# It is not just size that matters: shark cruising speeds are species-specific

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Short title: "Shark cruising speeds are species-specific"

#### Abstract

Speed of locomotion plays an important role in an animal's biology and ecology, and is of particular interest in aquatic animals. Determining cruising speeds of shark-for which such data are scarcemay help to better understand their interactions with prey, the size of the home ranges they maintain, their energetic costs, and how they interact with their environment through sensory perception. In this study, the cruising speeds of a range of different shark species were measured using stereo-Baited Remote Underwater Video Systems (stereo-BRUVS). The relationship between cruising speeds and fork length, species, order, habitat, trophic level, temperature and tail shape was then modelled. Fork length and species best explained the cruising speeds of the eight species of shark studied: *Carcharhinus* amblyrhynchos, Carcharhinus albimarginatus, Carcharhinus obscurus, Furgaleus macki, Carcharhinus obesus, Mustelus antarcticus, Heterodontus portusjacksoni and Parascyllium variolatum. This linear model had a slope that did not differ statistically from that of the theoretical model proposed by Weihs (1977), which suggests that the relationship between cruising speed and length appears to be dominated by energetics. The results suggest that existing allometric estimates of cruising speeds can be improved by defining cruising speeds for each species as a function of length. Currently literature presents cruising speed data for only a few species of shark; therefore, we provide a second, generalised model, which predicts cruising speed as a function of length and tail shape. The length + tail shape model was selected based on its generality and accuracy in estimating shark cruising speeds obtained from acoustic tags. This length + tail shape model was significantly better than a length only model; it explained a further 76% of the variation in cruising speed derived from stereo-BRUVS and acoustic tagging data than a length only model. The more accurate prediction of the length + tail shape model is most likely because tail shape is correlated with a number of ecological factors.

Key Words: swimming speed, stereo-BRUVS, energetics, allometry, sensory perception, home range, acoustic telemetry

## Introduction

In many animals, locomotion is the primary cause of energy expenditure. The average rate of locomotion is often correlated with metabolic rate (Blaxter, 1989). Thus, the speed at which an animal moves through its environment represents a balance between energy expenditure and the need to perform a range of behaviours critical for survival, such as foraging (Ware, 1978; Schnell and Hellack, 1979) and predator avoidance (Boyd et al., 1995). The quantification of locomotive speed in an animal can, therefore, provide important ecological insights, such as the nature of predator-prey interactions (Hatle and Grimké Faragher, 1998; Ings and Chittka, 2008) and the maintenance of home ranges (Sainte-Marie and Hargrave, 1987).

Beyond energetic considerations, speed of locomotion is an important factor for understanding the evolution and adaptation of sensory systems, as speed determines the rate at which sensory information is encountered and must be processed by the animal as it moves through its environment. For example, in the visual system, speed of locomotion influences the rate at which the image moves across the retina (Eckert and Zeil, 2001). Animals that exhibit faster speeds of locomotion generally have higher temporal resolution in the visual system and are, therefore, able to process images much faster, reducing image blur (Autrum, 1958; McFarland and Loew, 1983; Lisney et al., 2011). Many animals go to the effort of adopting energetically costly adaptations in order to enhance temporal resolution. For example, swordfish Xiphias gladius achieve higher temporal resolution than other teleost fishes by warming their eyes and are, therefore, able to resolve images at faster swimming speeds, which may enhance their ability to identify and capture prey (Fritsches et al., 2005; Schieber et al., 2012).

Speed of locomotion in the aquatic environment is of particular interest from a sensory perspective; animals must control their movement in both the horizontal and vertical planes and deal with a complex three-dimensional sensory world. Vision is particularly challenging in the aquatic environment. The detection of objects is more difficult due to lower light intensity and lower contrast (Lythgoe, 1988). A better understanding of the sensory adaptations exhibited by aquatic animals is clearly dependent on a more complete characterisation and quantification of locomotion speed in relation to behaviour, which was the motivation for this study.

The speed at which an animal moves is dependent on the nature of the activity in which they are engaged. For instance, the maximum speed an animal is capable of—burst speed—is usually undertaken during escape from predators. In fishes, burst speeds reach velocities in excess of 6—18 body lengths s-1, but because burst swimming is powered anaerobically, it is usually brief (<20s) (Dieringer et al., 1983; Gioanni, 1988; Puzdrowski and Leonard, 1994; Watanabe et al., 2012). In contrast, cruising swimming is aerobically powered, slow swimming (~2—4 lengths s-1 in fish) that can be sustained for prolonged periods of time (>200 min) (Ware, 1978; Gioanni, 1988; Watanabe et al., 2012). Cruising swimming speed is the most common speed at which an animal travels (Beamish, 1978) and, therefore,

is the speed at which animals are most likely to be travelling when they first encounter predators, prey and other important sensory cues. This study, therefore, has focused on cruising speeds.

In fishes, the main factors affecting of cruising speeds are body size (Bainbridge, 1958; Weihs, 1977; Harahush et al., 2009), body shape (Harris, 1965; Walker and Westneat, 2002) and habitat (Peake et al., 1997). Cruising speed increases with body size but at a disproportionate rate with speed increasing at a slower rate than body size (Bainbridge, 1958; Weihs, 1977; Harahush et al., 2009). Body shapes that reduce drag increase swimming efficiency, allowing faster speeds to be achieved with lower energy consumption (Harris, 1965; Walker and Westneat, 2002). For example, labriform fishes with more efficient swimming performance have high aspectratio fins, with the centre of the fins located closer to the fin base and with a longer leading edge fin ray (Walker and Westneat, 2002). The relationships between cruising speed and both body length and shape generally reflect the optimisation of energy expenditure and may also be habitat-driven. For instance, in salmonid fishes, optimal cruising speeds are an adaption to their specific habitats (Peake et al., 1997). Brook trout live in slow moving pools and are adapted to slower swimming speeds than salmon parr, which are anadromous and live in areas with much faster currents. Evolving optimal swimming speeds for different habitats may also lead to a reduction in interspecific competition (Peake et al., 1997; Souza et al., 2011). Habitat has also been known to influence swimming speed, particularly with respect to temperature: the Greenland shark, Somniosus microcephalus, is much slower than other fish of its size, and this has been attributed to its ectothermy and habituation to cold waters (Watanabe et al., 2012).

Despite our knowledge about fish swimming speeds in general, there remains a gap with respect to understanding swimming speeds in sharks. Such knowledge is of particular significance because sharks are apex predators (Compagno, 1990) and play an important role in shaping population dynamics and ecosystem structure (Schor and Levi, 1980; Myers et al., 2007; Ferretti et al., 2010; Tappeiner et al., 2012). Where shark swimming speeds have been studied, estimates have predominately used data obtained from acoustic telemetry tagging (Klimley et al., 2002; Sundström and Gruber, 2002; Bruce et al., 2006), observations of captive animals swimming in aquaria or water flumes/tunnels (Weihs et al., 1981; Graham et al., 1990) and, more recently, accelerometers (Nakamura et al., 2011). However, such studies encompass only a limited number of species and can be expensive and intrusive. Acoustic tags may also have low temporal and spatial resolution; they measure mean speed from point-to-point and generally do not take into account specific swimming behaviour, which means it is difficult to distinguish cruising swimming from resting behaviour (Musyl et al., 2001). Observations of captive animals and the use of water tunnels have been beneficial in linking speed with behaviour (Weihs et al., 1981) and energetics (Harahush et al., 2009), but are limited in terms of the size of animals. Moreover, the ability of these methods to infer speed under natural conditions is also debated (Dickson and Graham, 2004; Grusha and Patterson, 2005; Hammerschlag et al., 2011). A small sample size is also common to all these types of studies. Previously, estimates of cruising speeds presume all individuals of the same length regardless of species to have the same cruising speed, for both sharks and teleosts (Weihs, 1977).

In this study, we measured cruising speeds in multiple species of shark using an innovative application of stereo-baited remote underwater video systems (stereo-BRUVS). We used stereo-BRUVS to generate speed measurements of sharks because they are a relatively non-intrusive method that is capable of generating large in situ data sets for a wide range of shark species and sizes. Measurements of cruising speed were used to generate a predictive model of cruising speed as a function of body size, body shape, habitat, trophic level, temperature and taxonomic order. The predictive capabilities of the model were then assessed by comparing it with a theoretical model based on energetics (Weihs, 1977) and to estimates of shark cruising speed derived from acoustic tagging data.

### Materials and methods

## Acquisition of video footage

Stereo-baited remote underwater video systems (stereo-BRUVS) were used to capture footage of sharks swimming in their natural environment. Video footage was selected from a database containing over 250 h of digital video footage obtained during 200 stereo-BRUVS deployments at six different locations along the western coast of Australia (supplementary info) as well as 16 samples from the Chagos Archipelago (central Indian Ocean). A range of habitats were sampled, from sandflats to high-profile reefs at depths between 5 and 85 m.

The stereo-BRUVS comprised two Sony HC15E video cameras mounted 0.7 m apart on a horizontal base-bar. The cameras were positioned such that their optical axes converged eight degrees towards the centre of the apparatus to create an optimized field of view (Harvey and Shortis, 1996; Harvey and Shortis, 1998). A bait basket was mounted in a central position in front of the cameras and contained 1kg of crushed pilchards. The stereo-BRUVS were deployed from a vessel onto the seabed for between one and two hours. Each unit, therefore, constituted a remote station, filming the fish and shark assemblage within its field of view.

#### Video Analysis

EventMeasure software (www.seagis.com.au) was used to estimate the length and position of individual animals from the stereo-video imagery. Sharks were first identified by size, sex,- and individual-specific markings if present. Only individuals that could be clearly identified were included in the analysis. Fork length (m) was then estimated for each individual. Position coordinates were taken from the same location on the animal, generally the eye or, when eyes were not clearly visible, from the tip of the snout. Repeated positional measurements were taken of each shark over time as it swam parallel to and within 5 m of both cameras for a minimum horizontal distance of 4 m. Care was taken to avoid

measuring swimming speed when the shark interacted directly with the bait. Measurements were also not made when sharks swam directly towards or away from the bait. Swimming speeds (m s<sup>-1</sup>) were then calculated as the distance moved as a function of elapsed time as the shark moved across the field of view. Swimming speeds were classified preliminarily as "cruising" when the shark displayed consistent slow rhythmic tail beats or as "burst" when the sharks exhibited obvious faster tail beat frequency and greater tail beat amplitude over short distances. If no tail beats were observed, measurements were not taken.

## Cruising speeds from tagging data

We reviewed the literature to compile published estimates of shark cruising speeds. Specifically, estimates from acoustic telemetry were used as these are the most prevalent in the literature. If speed was expressed separately for day and night, the day speed was used, given that all stereo-BRUVS footage was captured during the day. All lengths of tagged sharks were quantified as fork length based either on reported fork lengths or by calculating fork length from total length using conversions reported on Fishbase (Froese, 2013). The sampling intervals used for the estimation of cruising speeds were also recorded as the time interval (in minutes) between recordings of tagged shark coordinates. If multiple sampling intervals were used in a study, the average sampling interval was calculated.

#### Data analysis

As the focus of this study was to measure and predict cruising speeds, it was first necessary to remove burst speeds from the data set. For each species, a general linear model was used to regress all recorded speed measurements against body length. Outliers that were more than three standard deviations above the regression line (i.e. indicating burst swimming) were removed. The average cruising speed (hereafter referred to as speed) was then calculated for each individual as the mean of the remaining non-burst speeds. Potential factors that may affect cruising speed were compiled for each species to test generalisation of the model. These factors included phylogenetic order, maximum fork length (maximum recorded growth length), habitat temperature (temperate or tropical), trophic level and major habitat type (Froese, 2013) as well as classifying species by their tail shape (Thomson and Simanek, 1977).

The initial analysis included shark species with speed and length measurements for a minimum of eight individuals (hereafter referred to as "coreBRUVS"). Speed and length were log<sub>10</sub> transformed for all analyses in order to fulfil the assumption of homogeneity of variance (Zar, 1999). Multiple regression and ANCOVA were used to model the effects of length and species on speed for all individuals in R (Speakman, 1986).

#### Generalised cruising speed model

We also produced a model that would be capable of predicting cruising speed in other species of shark not measured in this study. Multiple regression analysis was performed on the residuals from a linear regression of speed against fork length to assess the ability of each of the following factors to replace the factor species in the original model: phylogenetic order, maximum species fork length (Max.FL), trophic level, temperature, habitat, and tail shape. Given that the number of factors varied between models, model fit was evaluated using the Akaike Information Criterion (AIC).

We selected three models that balance high AIC whilst still allowing predictions on a broad range of sharks. We tested the predictive capability of each of these general cruising speed models by applying them to (1) literature-derived estimates of speed from acoustic tagging studies (hereafter referred to as 'tag data') and (2) species with stereo-BRUVS derived estimates of speed with fewer than eight observations (hereafter referred to as 'extraBRUVS'). We first assessed whether the sampling interval of the tag data, i.e. the time in minutes between positions reported by the tags, influenced estimates of speed. Specifically, we predicted speed as a function of length using the general model and then regressed the residuals against sampling interval. Only studies where the sampling interval did not affect speed estimates were used for further analysis. The selected tag data and extraBRUVS data were compared to speeds predicted from our general model. Applicability of the model to these new species was assessed by regressing predicted versus observed values.

To increase the model's power to include a greater range of sharks, the model was also applied to the tag data to extend predictions to sharks with high aspect tail shape. A least squares fitting algorithm was used to calculate the intercept term for sharks in this group, which extended the model to include sharks for which only tag-based cruising speed estimates are currently available. Finally, the predictive capability of each of the models was assessed by comparing the variation explained by each of the generalised models and the best performing model selected as the generalised model. The selected model was then compared to predictions from a length only model.

### Results

Shark swimming speed and fork length estimates were derived from over 250 h of stereo-BRUVS footage. We recorded 611 speed measurements, 98.4% of which were classified as cruising speeds, providing data for 248 individual sharks representing fifteen species. For eight species of sharks (n = 216 individuals), cruising speeds were available for at least eight individuals, and these species formed the basis of the predictive model. These eight species represented three phylogenetic orders (Carcharhiniformes, Heterodontiformes and Orectolobiformes), ranged in fork length from 0.65m to 2.21 m, varied in trophic level from 3.5 to 4.5 and had three different tail morphologies (Table 1).

Fork length had a significant effect on speed (F  $_{(1,214)}$  = 144.9; p = < 0.0001). However, the addition of species increased the explanatory power of the model (F  $_{(7,207)}$  = 19.8; p = < 0.0001) (Figure 1). There was no significant interaction between length and species (F  $_{(7,200)}$  = 0.8; p = 0.62), indicating that all species shared a common slope of 0.44 (± 0.0196) (Table 2). The intercepts for individual species ranged from -0.454 for the slowest species, the necklace carpet shark (*P. variolatum*), to -0.158 for the fastest species, the grey reef shark (*C. amblyrhyncos*) (Table 2). Maximum species fork length (Max.FL), trophic level, habitatand tail shape all explained a significant amount of variation in cruising speeds; however, length and species were the most significant factors.

Table 1 Classification of shark species for which swimming speed measurements were made: phylogenetic order (Order), maximum fork length reported in literature (MaxFL), trophic level (Trophic) (defined as 1+ the mean trophic level of diet), habitat (Habitat) (Froese, 2013) and tails shape (Tail) (2= low heterocercal angle, 3= straight tail, 4= epicaudal lobe; (Thomson and Simanek, 1977). Summarized data for fork lengths (FL), cruising speeds (CS m s-1) and burst speeds (BS m s-1) for each species are based on (n) number of observations.

Order / species	MaxFL (m)	Trophic	Habitat	Tail	n		FL (m)			CS (m s <sup>-1</sup> )		Burst (m s <sup>-1</sup> )
						mean	min	max	mean	min	max	
Carcharhiniformes												
Carcharhinus albimarginatus <sup>1</sup>	3.00	4.2	reef-associated	2	8	1.13	0.74	1.6	0.73	0.5	1.11	-
Carcharhinus amblyrhynchos <sup>1</sup>	2.55	4.1	reef-associated	2	51	0.81	0.5	1.45	0.64	0.35	1.23	3.25
Carcharhinus brevipinna	3.00	4.2	reef-associated	2	5	1.11	0.73	1.62	0.65	0.45	0.91	-
Carcharhinus plumbeus	2.50	4.5	benthopelagic	2	5	1.12	0.84	1.42	0.73	0.43	1.24	-
Carcharhinus obscurus <sup>1</sup>	4.20	4.5	reef-associated	2	11	0.67	0.51	0.99	0.5	0.36	0.75	-
Furgaleus macki <sup>1</sup>	1.60	3.8	demersal	3	9	1.09	0.74	1.58	1.09	0.74	1.58	4.9
Galecerdo cuvier	7.50	4.5	benthopelagic	2	4	1.51	1.29	1.82	0.63	0.44	0.83	-
Hemitriakis falcata	-	4.3	reef-associated	3	3	0.71	0.66	0.74	0.61	0.53	0.71	2.12
Mustelus antarcticus <sup>1</sup>	1.75	4.3	demersal	3	27	0.94	0.81	1.14	0.52	0.29	0.77	1.72
Negaprion acutidens	3.80	4.1	reef-associated	2	6	1.81	1.7	1.93	0.53	0.39	0.63	3.49
Sphyrna lewini	4.30	4.1	pelagic-oceanic	2	5	1.53	0.98	2.14	0.69	0.3	0.84	-
Triaendon obesus <sup>1</sup>	2.13	4.2	reef-associated	2	49	0.86	0.52	1.23	0.5	0.29	0.8	-
Heterodontiformes												
Heterodontus portusjacksoni <sup>1</sup>	1.65	3.5	demersal	4	52	0.58	0.31	0.97	0.34	0.21	0.57	-
Orectolobiformes												
Nebrius ferrugineus	3.20	4.1	reef-associated	2	4	1.58	1.1	2.21	0.32	0.21	0.41	-
Parascyllium variolatum <sup>1</sup>	0.91	3.8	demersal	3	9	0.51	0.35	0.65	0.26	0.23	0.29	0.74

species with more than eight (n>8) individuals recorded and used in analysis



Figure 1 Cruising swimming speeds (m s-1) in free-swimming sharks measured by stereo-BRUVS for eight species; A) Carcharhinus amblyrhynchos (CAM), B) Carcharhinus albimarginatus (CAL), C) Carcharhinus obscurus (COB), D) Furgaleus macki (FM), E) Mustelus antarcticus (MA), F) Triaenodon obesus (TO), G) Heterodontus portusjacksoni (HP) and H) Parascyllium variolatus (PV). Lines represent the linear relationships between fork length (m) and cruise swimming speed (equation presented in table 3). I) Regression lines for all eight species.

Table 2 Species-specific intercepts (INT) estimated by the ANCOVA: log10(CS) = 0.44\*log10(FL) + INT where CS = cruising speed and FL = fork length. Results include 95% prediction intervals for the intercept (PI), mean FL (m). Mean FL was used with the INT to predicted CS (CSpr) as well as to predict lower (CSL) and upper limits (CSU) of CS (m s<sup>-1</sup>). The difference in the CSpred and limits are shown in m s<sup>-1</sup> (Dif) and as a percentage difference (%dif).

Species	INT	PI	mFL	CSpr	CSL	CSU	Dif	%dif
C. amblyrhynchos	-0.158	+/- 0.032	0.81	0.63	0.59	0.68	0.05	7.12
C.s albimarginatus	-0.164	+/- 0.035	1.13	0.72	0.67	0.78	0.06	7.72
C. obscurus	-0.223	+/- 0.027	0.67	0.50	0.47	0.53	0.03	6.07
F. macki	-0.24	+/- 0.042	1.09	0.60	0.54	0.66	0.06	9.24
C. obesus	-0.266	+/- 0.077	0.86	0.51	0.43	0.60	0.08	16.15
M.antarcticus	-0.28	+/- 0.090	0.94	0.51	0.42	0.63	0.10	18.68
H. portusjacksoni	-0.362	+/- 0.173	0.58	0.34	0.23	0.51	0.11	32.83
P. variolatum	-0.454	+/- 0.256	0.51	0.26	0.14	0.47	0.12	44.55

Generalised cruising speed model

The slope of the linear relationship between cruising speed and length from the empirical model (0.44  $\pm$ -0.0196) was not significantly different (p = 0.61) to the slope derived from a theoretical energetics model (0.43), derived by Weihs (1977). In order to develop a more generalised cruising speed model applicable to species not included in the original empirical model, we set the slope of the general model to 0.44, given the empirical and theoretical support for this value. The mean intercept for the eight coreBRUVS species with a fitted slope of 0.44 was -0.266. ANCOVAs performed on the residuals of the length model with a fixed slope found phylogenetic order to account for most additional variation in speed (Table 3), although it explained less variation than the length–species model. The other factors of tail shape, habitat, temperature, trophic level and maximum fork length were all significant, but did not explain as much variation as order (Table 3). Combining all factors (Order + Tail + Max.FL + Temperature + Trophic + Habitat) had the greatest explanatory power but limited the generality of the model. The best predictive models were selected based on the balance between explanatory power and keeping the model sufficiently generalised to allow predications on a range of sharks. Therefore, we looked at the predictive capabilities of a model with the three most influential terms length, order and tail shape.

Table 3 ANCOVA table based on the eight core BRUVs species (n=216) after fixing the length slope at 0.44. The table shows the significance of model terms in comparison to the length model with a set slope (Log10 (Cruising Speed) ~  $0.44 * \log 10$  (Length)). Model terms include; species, phylogenetic order (Order), temperature (Temp), maximum fork length (Max.FL), trophic level (Trophic), Habitat (Hab), and tail form (Tail). Akaike information criterion (AIC) values show the variation explained by length and model terms.

Model	df	SS	MS	F	P- value	AIC
Length	1	3.37	3.37			
+ Species	7	1.25	0.17	24.1	< 0.0001*	-395
+ Order	2	1.08	0.54	50.4	< 0.0001*	-360
+ Temp	1	0.74	0.74	60.8	< 0.0001*	-333
+ Tail	1	0.94	0.94	81.8	< 0.0001*	-348
+ Habitat	1	0.87	0.87	74.7	< 0.0001*	-343
+ Max.FL	1	0.77	0.77	63.2	< 0.0001*	-335
+ Trophic	1	0.60	0.60	47.0	< 0.0001*	-322
+ Tail + Max FL	3	1.04	0.34	31.8	< 0.0001*	-355
+ Tail + Max.FL + Temp + Trophic + Hab	4	1.08	0.27	25.1	< 0.0001*	-391
Length + Order	3	2.29	0.76			
$+ Tail^1$	1	0.10	0.10	10.1	< 0.002*	-369
+ Habitat <sup>1</sup>	1	0.10	0.10	10.1	< 0.002*	-369
+ Max.FL <sup>1</sup>	1	0.10	0.10	10.0	< 0.002*	-369
+ Trophic <sup>1</sup>	1	0.06	0.06	5.5	< 0.02*	-364
+ Tail + Max.FL + Temp + Trophic + Hab <sup>1</sup>	3	0.29	0.10	16.7	< 0.0001*	-394

1 model terms tested against Log10 (Cruising Speed) ~ 0.44 \* log10 (Length) + Order

### Predictive capabilities of the model

Literature-derived cruising speeds were obtained for 101 tagged individuals representing thirteen species (Table 4). Sampling intervals ranged from "continuous" (Parsons and Carlson, 1998) (coded as 0.5 min) to 45 min (Ackerman et al., 2000). The analysis of residuals as a function of sampling interval demonstrated that sampling interval had a significant effect on the size of the residuals (p = 0.04). Sampling intervals greater than 10 min produced residuals that were usually negative and large (Figure 2), suggesting that the general model would overestimate speed for individuals where sampling intervals exceeded this duration. We thus restricted our analysis to data derived from individuals for which sampling intervals were less than or equal to 10 min (n = 61 individuals from 9 species). We compared the observed speeds with predicted speed from three generalised models: (1) length + order, (2) length + tail shape and (3) length + order + tail shape. All models had a significant relationship between predicted and observed speeds obtained from tagged animals (tag data, n = 50 individuals from 6 species) and also the additional animals for which stereo-BRUVS (extraBRUVS, n = 32 individuals from 4 additional species)- derived speeds were obtained but not used to develop the model (Table 5).

Order / Species	n	FL (m)	CS (m s <sup>-1</sup> )	SI (min)	Ref
Carcharhiniformes					
Carcharhinus amblyrhynchos	23	1.16-1.71	0.07-0.97	35 <sup>1</sup>	(McKibben and Nelson, 1986)
Carcharhinus plumbeus	25	0.50-1.11	0.31-0.69	5	(Rechisky and Wetherbee, 2003)
Carcharhinus obscurus	10	0.53-0.78	0.03- 0.36	15	(Huish and Benedict, 1977)
Mustelus antarcticus	1	0.925	0.33	2	(Barnett et al., 2010)
Negaprion brevirostris	11	0.64-1.95	0.22-0.74	1	(Sundström and Gruber, 1998; Sundström et al., 2001; Sundström and Gruber, 2002)
Prionace glauca	2	1.233	0.3-0.6	1	(Klimley et al., 2002)
Rhizoprionodon terraenovae	9	0.54 -0.82	0.28-0.59	9	(Gurshin and Szedlmayer, 2004)
Sphyrna lewini	2	0.31	0.16-0.17	15	(Holland et al., 1993)
Sphyrna tiburo	2	0.76-0.79	0.34-0.36	$0.5^{2}$	(Parsons and Carlson, 1998)
Triakis semifasciata	2	0.91-1.19	0.23- 0.42	45	(Ackerman et al., 2000)
Lamniformes					
Carcharodon carcharias	6	1.41-4.26	0.61- 0.89	4, 1	(Carey et al., 1982; Klimley et al., 2002; Bruce et al., 2006)
Isurus oxyrinchus	6	1.10-1.67	0.49-1.2	1, 15	(Holts and Bedford, 1993; Klimley et al., 2002)
Orectolobiformes					
Rhincodon typus	2	4.44-5.38	0.6-0.75	10	(Gunn et al., 1999)

Table 4 Acoustic tagged data derived from the literature, where CS = cruising speed and FL = fork length. Number of observations for each species (n), sampling interval (SI) and the referenced literature (Ref) are also presented.

<sup>1</sup>Sampling interval is an average of the intervals used in the study <sup>2</sup>Reported as continuous; estimated as every 30 seconds

However, the three models were similar in their predictive power (maximum difference in mean residuals = 0.016m/s). Therefore, we performed further analysis on tail shape as it is more directly related to the physical process of swimming.



Figure 2 The sampling interval time of tagged data had a significant effect on cruising speed (p = 0.04). Speeds have been adjusted to account for length by using the residuals of the length model with a set slope of 0.44 found in our model table 3.

The length + tail model was significantly better at predicting cruising speeds than a length only model (t-test,  $t_{155} = -24.87$ ; p = <0.0001). The residual from the length + tail model (+/- 0.072 m s<sup>-1</sup>) was 76% lower than a length only model (+/- 0.30 m s<sup>-1</sup>). Residuals from the length + tail model were compared between the tag data and the extraBRUVS (ttest,  $t_{48} = -0.45$ ; p = 0.65); the model predicted cruising speed equally well for the two data sets, even though they were measured using different methodologies. The mean residual for tag data sharks was calculated to be 0.084 m s<sup>-1</sup> (+/- 0.016 m s<sup>-1</sup>) and the mean residual for sharks from the extraBRUVS data was calculated to be 0.068 m s<sup>-1</sup> (+/- 0.031 m s<sup>-1</sup>). The residuals from both the extraBRUVS and tag data were positive relative to the coreBRUVS from which the generalised model was constructed (t-test,  $t_{118} = -4.6$ ; p = < 0.001).

In order to extend the length + tail model, the intercept for sharks with a tail shape 1, which is characterised by a high aspect ratio, was calculated from tag data. We fitted a length only model to tag data from 17 individuals from three species with a high aspect tail shape (tail shape 1) (Table 5). From the residuals of this regression the intercept for sharks in with this tail shape was calculated to be -0.267.

Table 5 ANOVA results comparing the observed and predicted cruising speeds from the three models 1) length tail 2) length—order 3) length, order—tail. Intercepts (INT) estimated by the ANCOVA: log10(CS)=0.44\*log10(FL) + INT where CS = cruising speed and FL = fork length. The intercept from animals with tail shape 1 which is based on tag data. We have also included the mean residuals of each model and the results of t-test comparing the residuals of the three models.

Model (df)	INT	F	P-value	Mean residuals
<sup>#1, #2</sup> Length + Tail (1, 81)		13.57	0.0004*	0.077 (+/- 0.141)
Tail 1 (high aspect ratio) $^*$	-0.267			
Tail 2 (low heterocercal angle)	-0.211			
Tail 3 (straight tail)	-0.309			
Tail 4 (epicaudal lobe)	-0.365			
$^{\#1,\ \#3}$ Length + Order (1, 83)		30.63	0.0001*	0.061 (+/- 0.127)
Carcharhiniformes	-0.224			
Heterodontiformes	-0.365			
Orectolobiformes	-0.453			
$^{#2, #3}$ Length + Tail + Order (1, 81)		24.65	0.0001*	0.072 (+/-0.131)
Tail 2 (low heterocercal angle)	-0.211			
Tail 3 (straight tail)	-0.271			
Tail 4 (epicaudal lobe)	-0.365			
Orectolobiformes	-0.183			

<sup>#1</sup> (n=161, t=-0.80, p=0.42), <sup>#2</sup> (n=161, t=-0.27, p=0.79), <sup>#3</sup> (n=163, t=0.55, p=0.58) *\*intercept based on tag data* 

### Discussion

Factors affecting cruising speed of sharks

Our study found the slope of the relationship between speed and body size was constant across all species, whereas the offset (or intercept) was species-specific. The consistency of this slope with that of Weihs' (1977) theoretical model suggests a strong energetic influence on swimming speed. Indeed, Weihs (1977) identified energetics as a major influence on the logarithmic relationship between speed and length in aquatic animals. His model stated that an animal will swim at the speed that requires the least amount of energy and defined optimal cruising speed as the speed at which total metabolic rate is approximately double the metabolic rate of the individual at rest. Weihs (1977) used drag coefficients based on trout species to derive optimal cruising speed (CS, in m s<sup>-1</sup>) as a function of length (L, in m) where

$$CS = L^{0.43} + 0.503 \tag{1}$$

Based on our analysis of eight species ranging in size from 0.31m to 2.21m (Max.FL 0.9m to 7.5m) under natural conditions, we derived the general equation:

$$CS = L^{0.44} + 10^{species}$$
 (2)

where the species-specific intercept (*species*) for each of the eight species is presented in Table 2.

Weihs' (1977) theoretical model is consistent with empirical observations of cruising speed in a number of aquatic species, including sockeye salmon (*Oncorhylnchus nerka*) (Ware, 1978), white crappie (*Pomoxis annularis*) (Parsons and Sylvester Jr, 1992), bonnethead sharks (*Sphyrna tiburo*) (Parsons, 1990) and blacknose sharks (*Carcharhinus acronotus*) (Carlson et al., 1999). The cruising speed measurements of the bonnethead and blacknose sharks were made from sharks swimming in flumes, which allowed simultaneous measurements of metabolic rate and cruising speed. Both speed and metabolic rate increased with body length (Carlson et al., 1999) and differed between species (Scharold et al., 1988; Scharold and Gruber, 1991). The species effect and relationship between length and cruising speed may reflect difference in metabolic rate. Metabolic rates of larger individuals and faster cruising species may be higher than those with slower cruising speeds.

The species model best explains the cruising speed of sharks because a number of factors affect movement and thus energetic expenditure (Shirai, 1996). In addition to body size (Ware, 1978; Parsons, 1990), morphological traits such as body shape (Walker and Westneat, 2002) and fin placement (Standen and Lauder, 2005) can influence cruising speed by improving propulsion, reducing drag (Walker and Westneat, 2002) and maintaining balance (Standen and Lauder, 2005). Cruising speed can also be effected by physiological traits such as metabolism (Parsons, 1990), in particular the efficiency of red muscle fibres (Rome et al., 1984). Red muscle fibres are used at low speeds (i.e. aerobic activities) and their maximum power output limits cruising speed (Johnson et al., 1994; Bernal et al., 2001; Syme and Shadwick, 2002; Bernal et al., 2003). For example, the increased temperatures associated with endothermy require less activation of muscle fibres making for more energy efficient swimming (Dickson and Graham, 2004).

### Predicting swimming speeds

Our study presents one of the largest data sets on cruising speeds for a range of shark species and sizes, in their natural environment. We have built on this data set to develop a second, more general model to predict cruising speeds of sharks for which empirical observations are currently unavailable. The general model aims to replaces the species term with tail shape. The length + tail shape model developed from core-BRUVS data was tested on new species and was found to generate predictions of cruising speed with considerable accuracy. The length + tail model is significantly better at predicting the tag and extraBRUVS data and explained a further 76% of the variation in cruising speed compared to a length only model (residuals:  $\pm 0.072 \text{ m s}^{-1} \text{ Vs} \pm 0.300 \text{ m s}^{-1}$ ). Although, it must be stressed that a model incorporating species would, of course, be more accurate. This is currently the most accurate model for predicating the cruising speeds of shark species where direct measurements are unavailable.

The length + tail shape model produced similar residuals for species represented by either the extraBRUVS or tag data. This result suggests that the stereo-BRUVS method and tagging method

produced similar speed measurements. The mean residuals from both the extraBRUVS and tag data were positive, suggesting the model may have a tendency to overestimate cruising speeds. However, this difference equates to an overestimation of 0.085 m s<sup>-1</sup>, which is small in relation to how fast the animals are moving (0.21 to 1.58 m s<sup>-1</sup>) and may reflect the large amount of variation in individual cruising speed resulting from uncontrolled environmental factors, such as habitat (Vásquez et al., 2002), water temperature and currents (Salinger and Anderson, 2006). It is to be expected that the coreBRUVS data have a mean residual close to zero as these measurements were used to build the model. However, the difference between the coreBRUVS and extraBRUVS data highlights the need for large sample sizes to accurately identify trends in speed data.

The success of the length + tail shape model in accurately predicting cruising speeds may be attributed to its ability to cover a range of ecological and morphological characteristics. The ability of all factors (trophic level, habitat, tail shape and temperature) to explain cruising speed highlights the fact that cruising speed is probably dependent on a number of ecology and morphological factors. Tail shape is correlated to a number of ecological and morphological factors such as habitat, order and overall body shape. For example, most lamnid sharks have high aspect ratio tail shape, conical head (Thomson and Simanek, 1977) and are highly active pelagic predators (Northmore and Dvorak, 1979); their relatively quick cruising speed potentially reflect their feeding ecology in that they track fast, elusive prey (Speakman, 1986; Kramer and McLaughlin, 2001; Zeil et al., 2008). In contrast, Heterodontiformes are characterised by a tail with a marked epicaudal lobe and the absence of an anal fin (Thomson and Simanek, 1977). All Heterodontiformes are benthic and feed on smaller, less mobile prey, which do not require great speed to track or capture (Speakman, 1986; Kramer and McLaughlin, 2001; Zeil et al., 2008).

The length + tail shape model, the length + order model and the length + order + tail shape model predicted cruising speed with similar accuracy. However, we suggest that length + tail shape would make the best general model because the order model is also more likely to produce inaccurate estimates for the more atypical sharks within an order. For example, the Lamniformes are a diverse group that includes unusual deep sea species such as the megamouth (*Megachasma pelagios*) and goblin (*Mitsukurina owstoni*) sharks (Froese, 2013). A model built on white (*Carcharodon carcharias*) and short fin mako (*Isurus oxyrinchus*) sharks is less likely to reflect these sharks.

In the absence of species-specific information, tail shape is a suitable alternative to predict cruising speed. Care should also be taken with sharks with the tail shape 1 (high aspect ratio tail) as the model for these groups were based only on data from acoustically tagged sharks. However, there was a large (n = 18) dataset and—considering the similarities between speeds derived from the two methodologies for other shark species—it is unlikely that the estimates derived from tag data and stereo-BRUVS will differ substantively.

#### The use of stereo-BRUVS and acoustic tags for measuring cruising speed

Stereo-BRUVS are a useful method for measuring the cruising speed of sharks. The relatively low cost and widespread use of stereo-BRUVS means that large multispecies data sets can be obtained. With the development of mid-water camera systems (Letessier et al., 2013), footage of pelagic species is also becoming increasingly available such that swimming speeds for relatively elusive open-ocean species can be determined. Stereo-BRUVS also allow behaviours such as burst and cruising speed to be isolated. For many species of sharks, this paper provides the first measurements of potential burst speeds. Finally, stereo-BRUVS allow swimming speeds to be measured in the sharks' natural environment in a largely non-invasive manner.

The stereo-BRUVS methodology does introduce the possibility that the bait used to lure sharks into the frame may alter the behaviour, and therefore cruising speed (Maioli, 1988; Dieringer et al., 1992). Although bait was present during sampling, speeds were not measured while the sharks were feeding or interacting with the bait. Moreover, the similarities seen between cruising speed estimates from the stereo-BRUVS data the tag data and Weih's (1977) model suggests that bait has little effect on the overall cruising speed of the sharks. Although it appears that the bait had no great effect on the cruising speed of sharks, comparing the cruising speed of sharks measured using stereo-BRUVS with and without bait present would determine the influence of the bait on cruising speed, but such a study would be hampered by the reduced likelihood of observing sufficient numbers of sharks in the baitless trials.

Speeds derived from acoustic telemetry were comparable to those predicted from the model based on stereo-BRUVS, although the sampling interval of the tag data did affect estimates of cruising speed. Predicted cruising speeds based on sampling intervals greater than 10 min were generally slower than those estimated at sampling intervals of less than 10 min. This bias may reflect deviations from straight-line (point-to-point) navigation by the sharks over longer sampling intervals and result in an apparent decrease in swimming speed because, in fact, animals are covering more ground. Measuring speed with acoustic (or satellite) tags may also be subject to other inaccuracies due to the device affecting locomotion (e.g. by increasing drag) (Dickson and Graham, 2004; Grusha and Patterson, 2005; Hammerschlag et al., 2011) and behavioural responses to externally attached tags (Davidson et al., 1999).

Tagging data have the benefit of recording speed over much larger distances and under low visibility or dim lighting conditions (Hammerschlag et al., 2011), and improvements to tag technology, such as the incorporation of accelerometers, are providing the potential for increasingly accurate measurements of swimming speed. Accelerometers are also advancing the ability of scientists to relate swimming speed and body movement with specific behaviours (Whitney et al., 2010; Gleiss et al., 2011; Nakamura et al., 2011; Whitney et al., 2012). Studies using accelerometers rarely isolate cruising speed but present mean swimming speed, which can include gliding and burst swimming (Nakamura et al., 2011).

Isolating cruising speed from these data would make a useful contribution to assess the model developed in this study. As data on swimming speed increase, it will be possible to investigate the patterns observed in this study across a greater range of shark species. In order to extend the range of sharks in which cruising speed has been investigated, stereo-BRUVS may be designed to target specific habitats, i.e. pelagic environments using midwater stereo-BRUVS (Letessier et al., 2013).

## Conclusion

Cruising speeds in sharks are species-specific. However, in order to estimate cruising speeds of sharks for which no measurements currently exist, predictions can be made based on a general model taking into account fork length and tail shape. It is anticipated that our empirical model will be of use in a range of ecological research. The model may be used in conjunction with other methodologies to better understand predator-prey interactions, sensory perception and habitat use in marine ecosystems. For example, combining the model estimates of cruising speed with arrival times from baited remote underwater video data may provide insights into home range size, which may help to inform decisions about the size and location of marine protected areas designed for shark conservation. Accurate predictions of cruising speed may also allow fine- scale movements to be assessed from tag data by predicting the probability of straight line swimming. Of particular interest to our research is the degree to which interspecific differences in swimming speed are reflected in functional adaptations of sharks' sensory systems to process new sensory information, which in turn impacts upon critical behaviours such as prey detection and predator avoidance. Swimming speed is a fundamental attribute of aquatic animals, influenced by their sensory capabilities, their behaviour and their interaction with their environment. General models quantifying swimming speed in sharks have the potential to provide insight into their neurobiology and ecology and may contribute to the conservation of this diverse and ecologically important taxa.

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