

# 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:

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

$$98 \quad S \propto R/A$$

99

100 Thus predicted swim speed should therefore scale as follows:

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

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 ( $\lambda$ ) 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

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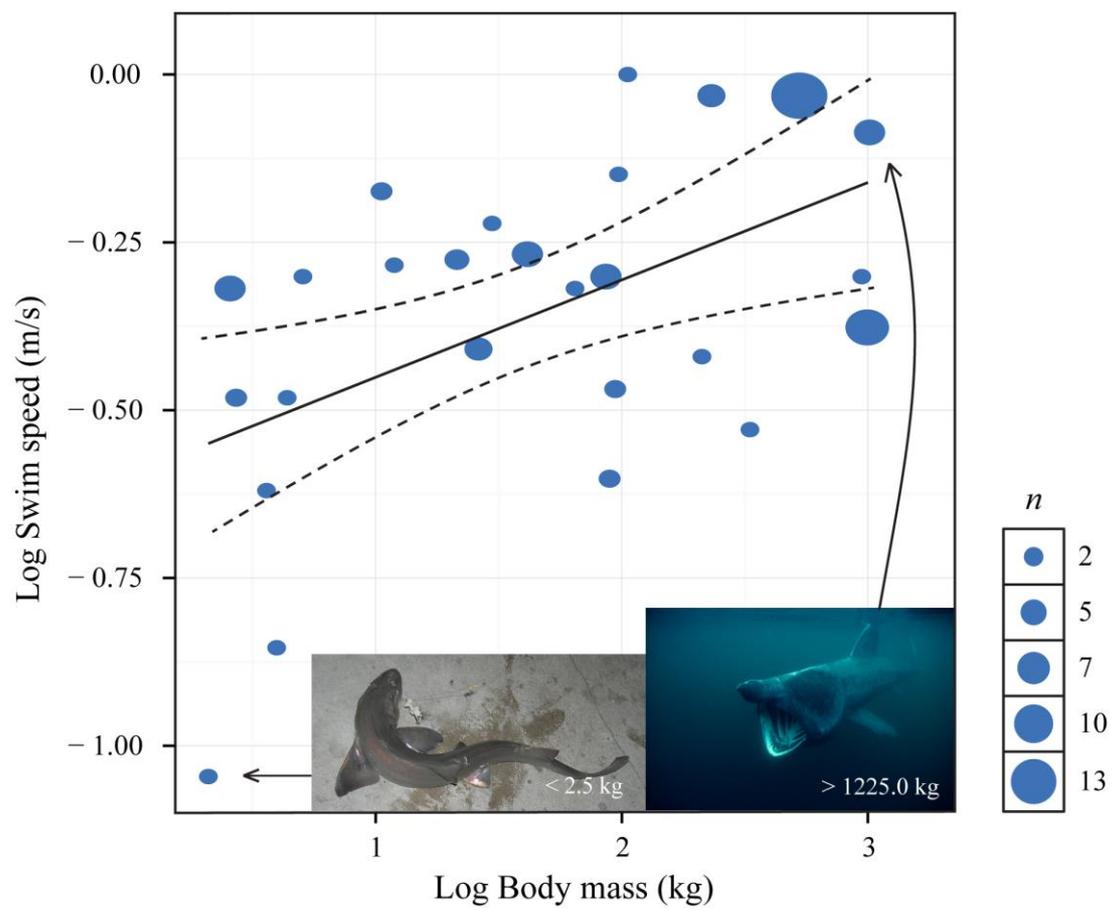
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249 **Figure 1.** The scaling relationship of shark swim speed (m/s) with body mass (kg) for  
250 26 species (geometric mean taken across  $n$  studies denoted by point size), fitted with  
251 a linear model (solid line) and 95% confidence intervals (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