

CORRESPONDENCE

On the importance of understanding physiology when estimating energetics in cetaceans

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We have, with great interest, read the paper entitled ‘Estimating energetics in cetaceans from respiratory frequency: why we need to understand physiology’ by Fahlman et al. (2016), hereafter referred to as Fahlman et al., and we are particularly pleased by their emphasis of the need to understand physiology when estimating field metabolic rates (FMR) of cetaceans.

In this paper, Fahlman et al. have employed their own detailed data collected from captive bottlenose dolphins (*Tursiops truncatus*), at rest and at rest after a swimming bout at surface, to test the validity of using respiratory variables of free-living large mysticete cetaceans for the estimation of their FMR. This approach was first used in the blue whale (*Balaenoptera musculus*) by Nobel laureate August Krogh, who definitely knew physiology (Krogh, 1934), and has hitherto been the only way to obtain useful estimates of energy expenditure in free-living large cetaceans, which are not easily accommodated in laboratories. It takes advantage of the fact that diving mammals are breath-hold divers which benefit from maximizing their time under water by conducting respiratory exchange during brief surface periods, in which large volumes of air are rapidly exchanged (e.g. Blix and Folkow, 1995).

The approach is based on the equation:

$$V_{O_2} = VT \times \Delta O_2 \times f, \quad (1)$$

where V_{O_2} is the rate of oxygen uptake ($l \text{ min}^{-1}$); VT is tidal volume ($l \text{ breath}^{-1}$); ΔO_2 is the difference in oxygen concentration between inspired (O_{2in}) and expired air (O_{2ex}); $\Delta O_2 = O_{2in} - O_{2ex}$ (%); and f is breathing rate (breaths min^{-1}).

In their analysis, Fahlman et al. have evaluated three methods, all based on Eqn 1 (Methods A, B and C). In Method A, data from Armstrong and Siegfried (1991) and Dolphin (1987) were used, and in B our data (Blix and Folkow, 1995) were used, in both cases to estimate FMR in large mysticetes; whereas in Method C, Fahlman et al. used their own data from their dolphins. In all cases the method outputs were compared to Fahlman et al.’s own direct measurements of V_{O_2} in the same dolphins. In so doing it is hardly surprising that Method C performed well, whereas Methods A and B were found to overestimate the ‘true’ value by some 200-500% and, although Fahlman et al. offer some reservations on the validity of their comparison, this remains to be the take-home message, both from the abstract and the full paper.

However, we want to emphasize that Fahlman et al. conducted their comparison across levels of activity, across suborders and across >20-orders-of-magnitude in body mass, and in doing so, even chose to use empirical allometric relationships for prediction of lung volumes in large mysticetes to predict the lung volumes of their dolphins, instead of using their own measured values. That the

outputs of the different methods differ substantially should therefore come as no bigger surprise than that use of the Du Bois formula for estimation of surface area in man (Du Bois and Du Bois, 1916) would prove inappropriate for estimating surface area, for example, in giraffes. Moreover, if Fahlman et al. instead had estimated the lung volumes of their dolphins by use of Wahrenbrock and coworker’s (1974) empirical equation for gray whales (*Eschrichtius robustus*), they would have obtained negative values.

To further illustrate our point, we have tested the validity of Fahlman et al.’s Method C, using existing data for a large mysticete. Wahrenbrock et al. (1974) have measured that a 4000 kg gray whale calf at rest has a V_{O_2} corresponding to about 2× Kleiber’s basal metabolic rate (BMR), i.e. as expected for any immature and growing mammal (Kleiber, 1961). Using Method C with Fahlman et al.’s data for resting VT (32% of total lung capacity) and ΔO_2 (4.94%), and Wahrenbrock and coworker’s (1974) measured values of lung volume (236 liter) and resting breathing rate ($\sim 1 \text{ breath min}^{-1}$) for a calf of 4000 kg, we obtain a V_{O_2} of 3.7 liter min^{-1} , which is less than 35% of the V_{O_2} of 10.7 liter min^{-1} that was measured. If Fahlman’s Method C is applied to our data (Blix and Folkow, 1995), it suggests that a minke whale (*Balaenoptera acutorostrata*) would be able to swim at 2–3 m s^{-1} at a FMR that is 20% below Kleiber’s BMR of mammals in general (Kleiber, 1961), or for good measure, at similar FMR (in $\text{W kg}^{-0.75}$) as in the three-toed sloth (*Bradypus variegatus*) (Nagy and Montgomery, 1980).

One would assume that, with proper physiological insight, the extraordinarily large discrepancies between the outcomes of the different methods would have inspired similar exercises, and that Fahlman et al.’s paper, in consequence, would not have been published in its present form.

Competing interests

The authors declare no competing or financial interests.

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Response to 'On the importance of understanding physiology when estimating energetics in cetaceans'

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We are grateful for the interest in our paper by two eminent physiologists and hope this response to their comments will clarify the objectives of our paper. The analysis in Fahlman et al. (2016) was not intended to provide an accurate method to estimate field metabolic rate (FMR) in large mysticetes; the objective was to measure the dynamic changes in physiology associated with recovery from exercise and show that they are important to consider when estimating FMR. While static averages can provide useful estimates of FMR for a variety of situations, these need to be appropriately selected. For example, we illustrate that it is not possible to use selected average values chosen from excised tissues or resting animals (as in Blix and Folkow, 1995) to provide meaningful estimates of FMR for animals at different activities (i.e. the dolphins in our study). Our study highlights the importance of temporal variation in physiological models: the Blix and Folkow (1995) estimates rely on the assumption that only breathing frequency (f_R) changes with activity, while we argue that both the tidal volume (VT) and mixed lung O₂ content also vary with activity and recovery from a dive (Ridgway et al., 1969). Including this variation in all three parameters reduces temporal uncertainty in the same conceptual model (see Eqn. 1 in Fahlman et al., 2016).

Mathematical models are important tools in eco-physiology as they can create a framework with which to investigate complex physiological problems. It is therefore important to evaluate and revise these models as new information is gained or technological advancements are made. A recent example is how a theoretical model developed to improve our understanding of how mammalian gas exchange is altered during breath-hold diving (Fahlman et al., 2006) was repeatedly updated as new information became available (Fahlman et al., 2009; Hodanbosi et al., 2016). In this study, improved parameter estimates illustrated discrepancies in previous models and allowed us to identify the sensitivity of the system to specific inputs. Similarly, it is not surprising that our Model C (Fahlman et al., 2016) provided the best estimates in our study species, as empirical data from those dolphins were used to revise the input parameters. By doing so, we illustrated how the use of our data in Model C accounts for empirical uncertainties and temporal variation, as we were able to measure aspects of the system (VT and O₂ content) that are difficult to record in a free-swimming cetacean, thus highlighting the dynamic nature of recovery from exercise.

Estimating FMR in large whales is not a straightforward exercise as there is limited information available for use with Eqn 1. The main critique in Folkow and Blix's Correspondence is that we

inappropriately apply allometric relationships within the order *Cetacea*. While we agree that species-specific parameters and variables should be used when available, many theoretical models use estimates from closely related species. For example, even Blix and Folkow themselves (Blix and Folkow, 1995) used mixed pulmonary O₂ from the harbor porpoise and bottlenose dolphin for their estimated O₂ exchange ratio in minke whales, and picked a value for VT to be 60% of total lung capacity (TLC) while the measured VT was from 25-60% of TLC, which resulted in a metabolic rate that was 2×Kleiber (Wahrenbrock et al., 1974). Dolphin (1987) used a value for VT that was 80% of the vital capacity (VC) estimated from the bottlenose dolphin and pilot whale, resulting in surface and diving metabolic rates for humpback whales that were 6–10×Kleiber. Finally, Armstrong and Siegfried used an allometric equation for terrestrial mammals to estimate VC and multiplied this by 80% to estimate VT in minke whales, which resulted in daily metabolic rates around 3–4×Kleiber (Armstrong and Siegfried, 1991). In our study, we showed that both VT and ΔO_2 are probably significantly lower compared to the estimates used in these previous studies and that these parameters vary with both activity level and recovery time.

In their Correspondence, Folkow and Blix further argue that our Model C results in a resting metabolic rate for a 4000 kg minke whale (~7.3 m) that is approximately 0.74×Kleiber. Their argument assumes that the physiology of all mysticetes is comparable, so we will follow this assumption for the following counter-argument. We would like to point out a few necessary corrections to this estimate. Our data for resting VT is 37% of estimated TLC (TLC_{est}; Fahlman et al., 2011; Kooyman, 1973) or 103 l. With an O₂ exchange ratio of 4.92% and respiration rate of 1.38 breaths min⁻¹ (estimated from figures 4 and 5 in Wahrenbrock et al., 1974) the metabolic rate would be 7.0 l O₂ min⁻¹. A similar calculation using the assumptions by Blix and Folkow (1995) results in a value approximately 3.4×Kleiber or 68% higher than the measured value in Wahrenbrock (1974) for a gray whale. For a sleeping, swimming, and feeding minke whale ($f_R=0.59-0.89$, $M_b=4000$ kg), the estimate by Blix and Folkow (1995) would be approximately 2.0 to 2.9×Kleiber. Using our results where we measured the changes in continuous O₂ uptake during recovery from exercise, and assuming that the first breath represents a close estimate of the instantaneous O₂ consumption rate during steady-state exercise performed by the dolphins, we would get a VT of 146 l (53% of TLC_{est}=278 l) and ΔO_2 (6.6%). Thus, the O₂ consumed per breath would be approximately 9.6 l, or 1.4×Kleiber (7 l O₂ min⁻¹) for a cruising minke whale.

The point of this exercise is to show how new data can be used to improve models by allowing us to evaluate past efforts and to illustrate their limitations. We agree with Folkow and Blix that we must use 'proper physiological insight' when considering parameter assumptions and application across species groups. The basic models A and B (Armstrong and Siegfried, 1991; Blix and Folkow, 1995; Dolphin, 1987) are widely applied across marine mammal species (e.g. Christiansen et al., 2014; Williams and Noren, 2009) and we encourage their evaluation (e.g. Fahlman et al., 2016; Roos,

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2015) as they are applied to new species and in light of new developments in physiological research. We therefore argue that it is not possible to use static average values to estimate FMR for a range of activity levels to estimate metabolic rate from f_R with two unknown variables that are known to vary with exercise. It is well known that V_T , f_R , and ΔO_2 vary with exercise and following diving (Fahlman et al., 2008, 2016; Kooyman et al., 1973; Ponganis et al., 1991, 1990; Reed et al., 1994, 2000; Ridgway et al., 1969), and we argue that this has to be accounted for to improve estimates of FMR.

We believe that our study (Fahlman et al., 2016) has helped provide insight into the dynamic nature of cardiorespiratory physiology of cetaceans, and that future studies will help improve our understanding. We agree with Folkow and Blix that our study has limitations; however, this discussion clearly shows how and why we need to be willing to evolve our understanding of physiology.

Competing interests

The authors declare no competing or financial interests.

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