

Morphological predictors of swimming speed: a case study of pre-settlement juvenile coral reef fishes

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Summary

The swimming abilities of fishes are of vital importance to their ecology, and studies on fish swimming have been the focus of research for over a century. Here we explore the relationship between swimming ability and external body morphology, using data on U_{crit} swimming speeds of 100 species of pre-settlement juvenile coral reef fishes (at the transition between the larval and adult habitats), comprising 26 different families from 5 orders. The taxonomic diversity of this methodologically consistent dataset provides a unique opportunity to examine the relationship between form and function in fish swimming across a broad taxonomic range. Overall, we found that a predictive model incorporating total length (TL), the square of caudal peduncle depth factor ($CPDF^2$) and aspect ratio (AR) can be used to accurately predict swimming performance of a wide range of fish families, and was able to explain 69% of the variability in swimming performance of these pre-settlement juvenile fishes. The model was also

able to successfully predict the swimming speed of an out-group salmonid species (*Oncorhynchus mykiss*). There was no evidence that the model fit differed among taxonomic groups, despite the inclusion of five different orders of fishes, suggesting that body morphology sufficiently explains the bulk of differences in swimming performance. Furthermore, the model appears to work equally well for fishes from the Great Barrier Reef and the Caribbean, and for families with different adult habitat associations and swimming modes. It remains to be determined how well the model predicts the swimming abilities of temperate species as well as adults of these same species. This model provides an invaluable means of predicting swimming abilities of pre-settlement juvenile fishes that are unable to be reared in the laboratory, do not perform well in swimming flumes or are unable to be captured live in the field.

Key words: swimming, morphology, dispersal, behaviour, U_{crit} .

Introduction

Swimming performance affects every aspect of a fish's ecology, from the acquisition of food and avoidance of predators (Videler, 1993), to successful migration (Fisher and Bellwood, 2003), ultimately influencing Darwinian fitness (Plaut, 2001; Reidy et al., 2000). Consequently, swimming performance has long been a topic of considerable interest to ecologists. Perhaps the earliest published measurements of fish swimming speed are from 1893, where Regnard measured the maximum swimming speed of small fishes in an annular, rotating channel (Regnard, 1893). Since then, many researchers have measured the swimming performance of fishes (Bainbridge, 1958; Beamish, 1970; Brett, 1964; Fry and Hart, 1948; Magnan, 1930), and such studies have been viewed as a prelude to, or put in the context of, the functional design, physiology and ecology of fish swimming (Blake, 2004).

While much work has been done measuring swimming performance of fishes in the last century, data have been biased toward particular taxa or groups, and are most abundant for temperate fishes. Excellent data are available on the swimming performance of the cod-like fishes (Claireaux et al., 1995; Lough and Potter, 1993; Reidy et al., 2000), as well as the

Salmonidae such as salmon and trout (e.g. Brett, 1964; Greenland and Thomas, 1972; Paulik and DeLacy, 1957; Small and Randall, 1989; Taylor and McPhail, 1985) and the Scombridae such as tunas, mackerel (e.g. Blake et al., 2005; Dewar and Graham, 1994; Korsmeyer et al., 1996). For these groups, differences in overall body shape, along with other physiological differences such as muscle type, can account for differences in their swimming performance, with faster swimming taxa showing a generally more streamlined body form (Wardle, 1977).

Tropical ecosystems are characteristically much more diverse than their temperate counterparts, and coral reefs in particular often house thousands of fish species that include both perciform families, and less derived teleost orders (Sale, 1991). As such, coral reef fish fauna represent the most diverse group of fishes in the world (Sale, 1991). Examination of the swimming abilities of coral reef fish species is comparatively recent, with an explosion of research occurring over the last decade. Much of this research has focused on the late-larval/early-juvenile stages of coral reef associated fishes (Fisher and Bellwood, 2003; Fisher et al., 2000; Fisher et al., 2005; Fisher and Wilson, 2004; Hogan et al., 2007; Leis and

Carson-Ewart, 1997; Stobutzki, 1997; Stobutzki and Bellwood, 1994), and the potential for active swimming behaviour to be used to modify dispersal distances (Fisher, 2005; Stobutzki and Bellwood, 1997). Several studies have also shown the importance of swimming performance in structuring adult distributions on coral reefs (see Fulton et al., 2001; Fulton et al., 2005; Wainwright et al., 2002).

The swimming performance of different species and taxonomic groups of fishes within the coral reef ecosystem are known to vary widely, even when fishes are examined at the same developmental stage. For example, the maximum swimming speeds of pre-settlement juvenile coral reef fishes range from 5 to 100 cm s⁻¹ (Fisher et al., 2005). Although hydrodynamic theory and bio-energetics indicate that the optimal swimming speeds of fish should be dependent on their body length (Ware, 1978), variation in swimming performance among taxonomic groups are often only explained weakly by total length (Bainbridge, 1960; Blake, 2004; Fisher et al., 2005; Stobutzki and Bellwood, 1997), and it is clear that other morphological and physiological factors must be important.

There are numerous aspects of the body morphology of fishes that have been identified as important in defining swimming performance, including aspect ratio (Sambily, 1990), fineness ratio (Bainbridge, 1960), caudal peduncle depth factor (Webb and Weihs, 1986) and propulsive area (Fisher et al., 2000). However, with the exception of some work on pectoral fin locomotion (Wainwright et al., 2002) and a brief correlative study (Fisher et al., 2005), no attempt has been made to use the diverse range of reef fish families available to examine the extent to which swimming capabilities correlate with, and can be predicted by, external body morphology. The large amount of data available on the swimming speeds of pre-settlement juvenile coral reef fishes provides an excellent opportunity to examine the relationship between form and function in fish swimming, and to determine how this varies among taxonomic groups, different swimming modes, among different coral reef regions, and with habitat. Although perhaps not as diverse as their adult counterparts, these pre-settlement juvenile fishes still represent a wide range of body forms and swimming modes, allowing an examination of factors influencing swimming performance across a broad range of body types.

Importantly, it is not possible to measure the swimming performance of many fish species because such data are difficult and time consuming to collect, requiring specialized equipment. Additionally, some taxa can only be caught in the field using methods that injure or kill individuals (such as towed nets), or are caught so rarely that good swimming data are unlikely to ever be collected. If morphological characteristics can be reliably used to predict fish swimming performance, this could provide an invaluable means of estimating the abilities of unstudied taxa, and allow the incorporation of essential swimming parameters into ecological studies.

Despite its potential utility, no studies have developed a general model for predicting the swimming ability of coral reef fishes. Here we explore the relationship between swimming ability and external body morphology across a broad range of coral reef fish taxa, using existing data on U_{crit} swimming speeds of early-juvenile-stage coral reef fishes. U_{crit} speeds represent the maximum sustainable speeds of fishes, and at

these speeds fish predominantly utilize a body-caudal fin swimming mode. The best model for estimating swimming performance is determined, and the fit of the model is examined in relation to a variety of ecological characteristics of each family, including its taxonomic order, preferred swimming mode at cruising speed, adult habitat (pelagic/demersal) and geographic region.

Materials and methods

Swimming data

U_{crit} swimming speed data were obtained from published sources (Fisher, 2005; Fisher et al., 2005; Hogan et al., 2007), representing 100 species of fishes from 26 different families. These data were collected from fish in the Great Barrier Reef in the Pacific and from both the Turks and Caicos Islands and Turneffe Atoll off Belize in the Atlantic (Caribbean). The experimental protocol adopted at all locations was identical, using similarly designed and calibrated swimming flumes. All swimming experiments were conducted at ambient seawater temperatures, which ranged between 28 and 30°C at both locations. The majority of larvae were swum within 6 h of capture and all were swum within 12 h, using the swimming flumes described by Stobutzki and Bellwood and others identical in design to them (Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997). U_{crit} was measured by placing larvae in the swimming flume and increasing the speed incrementally over time until the larva could no longer maintain position for the full time interval, and then calculated following Brett (Brett, 1964) as:

$$U_{crit} = U + (t/t_i \times U_i),$$

where U is the penultimate speed expressed in cm s⁻¹, U_i is the velocity increment expressed in cm s⁻¹, t is the time swum in the final velocity increment and t_i is the set time interval for each velocity increment. Although speed and time increments varied between studies (see Fisher et al., 2005), the most common values used were a speed increment of 3 body lengths (BL) s⁻¹ and a time interval of 2 min. There is no evidence that variation in either speed or time interval influences U_{crit} speed estimates over the range used (see Fisher et al., 2005; Hogan et al., 2007).

Samples were obtained for these studies predominantly using light traps, although some were also captured using crest nets. Both light traps and crest nets capture coral reef fishes at the end of their pelagic phase, and most specimens swum are best described as pre-settlement juveniles. For most families, this stage represents the transition from the pelagic to the benthic habitat, and most families have largely developed into the adult body form. The size of the different families of fishes at this developmental stage varied widely, from an average of 6.37 mm for the Ogocephalidae up to 37.27 mm for the Holocentridae. The average size across all families was 19.30 mm. The families captured were generally reef associated (occur in the vicinity of reefs), however several are distinctly more 'pelagic' (including the Sphyrnidae, Carangidae, Clupeidae and Nomeidae). Predominantly demersal families consisted of archetypical reef fish families, closely associated with coral reef habitat see (Bellwood, 1996), as well as more generalist families associated with a range of benthic habitats. The families swum also

represented a range of swimming modes, including pectoral fin, pectoral-caudal fin, caudal fin and dorso-ventral fin locomotors. In all, families from five different orders of fishes are represented, including six sub-orders of the highly diverse Perciformes.

Morphological measurements

Data for morphological measurements were obtained from digital images of the fish taken immediately after the swimming trials. These images were obtained from the same individuals that comprised the swimming data used in analysis (Fisher et al., 2005; Hogan et al., 2007). Variables used for analysis are shown and defined in Fig. 1. All measurements were taken to the nearest 0.1 mm, using the image analysis software, ImageTool (UTHSCSA 2002). Body width (*BW*, measured at

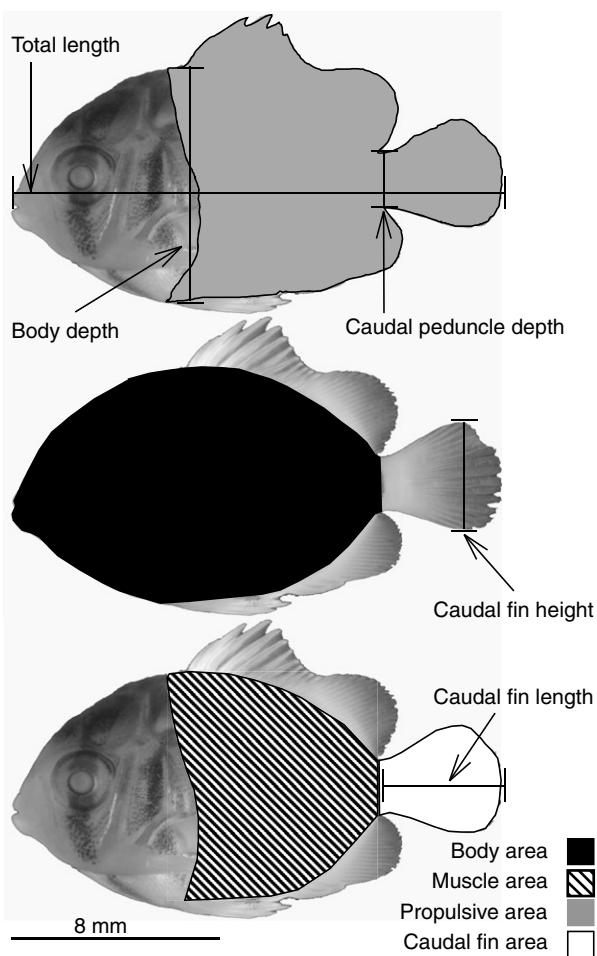


Fig. 1. Morphological measurements of pre-settlement juveniles, including: total length (*TL*; outer edge of the caudal fin to the tip of the upper jaw), caudal fin length (*CFL*; tip of the caudal fin to the caudal peduncle), body depth (*BD*; height at the deepest region), body area (*BA*; area in lateral view excluding the fins), propulsive area (*PA*; area including the fins (naturally fully extended) but excluding the head and gut region where they are inflexible or lack overlaying muscle and can not be used for propulsion), muscle area (*MA*; area excluding the fins and the head and gut region), caudal fin depth (*CFD*; widest section when fully extended), caudal peduncle depth (*CPD*; height at the narrowest point between the caudal fin and the fish's body) and caudal fin area (*CFA*; area with the caudal fins naturally fully extended).

the widest region, usually the head) was also measured to the nearest 0.1 mm using vernier calipers.

Developing the morphological model

The shape of different families of pre-settlement juveniles was characterised using several morphological variables and five morphometric ratios that were identified from the literature as being potentially important for describing swimming abilities in fishes (Table 1). Because all of the raw morphological variables were highly correlated with length, rather than using them directly, they were used to calculate various morphometric ratios obtained from the literature, which were known to be important in swimming. Although residual analysis provides an effective and alternative means of removing co-variance with length in morphometric studies, this approach was not adopted here because of the potential confounding effect between size and the magnitude of the residuals: as size increases the magnitude of the residual values increase, even when the actual body shape remains the same. Initial analysis indicated that models incorporating residual values were highly unstable outside the observed range of data.

Morphometric ratios considered in the analysis included: muscle ratio (*MR*, the ratio of the muscle area of the fish relative to the total body area), propulsive ratio (*PR*, the ratio of the propulsive area to total body area), fineness ratio [*FR*, length divided by the average between the body width and body depth (Bainbridge, 1960)], aspect ratio [*AR*, caudal fin height divided by the square root of caudal fin area (Sambily, 1990)] and caudal peduncle depth factor [*CPDF*, caudal peduncle depth divided by body depth (Webb and Weihs, 1986)] (Table 1B). Initially a correlation matrix and a PCA were used to examine the relationships among the different ratios, and the spread of the different families among the different body shapes.

A best-subsets multiple regression approach was used to develop a morphological model that could be used to predict

Table 1. Morphological variables and morphometric ratios used in the best-subsets multiple regression analyses for predicting U_{crit}

Variable	Calculation
Morphological variables	
Total length (<i>TL</i>)	MD
Body depth (<i>BD</i>)	MD
Body width (<i>BW</i>)	MD
Body area (<i>BA</i>)	MD
Propulsive area (<i>PA</i>)	MD
Muscle area (<i>MA</i>)	MD
Caudal peduncle depth (<i>CPD</i>)	MD
Caudal fin depth (<i>CFD</i>)	MD
Caudal fin area (<i>CFA</i>)	MD
Morphometric ratios	
Muscle ratio (<i>MR</i>)	MA/BA
Propulsive ratio (<i>PR</i>)	PA/BA
Fineness ratio (<i>FR</i>) ^a	$TL/[(BW+BD)/2]$
Aspect ratio (<i>AR</i>) ^b	$CFD/CFA^{1/2}$
Caudal peduncle depth factor (<i>CPDF</i>) ^c	CPD/BD
^a (Bainbridge, 1960); ^b (Sambily, 1990); ^c (Webb and Weihs, 1986). MD, measured directly; see Fig. 1.	

U_{crit} swimming speeds across families. A forward stepwise approach was not adopted because of moderately high levels of multi-collinearity in the data, which can cause problems when testing for the significance (and therefore inclusion/exclusion) of predictor variables (Graham, 2003). The regsubsets function in the leaps package contributed to R [written by Thomas Lumley using Fortran code by Alan Miller (see Miller, 1990)] was used for best sub-sets regression analyses. Although generally weak, at the family level U_{crit} is positively related to size for pre-settlement juvenile coral reef fishes (Fisher et al., 2005). To account for the overall influence of size on swimming performance, total length was forced as the first variable in the best-subsets multiple regressions. Because shape is not necessarily linearly related to swimming speed, the squares of all variables were also entered, allowing the best-subsets regression to fit both linear or quadratic functions to obtain the best-overall model for predicting swimming performance. Including the scope for quadratic functions allows for the likely possibility that shape measurements and/or morphometric ratios will have an optimal-response relationship with swimming speed, where swimming speed increases up to some optimal value, after which point there is no longer an increase (and perhaps even a decrease) in swimming performance.

Best-fit predictive equations were obtained for sequentially greater numbers of variables included in the model. Observed values of U_{crit} were plotted against predicted values and R^2 (both regular and adjusted) (Zar, 1999) were calculated to evaluate the performance of the predictive relationships. We used a second-order Akaike information criterion for small sample sizes (AICc) (Burnham and Anderson, 2002) to select the best model that contained the least number of predictor variables, evaluating the relative fit of each model using Akaike weights (ω_i) (Burnham and Anderson, 2002).

All regressions were performed on the means for each species using the statistical programming language R. The mean for each species was weighted according to their percentage contribution to each family (such that the sum of the weights of all species in a family were equal to 1), to ensure that all families were equally represented in the analysis (so the analysis would not be biased towards the specious families).

Evaluating the model

A bootstrap analysis was carried out to examine the stability of the size of the best selected model as well as to determine the relative usefulness of the different morphometric ratios for predicting swimming ability. The full analysis was carried out using 10 000 bootstrap iterations, each based on a randomly selected set of families (with replacement). From these, the mean Akaike weight and the proportion of iterations in which each variable was included in the best-fit model of each model size was calculated.

An independent test of the model was carried out by using the best models to predict swimming ability of steelhead trout (*Oncorhynchus mykiss*, total length=18.4 cm), and comparing the predicted value to empirical data obtained from specimens swum at the National Marine Fisheries Service Laboratory in Santa Cruz, CA, USA. The average size of the individual steelhead was 179 mm (fork length, *FL*). (Data are courtesy of A. Ammann, unpublished.)

An ANOVA based on the residuals from the best-fit model was used to examine how well a purely morphological model was able to predict swimming speed across families caught in different oceans (Caribbean and Great Barrier Reef). A similar analysis was also carried out for families from different orders of fishes, different swimming modes and different adult habitat characteristics (demersal or pelagic).

Results

Body shape and the morphological measurements

A large range of body morphologies were represented by the 26 different families, ranging from those with very wide bodies, small amounts of body area dedicated to swimming, small values of fineness ratio and caudal peduncle depth factor and a low aspect ratio (such as the Ostraciidae), to those with the opposite characteristics (such as the Holocentridae and Siganidae) (Fig. 2). Many of the morphological parameters were either strongly or moderately correlated, and a large amount of variance was explained by the first axis of the principle components analysis (61.2%), which largely represented strong positive associations between *FR*, *CPDF* and the two measurements of the proportion of the body area dedicated to swimming (*PR* and *MR*; Fig. 2). The second axis also explained considerable variance (24.5%), and represented high positive associations between *CPDF* and *FR*, which were in turn negatively related to *AR* (Fig. 2). In total, 88% of the variability in body shape among families could be represented by only two axes.

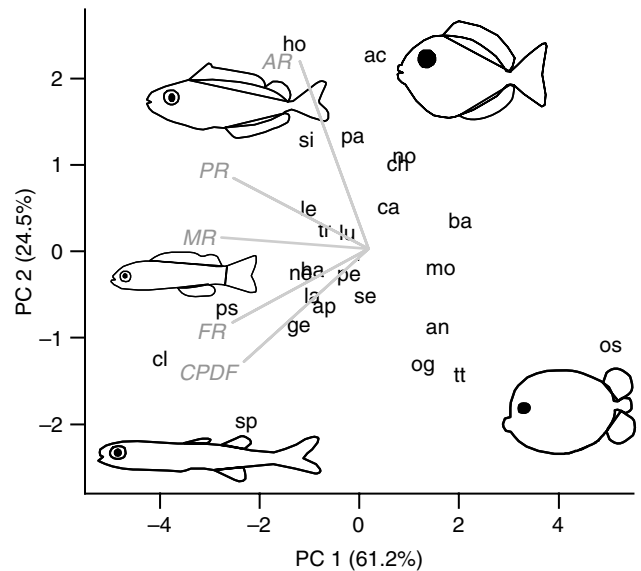


Fig. 2. Principal components (PC) analysis of five morphometric ratios across 26 families of pre-settlement juvenile fishes. The solid grey lines indicate the relative eigenvectors for each variable. The variables (also in grey) are defined in Table 1. Families: ac, Acanthuridae; ap, Apogonidae; an, Antennariidae; ba, Balistidae; ca, Carangidae; ch, Cheatodontidae; cl, Clupeidae; ge, Gerridae; ha, Haemulidae; ho, Holocentridae; la, Labridae; le, Lethrinidae; lu, Lutjanidae; mo, Monacanthidae; ne, Nemipteridae; no, Nomeidae; og, Ogcocephalidae; os, Ostraciidae; pa, Pomacanthidae; pe, Pomacentridae; ps, Pseudochromidae; se, Serranidae; si, Siganidae; sp, Sphyraenidae; tt, Tetraodontidae; tr, Terapontidae.

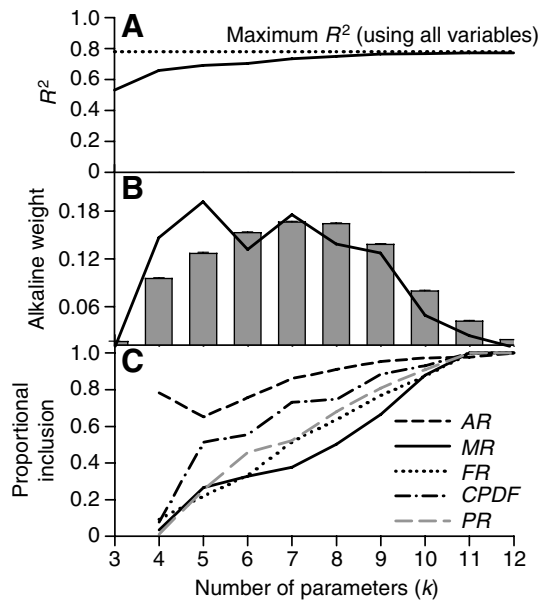


Fig. 3. The change in R^2 (A) and Akaike weights, ω_i (B, solid line) and the frequency different variables were included in the best-subsets model (for 1000 bootstrap iterations) as the number of parameters (k) included in the model is increased (C). The error and intercept terms make up the first two parameters of the model, and total length (TL) was forced as the first variable included (in order to account for size). The bars in B show the mean Akaike weight for each model size for 10 000 random iterations ± 1 s.e.m.

The morphological model

As variables are added to the morphological model, the proportion of variance explained increases from $R^2=0.56$ up to a maximum of about 78%, when all six variables (12 parameters) were included (Fig. 3A). The Akaike weights (ω_i) identify the 5-parameter model (which includes three variables) as the most likely best model (Fig. 3B). As the number of parameters increases beyond 5, ω_i dips and then drops off steadily, despite a gradual increase in R^2 (Fig. 3).

According to the best sub-sets regression on the raw data, the best 3-variable model included TL , AR and $CPDF^2$ (five parameters, including the intercept and error terms; Table 2).

Evaluating the model

Although the raw data indicated that the 5-parameter model was probably the best, the selection of this sized model was relatively unstable based on the bootstrap analysis, which indicated that, on average, the 7-parameter model had a higher average Akaike weighting. Despite some instability in selection of the best model size, the bootstrap analysis showed consistency in the variables included in the best model. For smaller sized models, AR and $CPDF$ were almost always included (Fig. 3C), and the bootstrap did confirm that a model including TL , AR and $CPDF^2$ was most frequently chosen as the best 3-variable model (Table 2). As the number of parameters increases, either PR or FR were included in the best model, with similar frequency (Fig. 3C). The best 7-parameter model included four variables: TL , AR , $CPDF$ and PR , with linear and squared terms for PR , and was consistent with that obtained using the raw data (Table 2).

Although the bootstrap analysis indicated that a 7-parameter model may be preferable, an independent test of the model using data for Californian steelhead trout (*Oncorhynchus mykiss*, mean $FL=179$ mm, mean $U_{crit}=82.3\pm 2.17$ cm s^{-1}) indicated that the larger sized models were unstable when used to predict swimming speeds for fishes outside the observed data range (Table 2). While the 3-variable model was able to reliably predict the swimming speeds of this species, the larger model substantially underestimated their swimming speed (Table 2). For this reason, the 3-variable model was used for further analysis.

Overall, the best-fit model fitted equally well to the different reef fish families, and was able to explain 69% of the variation in swimming speeds among species from both regions (Fig. 4). The fastest swimming species belonged to the Holocentridae, followed by the Carangidae, Siganidae and Acanthuridae (Fig. 4). The slowest swimmers were the Ogcocephalidae and Antennariidae (Fig. 4).

An analysis of the residuals from the best model indicated that there was no significant difference in the fit of the model between fishes from the Caribbean and those from the Great Barrier Reef (ANOVA, $F_{1,36}=1.7$, $P=0.20$), suggesting that the model works equally well across both regions (Fig. 5). There was also no difference in the residual fits across families with different adult habitat (benthic/pelagic) (ANOVA, $F_{1,24}=3.15$, $P=0.10$), from different taxonomic orders (ANOVA, $F_{4,21}=1.70$,

Table 2. Best-subsets multiple regression equations for predicting U_{crit} (cm s^{-1}) using the morphological ratios described in Table 1

Best-fit model	N	k	R^2	Out-group
(A) Raw dataset				
$17.9\log(TL)+42.9AR-30.8CPDF^2-66.1$	3	5	0.69	81.8
$18.2\log(TL)+32.0AR-53.5CPDF^2-313PR+202PR^2+62.4$	4	7	0.73	75.7
(B) Bootstrap analysis				
$18.3\log(TL)+41.5AR-26.7CPDF^2-66.2$	3	5	0.69	82.8
$17.6\log(TL)+34.0AR+44.6CPDF^2-287PR+186PR^2+50.7$	4	7	0.73	75.4

Shown are the best-fit models obtained using (A) the raw dataset and (B) the bootstrap analysis. N refers to the number of unique variables included in the model, and k refers to the number of total parameters (includes the intercept and error term). R^2 values are for the fit of each model to the raw data. Out-group values are the U_{crit} values (cm s^{-1}) for steelhead trout (*Oncorhynchus mykiss*, mean fork length=179 mm) predicted by each model. The measured empirical U_{crit} speed for the out-group was 82.3 ± 2.17 cm s^{-1} .

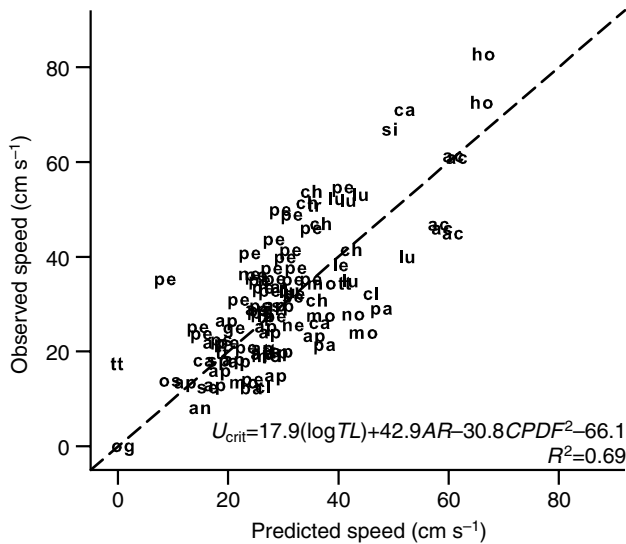


Fig. 4. Selected best-fit predictive models for U_{crit} swimming speeds for the 3-variable model obtained using the raw data (Table 2). The broken line shows the expected 1:1 relationship. Family abbreviations as in Fig. 2.

$P=0.19$), or those families with different swimming modes (ANOVA, $F_{4,21}=0.63$, $P=0.65$) (Fig. 5).

Discussion

Here we demonstrate the utility of using morphological variables to predict U_{crit} swimming speeds in coral reef fishes. A predictive model incorporating total length (TL), the square of caudal peduncle depth factor ($CPDF^2$) and aspect ratio (AR) can be used to predict swimming performance of a wide range of fish families, from five different orders. The inclusion of these parameters in a model for predicting maximum sustained swimming performance is consistent with predictions of hydro-mechanical theory, which suggests that the optimal functional design should reflect those features that maximize thrust while minimizing drag, namely: a high aspect ratio, narrow caudal peduncle, large anterior body depth and a near optimal finness-ratio (Blake, 2004).

Aspect ratio is believed to have a strong influence on the swimming abilities of fishes (e.g. Fisher et al., 2005; Sambilya, 1990; Webb and Weihs, 1986), and this variable was consistently included in the best-subset regression models, regardless of how many other variables were added. A high aspect ratio is thought to be characteristic of pelagic marine fish that have enhanced cruising speeds, enabling them to travel over wide areas in search of food and breeding grounds (Webb, 1994).

Caudal peduncle depth (expressed as a ratio of body depth) was also strongly related to swimming speed across families, confirming the importance of this variable to swimming ability in fishes. A deep caudal peduncle is found in fish that are described as ‘accelerators’ (Webb, 1994). These hover in the water column and ambush prey but have poor sustained swimming speeds (Webb, 1994). On the other hand a narrow caudal peduncle is characteristic of thunniform fish, which use an axially oscillating caudal fin to generate thrust for cruising at high speed (Webb, 1984; Webb and Weihs, 1986). U_{crit}

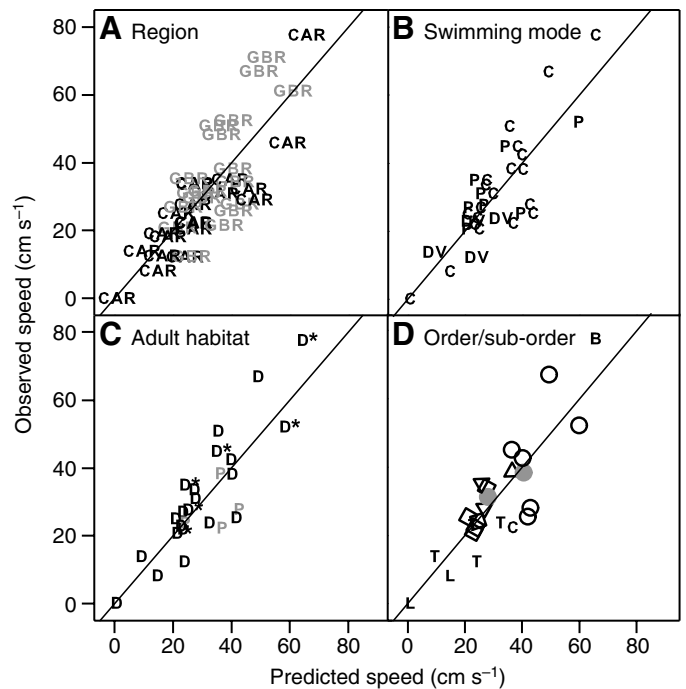


Fig. 5. An examination of the fit of the best-fit model (Fig. 4) across fishes from different regions (A; Great Barrier Reef, GBR, and Caribbean, CAR), with different swimming modes (B; C, caudal; P, pectoral; DV, dorso-ventral; PC, pectoral-caudal fin locomotors), adult habitat characteristics (C; D, ‘demersal’; P, ‘pelagic’) and orders (D; B, Beryciformes; C, Clupeiformes; L, Lophiiformes; T, Tetraodontiformes). Asterisks indicate families that are considered an archetypal coral reef fish (see Bellwood, 1996). Because of their dominance in the dataset and their high diversity, the sub-orders of the order Perciformes are shown individually (symbols).

measures the prolonged, high speed swimming capabilities of fishes (Plaut, 2001) and appears to be closely correlated with their fastest sustainable speed (over 24 h) (Fisher and Wilson, 2004). As such, it closely represents ‘cruising’ behavior, as opposed to rapid acceleration, although there may be some component of maneuverability that is important when measuring swimming performance using flumes.

Propulsive ratio and fineness ratio both appear to produce similarly viable 4-parameter models when combined with the best 3-parameter model. Both of these variables are related to the muscle mass of the fish, with PR measuring the proportion of the fish’s body able to be used in swimming, and FR estimating the combined total drag of the body due to frictional resistance and form drag, with an optimal value of 2.5 thought to allow the greatest amount of muscle mass (Bainbridge, 1960). However, the inclusion of a fourth variable in the model added little in terms of explained variance, and appeared to make the model’s predictive ability outside the observed range of data unstable (Table 2). The fact that TL , $CPDF^2$ and AR are able to explain nearly 70% of the variability in U_{crit} is remarkable, given the wide range of body shapes exhibited by the different families. Although not necessarily the only factor of importance in fish swimming (physiological factors such as muscle type must also be considered), body morphology is clearly highly correlated

with, and therefore can be used to predict swimming performance.

Pectoral fins have not been considered in this study, despite being valuable predictors of swimming abilities of adult fishes, especially among those that use pectoral fin locomotion (Fulton et al., 2005; Wainwright et al., 2002), and being well developed even at this pre-settlement juvenile stage. For pre-settlement juvenile fishes, pectoral fins are very small and transparent, making them impossible to view on whole photographs and difficult to dissect and pin. For these reasons they were not considered in this study, although they could prove useful for predicting endurance swimming (which may be affected by swimming mode) and are strongly correlated with gait transition speed in adult fishes (Fulton et al., 2005). Given that body and caudal fin undulation replace median and paired fin undulation at higher speeds (Webb, 1994), body and caudal fin morphometrics may provide a more useful predictor of U_{crit} performance than pectoral fin morphology. This is confirmed by the fact that there was little difference in the predictive ability of the model among families from different swimming modes, and it seems unlikely that our predictive power would be greatly improved with the inclusion of pectoral fin morphology, at least for the purposes of predicting maximum swimming speeds.

Fishes that occupy different habitats or environments might be expected to have evolved to thrive in their particular habitat. Given that different swimming modes and gaits occur for fishes among different habitats and with different feeding modes (Webb, 1984; Webb, 1994), we might expect to see systematic differences in the fit of our morphological model for fishes that live in different habitats. In the present study we included fishes of which the adult and juvenile forms are relatively sedentary and associated with the benthic, coral reef habitat, as well as fishes that are more mobile and associated with pelagic habitat. Despite the potential for differences in morphology relating to these different habitat specialties, we found that the fit of the model was unaffected by adult habitat characteristics. This may reflect the fact that these fishes are all pre-settlement, and potentially exhibit pelagic behavioural and physiological traits. We used measurements of fishes that can be best described as pre-settlement early-juvenile fishes, although for most families these individuals have largely developed into the adult body form. They are at the transition point from a pelagic to a benthic existence, and it is possible that the relationship between body morphology and swimming ability of these juvenile fishes may differ to that of their adult counterparts. Previous studies have reported a drop in swimming performance following settlement (Bellwood and Fisher, 2001; Stobutzki and Bellwood, 1994) and this could be due to both physiological and behavioral changes over this transition period.

Furthermore, the smaller size of these fishes relative to their adult forms may influence the relationship between body shape and swimming speed. Reynolds number Re is related to the viscosity of the water around a body; at low Reynolds numbers viscous forces act on the body, at high Reynolds numbers inertial forces take over (Vogel, 1994), and Re has been closely linked to changes in swimming modes of larval fishes during development (Weihs, 1980). The Reynolds values that correspond to the shift between viscous forces and inertial forces are believed to be between 200 and 400 (Fuiman and

Batty, 1997; Weihs, 1980). With the exception of the very slow swimming *Ogcocephalidae*, all of our fish species swam in an environment above a Reynolds number of 1000 and so should experience inertial forces whilst swimming, similar to that expected for adult forms. Large herring larvae (18.2 mm *TL*), experiencing Reynolds environments of 100–500 had similar locomotor mechanics to juvenile and adult fishes (Fuiman and Batty, 1997). Therefore, Reynolds number at least is unlikely to influence the observed relationships, and barring physiological and behavioural differences, the developed model may work equally well for adults.

There was no evidence that the model fit differed among taxonomic groups, despite the inclusion of five different orders of fishes. This suggests that body morphology alone appears sufficient to explain the bulk of the differences in swimming performance among taxonomic groups and that phylogenetic constraint of body morphology may limit maximum sustainable swimming speeds. The fastest groups are the Beryciformes (Holocentrids), followed by the Siganidae and the Acanthuridae, both members of the Perciformes. These groups appear to have evolved similar streamlined body forms, not unlike that of the tunas (also from the order Perciformes), optimized for fast steady swimming (Blake, 2004). These morphological adaptations have evolved independently in a number of phylogenetically distant groups (Blake, 2004). A handful of species (notably those from the orders Tetraodontiformes and Lophiiformes), exhibit exceptionally slow swimming speeds, having body morphologies clearly incapable of sustained swimming at high speed. Such species must have quite unique ecological characteristics that allow their slow swimming existence, and it is perhaps not surprising that at least some of their representatives exhibit factors such as chemical or cryptic defenses from predation. The majority of fishes swim at intermediate speeds, with most families swimming between 20 and 50 cm s⁻¹. It is at these medium range speeds that the largest variation in body form is found, and may reflect the fact that a diversity of body morphology is probably adequate for producing a reasonable level of swimming proficiency. For medium pace swimmers, design factors beneficial to other swimming skills, such as acceleration or maneuverability, may result in a diversity of morphological shape.

We have examined only marine tropical fishes in this study, which may bias model predictions if salinity and temperature affect swimming performance. Although seawater has a moderately higher density than freshwater, this slight change should have little effect on their relative viscosities. It is therefore likely that model predictions should hold for freshwater fishes providing there are no other physiological differences between marine and freshwater fishes. Temperature, on the other hand, may be expected to have a large effect on the swimming performance of fishes. Although temperature effects on the viscosity of seawater should also have little effect on swimming performance of fishes of this size, colder water is expected to have a considerable physiological effect on swimming performance by causing lower tail-beat frequencies and slower swimming speeds (Fuiman and Batty, 1997). As a result, it is likely that the presented model may over estimate swimming performance in temperate and possibly sub-tropical fishes, although the independent out-group test using the salmonid

Oncorhynchus mykiss suggests that this may not be the case, as these fish were swum at a temperature of around 12°C. Further comparisons are required using a larger range of temperate species to determine the extent to which the model can be used for predicting swimming speeds of fishes in colder regions.

Here we clearly show the utility of using a small number of easily measured external morphological parameters to predict maximum (U_{crit}) swimming speeds in coral reef fishes. The model appears to work equally well for fishes in the Great Barrier Reef and the Caribbean, and for families with different adult habitat characteristics and swimming modes. This model provides an invaluable means of predicting swimming abilities of fishes that are unable to be reared in the laboratory, do not perform well in swimming flumes or are unable to be captured live in the field.

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