Scaling of swim speed in sharks: a comment on Jacoby et al. (2015)

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Jacoby et al. [1] recently proposed that the cruise swim speeds (S) of ram-ventilating sharks can be predicted by body mass (M), which they use as ‘a surrogate for metabolic rate’ (R; i.e. oxygen uptake rate). They reasoned that ‘overall scaling of swim speed can be predicted by metabolic need’ based on their ‘expectation that swim speed will increase with increasing body size in order to meet higher whole-body metabolism relative to gill surface area’ (A_g). However, the authors assumed that for ram-ventilating sharks A_g scales with M raised to the power of 0.667. Here I propose that if a more appropriate exponent is used (0.84; electronic supplementary material, table S1), then the authors’ theoretical predictions of S are not valid.

The authors presumed that if it is known how both R and A_g scale with M, as described by the allometric equation $Y = aM^b$, then S can be reasonably predicted by M following from the theoretical relationship they developed in which $S \propto (R/A_g)$. Although the authors justifiably assumed that R scales with M where $b = 0.84$ (according to [2]), it is unclear why they assumed that A_g scales with M in direct proportion to body surface area ($b = 0.667$) because this assumption is not substantiated by the available evidence [3], including the study that the authors referenced in support of their assumption [4]. If the scaling exponent for A_g (as a function of M) was less than that for R, then there would be an increasing mismatch between oxygen demand and supply with increasing M, which led the authors to presume that S needs to increase with increasing M to maintain ram ventilation rate (F) to maintain R. However, this does not appear to be the case for the few sharks for which data are available (including data from [4]) where the mean mass scaling exponent for A_g is 0.84 (electronic supplementary material, table S1), identical to the value for R [3]. Thus, the theoretical relationship would be modified to $S \propto (R/A_g) \propto M^{0.84 \cdot 0.84 \cdot 1}$, indicating that S would not need to increase with increasing M to maintain F as proposed by the authors.

The swim speed data used by Jacoby et al. [1] and the confidence interval around the slope of their empirical model span a wide range at a given mass. Consequently, it is difficult to justify the predictive insight of their model, and unconvincing to implicate a respiratory dependence on swim speed as a physiological causality between swim speed and mass. Furthermore, the authors did not provide an intercept for their linear model and conceded that ‘further information would be needed to predict the intercept’. However, without this parameter the empirical model cannot be used to estimate swim speeds. This was inadvertently demonstrated by the authors when, ‘as a proof of concept,’ they appear to have incorrectly derived the speed for megalodon by using just the slope from their linear model.

An alternative hypothesis predicts that cruise swimming speeds are optimal where the total cost of transport (i.e. the energy required to move one unit distance) is minimized [5,6]. Within species of ram-ventilating sharks the cost of transport decreases with increasing mass [7]. Thus, at cruising speeds it is less energetically costly for a large shark to swim a given distance compared with a smaller shark of similar body morphology. In support of this, the
exponent determined for a recent empirical model [8] that relates shark cruising speed to length \( S = a \text{Length}^b \) is very similar to that of Weihs's [5] theoretical bioenergetics model, in which \( b = 0.43 \) (exponent range: 0.35–0.5). Therefore, for ram-ventilating sharks the hypothesis that \( S \) is driven by energetics is more physiologically rational than the authors' hypothesis that \( S \) is driven by a mismatch between \( R \) and \( A_g \) with increasing \( M \), which does not appear to exist.

**Competing interests.** I declare I do not have competing interest.

**Funding.** This study was funded by Natural Sciences and Engineering Research Council of Canada (grant no. 6564).

### References