

Body shape and mode of propulsion do not constrain routine swimming in coral reef fishes

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Abstract

- 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 behaviour and dominates the ecomorphological literature, despite the paucity of field measurements.
- In this study, we measured variation in swimming behaviour 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.
- We find little evidence of the expected relationships between swimming behaviours 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 behaviours.
- Our results indicate that swimming behaviour is not easily predicted from simple measures of body shape and that alternative swimming modes can produce comparable behavioural profiles.

KEY WORDS

body shape, coral reefs, fish behaviour, fish ecology, locomotion, morphology, propulsion, swimming

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, 1984b). 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 et al., 2010). Webb (1984a) originally called these three categories maneuverers, cruisers and accelerators, respectively (Figure 1).

These three archetypes represent specialization in their respective behaviours 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, generalists have poorer maximum abilities than specialists on their respective axes but greater performance than specialists on the opposing axes (Figure 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 (Breder, 1926; 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 & Piller, 2015; Ehlinger & 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 & Dickson, 2000; Walker et al., 2013), 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 & 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 behaviour can be predicted by body shape (Figure 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 behavioural assumption is that these ‘cruising’

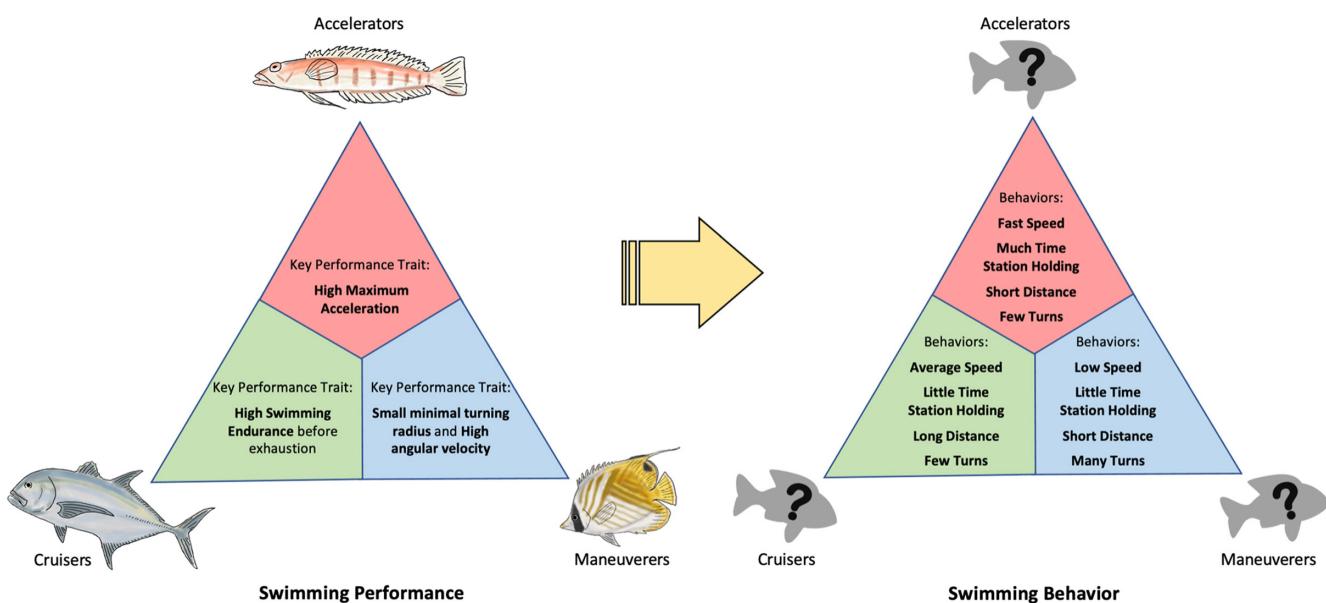


FIGURE 1 Fish swimming paradigm. An adaptation of Webb (1984a, Figure 1). On the left-hand triangle, corners represent swimming specialists while generalists have intermediate traits. Webb classifies swimming variation in terms of key performance traits. His hypothesis was that high performance in each 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 behaviour. On the right triangle, we show how four behavioural axes can be used to distinguish routine behaviours 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 behaviours to test for relationships between routine behaviour and body shape.

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 behavioural 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 barracuda, are expected to be capable of rapid acceleration from a halt. As such, elongate fishes are expected to use sit-and-wait behaviours, or long periods of station holding between short, rapid burst-swimming, often used to catch prey or evade predators (Porter & Motta, 2004; Tytell et al., 2010; Villéger et al., 2017). Despite the longstanding use of the cruiser–accelerator–maneuverer paradigm to infer routine behaviours, many of these relationships between body shape, axes of swimming performance and routine behaviours 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 behaviours used by fishes will also trade-off (Table 1). The behavioural 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 behaviours are characteristic of cruisers. Accelerators are characterized by long periods of sit and wait behaviour 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 behaviours 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 & 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 favourable for tight turns and fine directional control (Blake, 2004; Borazjani & Sotiropoulos, 2010; Lauder & Madden, 2007; Lauder & 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 & Sotiropoulos, 2010; Lauder & Madden, 2007; Lauder & 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 & Korsmeyer, 2019). Furthermore, deeper levels of complexity within locomotor modes can contribute to variation in swimming behaviours. 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 & 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 behaviour 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 behaviour 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 dataset of 48 species, we first look for predicted trade-offs and positive correlations between these behaviours (Table 1, Figure 1). We then test for an effect of species body shape on each of the swimming metrics. Finally, we contrast swimming behaviour in BCF and MPF swimmers, testing for the expected differences in average swimming speed and turning frequency. If swimming

TABLE 1 Predicted correlations between swimming variables versus observed relationships. Predicted pairwise relationships among four variables that describe swimming behaviour, as measured in this study. Expected correlations (positive or negative) are based on interpretation of properties of specialist swimmers as discussed in Section 1. The results column reports the results from PGLS regressions that test for each relationship. Results were counter to predictions in four of six cases

| Behaviour 1 | Behaviour 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 |

behaviours are constrained by body shape, this should lead to the expected relationships between the behavioural 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 | MATERIALS AND METHODS

2.1 | Behavioural 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 (26.5–29.5°C) and February (28.0–30.5°C). We selected videos in which water conditions were calm. The videos were recorded between 8:00am and 4:00pm and span 10 reef locations that range in depth from 2 to 81 m. 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 hr before recovery. Cameras were set to film in 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 $2 \times 2 \times 1$ m cubic contraption with 3D known coordinates positioned in two parallel planes for distance measurements 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 field-work or animal ethics permits were required for the collection of videos.

We collected swimming behaviour 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 $29 \text{ s} \pm 35.1 \text{ SD}$, representing an average of 424.6 s of observation on each species. To ensure that each sample video was of a unique individual, we allowed for at least 5 min of video time between selected observation clips. We began the measurements of behaviour 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 behaviours of fishes swimming around the reef. We digitized behaviours manually by marking the position of the fish in both camera views when behaviours of interest occurred. During the observation interval, we calculated the **net frequency of turns** to characterize routine use of maneuvers, and the percent of **time spent holding position** to characterize sit and wait behaviour. 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°. 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 labelled 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 (SL) of each subject fish. Averaging across samples (i.e. individual fishes), we calculated the species mean values of four behavioural traits, including turning frequency, average straight-line swimming speed, average straight-line swimming distance, station holding proportion and SL.

We categorized species by locomotor mode based on behaviour during routine straight-line swimming. Species were scored based on our observations and consultation of the literature. 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 used a publicly available dataset of eight body shape variables measured on museum specimen (Price et al., 2022). The body shape dataset 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).

The first three of the body shape variables we selected from this dataset were SL, maximum body depth (BD) and maximum fish width (FW). From these variables, we calculated body elongation (BE) as BD divided by SL. Elongation is the primary axis of body shape diversity in reef fish (Claverie & 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 BE alone is less predictive of swimming efficiency than when mode of propulsion and other axes

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 | | | | | | | | | | | |
| <i>Ctenochaetus striatus</i> | 20 | 0.47 | 3.03 | <i>Kyphosidae</i> | | | | <i>Pomacanthidae</i> | | | |
| <i>Acanthurus thompsoni</i> | 13 | 0.52 | 2.96 | <i>Kyphosus cinerascens</i> | 7 | 0.44 | 1.94 | <i>Pygoplites diacanthus</i> | 14 | 0.53 | 2.98 |
| <i>Naso brachycentron</i> | 9 | 0.43 | 3.59 | <i>Labridae</i> | | | | <i>Pomacentridae</i> | | | |
| <i>Naso brevirostris</i> | 13 | 0.39 | 2.79 | <i>Anampseseleotridae</i> | 13 | 0.28 | 2.14 | <i>Abudefduf sexfasciatus</i> | 14 | 0.54 | 2.85 |
| <i>Naso elegans</i> | 31 | 0.44 | 2.79 | <i>Chelmon fasciatus</i> | 12 | 0.40 | 2.00 | <i>Abudefduf spadiceus</i> | 10 | 0.55 | 2.67 |
| <i>Naso unicornis</i> | 25 | 0.44 | 3.09 | <i>Chlorurus sordidus</i> | 7 | 0.35 | 1.98 | <i>Chromis fieldi</i> | 15 | 0.56 | 2.51 |
| <i>Naso vlamingii</i> | 17 | 0.40 | 2.61 | <i>Epibulus insidiator</i> | 12 | 0.47 | 2.50 | <i>Chromis ternensis</i> | 15 | 0.49 | 2.84 |
| <i>Zebrafoma scopas</i> | 12 | 0.60 | 3.89 | <i>Gomphosus caeruleus</i> | 11 | 0.27 | 2.13 | <i>Chromis viridis</i> | 11 | 0.48 | 2.72 |
| Ballistidae | | | | | | | | | | | |
| <i>Hemigymnus fasciatus</i> | | | | <i>Hemigymnus fasciatus</i> | 10 | 0.39 | 2.03 | <i>Plectroglyphidodon dickii</i> | 9 | 0.56 | 2.68 |
| <i>Labrichthys unilineatus</i> | | | | <i>Labrichthys unilineatus</i> | 15 | 0.34 | 2.26 | <i>Plectroglyphidodon 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>Caesio xanthonota</i> | 15 | 0.37 | 2.31 | <i>Oxycheilinus orientalis</i> | 10 | 0.36 | 2.36 | | | | |
| <i>Caesio xanthonota</i> | | | | <i>Scarus caudofasciatus</i> | 26 | 0.38 | 2.11 | <i>Tetraodontidae</i> | | | |
| | | | | <i>Thalassoma hardwicke</i> | 11 | 0.33 | 2.21 | <i>Arthron meleagris</i> | 12 | 0.29 | 1.00 |
| | | | | <i>Thalassoma lunare</i> | 11 | 0.31 | 2.17 | | | | |
| Carangidae | | | | | | | | | | | |
| <i>Caranx melampygus</i> | 14 | 0.36 | 2.64 | <i>Monacanthidae</i> | | | | <i>Zanclidae</i> | | | |
| <i>Caranx melampygus</i> | | | | <i>Oxymonacanthus longirostris</i> | 11 | 0.41 | 3.00 | <i>Zanclus cornutus</i> | 14 | 0.83 | 5.23 |
| Chaetodontidae | | | | | | | | | | | |
| <i>Chaetodon auriga</i> | 10 | 0.59 | 4.10 | <i>Mullidae</i> | | | | | | | |
| <i>Chaetodon lunula</i> | 11 | 0.66 | 3.85 | <i>Parupeneus macronemus</i> | 9 | 0.33 | 2.12 | | | | |
| <i>Chaetodon mitratus</i> | 23 | 0.60 | 3.49 | | | | | | | | |
| <i>Chaetodon trifascialis</i> | 12 | 0.54 | 3.00 | <i>Cirrhitidae</i> | | | | | | | |
| <i>Chaetodon trifascialis</i> | 9 | 0.61 | 3.69 | <i>Paracirrhites arcatus</i> | 13 | 0.42 | 2.56 | | | | |
| | | | | <i>Paracirrhites forsteri</i> | 11 | 0.37 | 1.98 | | | | |
| Epinephelidae | | | | | | | | | | | |
| <i>Cephalopholis argus</i> | 13 | 0.34 | 1.74 | <i>Pinguipedidae</i> | | | | | | | |
| <i>Cephalopholis polleni</i> | 28 | 0.36 | 1.70 | <i>Parapercis hexophtalma</i> | 12 | 0.20 | 1.04 | | | | |
| <i>Cephalopholis spiloparaea</i> | 25 | 0.35 | 2.02 | | | | | | | | |

of shape diversity such as caudal peduncle and fin shape are included (Tytell et al., 2010; Tytell & Lauder, 2004). Additionally, we calculate cross sectional area, accounting 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; Tokić & Yue, 2012; Tytell et al., 2010; Webb, 1984a).

Additionally, we calculated size corrected head depth (HD), lower jaw length (JL), mouth width, 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 ($\left(\frac{\pi \times BD \times FW^3}{4}\right)$; 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 $\ln(\text{SMA})$ and $\ln(\text{SL})$.

2.3 | Analyses

Behavioural 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 (Figure 2a–c). We removed size effects by using residuals from linear regressions of the log-transformed behavioural variables versus the log of fish SL: $X' = \ln(X) - k \ln(L) - b$, where X' is the residual size corrected behavioural 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 behavioural variables in all subsequent analyses. We found no relationship between the time spent station holding and fish SL, so no size correction was performed on this variable (Figure 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 et al., 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., 2012]). Additionally, we used phylogenetic ANOVAs (GeoMorph [Adams et al., 2022; Baken et al., 2021]) to test if BCF and MPF swimmers differ in each swimming variable. To test for the effects of body shape on swimming behaviour, 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 behaviour, we ran a principal component analysis (PCA) on the eight body shape variables (body shape PCA). We then tested for the relationships between PC1 of the body shape PCA and our swimming behaviours using PGLS regressions.

3 | RESULTS

3.1 | Relationships between swimming variables

If body shape induces behavioural trade-offs, we would expect to find negative correlations between behaviours that typify the maneuverers, accelerators and cruisers, and positive correlations between behaviours that are both associated with one archetype. Using PGLS, we first tested the suspected trade-off between the use of maneuvers versus distance and swimming speed (i.e. between maneuverers and cruisers, Figure 1, Table 1). Opposite of expectations, we found a positive correlation between the average swimming speed and turning frequency ($p: 0.0004$, $r: 0.49$, Figure 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 ($p: 0.002$, $r: 0.43$, Figure 3b), as predicted. In line with expectations, we found swimming distance and turning frequency to be negatively correlated ($p: 0.002$, $r: -0.44$, Figure 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 versus the amount of time spent not swimming (between cruisers and accelerators, Figure 1, Table 1). However, our test for a correlation between the proportion of time spent station holding and swimming distance was not significant ($p: 0.63$, $r: 0.07$, Figure S1). Furthermore, we did not detect a significant correlation between the proportion of time spent station holding and swimming speed ($p: 0.24$, $r: 0.17$, Figure 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 dataset 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 (Figure 2d).

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

The PGLS analyses used to independently compare the body shape variables and swimming behaviours showed no significant relationships (Figure 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 shape PCA (Figure 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

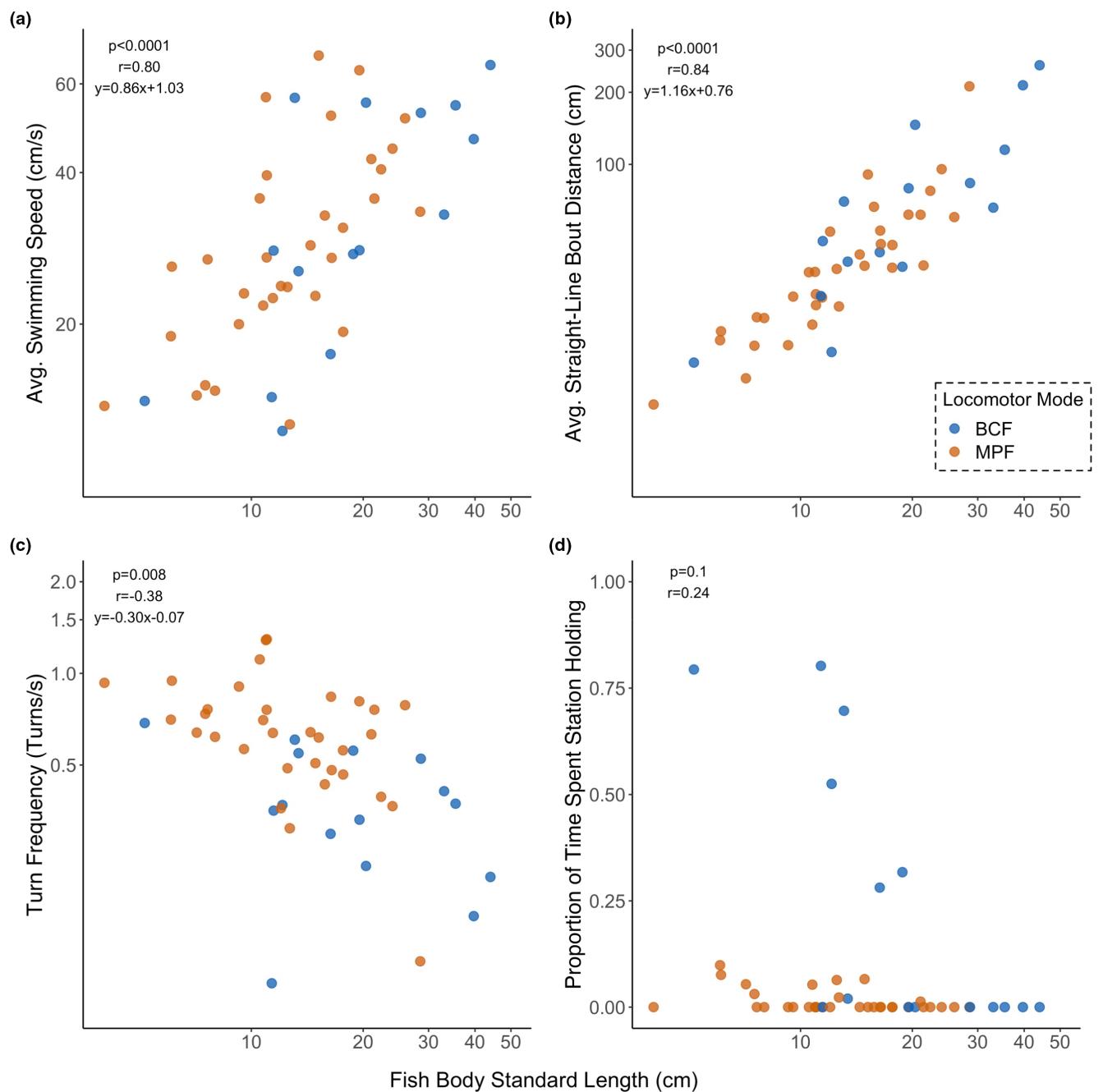
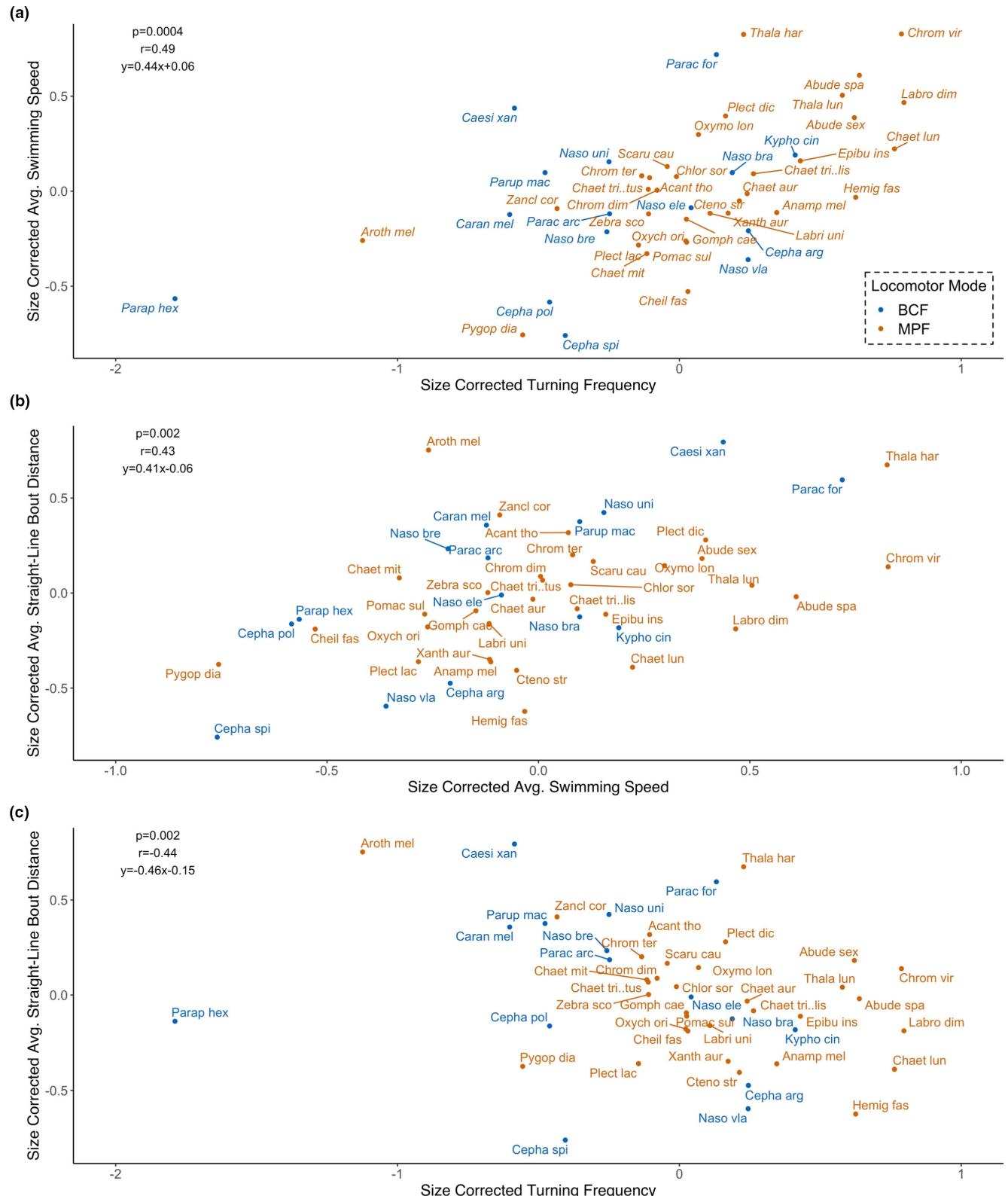


FIGURE 2 Body size is correlated with most swimming behaviours. The relationships between the average SL of each species and (a) the average swimming speed during bouts of straight-line swimming, (b) the of average distance travelled during bouts of straight-line swimming, (c) the of average number of turns made per second, and (d) the proportion of time spent holding position to total observation time. Species are colour coded by locomotor mode. Blue points represent body caudal fin swimmers, orange points represent median paired fin swimmers. p -values, r , and equations were calculated using phylogenetic general least squares regression.

area (CS), BE and 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 (Figure 4). We found no effects of PC1, PC2 or their interaction on average swimming speed or swimming bout distance (Figure 4b,c). There were also no effects of PC1 or PC2 individually on turning frequency, however there was a weakly significant interaction effect ($p: 0.043$; Figure 4d). This trend is driven by the presence of *Parapercis hexophtalma*, which has the highest BE 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 dataset 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 dataset were the five 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 (Figure 3a); *Chaetodon lunula* had a high turning frequency. *Parapercis hexophtalma* was the most

FIGURE 3 Behavioural 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 labelled by the first five letters of the genus and first three letters of the species. For very similar species, the last three 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 Figure 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 Figure 2b. Average straight-line distance values are the residuals of the relationship between the natural log of the species average for distance travelled during straight-line swimming and the natural log of the average fish body length (cm), shown in Figure 2c. Species are colour coded by locomotor mode. Blue points and bars represent body caudal fin swimmers, orange points and bars represent median paired fin swimmers. *p*-values, *r*, and equations were calculated using phylogenetic general least squares regression.

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 BE. 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 behaviours

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; Figure 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 behaviour. 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 behaviour (Costa & 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 behaviour. 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 behaviour in coral reef fishes.

4.1 | Trade-offs and correlations between behavioural 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 trade-offs with the other axes. The behavioural analog of these predictions is the expectation of trade-offs between suites of behaviours that would distinguish maneuverers, cruisers and accelerators (Figure 1, Table 1). We did not observe strong evidence of the expected relationships between our four differentiating behaviours: average swimming speed, swimming bout distance, turning frequency and the proportion of time spent station holding.

Only two of the six expected relationships between behaviours 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; Breder, 1926; Ellerby & 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 behaviour swim fast over short distances and do not turn frequently when they are swimming (Higham, 2007; Villéger et al., 2017). We observed that fishes that use sit-and-wait behaviour 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.

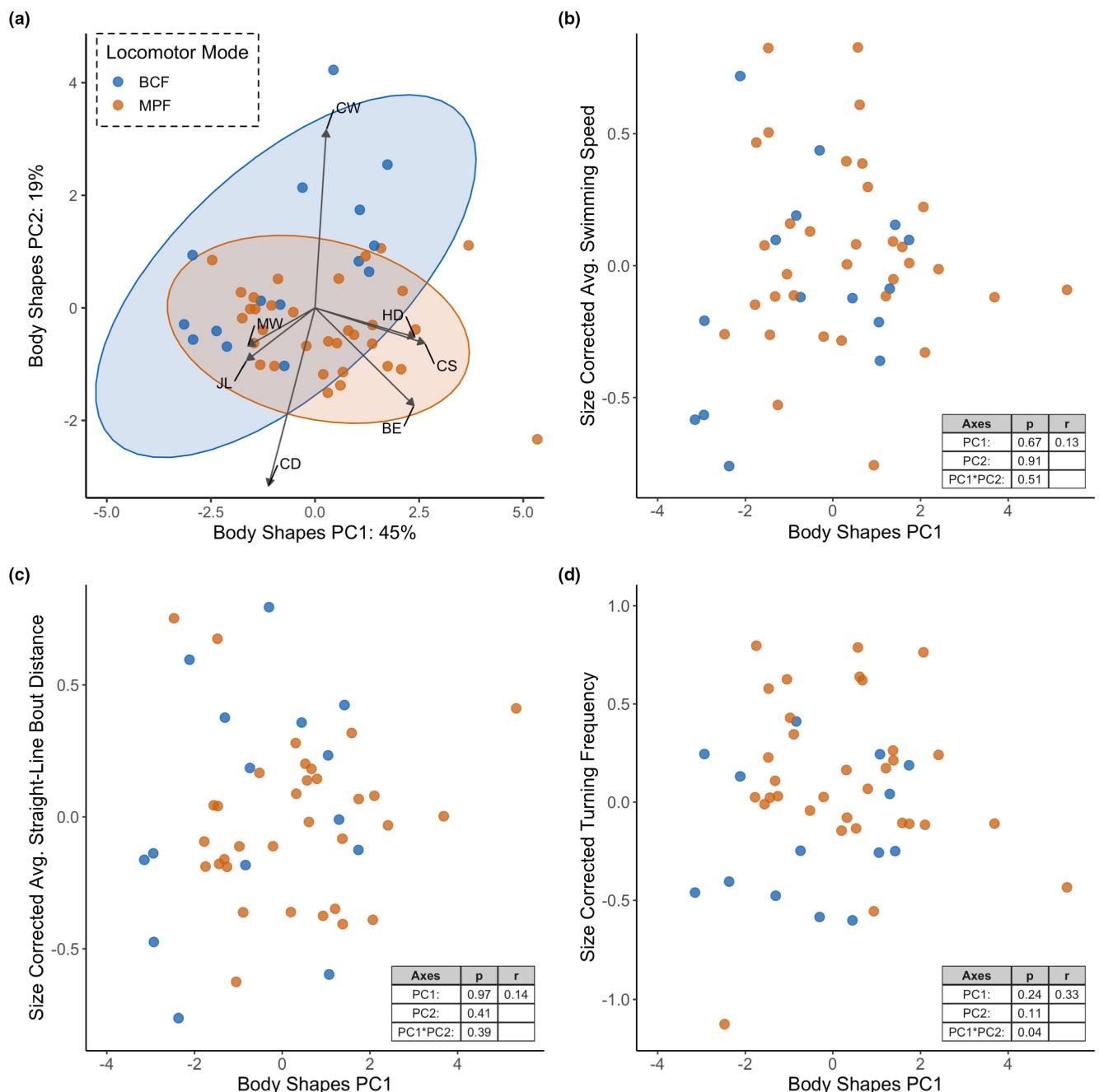


FIGURE 4 The effects of body shape on swimming Behaviours. (a) a morphospace principal component analysis modified from Friedman et al. (2021) and Price et al. (2022), where species scores are plotted on the first two principal components axes, PC1 versus PC2. Body shape ratios included as loadings are 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 versus PC1. Average straight-line distance values are the residuals of the relationship between the natural log of a species' average distance travelled during straight-line swimming and the natural log of the average fish body length (SL; cm). (c) Average straight-line distance versus PC1. Average straight-line distance values are the residuals of the relationship between the natural log of the species average for distance travelled during straight-line swimming and the natural log of SL. (d) Turning frequency versus 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 colour coded by locomotor mode. Blue points represent body caudal fin swimmers, orange points represent median paired fin swimmers. 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 behaviours versus the body shape PCs.

However, as this relationship is weak and highly sensitive to the inclusion of one species, *Parapercis hexophtalma*, 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 behaviours. A possible explanation for why our findings did not match expectations is that peak performance may not be a strong predictor of routine swimming behaviour. It is possible that the use of maximum performance is uncommon in the daily life of animals and routine behaviours may usually fall well below maximum capacity. While many studies find that maximum swimming performance and routine behaviour are significantly correlated (Fisher & 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 behaviour in reef fishes, so that these relationships are not manifested in average swimming profiles.

4.2 | Effects of body shape on swimming

Body shape is classically expected to underly the expected trade-off between axes of swimming performance (Blake, 2004; Webb, 1984a). It is intuitive that to maintain low fitness costs, fishes would be unlikely to routinely use behaviours that are energetically expensive and that the routine behaviours used by a fish would reflect the body shape. However, we found that variation among species in most routine swimming behaviours 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 behaviour 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 behavioural axes (Figure 3). One of the many examples of the lack of morphological similarity among fishes in the same region of behaviour-space (high-distance/low-turning frequency) can be found between *Zanclus cornutus*, the most deep-bodied species in the dataset (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 behaviour. 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 good examples of how much behavioural 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 behaviours.

Although theory suggests that maximal swimming performance is limited by body shape, our observations show that routine behaviours 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 behaviours. However, a second possible explanation is that the mapping of morphology to swimming performance in fishes is more complex than previously thought.

Although 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 & Gerry, 2011; Gerry et al., 2012; Langerhans, 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 et al., 2016; Friedman et al., 2016; Jastrebski & Robinson, 2004), increased maneuvering (Ehlinger & 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 & Nipper, 1996; Wainwright et al., 2002; Walker, 2000; Walker & 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.

4.3 | 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 behaviours available to fish. Biomechanical analyses suggest that MPF swimming offers maximum control during slow-speed maneuvering (Lauder & 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 & Lynch, 2004; Korsmeyer et al., 2002; Lauder & Tytell, 2005; Sfakiotakis et al., 1999; Webb, 1984a). Although numerous species have been shown to transition from MPF to BCF as swimming speed increases (Cannas et al., 2006; Drucker & Jensen, 1996; George & Westneat, 2019; Korsmeyer et al., 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 behavioural profile while swimming.

We found no significant difference between the behavioural profiles of MPF and BCF swimmers. Furthermore, species that emphasize either locomotor mode can achieve behavioural extremes in turning frequency, average swimming and straight-line distance (Figures 3 and 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 behaviour and support the previous findings that MPF swimmers can be highly efficient over a wide range of speeds (Korsmeyer et al., 2002). Furthermore, our findings indicate behaviours are not sensitive to the additional drag experienced by BCF swimmers due to the undulating body, compared with the fixed body of MPF swimmers (Lighthill, 1969; Lighthill & 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 & Wainwright, 2001; Fulton & Bellwood, 2004, Fulton et al., 2005).

5 | CONCLUSIONS

With the advancing tools available to study fish undisturbed in situ, it is likely that our dataset is only the beginning of what will become a large and diverse record of routine behaviour in fish. Analyses of the effects of factors other than body shape and locomotor mode will help to elucidate predictors of diversity in routine behaviour. 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 behaviour. As such, inferring routine behaviour in fishes based on body shape should be avoided.

AUTHOR CONTRIBUTIONS

Darien R. Satterfield, Thomas Claverie and Peter C. Wainwright designed the research questions and methodology. Thomas Claverie did the fieldwork and collection of videos. Darien R. Satterfield collected data from the videos. Darien R. Satterfield and Peter C. Wainwright analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

We have no conflicts of interest to report.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.25338/B8R056> (Satterfield et al., 2022).

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