Scaling of swim speed in sharks: A reply to Morrison (2016)

David M.P. Jacoby[a*], Penthai Siriwat[a,b], Robin Freeman[a] and Chris Carbone[a]

[a] Institute of Zoology, Zoological Society of London, Regent's Park, NW1 4RY, UK

[b] CBER, Department of Genetics, Evolution and Environment, Division of Biosciences, University College London, Gower Street, London,WC1E 6BT, UK

* Correspondence: davidjacoby1@gmail.com

Morrison (2016) raises concerns about the parameterisation of our scaling model and its wider relevance to swim speeds among this group of marine predators. We welcome the opportunity to discuss these issues further and feel that this conversation highlights several interesting points for debate.

Our original approach includes a focus on frontal area which we believe is a critical factor determining water flow to the gills in ram-ventilating sharks and this typically scales to 2/3 of body mass. In support of this, a study on shark body form found that the scaling of frontal length measured in terms of ventral, lateral and dorsal spans all scaled isometrically with total body length (1), which in turn scales to the 1/3 of body mass. Notably, with these assumptions our predictions are consistent with the empirical data we gathered across 26 species of shark. Morrison noted that gill surface area scales more steeply than 2/3, and therefore, sharks need not increase speeds with increasing size to maintain respiratory balance. We believe, oxygenated water flow over the gills will be regulated by frontal area and swim speed as oxygen levels will be at their highest as they enter the animal, then becoming increasingly more depleted with increasing contact with the gills themselves. As such, we would argue that there is a complex relationship between gill area, water flow, and oxygen exchange.

We would argue that the weak scaling of swim speed with mass predicted by our model is consistent with that observed among sharks and other fish ranging between 0.08 and 0.2 (2,3,4). While we concede that alternative theoretical models like Weihs (5) may produce similar scaling estimates, the fact that alternative models have similar predictions is not unusual across scientific disciplines. Indeed it is interesting that the two approaches, Weihs based on fluid mechanics and ours based on oxygen uptake, have convergent predictions. In addition, our model differs from Weihs' (5) in that it makes a mechanistic link between swim speed and oxygen uptake and therefore could be adapted to explore respiratory adjustments, during different states of behaviour among fish, where oxygen uptake potentially matches the costs of movement, such as during high speed hunting bouts or higher cruising speeds in low oxygen environments (6).

We acknowledge that we made an unfortunate error in our calculation of megalodon swim speed and thank Morrison for drawing our attention to this. A correction, including a revised prediction of 1.34 m/s, has now been published.

1. Irschick, D. J., & Hammerschlag, N. (2015). Morphological scaling of body form in four shark species differing in ecology and life history. *Biological Journal of the Linnean Society*, *114*(1), 126–135.
2. Watanabe, Y., Lydersen, C., Fisk, A. T., & Kovacs, K. M. (2012). The slowest fish: Swim speed and tail-beat frequency of Greenland sharks. *Journal of Experimental Marine Biology and Ecology*, *426-427*, 5–11. http://doi.org/10.1016/j.jembe.2012.04.021
3. Jacoby, D. M. P., Siriwat, P., Freeman, R., & Carbone, C. (2015). Is the scaling of swim speed in sharks driven by metabolism? *Biology Letters*, 11 20150781; DOI: 10.1098/rsbl.2015.0781.

4. Watanabe, Y. Y., Goldman, K. J., Caselle, J. E., Chapman, D. D., & Papastamatiou, Y. P. (2015). Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *Proceedings of the National Academy of Sciences*, *112*(19), 201500316. http://doi.org/10.1073/pnas.1500316112
5. Weihs D. 1977 Effects of size on sustained swimming speeds of aquatic organisms. In Scale effects in animal locomotion (ed. T Pedley), pp. 333–338. New York, NY: Academic Press.
6. Parsons G. & Carlson J.K. 1998 Physiological and behavioral responses to hypoxia in the bonnethead shark, *Sphyrna tiburo*: routine swimming and respiratory regulation. *Fish Physiology and Biochemistry* 19, 189-196.