

1 **Is the scaling of swim speed in sharks driven by metabolism?**

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9 **Abstract:**

10 The movement rates of sharks are intrinsically linked to foraging ecology, predator-
11 prey dynamics and wider ecosystem functioning in marine systems. During ram-
12 ventilation, however, shark movement rates are not only linked to ecological
13 parameters, but also physiology, as minimum speeds are required to provide
14 sufficient water flow across the gills to maintain metabolism. We develop a
15 geometric model predicting a positive scaling relationship between swim speeds in
16 relation to body size and ultimately shark metabolism, taking into account estimates
17 for the scaling of gill dimensions. Empirical data from 64 studies (26 species) were
18 compiled to test our model while controlling for the influence of phylogenetic
19 similarity between related species. Our model predictions were found to closely
20 resemble the observed relationships from tracked sharks providing a means to infer
21 mobility in particularly intractable species.

22

23 *Keywords: body size scaling, elasmobranch; metabolic rate, rate-of-movement, swim*

24 *speed*

25 **Introduction:**

26 Metabolic rate (R) is one of a few fundamental metrics in determining an animal's
27 daily energy expenditure. The link between metabolism and behaviour, however, is
28 complex and remains poorly understood. In three-dimensional marine landscapes,
29 swim speeds among fish were found to scale positively with body mass raised to a
30 power of 0.08 [1], where highest swim speeds were amongst species capable of red
31 muscle endothermy [2]. In an early theoretical study, Weihs [3] predicted fish ideal
32 swim speeds should be proportional to body length with recent empirical support
33 found for this relationship [4], however, others have predicted a scaling of
34 movement rates of 0.16 in swimming migratory vertebrates [5]. For many shark
35 species that ram ventilate, there should be fundamental links between swim speed
36 and metabolism, with sharks maintaining minimum speeds to optimise water flow
37 across the gills to meet oxygen requirements for metabolism. General models
38 allowing us to predict speed of locomotion and relate it to daily energy expenditure,
39 will aid our understanding of these elusive predators, providing broader insights into
40 the functioning of marine predator-prey dynamics [6,7].

41 The swim speeds of predatory elasmobranchs will influence prey encounter
42 rates and thus directly impact species at lower trophic levels [6]. While elusive and in
43 many cases threatened, sharks also attract considerable behavioural research using
44 animal-borne biologging techniques from which swim speeds can often be measured
45 or inferred [8]. This provides an opportunity to compare swim speeds with body size
46 across a wide range of species to improve our understanding of variation in mobility
47 across species with size and trophic level.

48

49 Here we explore whether overall scaling of swim speed can be predicted by
50 metabolic need by developing a simple geometric model that predicts the scaling
51 relationship between minimum swim speeds and body mass (a surrogate for
52 metabolic rate) among shark species, accounting for the influence of the scaling of
53 gill dimensions on oxygen uptake. We test our model empirically using data from 26
54 species tracked in the wild with the expectation that swim speed will increase with
55 increasing body size in order to meet higher whole-body metabolism relative to gill
56 surface area. We also argue that among sharks, variation in swim speeds may be
57 linked with trophic level of prey types [9] such that higher swim speeds will be
58 associated with more mobile, higher trophic-level prey species [2]. We test for
59 potentially confounding effects using phylogenetic generalised least squares (PGLS).
60

61 **Methods:**

62 *Model*

63 We assume that oxygen uptake rates in elasmobranchs are directly related to swim
64 speed and thus uptake rate will scale with minimum speed and body dimensions.
65 Knowing how body dimensions (in particular the gills) scale with size in
66 elasmobranchs, we can predict the scaling of shark speed required to meet
67 metabolic needs of different species.

68 Shark metabolic rate, R , is estimated to increase with body mass to the power
69 0.84 [10]. We then argue that in ram ventilating fishes, metabolic rate is a function
70 of body mass, and is proportional to ram ventilation rate or flow F , so that $F \propto R$.
71 Using arguments developed for predators in 3D marine environments feeding on

72 small prey [6], we assert that intake rate of oxygen (i.e. respiration rate) is
73 proportional to swim speed and the square of the body width or a linear dimension
74 of the gills. This is because in 3D environments, flow rate of water through the gills,
75 should be related to the surface area of the gills (or width, w) squared [6] and its
76 speed. Across species of different sizes we expect the rate of oxygen intake to scale
77 with the product of swim speed S , and surface area A , both of these can be
78 described as power equations with respect to body mass:

79
$$S \propto M^b$$

80
$$A \propto M^{2w}$$

81

82 where b and w represent the scaling exponents for speed and gill width
83 respectively.

84
$$F \propto AS$$

85 If...

86
$$F \propto R$$

87 then...

88
$$AS \propto R$$

89
$$S \propto R/A$$

90

91 In accordance with [6], width was estimated to scale to mass in marine predators to
92 the power 0.349, however, overall gill area ($2x w$) was estimated to be 0.667 [11]:

93
$$A \propto M^{0.667}$$

94

95 According to a study using eight shark species, oxygen consumption is thought to
96 scale with body mass to the power 0.84 [9] giving rise to the relationship:

97
$$R \propto M^{0.84}$$

98
$$S \propto R/A$$

99

100 Thus predicted swim speed should therefore scale as follows:

101
$$S \propto M^{0.84-0.667} \propto M^{0.173}$$

102

103 *Elasmobranch mass and swim speeds*

104 To test our model, instantaneous swim speeds (ISS) were obtained from primary
105 sources (64 studies) across a range of shark species (26 benthic, demersal and
106 pelagic species) for which swim speeds could be calculated (see ESM1 and table S1).
107 Sampling frequency which was highly variable, was included as a factor in our
108 empirical model. Where body mass was not reported, it was estimated from the
109 total length (L_T) using length-weight power equations [12]. Due to its unique
110 specialist adaption to very low water temperatures [1], the Greenland shark,
111 *Somniosus microcephalus* was excluded from the analyses.

112

113 *Statistical analysis*

114 The geometric mean of body mass, swim speed and sampling rate were calculated
115 across studies and log transformed along with trophic levels obtained from [12] to
116 achieve normality. To address whether model parameters were correlated to the
117 phylogenetic relatedness of the species, we estimated the phylogenetic signal (λ) for

118 each relevant predictor by testing trait correlation with a published shark
119 phylogenetic tree [13] using the R package: *phytools* [14]. Then, we performed a
120 Phylogenetic Generalised Least Squares (PGLS), with branch length transformations
121 optimised using maximum likelihood (R package: *caper*, [15]). Data type did not
122 significantly improve our model and also varied within species so this was not
123 deemed to influence our results (ESM1).

124

125 **Results:**

126 Species size with respect to body mass spanned approximately three orders of
127 magnitude, from the brown smoothhound, *Mustelus henlei* (2.1 kg, $n=1$) to the two
128 largest fish in the ocean, the basking shark, *Cetorhinus maximus* (mean = 1,234.9 kg,
129 $n=5$) and the whale shark, *Rhinocodon typus* (mean = 1,090.0 kg, $n=10$), with swim
130 speeds ranging from 0.09 to 1.06 m/s. Sampling rate varied considerably between
131 studies from 3600 samples/hr to 0.04 samples/hr.

132 Overall, data on body size and swim speed closely matched the scaling
133 predictions of our geometric model (Fig. 1). Of the parameters included in the
134 model, a phylogenetic signal was found for mass only ($\lambda = 0.66$, $p = 0.023$).
135 Correcting for phylogeny, minimum swim speeds scaled positively with body mass
136 according to a power function with an exponent of 0.15 (95% CI = 0.053 to 0.249,
137 PGLS: $R^2 = 0.28$, AIC = 37.15, $p < 0.01$). The above CI range includes the scaling of
138 0.173 from our model, but excludes the scaling of 0.33 predicted by Weihs [3]. While
139 sampling rate did not significantly influence the model ($p = 0.323$), trophic level,
140 which has been shown to correlate with body size in marine predators [7],

141 temperature and habitat type were all significant, positive predictors of speed (p
142 <0.05). Indeed the inclusion of these factors substantially improved the quality of
143 our model (AIC = 14.69) and explained 90% of the variation ($p <0.01$).

144

145 **Discussion:**

146 We present a novel model to predict shark swim speeds required to maintain
147 metabolic rate using body mass as a surrogate, assuming that water/oxygen flow
148 rates are related to the scaling of body form (gill dimensions) and swim speed.
149 Controlling for phylogeny, our predictions were consistent with empirical data from
150 26 species across 64 studies.

151 In support of our prediction that metabolic rate drives minimum swim speed in
152 sharks, Watanabe et al. [2] demonstrate that air-breathing swimming vertebrates
153 appear unconstrained due to their ability to stop and breath at the surface and thus
154 have a lower scaling exponent (<0.1). Our simple geometric model, however, makes
155 a number of key assumptions that require discussion. We assume that respiration
156 occurs through ram ventilation (F) during motion and further ISSs may include
157 periods of swimming with and against currents, however, we expect oxygen intake
158 rates to fluctuate about a mean, relative to swim speeds. More data that explicitly
159 measure speed in relation to active swimming using animal-borne sensors [e.g. 3],
160 will allow us to further refine the model. There is a clear need to improve estimates
161 of elasmobranch swim speeds and recent research, demonstrates that technological
162 advancements such as stereo-baited underwater video systems (stereo-BRUVS), now
163 offer a means to directly measure cruising speeds *in situ* [4]. Indeed, the authors of

164 this study suggest that shark swim speed can be defined as a function of fork length
165 using a model with slopes comparable to the theoretical work by Weihs [3].
166 However, our model slope is consistent with the predicted migrational speeds from
167 Hedenstrom [5], but falls midway between the observed estimated scaling of 0.08
168 [1] and the 0.33 predicted by Weihs [3].

169 The described model attempts to predict the slope of the relationship between
170 swim speeds and body mass, however, further information would be needed to
171 predict the intercept (exact swim speeds of sharks), including physiological,
172 environmental and ecological factors. Indeed we explored the influence of water
173 temperature (warm/cold/mixed) and habitat type to explore the additional
174 variation, both of which significantly improved the model ($p < 0.05$). Recent empirical
175 evidence suggests that some shark species have evolved elevated cruising speeds,
176 made possible by warm endothermic muscles, allowing them to increase prey
177 encounter rates and migrate greater distances than their cold blooded relatives [2].
178 Such physiological adaptations will undoubtedly significantly impact the predictions
179 of our model. Despite this, we observe a striking relationship that holds across
180 species in five different taxonomic Orders spanning a size range of three orders of
181 magnitude. As a proof of concept, we extrapolated from our empirical model an ISS
182 of 5.04 m/s for Megalodon, an enormous (15-20 m, ~48,000 kg) apex predatory
183 shark thought to have gone extinct 2.6 million years ago [16]. Though high, this
184 estimate is consistent with typical swim speeds of an equivalently-sized marine
185 mammal (fin whales, 4-6 m/s [17]). At a time when it remains a considerable
186 challenge to deploy, track and retrieve data from the majority of elasmobranch

187 species, we argue that such models will prove insightful for inferring a rudimentary
188 ecology in poorly understood and threatened shark species.

189

190 *Authors' contributions*

191 C.C. and R.F conceived the study, D.J. and P.S. acquired and analysed the data and all
192 authors contributed to the preparation of the manuscript.

193 *Competing interests*

194 The authors declare they have no competing interests.

195 *Data accessibility*

196 References for the empirical data are provided in the electronic supplementary
197 material.

198

199 *References*

- 200 1. Watanabe, Y. Y., Lydersen, C., Fisk, A. T. & Kovacs, K. M. 2012 The slowest fish:
201 Swim speed and tail-beat frequency of Greenland sharks. *J. Exp. Mar. Biol.*
202 *Ecol.* **426-427**, 5–11. (doi:10.1016/j.jembe.2012.04.021)
- 203 2. Watanabe, Y. Y., Goldman, K. J., Caselle, J. E., Chapman, D. D. &
204 Papastamatiou, Y. P. 2015 Comparative analyses of animal-tracking data
205 reveal ecological significance of endothermy in fishes. *Proc. Natl. Acad. Sci. U.*
206 *S. A.* **112**, 1500316112–. (doi:10.1073/pnas.1500316112)
- 207 3. Weihs, D. 1977 Effects of size on sustained swimming speeds of aquatic
208 organisms. In *Scale effects in animal locomotion* (ed T. Pedley), pp. 333–338.
209 New York.
- 210 4. Ryan, L. a., Meeuwig, J. J., Hemmi, J. M., Collin, S. P. & Hart, N. S. 2015 It is not
211 just size that matters: shark cruising speeds are species-specific. *Mar. Biol.*
212 **162**, 1307–1318. (doi:10.1007/s00227-015-2670-4)

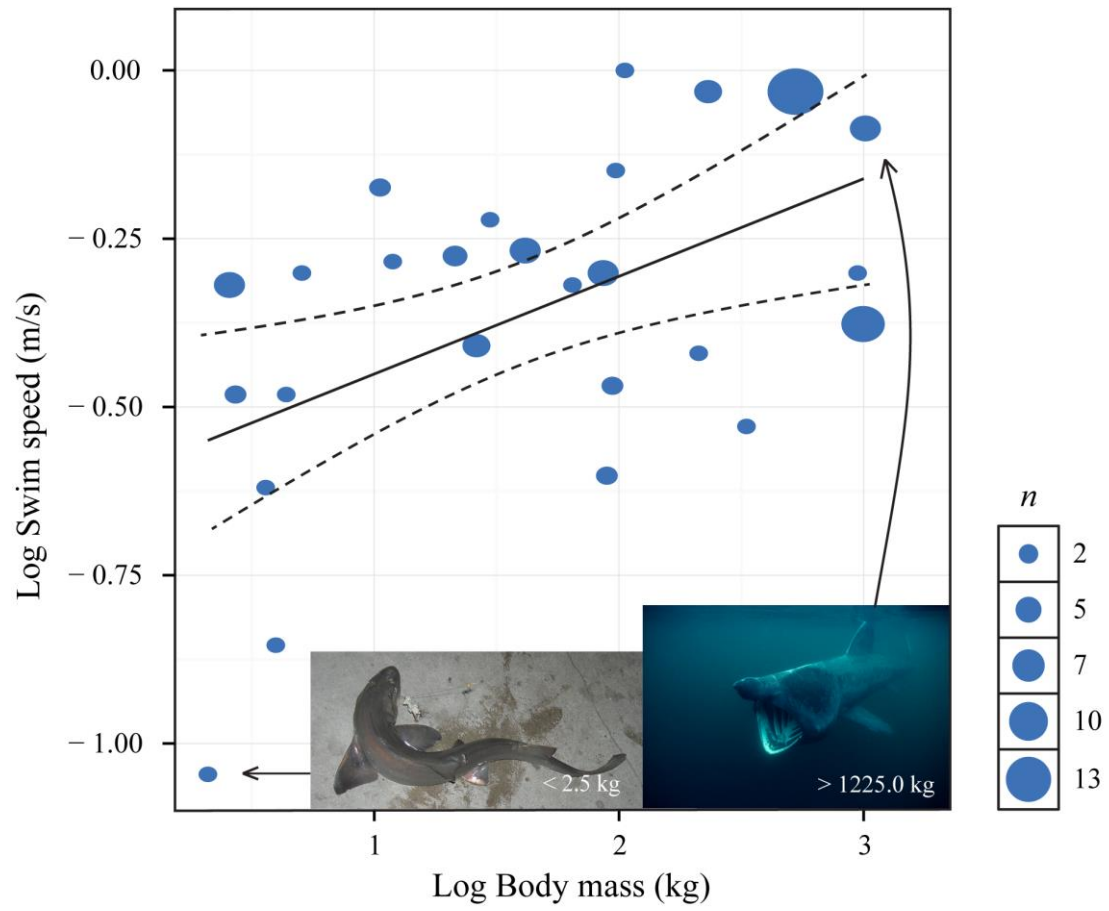
- 213 5. Hedenström, A. 2003 Scaling migration speed in animals that run, swim and
214 fly. *J. Zool.* **259**, S0952836902003096. (doi:10.1017/S0952836902003096)
- 215 6. Carbone, C., Codron, D., Scofield, C., Clauss, M. & Bielby, B. 2014 Geometric
216 factors influencing the diet of vertebrate predators in marine and terrestrial
217 environments. *Ecol. Lett.* **17**, 1553–1559.
- 218 7. Costa, G. 2009 Predator size, prey size, and dietary niche breadth relationships
219 in marine predators. *Ecology* **90**, 2014–9. (doi:10.1890/08-1150.1)
- 220 8. Sims, D. 2010 Tracking and Analysis Techniques for Understanding Free-
221 Ranging Shark Movements and Behavior. In *Sharks and Their Relatives II*
222 *Biodiversity, Adaptive Physiology, and Conservation*, pp.
223 351.(doi:10.1201/9781420080483)
- 224 9. Bowen, W. D., Tully, D., Boness, D. J., Bulheier, B. M. & Marshall, G. J. 2002
225 Prey-dependent foraging tactics and prey profitability in a marine mammal.
226 *Mar. Ecol. Prog. Ser.* **244**, 235–245. (doi:10.3354/meps244235)
- 227 10. Sims, D. W. 2000 Can threshold foraging responses of basking sharks be used
228 to estimate their metabolic rate? *Mar. Ecol. Prog. Ser.* **200**, 289–296.
229 (doi:10.3354/meps200289)
- 230 11. Emery, S. H. & Szczepanski, a. 1986 Gill dimensions in pelagic elasmobranch
231 fishes. *Biol. Bull.* **171**, 441–449. (doi:10.2307/1541685)
- 232 12. Froese, R. & Pauly, D. 2014 FishBase. *World Wide Web Electron. Publ.*
- 233 13. Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., Straube, N. & Lakner,
234 C. 2012 Elasmobranch Phylogeny: A mitochondrial Estimate Based on 595
235 Species. In *Biology of sharks and their relatives, second edition* (eds J. C.
236 Carrier J. A. Musick & M. R. Heithaus), pp. 227–
237 227.(doi:10.1080/17451000.2012.745005)
- 238 14. Revell, L. J. 2012 phytools: an R package for phylogenetic comparative biology
239 (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-
240 210X.2011.00169.x)
- 241 15. Orme, C. D. L., Freckleton, R. P., Thomas, G. H., Petzold, T. & Fritz, S. A. 2013
242 caper: comparative analyses of phylogenetics and evolution in R.
- 243 16. Gottfried, M. D., Compagno, L. J. V. & Bowman, S. C. 1996 Size and skeletal
244 anatomy of the giant ‘megatooth’ shark *Carcharodon megalodon*. In *Great*
245 *White Sharks: The Biology of Carcharodon carcharias* (eds A. P. Klimley & D. A.
246 Ainley), pp. 55–66. San Diego: Academic Press Inc.
- 247 17. Goldbogen, J. a. 2006 Kinematics of foraging dives and lunge-feeding in fin
248 whales. *J. Exp. Biol.* **209**, 1231–1244. (doi:10.1242/jeb.02135)

249 **Figure 1.** The scaling relationship of shark swim speed (m/s) with body mass (kg) for
250 26 species (geometric mean taken across n studies denoted by point size), fitted with
251 a linear model (solid line) and 95% confidence intervals (dashed lines). Photographs
252 (L-R) courtesy of Butko CC BY-SA (brown smoothhound, *Mustelus henlei*) and Jeremy
253 Stafford-Deitsch (basking shark, *Cetorhinus maximus*).

254

255

256 Figure 1.



257