
Body Shape and Mode of Propulsion Do Not Constrain Routine Swimming in Coral Reef Fishes

Satterfield Darien R. ^{1, 2, *}, Claverie Thomas ^{3, 4}, Wainwright Peter C. ^{1, 2}

¹ Department of Evolution and Ecology University of California Davis CA, USA

² Center for Population Biology University of California Davis CA, USA

³ Centre Universitaire de Formation et de Recherche de Mayotte, Dembeni , Mayotte

⁴ MARBEC laboratory Université de Montpellier, CNRS, Ifremer, IRD Montpellier , France

* Corresponding author : Darien R. Satterfield, email address : drsatterfield@ucdavis.edu

Abstract :

1. It is widely believed that because of biomechanical trade-offs, fish body shape and the mode of propulsion are strong predictors of swimming performance, with the best cruisers, maneuverers, and accelerators having different body forms and emphasizing different propulsion mechanisms. This paradigm is regularly projected onto routine swimming behavior and dominates the ecomorphological literature, despite the paucity of field measurements.

2. In this study, we measured variation in swimming behavior among 48 species of Indian Ocean coral reef fishes using recordings from a remote stereo video system. We measured average swimming speed, average swimming bout distance, frequency of turns, and percent of time spent station-holding and looked for the predicted trade-offs between them.

3. We find little evidence of the expected relationships between swimming behaviors across species, little evidence that body shape affects swimming, and few differences between species that swim by undulating the body and those that emphasize the use of median and paired fins. Taxa widely thought of as archetypical maneuverers (Chaetodon) and cruisers (Caranx) were not outliers in any behaviors. Our results indicate that swimming behavior is not easily predicted from simple measures of body shape and that alternative swimming modes can produce comparable behavioral profiles.

Keywords : fish behavior, swimming, locomotion, morphology, coral reefs, fish ecology, body shape, propulsion

1. Introduction

Three axes of swimming performance have dominated thinking about locomotor ecomorphology in fishes: maneuverability, swimming endurance, and acceleration (Blake 2004; Lighthill 1975; Videler 1993). Biomechanical evaluations indicate that specific body shapes correspond to maximum performance on each of these three axes (Webb, 1984a,b). Because of their shape and distribution of fins around the center of mass, laterally compressed, deep-bodied fishes, such as butterflyfishes, are able to turn easily and thought of as highly maneuverable (Konow & Ferry-Graham, 2013; Larouche et al., 2020). In contrast, a body that is deepest in the middle but tapered towards the ends with a thin caudal peduncle, as seen in carangids and scombrids, is considered advantageous for sustained swimming due to low drag from its streamlined shape and low lateral forces at the caudal peduncle (Dewar & Graham, 1994; Donley et al., 2004; Larouche et al., 2020; Videler & Wardle, 1991). Finally, an elongate body with comparatively tall fins and a deep caudal peduncle, as is found in sand perch, supports short bursts of acceleration between periods of station holding because of the large lateral surface area near the posterior end of the fish and long body that can bend into high-amplitude curves (Porter & Motta, 2004; Tytell, 2010). Webb (1984a) originally called these three categories maneuverers, cruisers, and accelerators, respectively (Fig. 1).

These three archetypes represent specialization in their respective behaviors and are thought to reflect trade-offs that prevent fishes from simultaneously achieving high performance on all axes (Webb, 1984b). Fishes with intermediate body morphologies are considered generalists with intermediate performance on multiple axes. As such, generalist have poorer maximum abilities than specialists on their respective axes but greater performance than specialists on the opposing axes (Fig. 1). This classic fish swimming paradigm is pervasive in literature on the ecomorphology of fish locomotion and generally characterizes how fish body form is thought to influence locomotion (de Barros et al., 2019; Villéger et al., 2017; Wikramanayake, 1990; Winemiller, 1991).

Despite the prominence and usefulness of this model (Astudillo-Clavijo et al., 2015; Bower and Piller, 2015; Ehlinger and Wilson, 1988; Fulton, 2007; Langerhans, 2009; Videler, 1993; Villéger et al., 2017), some empirical comparative studies of swimming performance have found surprising degrees of mismatch between fish morphology and swimming performance (Feilich, 2017; Gerstner, 1999; Pettersson, 2007; Sepulveda and Dickson, 2000; Walker et al., 2013),

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suggesting that the factors linking swimming ability and body shape can be complex (Hodge et al., 2018; Price et al. 2015). Others have noted that there are many challenges associated with measuring relationships between body shape and swimming efficiency, such as estimating drag, thrust, and energy consumption for a constantly undulating body, as well as accounting for differences in muscle composition, body size, and mode of propulsion (Bainbridge, 1958; Schultz & Webb, 2002; Tytell, 2007; Videler 1993). Due to these difficulties, there is still much debate over how strongly body shape limits performance capacities. Nevertheless, the proposed relationships between body shape and swimming performance are often used to substantiate predictions that body shape evolves in response to pressure for greater swimming performance. For example, the evolution of laterally compressed deeper bodies is often chalked up to an ecological need to turn more, and the evolution of an elongate, streamlined body is attributed to selection for faster or more efficient cruising (Costa and Cataudella, 2007; Ehlinger, 1990; Friedman et al., 2020, Larouche et al., 2020, Martinez et al., 2021, Rincón et al., 2007).

More generally, the body shape-swimming performance paradigm is often used as a justification that routine behavior can be predicted by body shape (Fig. 1). Where the paradigm asserts that a fish similar in morphology to a carangid should be able to achieve a high maximum swimming speed and sustainably swim for long distances, the parallel behavioral assumption is that these ‘cruising’ fishes are regularly using fast speeds and sustaining prolonged bouts of swimming (Blake, 2004; Villéger et al., 2017; Webb, 1994). For fishes similar in shape to butterflyfish, which are described as highly maneuverable, the behavioral expectation is that these fish use maneuvers or turns frequently (Villéger et al., 2017; Webb, 1994). Finally, elongate fish with a deep caudal peduncle, like sand perch and baracuda, are expected to be capable of rapid acceleration from a halt. As such, elongate fishes are expected to use sit-and-wait behaviors, or long periods of station holding between short, rapid burst-swimming, often used to catch prey or evade predators (Porter & Motta, 2004; Tytell, 2010; Villéger et al., 2017). Despite the longstanding use of the cruiser-accelerator-maneuverer paradigm to infer routine behaviors, many of these relationships between body shape, axes of swimming performance, and routine behaviors have yet to be tested, largely due to the difficulties of observing fishes undisturbed *in situ* and measuring these features of swimming.

Just as the paradigm suggests that body shape induces trade-offs in swimming performance, we expect that suites of routine behaviors used by fishes will also trade-off (Table 1). The

behavioral characteristic of a maneuverer is high turning frequency, which we would expect to trade-off with the traits of a cruiser - swimming speed and distance. In contrast, we expect speed and distance to be positively correlated as both behaviors are characteristic of cruisers.

Accelerators are characterized by long periods of sit and wait behavior and achieve high speeds during burst starts, but do not sustain a high speed over a long distance or use turns frequently. Thus, we expect the proportion of time a fish spends station holding will be negatively correlated with the traits that distinguish them from cruisers (swimming distance) and maneuverers (turning frequency).

A factor that potentially complicates the expected relationships between swimming behaviors and body shape is that the propulsive mechanisms used by swimming fishes differ among taxa. Two general locomotor modes are used for propulsion: body and caudal fin undulation (BCF) and median paired fin (MPF) swimming (Fulton, 2007; Sfakiotakis et al., 1999). Most species consistently use one of these modes for routine straight-line swimming (Blake, 2004; Fulton, 2007; Pink and Fulton, 2014). However, many fishes transition from MPF to BCF as swimming speed increases (Cannas et al., 2006; Feilich, 2017; Webb, 1994), and use different propulsors during bursts of acceleration and steady swimming. Nearly all fishes use median and paired fins to control turns, but straight-line swimming can be accomplished by both BCF and MPF swimming (Blake, 2004).

Biomechanical analyses suggest that BCF swimming is advantageous for long-distance and high-speed swimming, and MPF swimming is favorable for tight turns and fine directional control (Blake, 2004; Borazjani and Sotiropoulos, 2010; Lauder and Madden, 2007; Lauder and Tytell, 2005; Sfakiotakis et al., 1999; Webb, 1984a). As such, it has been argued that fishes that routinely use MPF swimming are more suited for maneuvering but incur the cost of lower swimming speeds, while routine BCF swimmers are expected to be capable of generating faster speeds but are less maneuverable (Borazjani and Sotiropoulos, 2010; Lauder and Madden, 2007; Lauder and Tytell, 2005; Sfakiotakis et al. 1999; Villéger et al., 2017). Like the body shape paradigm, this generalization has met with mixed results in comparative studies (Fulton, 2007; Fulton et al., 2013; Marcoux and Korsmeyer, 2019). Further, deeper levels of complexity within locomotor modes can contribute variation in swimming behaviors. For example, in BCF swimmers it has been noted that modulation of body stiffness through muscle tension can increase the range of routine speeds that are accessible to a fish (Long and Nipper, 1996;

McHenry et al., 1995). Additionally, MPF swimming acts as the mechanism allowing extremely stiff bodied fish to turn efficiently given their lack of bending potential (Walker, 2000; Webb, 2004; Weihs, 2002). Quickly it becomes clear that diversity in swimming behavior among fish species is likely to be driven by a more intricate set of kinematic related variables than body shape alone.

In the present study, we measure routine, daytime swimming behavior of coral reef fishes, focusing on four parameters: average straight-line swimming speed between turns, the distance covered in these bouts of straight-line swimming, the frequency of turns, and the percent of time spent station-holding. We use these data to explore several expectations from the fish ecomorphology literature. With a data set of 48 species, we first look for predicted trade-offs and positive correlations between these behaviors (Table 1, Fig. 1). We then test for an effect of species body shape on each of the swimming metrics. Finally, we contrast swimming behavior in BCF and MPF swimmers, testing for the expected differences in average swimming speed and turning frequency. If swimming behaviors are constrained by body shape, this should lead to the expected relationships between the behavioral axes. For example, a fish that turns frequently should not also be a high-speed cruiser. If BCF swimming results in better cruising performance and MPF swimming results in better maneuverability, we expect to find higher average swimming speeds in BCF swimmers and more frequent turning in the MPF swimmers.

2. Methods

2.1 Behavioral Observation

Videos were obtained from coral reefs in the Mozambique channel in Mayotte in November 2018 and February 2021. The water temperature is similar in the months of November (26.5 to 29.5 °C) and February (28.0 to 30.5 °C). We selected videos in which water conditions were calm. The videos were recorded between 8:00 am and 4:00 pm and span 10 reef locations that range in depth from 2 to 81 meters. The recordings were taken using 5 camera rigs placed in position by snorkelers up to 5 m depth or directly from the boat and lowered with strings when depth was greater than 5 m and left to record for 2 hours before recovery. Cameras were set to film on full HD at a rate of 30 frames per second. Each Camera rig consisted of a pair of GoPros separated by 80 cm and oriented 8° inward to maximize field of view overlap (Letessier et al. 2015). Calibration was done before each recording session using a 2*2*1 m cubic contraption

with 3D known coordinates positioned in two parallel planes for distances measurement and chess boards for camera distortion (Neuswanger et al., 2016). This set up allowed 3D video measurement of fish size and movement, including measurements of distance, speed, and changes in direction, all undisturbed by human presence. No fieldwork or animal ethics permits were required for the collection of videos.

We collected swimming behavior parameters from the videos on 48 fish species belonging to 16 families common on coral reefs. Sample sizes per species ranged from 7 to 31 individuals (Table 2), and the duration of each sample video was 29 seconds \pm 35.1 sd, representing an average of 424.6 seconds of observation on each species. To ensure that each sample video was of a unique individual, we allowed for at least five minutes of video time between selected observation clips. We began the measurements of behavior when the subject fish entered the field of view of both cameras and ended when the fish left the field of view of one of the cameras.

We used VidSync software (Neuswanger et al., 2016) to collect measurements of body size and behaviors of fishes swimming around the reef. We digitized behaviors manually by marking the position of the fish in both camera views when behaviors of interest occurred. During the observation interval, we calculated the **net frequency of turns** to characterize routine use of maneuvers, the percent of **time spent holding position** to characterize sit and wait behavior. The **average speed (cm/s)** and **distance traversed (cm)** among all bouts of straight-line swimming was measured to characterize routine swimming speeds and distances. Straight-line swimming was defined as the bout of swimming between two turns. Turns were defined here as a near-instantaneous change in direction larger than 45 degrees. Turn frequency was calculated as the number of turns made by a fish divided by the total amount of time that the fish spent moving (not when a fish was station-holding). A fish was labeled as station holding any time it was not swimming forward. Most often this looked like a fish physically resting on or hovering just above a coral structure. We only observed fish hovering high in the water column in a few instances. We also measured the standard length of each subject fish. Averaging across samples (i.e., individual fishes), we calculated the species mean values of four behavioral traits, including turning frequency, average straight-line swimming speed, average straight-line swimming distance, station holding proportion, and standard length.

We categorized species by locomotor mode based on behavior during routine straight-line swimming. Species were scored based on our observations and consultation of the literature. Median paired fin (MPF) swimming species used either their pectoral fins or dorsal and anal fins for locomotion and some taxa routinely mixed these (e.g., chaetodontids, tetraodontids). Body caudal fin (BCF) swimmers used the undulation of the body and the caudal fin for locomotion, holding the paired fins against the body except during turns. The species of Chaetodontidae and Pomacentridae included in this study frequently mix median and paired fin propulsion with body undulations (Fulton, 2007). We placed these species in the MPF group because of their extensive use of paired fins during straight-line swimming.

2.2 Body Shapes

To examine body shape diversity among the 48 species in this study we utilized a publicly available dataset of eight body shape variables measured on museum specimen (Price et al., 2022). The body shape data set contains 37 of the 48 species in our study, and for the 11 species not in the body shape dataset we used closely related species as replacements. A list of replaced species and their substitutions can be found in the supplemental material (See Table S1 in the Supporting Information).

The first three of the body shapes variables we selected from this data set were standard length (SL), maximum body depth (BD), and maximum fish width (FW). From these variables we calculated body elongation (BE) as the BD divided by SL. Elongation is the primary axis of body shape diversity in reef fish (Claverie and Wainwright, 2014). Diversity along this axis of body shape is also thought to have a substantial impact on swimming ability. While, measuring hydrodynamic efficiency is difficult due to the challenges of estimating drag and energy consumption (see Schultz & Webb, 2002; Tytell, 2007), some hydrodynamic models suggest that elongate species may experience less drag and have a lower energetic cost of high-speed swimming (Lighthill, 1969) Meanwhile, other models find that body elongation alone is less predictive of swimming efficiency than when mode of propulsion and other axes of shape diversity such as caudal peduncle and fin shape are included (Tytell et al., 2010; Tytell and Lauder, 2004). Additionally, we calculate cross sectional area, which accounts for lateral compression which is expected to have significant impacts on turning ability as deep-bodied

fishes experience greater drag and are less efficient cruisers but can make more acute turns (Eloy, 2013; Sfakiotakis et al., 1999; Tytell et al., 2010, Tokić and Yue, 2012; Webb, 1984a).

Additionally, we calculated size corrected head depth (HD), lower jaw length (JL), mouth width (MW), minimum caudal peduncle depth (CD), and maximum caudal peduncle width (CW) by dividing each of these variables by SL. Additionally, we calculated the second moment of area ($[\frac{\pi * BD * FW^3}{4}]$; Porter et al., 2009; abbreviated as SMA), a factor contributing to body stiffness. We size corrected SMA by transforming the variable to be the residuals of the linear regression between Ln(SMA) and Ln(SL).

2.3 Analyses

Behavioral variables were natural log-transformed to achieve normal distributions. However, normalization was not possible for the proportion of time spent station-holding; thus, no transformation was applied. Average swimming speed and distance were strongly positively correlated with fish body length, and turning frequency was negatively correlated with fish body length (Fig. 2A, B, &C). We removed size effects by using residuals from linear regressions of the log-transformed behavioral variables versus the log of fish standard length: $X' = \ln(X) - k \ln(L) - b$, where X' is the residual size corrected behavioral variable such as size corrected swimming speed, L is body length, and k and b are the coefficients from the regression. We used the residuals in place of the behavioral variables in all subsequent analyses. We found no relationship between the time spent station holding and fish standard length, so no size correction was performed on this variable (Fig. 2D).

For our phylogenetic analyses, a phylogeny including the species in our study was trimmed from a larger time-calibrated phylogeny of ray-finned fishes (Rabosky, Chang, Title, et al. et Alfaro, 2018). The larger phylogeny did not include *Gomphosus caeruleus*, *Oxycheilinus orientalis*, or *Scarus caudofasciatus*. We used *Gomphosus varius*, *Oxycheilinus arenatus*, and *Scarus festivus*, respectively, as proxies. We tested for significant correlations between the swimming variables using phylogenetic generalized least squares regressions (PGLS; Caper [Orme et al., 2013]). Additionally, we used phylogenetic ANOVAs (*GeoMorph* [Baken et al., 2021; Adams et al., 2022]) to test if BCF and MPF swimmers differ in each swimming variable. To test for the effects of body shape on swimming behavior, we ran PGLS regressions for each of the eight body shape variables against each of the four swimming variables (Table S2). To

examine the combined effects of body shape variation on multiple axes on swimming behavior, we ran a PCA on the eight body shape variables (body shapes PCA). We then tested for the relationships between PC1 of the body shapes PCA and our swimming behaviors using PGLS regressions.

3. Results

3.1 Relationships between swimming variables

If body shape induces behavioral trade-offs, we would expect to find negative correlations between behaviors that typify the maneuverers, accelerators, and cruisers, and positive correlations between behaviors that are both associated with one archetype. Using phylogenetic generalized least squares (PGLS), we first tested the suspected trade-off between the use of maneuvers versus distance and swimming speed (i.e., between maneuverers and cruisers, Fig. 1, Table 1). Opposite of expectations, we found a positive correlation between the average swimming speed and turning frequency ($p:0.0004$, $r:0.49$, Fig. 3A). This result indicates that fish which turn frequently also use high speeds. We also found a positive correlation between swimming distance and average swimming speed ($p: 0.002$, $r: 0.43$, Fig. 3B), as predicted. In line with expectations, we found swimming distance and turning frequency to be negatively correlated ($p: 0.002$, $r: -0.44$, Fig. 3C). Thus, there may be a trade-off between the rate of turns and the distance covered in bouts of swimming without turns.

We also expected trade-offs between swimming speed and distance vs the amount of time spent not swimming (between cruisers and accelerators, Fig. 1, Table 1). However, our test for a correlation between the proportion of time spent station holding and swimming distance was not significant ($p: 0.63$, $r: 0.07$, Fig. S1). Furthermore, we did not detect a significant correlation between the proportion of time spent station holding and swimming speed ($p: 0.24$, $r: 0.17$, Fig. S1). Fishes that used station-holding were diverse in swimming speeds and distances. However, this relationship should be interpreted with caution as only 33% (16) of the species in our data set had a non-zero amount of time spent station holding and only 12.5% (6) of species spent more than 10% of the time station holding (Fig. 2D).

Finally, we tested for a trade-off between the frequency of turns and the percent of time spent in sit and wait behavior (maneuverers vs accelerators). We found that the proportion of time spent station holding was weakly negatively correlated with turning frequency ($p: 0.04$, $r: -0.30$,

Fig. S1). This indicates that station holding fish turned less frequently when they were swimming, but the relationship was not strong and with a limited number of station-holding species in the data, this result should be interpreted with caution.

3.2 Swimming Behaviors and Body Shape

The PGLS analyses used to independently compare the body shape variables and swimming behaviors showed no significant relationships (Fig. 4, Table S2). The body shape variables used in this study were modified from Price et al., (2022). As such, that the patterns of body shape diversity in the body shapes PCA (Fig. 4A) reflect the patterns Price et al. report among their larger set of species. Among our species, PC1 accounts for 45% of the variation in body shape and is predominantly composed of cross-sectional area (CS), body elongation (BE), and head depth (HD). Deep-bodied and laterally compressed species are at the positive end of PC1 while elongate-bodied fish are at the negative end of PC1. PC2 accounts for 19% of the variation in body shape and represents diversity in caudal peduncle shape, specifically peduncle depth (CD) and peduncle width (CW). Fish with deep and narrow caudal peduncles are on the negative end of PC2 and those with short but wide peduncles are at the positive end of PC2. Using PGLS regressions we tested for relationships between PC1, PC2, and average swimming speed, swimming bout distance, and turning frequency (Fig. 4). We found no effects of PC1, PC2 or their interaction on average swimming speed or swimming bout distance (Fig. 4 B,C). There were also no effects of PC1 or PC2 individually on turning frequency, however there was a weakly significant interaction effect (p : 0.043; Fig. 4D). This trend is driven by the presence of *Parapercis hexophtalma*, which has the highest body elongation and a very low turning frequency. When this data point is removed the significant interaction effect is lost (p : 0.141).

The fish in our data set that was most emblematic of the “cruiser” body form, *Caranx melampygus*, had a relatively low average swimming speed. The species that best matched the deepest-bodied “maneuverer” specialist body shape in our data set were the 5 species of *Chaetodon*, along with *Zanclus cornutus*, and the acanthurid *Zebrasoma scopas*. All but one of these deep-bodied species were intermediate in turning frequency (Fig. 3A); *Chaetodon lunula* had a high turning frequency. *Parapercis hexophtalma* was the most elongate species, most similar to the specialist “accelerator” archetypal shape. *P. hexophtalma* had the highest station holding proportion. However, the two next most elongate species were both labrids, and neither

used station holding. The *Paracirrhites spp.*, which were also high in their proportion of time spent station holding, were average in body elongation. Finally, the three species with the fastest average swimming speed spanned the range of the elongation ratio (e.g., *Chromis fieldi*, *Paracirrhites forsteri*, and *Thalassoma hardwicke*).

3.3 Locomotor mode and Swimming Behaviors

The phylogenetic ANOVAs comparing BCF and MPF swimmers showed no significant differences in average swimming speed ($p: 0.72, F: 0.11, df: 1,46$), straight-line distance ($p: 0.58, F: 0.30, df: 1,46$), or turning frequency ($p: 0.36, F: 0.87, df: 1,46$). BCF swimmers spent more time station holding than MPF swimmers ($p: 0.03, F: 5.69, df: 1,46$; Fig. S1). The six species that spent greater than 10% of the time station holding are all BCF swimmers. However, eight BCF swimmers did not use station holding at all. Four of the top five species in turning frequency were BCF swimmers. Of the top five species in average swimming speed, three were MPF swimmers, and two were BCF swimmers. For straight-line distance, four of the top five species were BCF swimmers.

4. Discussion

This study assessed the validity of projecting widely used linkages between swimming mode, fish body form and swimming performance onto routine swimming behavior. The expectations that deep bodied fish are maneuverable, streamlined fish are efficient cruisers, and elongate fish can achieve fast accelerations, in addition to the assumption that body shape induces swimming performance axes have metamorphosed in the literature into the concept that body shape predicts routine behavior (Costa and Cataudella, 2007; Ehlinger, 1990; Friedman et al., 2020; Larouche et al., 2020; Martinez et al., 2021; Rincón et al., 2007; Villéger et al. 2017). We found limited evidence of the expected trade-offs between turning frequency, average swimming speed and distance, and station-holding as manifestations of maneuverers, cruisers, and accelerators. We also found little impact of body shape or mode of propulsion (BCF vs MPF swimming) on swimming behavior. Our results have important implications for studies of fish locomotion, as they indicate that classic and widely used ecomorphological expectations from the literature cannot be used to predict the diversity of routine swimming behavior in coral reef fishes.

Trade-offs and correlations between behavioral axes - A key concept in the classic fish swimming paradigm (Webb, 1984a) is that high abilities on one of the performance axes – maneuvering, cruising, or accelerating – will incur tradeoffs with the other axes. The behavioral analog of these predictions is the expectation of trade-offs between suites of behaviors that would distinguish maneuverers, cruisers, and accelerators (Fig. 1, Table 1). We did not observe strong evidence of the expected relationships between our four differentiating behaviors: average swimming speed, swimming bout distance, turning frequency, and the proportion of time spent station holding.

Only two of the six expected relationships between behaviors matched the classic expectations with significant correlations in the predicted direction. First, we observed a positive correlation between average swimming speed and swimming bout distance, as expected. Second, we observed a negative correlation between turning frequency and swimming distance, a pattern that confirms a classic expectation related to cruising and maneuvering. However contrary to expectations, there is a significant positive correlation between turning frequency and swimming speed. This result was unexpected, as the notion that fish can optimize body shape to perform well at either maneuvering or at high sustained swimming speed, but not both, is likely the most prevalent in swimming ecomorphology literature (see Astudillo-Clavijo et al., 2015; Bandyopadhyay et al., 1997; Ellerby and Gerry, 2011; Gaston et al., 2012; Rincón et al., 2007; Villéger et al., 2017; Weihs, 2002).

It is commonly expected that fish which use sit-and-wait behavior swim fast over short distances and do not turn frequently when they are swimming (Higham, 2007; Villéger et al., 2017). We observed that fishes which use sit-and-wait behavior are no more or less inclined to swim fast or travel far than fishes which are constantly swimming. We found a negative relationship between turning frequency and the proportion of time spent station holding. However, as this relationship is weak and highly sensitive to the inclusion of one species, *Parapercis hexophthalma*, we view it as weak if any evidence of a trade-off between these two variables.

While it may be that trade-offs prevent high performance on the key swimming traits that distinguish cruisers, maneuverers, and accelerators, we found little evidence that these distinctions are appropriate for describing diversity in routine behaviors. A possible explanation for why our findings did not match expectations is that peak performance may not be a strong

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predictor of routine swimming behavior. It is possible that the use of maximum performance is uncommon in the daily life of animals and routine behaviors may usually fall well below maximum capacity. While many studies find that maximum swimming performance and routine behavior are significantly correlated (Fisher and Bellwood, 2003; Plaut, 2001; Wainwright, 1987) this need not always be the case and there is evidence that the degree of the match varies by locomotor mode (Fulton, 2007). Thus, it may be that adaptations for high performance on each of the three traditional locomotor axes yield trade-offs among the performance traits, but that peak performance is a weak guide to routine swimming behavior in reef fishes, so that these relationships are not manifested in average swimming profiles.

Effects of body shape on swimming – Body shape is classically expected to underly the expected trade-off between axes of swimming performance (Webb, 1984a; Blake, 2004). It is intuitive that to maintain low fitness costs, fishes would be unlikely to routinely use behaviors that are energetically expensive and that the routine behaviors used by a fish would reflect the body shape. However, we found that variation among species in most routine swimming behaviors cannot be attributed to body elongation, cross sectional area, caudal peduncle shape, head and mouth shape, or second moment of area. Thus, it is not the case that for routine behavior fish can neatly be categorized as cruisers, maneuverers, or accelerators based on body shape. Rather, we observe fish of all shapes using many combinations of routine speeds and distances, turning frequencies, and periods of rest. Both elongate and deep-bodied species can be found along most of the range of all behavioral axes (Fig. 3). One of the many examples of the lack of morphological similarity among fishes in the same region of behavior-space (high-distance/low-turning frequency) can be found between *Zanclus cornutus*, the most deep bodied species in the data set (BE: 0.83) and a more elongate fish, *Parupeneus macronemus* (BE: 0.33). Finally, we observe that fishes of similar body shape can vary substantially in behavior. Our findings demonstrate that carangiform fish such as *Caranx* and *Caesio* are not necessarily prone to using higher speeds routinely than chaetodontiform fish such as *Chaetodon* and *Zebrasoma*. The labrids and acanthurids in this study are also a good example of how much behavior variation can exist among closely related species despite similarities in overall morphology. As such, we recommend that body shape should not be used to estimate routine swimming behaviors.

While theory suggests that maximal swimming performance is limited by body shape, our observations show that routine behaviors do not appear to be constrained by body shape. As discussed above, one possible explanation for the mismatch is that maximal performance profiles do not translate to routine behaviors. However, a second possible explanation is that the mapping of morphology to swimming performance in fishes is more complex than previously thought.

While there is positive evidence of the correlation between body shape and variation in swimming performance capacity from a number of laboratory studies (Blake et al., 1995; Ellerby and Gerry, 2011; Gerry et al. 2012; Langerhans et al., 2009; Oufiero et al., 2011) these studies usually focus on variation within species rather than comparative patterns. These studies have found consistent support for the expected morphological responses to greater use of sustained swimming (Aguilar-Medrano and Barber, 2016; Friedman et al., 2016; Jastrebski et al., 2004), increased maneuvering (Ellinger and Wilson, 1988; Mittelbach 1981; Robinson, 2000), and threats of predation (Ghalambor et al., 2003; Langerhans, 2009). However, studies of swimming performance require intensive laboratory effort and have therefore not been generated in a comprehensive way for large numbers of species. Those comparative studies that do exist often do not find the expected relationships between morphology and swimming performance (Feilich, 2017; Gerstner, 1999; Walker et al., 2013). This literature suggests that the mapping of body shape to swimming performance is complex, in part because descriptors of body shape do not account for the extensive variation found in the anatomical basis of locomotion (Aguilar-Medrano et al., 2016; Donatelli et al., 2021; Feilich, 2017; Gerstner, 1999; Walker et al. 2013), the mechanics of propulsion (Long and Nipper, 1996, Wainwright et al. 2002; Walker, 2000; Walker and Westneat, 2002) or flexibility in the mode of propulsion (Feilich, 2017). Indeed, we suggest that this is an area that requires renewed attention if we are to build a realistic and meaningful picture of swimming ecomorphology for fishes.

Effects of locomotor mode on swimming - In addition to body shape, the primary locomotor mode used for propulsion has been thought to limit the range of behaviors available to fish. Biomechanical analyses suggest that MPF swimming offers maximum control during slow-speed maneuvering (Lauder and Madden, 2007; Weihs, 2002) while BCF swimming is thought to allow for higher sustained speeds, and provide higher power during bursts, and thus has been suggested to perform best during sustained swimming or burst starts (reviewed by Blake, 2004; Colgate and Lynch, 2004; Korsmeyer, 2002; Lauder and Tytell, 2005; Sfakiotakis et al., 1999;

Webb, 1984a). Though numerous species have been shown to transition from MPF to BCF as swimming speed increases (Cannas, 2006; Druker, 1996; George, 2019; Korsmeyer, 2002), most species adopt a single locomotor mode that is used for routine travel. We have attempted to clarify if a species' standard locomotor mode shapes its behavioral profile while swimming.

We found no significant difference between the behavioral profiles of MPF and BCF swimmers. Further, species that emphasize either locomotor mode can achieve behavioral extremes in turning frequency, average swimming, and straight-line distance (Fig. 3 & 4). Thus, we find no support for the idea that MPF swimmers are routinely slower swimmers or that they turn more frequently. These patterns suggest that the locomotor modes are surprisingly comparable in behavior and support the previous findings that MPF swimmers can be highly efficient over a wide range of speeds (Korsmeyer et al. 2002). Further our findings indicate behaviors are not sensitive to the additional drag experienced by BCF swimmers due to the undulating body, as compared to the fixed body of a MPF swimmers (Lighthill, 1969; Lighthill and Blake 1990). Our findings are consistent with observations that MPF swimmers can thrive in environments where exceptional swimming endurance is needed such as high flow conditions and strong wave exposure (Bellwood and Wainwright, 2001; Fulton and Bellwood, 2004; 2005).

Conclusion - With the advancing tools available to study fish undisturbed *in situ*, it is likely that our data set is only the beginning of what will become a large and diverse record of routine behavior in fish. Analyses of the effects of factors other than body shape and locomotor mode will help to elucidate predictors of diversity in routine behavior. In the present there is limited evidence that it is valid to project the proposed relationships between body shape and swimming performance onto routine swimming behavior. As such, inferring routine behavior in fishes based on body shape should be avoided.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 [Species Replacements for Body Shape Data]

Table S2 [Correlations between Swimming Variables and Body Shapes]

Figure S1 [Relationships between Station Holding and other Behaviors]

Table and Figure Captions

Table 1. Predicted Correlations between Swimming Variables vs Observed Relationships.

Predicted pairwise relationships among four variables that describe swimming behavior, as measured in this study. Expected correlations (positive or negative) are based on interpretation of properties of specialist swimmers as discussed in the Introduction. The results column reports the results from PGLS regressions that test for each relationship. Results were counter to predictions in four of six cases.

Table 2. Species List. Videos (N) is the number of individual video sequences sampled for each species. Body Elongation (BE) is calculated as the body depth / standard length. Cross Sectional Area (CS) is the body depth / fish width.

Figure 1. Fish Swimming Paradigm. An adaptation of Webb (1984a, Fig. 1). On the left-hand triangle, corners represent swimming specialists while generalists have intermediate traits. Webb classifies swimming variation in terms of key performance traits. His hypothesis was that high performance in each swimming trait is best achieved by a particular body design. These body shape archetypes are shown in the corners. Accelerators which have a high maximum acceleration are elongate but have uniform body depth. Cruisers have a high sustained swimming speed and endurance, and have average elongation but have tapered bodies. Maneuverers are highly maneuverable with small minimal turning radius and can achieve high angular velocity. Maneuverers are deep bodied and laterally compressed. These hypotheses regarding swimming performance and body shape are often projected onto routine swimming behavior. On the right triangle, we show how four behaviors axes can be used to distinguish routine behaviors for the three swimming archetypes. The proportion of time spent station holding is expected to be highest for accelerators. Average swimming speed is expected to be low for maneuverers but higher for accelerators and cruisers. Straight-line distance should be greatest for cruisers. Finally, turning frequency should be highest for maneuverers. Here we use these behaviors to test for relationships between routine behavior and body shape.

Figure 2. Body Size is Correlated with Most Swimming Behaviors. The relationships between the average standard length of each species and A) the average swimming speed during bouts of

straight-line swimming, B) the of average distance traveled during bouts of straight-line swimming, C) the of average number of turns made per second, and D) the proportion of time spent holding position to total observation time. Species are color coded by locomotor mode. Blue points represent body caudal fin swimmers (BCF), orange points represent median paired fin swimmers (MPF). *P*-values, *r*, and equations were calculated using phylogenetic general least squares regression.

Figure 3: Behavioral distributions and relationships. A) The relationship between turn frequency and average swimming speed, B) The relationship between average swimming speed and average straight-line distance, C) The relationship between average straight-line distance and turn Frequency. Points are labeled by the first 5 letters of the genus and first 3 letters of the species. For very similar species, the last 3 letters are also provided. Average swimming speed values are the residuals of the relationship between the natural log of the species average swimming speed during bouts of straight line swimming (cm/s) and the natural log of the average fish body length (cm), shown in Fig. 2A. Turning frequency values are the residuals of the relationship between the natural log of the species average for number of turns per second and the natural log of the average fish body length (cm), shown in Fig. 2B. Average straight-line distance values are the residuals of the relationship between the natural log of the species average for distance traveled during straight line swimming and the natural log of the average fish body length (cm), shown in Fig. 2C. Species are color coded by locomotor mode. Blue points and bars represent body caudal fin swimmers (BCF), orange points and bars represent median paired fin swimmers (MPF). *P*-values, *r*, and equations were calculated using phylogenetic general least squares regression.

Figure 4. The effects of Body Shape on Swimming Behaviors. A) A morphospace PCA modified from Friedman et al., (2021) and Price et al., (2022), where of species scores are plotted on the first two principal components axes, PC1 vs PC2. Body shape ratios included as loadings are Body Elongation (BE), Cross Sectional Area (CS), Head Depth (HD), Minimum Caudal Peduncle Depth (CD), Maximum Caudal Peduncle Width (CW), Mouth Width (MW), and Lower Jaw Length (JL). B) Average swimming speed vs. PC1. Average straight-line distance values are the residuals of the relationship between the natural log of a species' average

distance traveled during straight-line swimming and the natural log of the average fish body length (SL; cm). C) Average straight-line distance vs. PC1. Average straight-line distance values are the residuals of the relationship between the natural log of the species average for distance traveled during straight line swimming and the natural log of SL. D) Turning Frequency vs. PC1. Turning frequency values are the residuals of the relationship between the natural log of the species average for number of turns per second and the natural log of SL. Species are color coded by locomotor mode. Blue points represent body caudal fin swimmers (BCF), orange points represent median paired fin swimmers (MPF). The ellipses contain 95% of the points in their respective locomotor mode, showing the significant interaction of PC1*PC2 and locomotor mode. Tables in the lower right corner of panels A, B, and C show the *P* and *r* values from the phylogenetic general least squares regressions of the swimming behaviors vs. the body shape PCs.

Tables and Figures

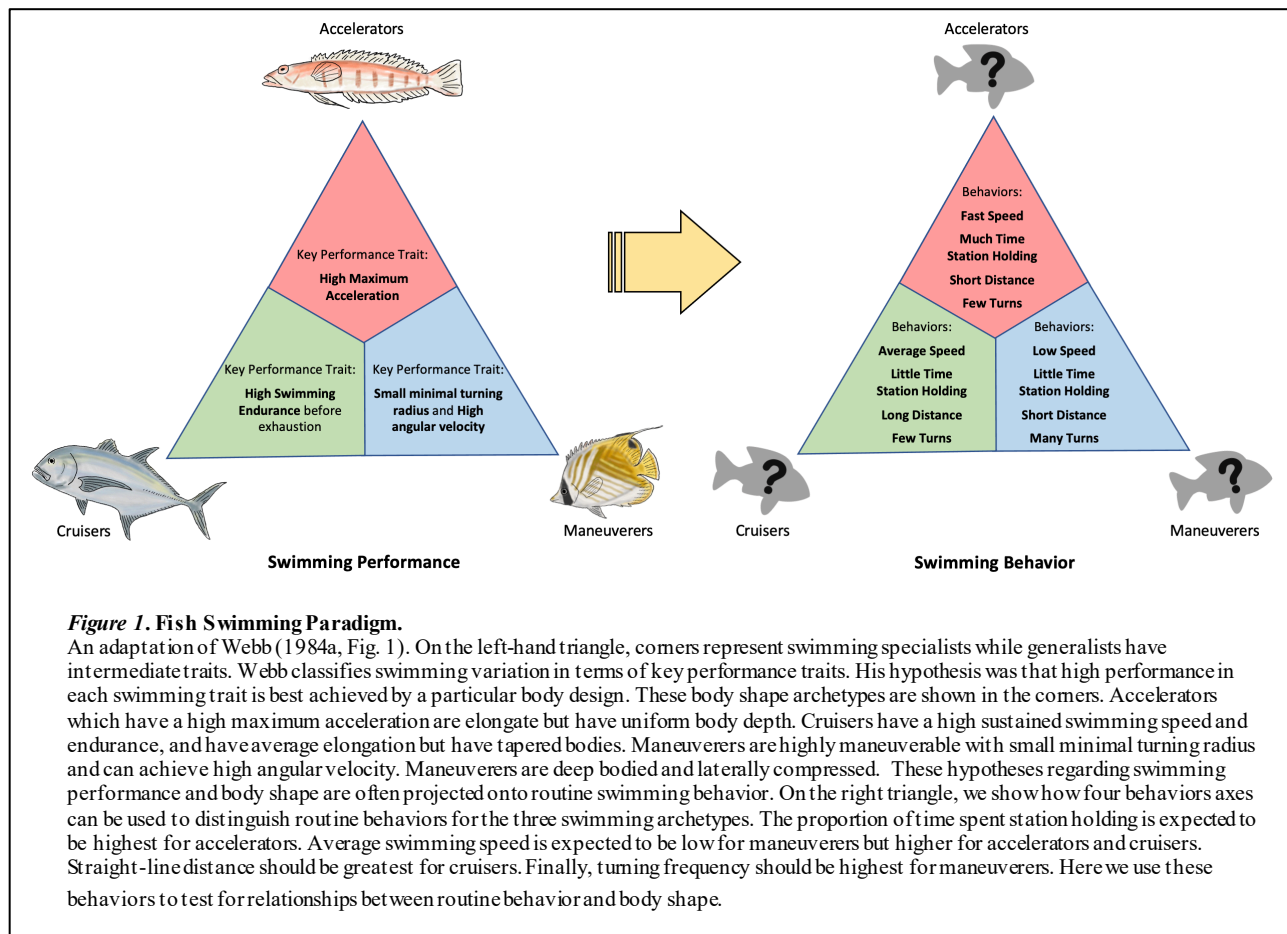
Table 1. Predicted Correlations between Swimming Variables vs Observed Relationships. Predicted pairwise relationships among four variables that describe swimming behavior, as measured in this study. Expected correlations (positive or negative) are based on interpretation of properties of specialist swimmers as discussed in the Introduction. The results column reports the results from PGLS regressions that test for each relationship. Results were counter to predictions in four of six cases.

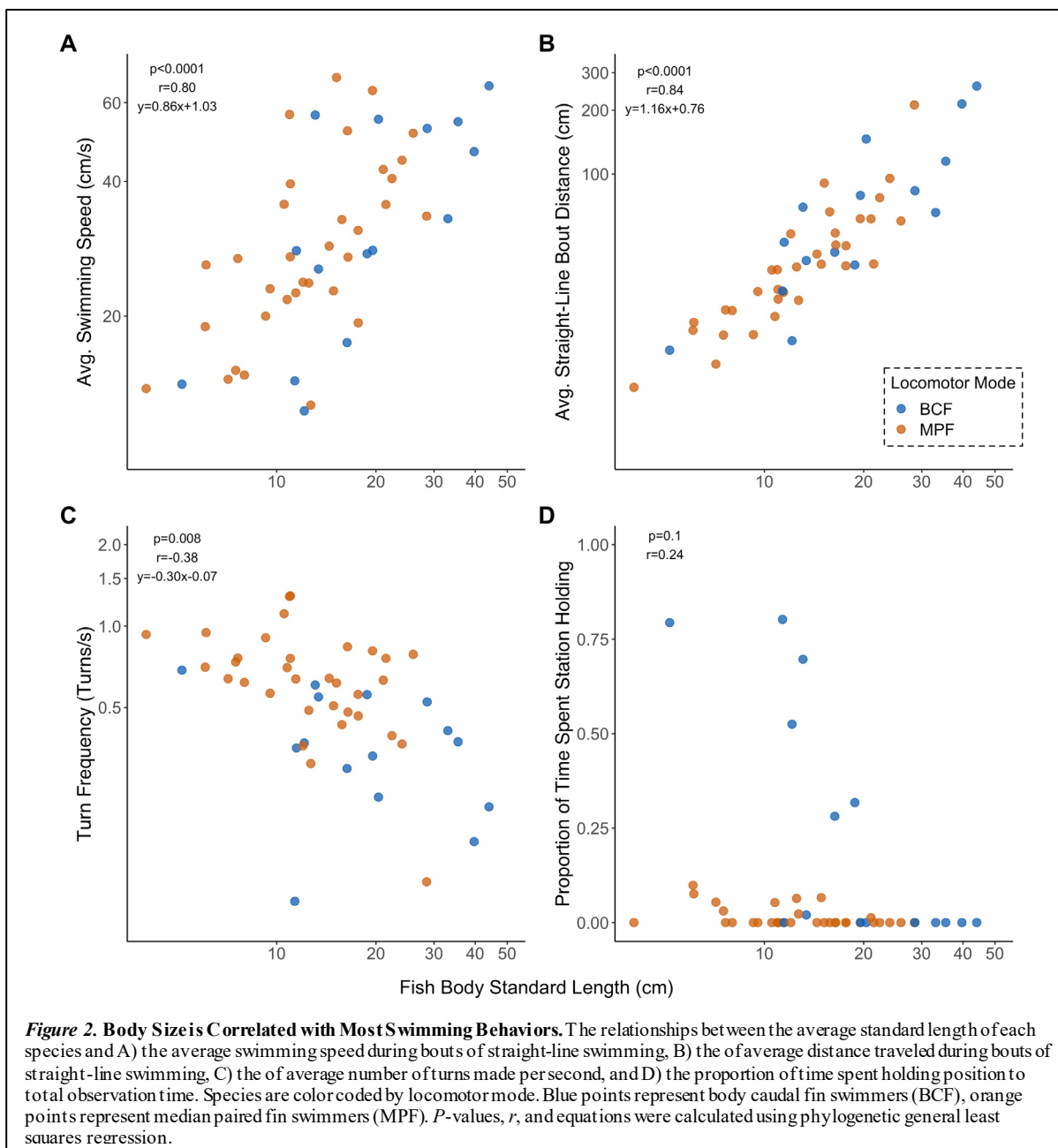
Behavior 1	Behavior 2	Expected Correlation	Results
Swimming Speed	Turning Frequency	-	+
Swimming Speed	Swimming Bout Distance	+	+
Swimming Speed	Proportion of Time Station Holding	+	0
Turning Frequency	Swimming Bout Distance	-	-
Turning Frequency	Proportion of Time Station Holding	-	- / 0
Swimming Bout Distance	Proportion of Time Station Holding	-	0

Table 2. Species List. Videos (N) is the number of individual video sequences sampled for each species. Body Elongation (BE) is calculated as the body depth / standard length. Cross Sectional Area (CS) is the body depth / fish width.

Species	Videos (N)	BE	CS	Species	Videos (N)	BE	CS	Species	Videos (N)	BE	CS
Acanthuridae				Kyphosidae				Pomacanthidae			
<i>Acanthurus thompsoni</i>	20	0.47	3.03	<i>Kyphosus cinerascens</i>	7	0.44	1.94	<i>Pygoplites diacanthus</i>	14	0.53	2.98
<i>Ctenochaetus striatus</i>	13	0.52	2.96	Labridae				Pomacentridae			
<i>Naso brachycentron</i>	9	0.43	3.59	<i>Anampses meleagrides</i>	13	0.28	2.14	<i>Abudefduf sexfasciatus</i>	14	0.54	2.85
<i>Naso brevirostris</i>	13	0.39	2.79	<i>Cheilinus fasciatus</i>	12	0.40	2.00	<i>Abudefduf sparoides</i>	10	0.55	2.67
<i>Naso elegans</i>	31	0.44	2.79	<i>Chlorurus sordidus</i>	7	0.35	1.98	<i>Chromis fieldi</i>	15	0.56	2.51
<i>Naso unicornis</i>	25	0.44	3.09	<i>Epibulus insidiator</i>	12	0.47	2.50	<i>Chromis ternatensis</i>	15	0.49	2.84
<i>Naso vlamingii</i>	17	0.40	2.61	<i>Gomphosus caeruleus</i>	11	0.27	2.13	<i>Chromis viridis</i>	11	0.48	2.72
<i>Zébrasoma scopas</i>	12	0.60	3.89	<i>Hemigymnus fasciatus</i>	10	0.39	2.03	<i>Plectrogyphidodon dickii</i>	9	0.56	2.68
Balistidae				<i>Labrichthys unilineatus</i>	15	0.34	2.26	<i>Plectrogyphidodon lacrymatus</i>	12	0.52	2.49
<i>Xanthichthys auromarginatus</i>	30	0.47	2.60	<i>Labroides dimidiatus</i>	12	0.24	2.04	<i>Pomacentrus sulfureus</i>	12	0.47	2.34
Caesionidae				<i>Oxycheilinus orientalis</i>	10	0.36	2.36	Tetraodontidae			
<i>Caesia xanthonota</i>	15	0.37	2.31	<i>Scarus caudofasciatus</i>	26	0.38	2.11	Arothron meleagris			
Carangidae				<i>Thalassoma hardwicke</i>	11	0.33	2.21	12	0.29	1.00	
<i>Caranx melampygus</i>	14	0.36	2.64	<i>Thalassoma lunare</i>	11	0.31	2.17	Zandriidae			
Chaetodontidae				Monacanthidae				<i>Zanclus cornutus</i>			
<i>Chaetodon auriga</i>	10	0.59	4.10	<i>Oxymonacanthus longirostris</i>	11	0.41	3.00	14	0.83	5.23	
<i>Chaetodon lunula</i>	11	0.66	3.85	Mullidae							
<i>Chaetodon mitratus</i>	23	0.60	3.49	<i>Parupeneus macronemus</i>	9	0.33	2.12				
<i>Chaetodon trifascialis</i>	12	0.54	3.00	Cirrhitidae							
<i>Chaetodon trifasciatus</i>	9	0.61	3.69	<i>Paracirrhites arcatus</i>	13	0.42	2.56				
Epinephelidae				<i>Paracirrhites forsteri</i>	11	0.37	1.98				
<i>Cephalopholis argus</i>	13	0.34	1.74	Pinguipedidae							
<i>Cephalopholis polleni</i>	28	0.36	1.70	<i>Parapercis hexoptalma</i>	12	0.20	1.04				
<i>Cephalopholis spiloparaea</i>	25	0.35	2.02								

Accepted Article





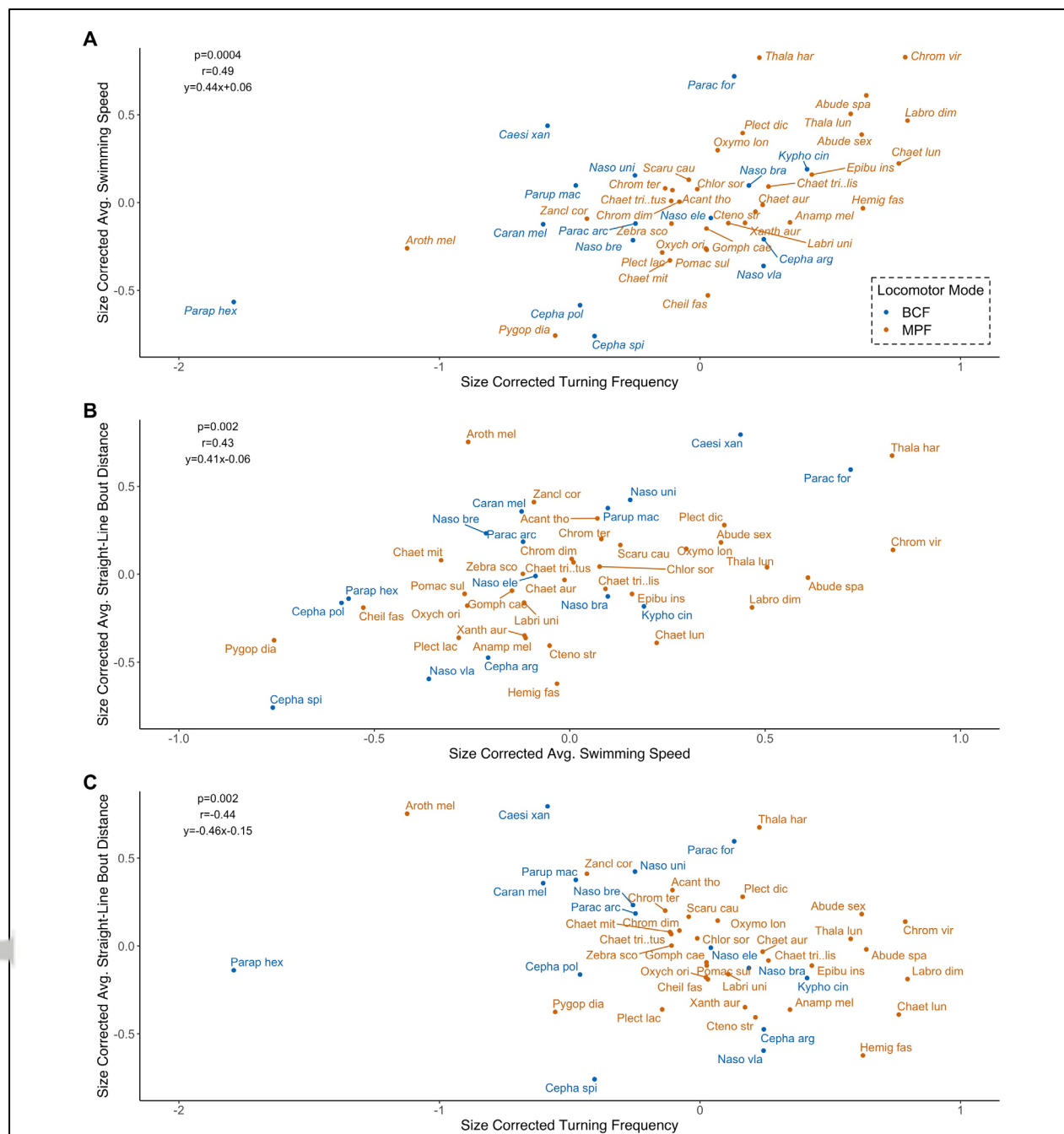


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