

Short Note

Resting Metabolic Rate of a Mature Male Beluga Whale (*Delphinapterus leucas*)

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The debate regarding whether marine mammals consume greater amounts of food than their terrestrial counterparts (Innes et al., 1987) has been heated at times because of the implications it holds for fisheries management. Some have argued that marine mammals are “gluttons” (Slijper, 1979) and “inefficient converters of fish flesh” (Sergeant, 1973), and that their numbers need to be controlled to preserve economically important fish stocks (see Yodzis, 2001). However, others have argued the need to preserve the prey species required by marine mammals to meet their high energy requirements by curtailing fishing effort (e.g., Williams et al., 2011).

Quantifying the amount of food a population of marine mammals requires usually entails constructing a bioenergetic model (Bowen, 1997; Winship et al., 2002). A critical input to the model is an estimate of resting metabolic rate (RMR), which is a standardized measure of the rate of heat production that is usually determined as the rate of oxygen consumption. RMR is a highly comparable measure of energy use obtained under a specific set of defined physiological and behavioural conditions. RMR not only forms a core individual component of bioenergetic models, but also mathematically affects estimates of other parameters within the models, such as the costs of activity, which are often estimated as multiples of resting metabolism.

The debate regarding whether marine mammals have elevated RMRs has been hampered by the difficulty in obtaining measurements that fulfilled the precise requirements of the parameter (Lavigne et al., 1986). These include measuring individuals that are quiescent but awake, unstressed, post-absorptive, and not pregnant (Kleiber, 1975). Estimates from wild individuals were often suspect given the stress imposed by temporary holding. Data from captive individuals also suffered from a lack of training to limit behavioural or physiological reactions that would

increase rates of oxygen consumption. However, the set of reliable measures has slowly increased as proper training and conditioning of captive animals became a recognized precursor to accurate measurements of RMR (reviewed by Hunter, 2005). Most of the reliable measurements of RMR for cetaceans have been limited to smaller species such as harbour porpoise (*Phocoena phocoena*; Karandeeva et al., 1973), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Ohizumi et al., 2009), and bottlenose dolphins (*Tursiops truncatus*; Williams et al., 1993, 2001). With the exception of one set of unreviewed values for killer whales (*Orcinus orca*; Kriete, 1995), direct data for larger cetaceans is essentially missing.

We conducted repeated measurements of rates of oxygen consumption on a mature (~17 y) male beluga whale (*Delphinapterus leucas*) held at the Vancouver Aquarium in British Columbia, Canada. Given the ability of small changes in activity or anxiety to elevate measurements of metabolism, the individual (“Imaq”) was trained over several months to rest quietly at the surface of his holding pool underneath a specially designed floating dome that completely contained the portion of his body above the water line. Air was drawn continuously through the dome at a rate of 500 L min⁻¹, sufficient to avoid build-up of carbon dioxide levels above 1%. Temperature, humidity, and pressure within the main airstream were continuously measured to adjust flow rates to meet standard temperature and pressure conditions. A subsample of dried excurrent air flow was measured for concentrations of oxygen and carbon dioxide using Sable System FC-1B and CA-1B analysers, respectively.

The metabolism of the whale was measured prior to its morning feed, and he was given small amounts of herring (< 500 g) about 5 min before the end of the trials to reinforce stationing behaviour within the dome. We presumed that there would be negligible effects of the heat increment of feeding

during the testing period given the long onset time of elevated metabolism exhibited in smaller marine mammals (Rosen & Trites, 1997). Each trial lasted ~20 min, and rates of oxygen consumption were calculated over the last 10 min of the trial. Raw instantaneous gas concentrations were converted to rates of oxygen concentration (VO_2) using LabAnalyst (M. Chappell, University of California at Riverside) that employed appropriate equations as given in Withers (1977). We converted oxygen consumption (L day^{-1}) to energy requirements (MJ day^{-1}) by assuming that 1 L of oxygen was equivalent to 20.1 kJ. Breaths were also monitored to calculate respiration rates. The behaviour of the whale was monitored, and trials where he breathed outside the dome or was distracted by external events (e.g., noises or movement that might increase activity or change respiration rates) were discarded. After a 4-mo training period to ensure the whale was calm within the dome, a total of 11 successful trials were run between 25 November and 23 December 2003. The body mass of the whale measured in July 2003 was 1,341 kg.

Measured metabolic rates were surprisingly consistent between trials. The average metabolic rate over 11 trials was $73,050 \pm 2,290 \text{ kJ d}^{-1}$ (mean \pm SE). This translated into approximately $54.48 \pm 1.71 \text{ kJ kg}^{-1} \text{ d}^{-1}$. In reference to Kleiber's (1975) classic mouse-to-elephant allometric relationship, the metabolism for this beluga whale was approximately 1.13 ± 0.035 times the predicted value for a similarly sized terrestrial mammal. Although this was statistically greater than 1.0 (Wilcoxon Signed Rank Test, $p = 0.0068$), it did not approach the much higher values reported for many other cetacean species (Figure 1).

Respiration rates were also very consistent between trials, averaging 1.82 ± 0.08 breaths min^{-1} . There was also a statistically significant linear relationship between mean metabolism and respiration rates with a moderate predictive capacity ($F_{1,9} = 7.28$, $p = 0.025$, $r^2 = 0.45$) such that

$$\text{RMR (kJ d}^{-1}\text{)} = 37869 + \text{Respirations min}^{-1} * 19350.$$

The narrow range of the data, however, means that caution should be used when employing this relationship to extrapolate metabolism from respiration for animals in more vigorous exercise states.

The metabolic rate exhibited by the male beluga in our study had a lower relative RMR than those reported previously for smaller cetaceans. When we fit the mean value into a larger dataset of RMR measurements of other cetaceans (summarized in Figure 1), the exact predictive relationship was

$$\text{RMR (kJ d}^{-1}\text{)} = 835.57 * \text{Mass (kg)}^{0.716} \text{ (} r^2 = 0.92\text{),}$$

with a mass-exponent that is similar to that typically displayed in mammalian energetics (Glazier, 2005).

Williams et al. (2001) constructed a similar comparative allometric equation and suggested that the higher metabolic rates reported for marine mammals were a result of longer small intestines required for their specific type of marine carnivory, even in comparison to their terrestrial counterparts. Although it is unclear whether beluga whales similarly have a relatively long small intestine, it has been noted that their total intestine to body length ratio (10:1) is among the highest reported for toothed whales (Stevens & Hume, 2004).

Although data were only obtained from a single individual, it is important to consider why the RMR of our beluga whale was significantly lower than that predicted by Williams et al.'s (2001) allometric equation for cetaceans and more similar to Kleiber's (1975) prediction for terrestrial mammals. It should be noted that our beluga whale was relatively old, although changes in metabolism with age are generally driven by changes in body composition rather than age *per se* (Bosy-Westphal et al., 2003). It is therefore possible that the effective metabolic mass of our beluga whale was relatively low due to large accumulated lipid stores. However, it is also likely that the lower rates of measured metabolism were due to the animal being in a calmer state (due to a prolonged training period) compared to cetaceans used in some other studies. Seemingly small changes in behaviour, posture, or vocalization can greatly elevate measured rates of oxygen consumption in cetaceans (Rechsteiner, 2012). It should also be noted that the only other measure of a large cetacean (*Orcinus orca*) was undertaken opportunistically, using a different methodology than other studies (Kriete, 1995), which may be skewing these allometric relationships.

Accurate estimates of resting metabolism are important ecologically as they are thought to be tied to food consumption requirements (Speakman & McQueenie, 1996). Certainly, the disparity in relative metabolic requirements between beluga whales and small cetaceans appear to be mirrored by their respective food requirements in captivity. For example, the average food intake of beluga whales at the Vancouver Aquarium is only about twice that of Pacific white-sided dolphins, despite a $10\times$ difference in body mass.

The assessment of interspecific relationships among cetaceans is aided by the data garnered from the single male beluga whale. However, more studies are required with larger, highly trained captive cetaceans under the specific physiological and behavioural requirements of resting

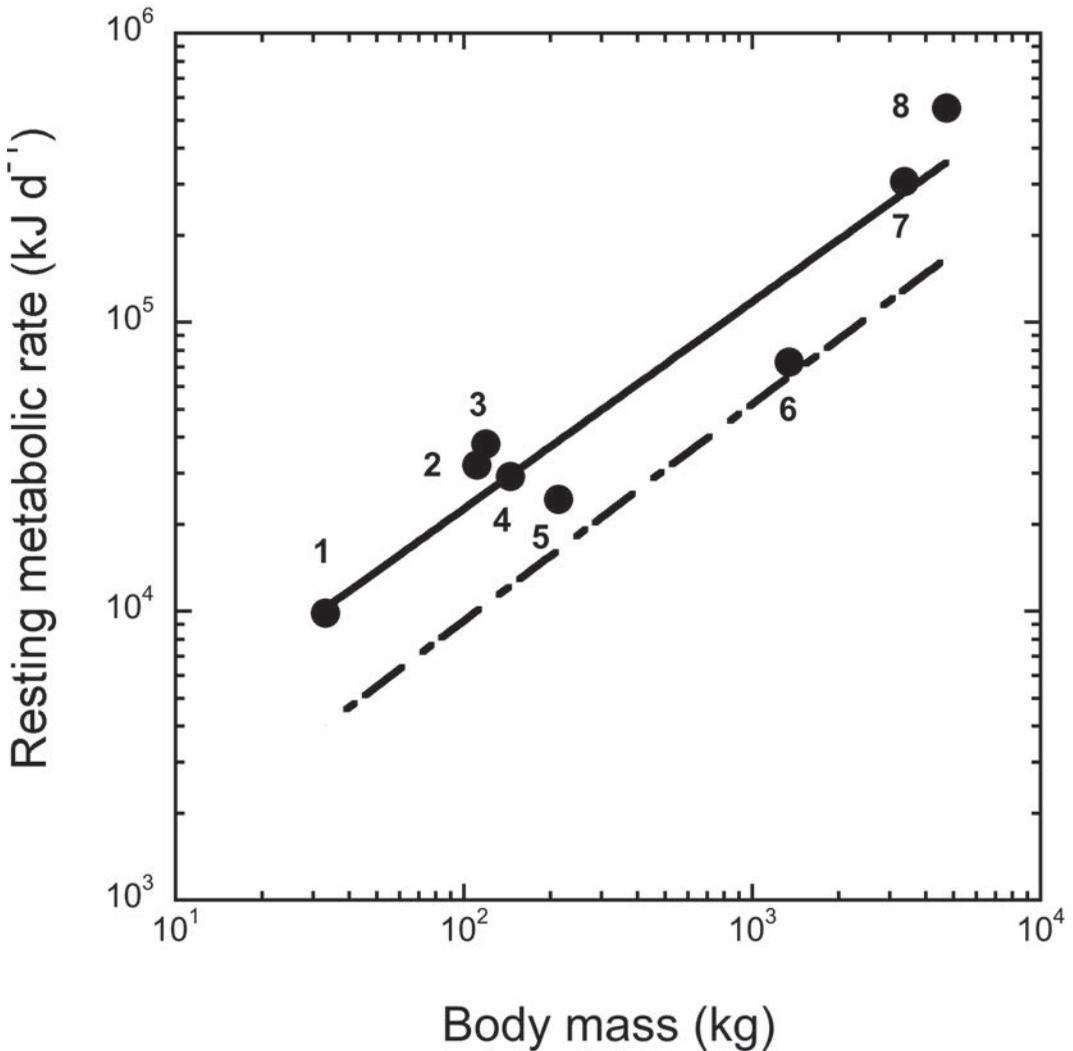


Figure 1. Interspecific comparison of estimates of resting metabolic rate (RMR) from studies of several cetacean species: 1 – Harbour porpoise (Karandeeva et al., 1973), 2 and 3 – Pacific white-sided dolphin (Rechsteiner, 2012, and Ohizumi et al., 2009, respectively), 4 and 5 – Bottlenose dolphins (Williams et al., 1993, and Karandeeva et al., 1973, respectively), 6 – Beluga whale (this study), and 7 and 8 – Killer whales (Kriete, 1995). The figure is modified from previous iterations by Williams et al. (2001) and Rechsteiner (2012). The predictive regression for cetacean species is designated by the solid line, while Kleiber's (1975) "mouse-to-elephant" curve appears as a dashed line for comparison. Note that both axes are logarithmic.

metabolism to fully understand the allometric and ecological relationships within this group of animals.

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