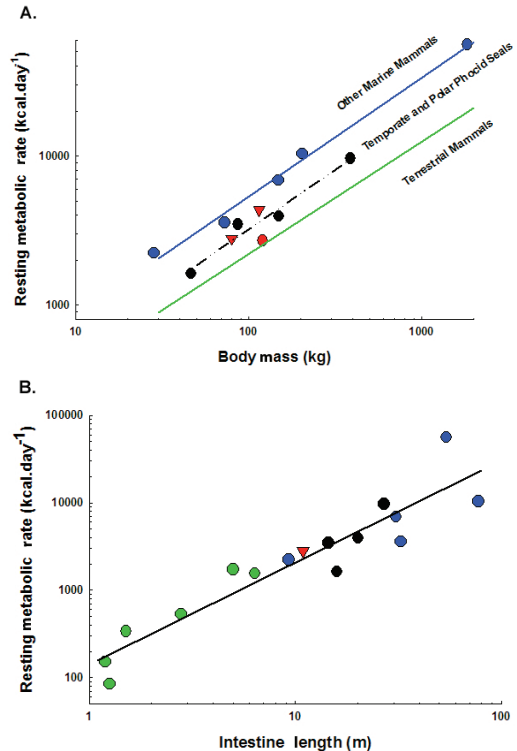


Figure 4. Resting metabolic rate in relation to body mass (A) and small intestinal length (B) for mammalian carnivores. In each graph, points represent individual terrestrial species (green); Hawaiian monk seals (red); temperate and polar phocid seals (black); and cetaceans, otariids, and sea otters (blue). In A, the green line denotes the allometric regression for terrestrial mammals from Kleiber (1975). The black dashed line is the regression for temperate and polar phocid seals and is described by metabolic rate = $82.8 \text{ mass}^{0.795}$ ($n = 4$ species, $r^2 = 0.97$, $p < 0.001$). The blue line describes the relationship for other marine mammal groups (from Williams et al., 2001). Data for monk seals are from Figure 2 and represent juveniles (downward facing triangles) and a mature seal (circle). In B, the black line denotes the least squares linear regression as described by metabolic rate = $141.9 \text{ small intestine length}^{1.162}$ ($n = 16$ species, $r^2 = 0.87$, $p < 0.001$). Note that the value for the monk seal (red downward facing triangle) is for the juvenile age class. Data for metabolic rates and intestinal length are from the present study and Williams et al. (2001, in prep.).

Admittedly, these results represent preliminary findings until further physiological research can be conducted on this species as well as the other remaining member of the *Monachus* genus, the Mediterranean monk seal (*M. monachus*). Despite this limitation, the available data can provide insight regarding the potential for resource demands by Hawaiian monk seals. Assuming that this species follows trends for other marine mammals in which field metabolic rate is approximately three times resting values (Costa & Williams, 1999; Williams et al., 2004a), the total daily caloric demand of a free-ranging 80 kg juvenile monk seal is predicted at 8,406.0 kcal.day⁻¹ ($3 \times 2,802.0$ kcal.day⁻¹). Based on common dietary items of Hawaiian monk seals (Goodman-Lowe, 1998), this demand translates into 10.3 kg of octopus, 4.6 kg of eel, or 8.7 kg of Labridae (wrasses) per day per individual depending on caloric value of the prey. Approximately 7.5 kg of spiny lobster, an important historical prey for both commercial fisheries and seals (NMFS, 1997), would be needed to satisfy the caloric needs of a juvenile seal per day. Thus, although mature Hawaiian monk seals demonstrate low metabolic demands compared to other marine mammals (Figure 4A), the elevated metabolism of juveniles and low caloric value of many of their preferred prey require that these immature seals consume 5.8 to 12.9% of their body mass per day in seafood in the wild.

Based on the results of this study, it is not surprising that the juvenile age class of Hawaiian monk seals appear more vulnerable to resource limitations than adults. Increased metabolic rates for juveniles (Figure 2) place two critical demands on this segment of the population—a comparatively large mass-specific nutritional requirement that is coupled with relatively higher aerobic metabolic costs during diving. Together, these conspire to make obtaining sufficient calories to maintain energetic balance physiologically challenging at this age compared to more mature individuals.

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