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

David M. P. Jacoby¹, Penthai Siriwat¹,², Robin Freeman¹ and Chris Carbone¹

¹Institute of Zoology, Zoological Society of London, Regent’s Park, London NW1 4RY, UK
²CBER, Department of Genetics, Evolution and Environment, Division of Biosciences, University College London, Gover Street, London WC1E 6BT, UK

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

1. Introduction

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

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

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

2. Material and methods

(a) Model

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

Shark metabolic rate, $R$, is estimated to increase with body mass to the power 0.84 [10]. We then argue that in ram ventilating fishes, metabolic rate is a function of body mass, and is proportional to ram ventilation rate or flow $F$, so that $F \propto R$. Using arguments developed for predators in three-dimensional marine environments feeding on small prey [6], we assert that intake rate of oxygen (i.e. respiration rate) is proportional to swim speed and the square of the body width or a linear dimension of the gills. This is because in three-dimensional environments, flow rate of water through the gills should be related to the surface area of the gills (or width, $w$) squared [6] and its speed. Across species of different sizes, we expect the rate of oxygen intake to scale with the product of swim speed $S$, and surface area $A$; both of these can be described as power equations with respect to body mass:

$$S \propto M^b$$

and

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

where $b$ and $w$ represent the scaling exponents for speed and gill width, respectively.

$$F \propto AS;$$

if

$$F \propto R,$$

then

$$AS \propto R$$

and

$$S \propto \frac{R}{A}.$$  

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

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

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

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

and

$$S \propto \frac{R}{A}.$$  

Thus, predicted swim speed should therefore scale as follows:

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

(b) Elasmobranch mass and swim speeds

To test our model, instantaneous swim speeds (ISSs) were obtained from primary sources (64 studies) across a range of shark species (26 benthic, demersal and pelagic species) for which swim speeds could be calculated (see electronic supplementary material, S1 and table S1). Sampling frequency that was highly variable was included as a factor in our empirical model. Where body mass was not reported, it was estimated from the total length ($L_T$) using length–weight power equations [12]. Owing to its unique special adaptation to very low water temperatures [1], the Greenland shark, Somniosus microcephalus, was excluded from the analyses.

(c) Statistical analysis

The geometric mean of body mass, swim speed and sampling rate were calculated across studies and log transformed along with trophic levels obtained from Froese & Pauly [12] to achieve normality. To address whether model parameters were correlated to the phylogenetic relatedness of the species, we estimated the phylogenetic signal ($\lambda$) for each relevant predictor by testing trait correlation with a published shark phylogenetic tree [13] using the R package: phytools [14]. Then, we performed a PGLS, with branch length transformations optimized using maximum likelihood (R package: caper [15]). Data type did not significantly improve our model and also varied within species so this was not deemed to influence our results (electronic supplementary material, S1).

3. Results

Species size with respect to body mass spanned approximately three orders of magnitude, from the brown smoothhound, Mustelus henleii (2.1 kg, $n = 1$), to the two largest fish in the ocean, the basking shark, Cetorhinus maximus (mean = 1234.9 kg, $n = 5$), and the whale shark, Rhincodon typus (mean = 1090.0 kg, $n = 10$), with swim speeds ranging from 0.09 to 1.06 m s$^{-1}$.Sampling rate varied considerably between studies, from 3600 to 0.04 samples h$^{-1}$.

Overall, data on body size and swim speed closely matched the scaling predictions of our geometric model (figure 1). Of the parameters included in the model, a phylogenetic signal was found for mass only ($\lambda = 0.66, p = 0.023$). Correcting for phylogeny, minimum swim speeds scaled positively with body mass according to a power function with an exponent of 0.15 (95% CI = 0.053–0.249; PGLS: $R^2 = 0.28$, Akaike information criterion (AIC) = 37.15, $p < 0.01$). The above CI range includes the scaling of 0.173 from our model, but excludes the scaling of 0.33 predicted by Weihls [3]. While sampling rate did not significantly influence the model ($p = 0.323$), trophic level, which has been shown to correlate with body size in marine predators [7], temperature and habitat type were all significant, positive predictors of speed ($p < 0.05$). Indeed, the inclusion of these factors substantially improved the quality of our model (AIC = 14.69) and explained 90% of the variation ($p < 0.01$).

4. Discussion

We present a novel model to predict shark swim speeds required to maintain metabolic rate using body mass as a surrogate, assuming that water/oxygen flow rates are related to the scaling of body form (gill dimensions) and swim speed.
Controlling for phylogeny, our predictions were consistent with empirical data from 26 species across 64 studies. In support of our prediction that metabolic rate drives minimum swim speed in sharks, Watanabe et al. [2] demonstrated that air-breathing swimming vertebrates appear unconstrained owing to their ability to stop and breathe at the surface and thus have a lower scaling exponent (less than 0.1). Our simple geometric model, however, makes a number of key assumptions that require discussion. We assume that respiration occurs through ram ventilation (F) during motion and also that some measures of ISSs reflect ground speeds and not true, through-water speeds. While data type was not a significant factor in our model, using animal-borne sensors (e.g. [3]) to collect more data that explicitly measure speed in relation to active swimming will allow us to further refine the model. There is a clear need to improve estimates of elasmobranch swim speeds, and recent research demonstrates that technological advancements such as stereo-baited underwater video systems (stereo-BRUVS) now offer a means to directly measure cruising speeds in situ [4]. Indeed, the authors of this study suggest that shark swim speed can be defined as a function of fork length using a model with slopes comparable to the theoretical work by Weihs [3]. However, our model slope is consistent with the predicted migrational speeds from Hedenstrom [5], but falls midway between the observed estimated scaling of 0.08 [1] and the 0.33 predicted by Weihs [3].

The described model attempts to predict the slope of the relationship between swim speeds and body mass; however, further information would be needed to predict the intercept (exact swim speeds of sharks), including physiological, environmental and ecological factors. Indeed, we investigated the influence of water temperature (warm/cold/mixed) and habitat type to explore the additional variation, both of which significantly improved the model (p < 0.05). Recent empirical evidence suggests that some shark species have evolved elevated cruising speeds, made possible by warm endothermic muscles, allowing them to increase prey encounter rates and migrate greater distances than their cold blooded relatives [2]. Such physiological adaptations will undoubtedly significantly impact the predictions of our model. Despite this, we observe a striking relationship that holds across species in five different taxonomic orders spanning a size range of three orders of magnitude. As a proof of concept, we extrapolated from our empirical model an ISS of 5.04 m s\(^{-1}\) for megalodon, an enormous (15–20 m, approx. 48 000 kg) apex predatory shark thought to have gone extinct 2.6 Ma [16]. Although high, this estimate is consistent with typical swim speeds of an equivalently sized marine mammal (fin whales, 4–6 m s\(^{-1}\) [17]). At a time when it remains a considerable challenge to deploy, track and retrieve data from the majority of elasmobranch species, we argue that such models will prove insightful for inferring a rudimentary ecology in poorly understood and threatened shark species.

**Figure 1.** The scaling relationship of shark swim speed (metres per second) with body mass (kilograms) for 26 species (geometric mean taken across n studies denoted by point size), fitted with a linear model (solid line) and 95% CIs (dashed lines). Photographs (left to right) courtesy of Butko CC BY-SA (brown smooth-hound, *Mustelus henlei*) and Greg Skomal/NOAA Fisheries Service (basking shark, *Cetorhinus maximus*). (Online version in colour.)

**Data accessibility.** References for the empirical data are provided in the electronic supplementary material.

**Authors’ contribution.** C.C. and R.F conceived the study, D.J. and P.S. acquired and analysed the data and all authors contributed to the preparation of the manuscript. All authors approve the final version and agree to be accountable for the work in the manuscript.

**Competing interests.** The authors declare they have no competing interests.

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References


Correction to ‘Is the scaling of swim speed in sharks driven by metabolism?’

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Following publication of our article, we acknowledge that there was an error in our extrapolated cruising speed for the megalodon shark. Our estimate of 5.04 m s\(^{-1}\) should have been 1.34 m s\(^{-1}\). However, we note that this corrected estimate for a 48 tonne individual may be low as its mass has been estimated as high as 100 tonnes [1].

This correction refers to a swim speed estimate for this extinct species only and does not influence the main analyses presented in our paper.

Reference