

RESEARCH ARTICLE

Swimming with multiple propulsors: measurement and comparison of swimming gaits in three species of neotropical cichlids

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ABSTRACT

Comparative studies of fish swimming have been limited by the lack of quantitative definitions of fish gaits. Traditionally, steady swimming gaits have been defined categorically by the fin or region of the body that is used as the main propulsor and named after major fish clades (e.g. carangiform, anguilliform, balistiform, labriform). This method of categorization is limited by the lack of explicit measurements, the inability to incorporate contributions of multiple propulsors and the inability to compare gaits across different categories. I propose an alternative framework for the definition and comparison of fish gaits based on the propulsive contribution of each structure (body and/or fin) being used as a propulsor relative to locomotor output, and demonstrate the effectiveness of this framework by comparing three species of neotropical cichlids with different body shapes. This approach is modular with respect to the number of propulsors considered, flexible with respect to the definition of the propulsive inputs and the locomotor output of interest, and designed explicitly to handle combinations of propulsors. Using this approach, gait can be defined as a trajectory through propulsive space, and gait transitions can be defined as discontinuities in the gait trajectory. By measuring and defining gait in this way, patterns of clustering corresponding to existing categorical definitions of gait may emerge, and gaits can be rigorously compared across categories.

KEY WORDS: Fish swimming, Gait, Kinematics, Fins, Biological propulsors

INTRODUCTION

Fishes are diverse and effective swimmers. There is much to be learned from the study of their swimming biomechanics, including different means of thrust generation and maneuvering, morphological design strategies, and effective kinematic motions for propulsion. The study of fish swimming, however, has been hampered by the lack of effective means of measuring and comparing fish gaits. There are myriad combinations of propulsive motions that fishes use across and within any given body shapes (e.g. Breder, 1926; Webb, 1973, 1984; Lindsey, 1978; Lauder and Madden, 2006; Korsmeyer et al., 2002; Arreola and Westneat, 1996; Lauder, 2006). Without the ability to measure and

compare these gaits, it is virtually impossible to disentangle the effects of fish morphology and steady swimming kinematics (gait) on swimming performance.

Efforts to create a means of gait measurement and comparison in swimming fish are aided by the rich literature in both descriptive classifications of fish gait and quantitative methods for comparing tetrapod gaits. Existing classification schemes for fish gaits provide easily identifiable categorical gait designations, and identify defining characteristics of different swimming modes, but preclude comparisons across these categories (e.g. Breder, 1926; Lindsey, 1978; Webb, 1984; Sfakiotakis et al., 1999). Any effective means of comparing gaits should be able to distinguish differences contributing to these existing classifications. The long history of gait study in terrestrial biomechanics (e.g. Hildebrand, 1965, 1976, 1977, 1989) inspired the approach taken here to quantitatively describe swimming gaits. Specifically, it suggested that if one could find repeatable, quantifiable parameters describing steady locomotion, these could be plotted on axes to define a gait space. The goal of the present study was to integrate these two bodies of literature (fish swimming kinematics and approaches to terrestrial gait description) to create and test a means of measuring and comparing fish gaits across taxa.

Fish gait classifications are traditionally based on differences in which anatomical structures (e.g. fins, body) are used in propulsion, and whether these propulsors are used in an oscillatory versus an undulatory motor pattern. Each classification is typically named after a fish or group of fishes that use that particular gait. For example, the thunniform gait (after the tunas of genus *Thunnus*) describes locomotion by caudal fin oscillation exclusively. The labriform gait (after wrasses, family Labridae) describes locomotion by pectoral fin oscillation. There are at least 16 of these gait categories (Sfakiotakis et al., 1999). Within a particular gait category, the magnitude of the frequency and amplitude of the undulation or oscillation determines swimming speed. Any suitable gait measurement system should then rightly include these kinematic parameters.

Although existing swimming gait categories have descriptive value, they preclude quantitative comparison across categories. In addition, the ability of fishes to use multiple propulsive elements while swimming steadily at a given speed – a fact typically not incorporated into gait classifications – should be explicitly incorporated into any new gait measurement. Existing gait categories focus on single dominant propulsors and, therefore, using these categories facilitates omission of the often considerable, simultaneous contributions of non-primary propulsors. For example, the traditional body–caudal fin undulatory mode of locomotion ignores the fact that median fins are active in addition to body undulation (Tytell et al., 2008; Standen and Lauder, 2005), and that the pattern of median fin activity changes as swimming

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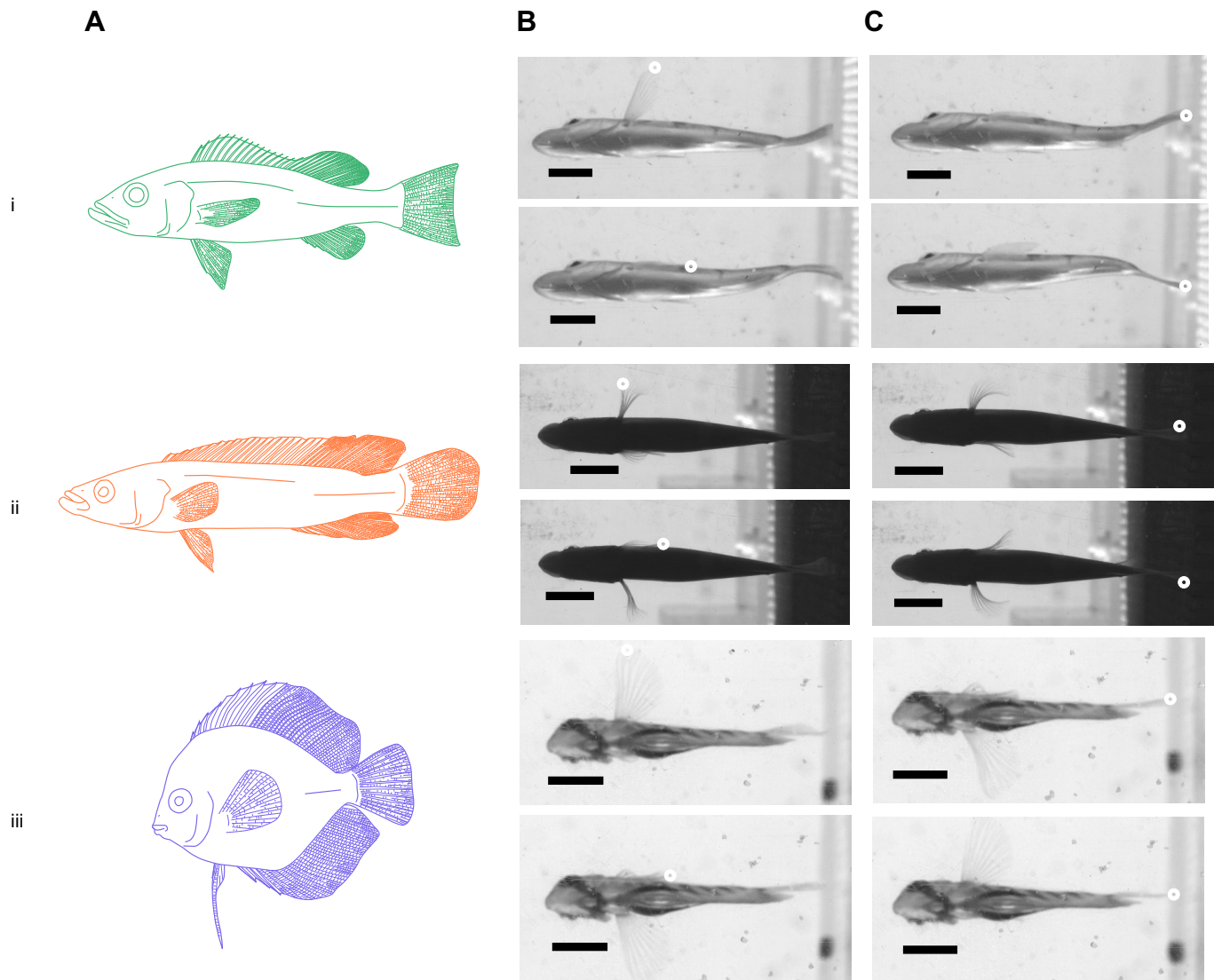


Fig. 1. The three species used in this study: (i) *Cichla ocellaris*, (ii) *Crenicichla saxatilis* and (iii) *Symphysodon aequifasciatus*. (A) Lateral profile. Colors for each fish correspond to those used for each species in Figs 3–7. (B,C) Representative pectoral (B) and caudal (C) fin beats at 1.5 body lengths (BL) s⁻¹. The points from which amplitude was calculated are shown by white circles. Scale bars, 2 cm.

speed increases (Drucker and Lauder, 2005; Standen and Lauder, 2005). Finally, the inability to quantify kinematic patterns complicates any attempt to associate gait with or isolate gait from other traits that may influence performance such as muscle physiology or morphology.

Here, I compare three species of neotropical cichlids of different body and fin morphology with respect to their gaits and steady swimming performance using a new framework for steady swimming gait comparison. These species, *Cichla ocellaris*, *Crenicichla saxatilis* and *Symphysodon aequifasciatus*, have body shapes that are typically associated with specific locomotor modes and performance capacities (see below and Fig. 1; hereafter these species will be referred to by genus only). *Cichla* has a typical perciform body shape: it is slightly laterally compressed, has a tapered caudal peduncle and what could be considered ‘generalist’ fin morphology (Webb, 1984). It was therefore predicted to have the best cruising (i.e. steady swimming) performance, measured as maximum prolonged swimming speed, and to use chiefly a body–caudal fin undulatory gait as opposed to labriform–pectoral fin–

based propulsion. *Crenicichla* has an ‘acceleration-specialist’ morphology, with a very cylindrical muscular body and caudally positioned fin area. Based on the hypothesized tradeoff between acceleration and cruising performance (Webb, 1984), it was predicted that *Crenicichla* would have the lowest steady swimming performance. *Symphysodon* has an extreme body shape associated with maneuvering performance (Webb, 1984): it is extremely laterally compressed, and has a deep disc-shaped body with large median fins, and was therefore predicted to have intermediate swimming performance. The likelihood of these species having different gaits made them an appropriate test case for a new approach to comparing swimming gaits.

MATERIALS AND METHODS

Fish care and maintenance

Five specimens each of *Symphysodon aequifasciatus* Pellegrin 1904 (standard length, SL 8.5±0.5 cm, mean±s.d.), *Crenicichla saxatilis* Linnaeus 1758 (SL 10.9±0.1 cm) and *Cichla ocellaris* Bloch and Schneider 1801 (SL 9.8±1.2 cm) were obtained through the pet

trade, and housed at 28°C with a 12 h:12 h light:dark cycle for at least 2 weeks in the lab before the beginning of experiments. *Symphysodon* and *Cichla* were maintained at pH 7, and *Crenicichla* were maintained at pH 6.2. *Symphysodon* are typically maintained at a lower pH, but these specimens were bred and raised by the breeder at pH 7. Experiments were conducted in water matching that used to house each species at 28°C. Experimental and fish care protocols were approved by the Harvard University Institutional Animal Care and Use Committee under protocol 20-03 to George Lauder.

Steady swimming performance trials and analysis

Three trials from each fish were used (if possible, but see Table S1 for sampling) to measure steady swimming kinematics and performance. Trials were conducted in a 600 l swimming flume with the working section restricted to 26 cm×26 cm×28 cm. For each trial, the fish swam for step increases from 0.5 body lengths (BL, measured as SL) per second, increasing by 0.2 BL s⁻¹ until burst and coast swimming was observed, following the procedure of Ellerby and Gerry (2011). Each swimming speed interval lasted 15 min, until burst-and-coast behavior was observed. Increases in speed were gradual over 30 s between 15 min intervals.

Steady swimming performance was measured as maximum prolonged swimming speed (He, 2010). Maximum prolonged swimming speed (U_{\max}) was calculated as a function of the fastest speed that could be sustained for 15 min (U_{last}) and the length of time spent at the subsequent speed before anaerobic burst-and-coast behavior was observed (t_{final}) (Ellerby and Gerry, 2011) as follows:

$$U_{\max} = U_{\text{last}} + \frac{t_{\text{final}}}{15 \text{ min}} (0.2 \text{ BL s}^{-1}). \quad (1)$$

Pectoral–caudal gait-transition speed (U_{trans}) was also recorded, as it is one of the few existing quantitative characterizations of kinematic steady swimming patterns. U_{trans} was defined as the speed at which a fish began to employ its caudal fin for propulsion, as many fishes never fully transitioned from exclusively pectoral to exclusively caudal propulsion.

Each of these metrics was best represented by a normal distribution, and each was compared using a linear mixed-effects model fitted by restricted maximum likelihood (REML) with species as a fixed factor and specimen as a random factor using the R package *lme4* (Bates et al., 2015). *Post hoc* Tukey HSD tests were conducted using R package *multcomp* (Hothorn et al., 2008) to determine which species had significantly different performance.

Kinematic data collection and analysis

From each trial, for each speed interval where possible, 10 s of steady swimming were recorded in lateral and ventral view at 250 frames s⁻¹ with 1024×1024 pixel resolution using two digital high-speed cameras (FASTCAM-1024PCI, Photron USA Inc., San Diego, CA, USA), with one pointed at a 45 deg angle front-faced mirror positioned under the flume working section. Both cameras were positioned far enough away from the flume that diffraction correction was not required. For some intervals, the fish position in the flume made video unattainable. Trials were included or excluded on the basis of the number of speed increments for which steady swimming video was recorded. If no swimming was recorded for three or more increments (typically for behavioral reasons), a trial was excluded. Table S1 gives the number of successful trials for each individual fish, and whether the individual was included in summary analyses.

For *Crenicichla*, successful trials were only obtained for three out of more than 20 attempts, and only with a black screen covering the

wall of the flume: therefore, for this species, only ventral view videos were possible.

Videos were calibrated using a 1 cm×1 cm grid pattern photographed at multiple positions in the working section in both lateral and ventral views. From measurements of these images, two linear equations were fitted to find pixel-to-centimeter conversion factors in both the vertical and horizontal plane.

Pectoral and caudal fin frequency and amplitude were recorded from the ventral view videos. Caudal fin amplitude was defined as the tip-to-tip displacement of the fin edge perpendicular to the direction of flow. Pectoral fin amplitude was as pectoral fin tip displacement, the farthest displacement of the tip of the pectoral fin from the position closest to the body during the fin beat (shown in Fig. 1). All amplitude measurements were made from the video in pixels using ImageJ, then converted to centimeters using the calibration factors for the fish's position in the working section (ImageJ v.1.51f, Fiji distribution; Schindelin et al., 2012; Schneider et al., 2012). Fin beat frequency, amplitude and the product of these were compared using linear mixed-effects models fitted by REML with species as a fixed factor and individual as a random factor, using unnormalized speed as a covariate using R package *lme4* (Bates et al., 2015).

Body midline kinematics were traced from ventral view video for representative individuals of *Cichla* and *Symphysodon*. For *Crenicichla*, midline traces were taken only from those rare trials where the fish actually swam, which were probably not 'representative' of typical behavior in the field. The midlines were taken from single body undulation cycles at every 10% of the undulatory cycle from 0%, resulting in 10 midline traces per speed. Midlines were compared qualitatively.

Parameterization of gait as a trajectory through propulsive space

Traditionally, fish gaits have been classified categorically and qualitatively, leaving researchers ill-equipped to address questions concerning the use of multiple propulsive elements including non-dominant propulsive structures, and how each propulsor may change kinematics with swimming speed. This prohibits quantitative comparison of gaits across fishes that use different categories of gait. For instance, under the existing categorization, there is no quantitative means to compare the 'gait-space' occupied by, say, a trout and a wrasse, or the extent of kinematic changes needed by either to produce an equivalent change in speed. Here, I propose a different means of defining gait that allows the treatment of multiple propulsors and quantitative analysis and comparison.

Gait can be thought of as the combination of propulsive inputs, be they from legs, bodies or fins, to produce a given locomotor output (i.e. speed or thrust). To quantify gait, then, one needs to parameterize those propulsive inputs and the output of interest (Eqn 2), where n is the number of propulsors:

$$\text{Output} = \sum_{i=1}^n \text{Input}_i. \quad (2)$$

The question arises, how does one parameterize the extent to which a given propulsor contributes to the locomotor output? One reasonable candidate for this is the product of frequency (f) and amplitude (A) of a propulsor, as in Webb (1973). For a fin, this is effectively the distance that fin travels per second to achieve a particular speed. This value is also proportional to the Strouhal number, a number that may be of particular importance for

swimming kinematics (Taylor et al., 2003; Eloy, 2012; Nudds et al., 2014). If we define the input, propulsor effort (Eff) for a given propulsor i as:

$$\text{Eff}_i = f_i \times A_i, \quad (3)$$

and speed (U) as the propulsive output, then we can express gait as the proportionality:

$$U \propto \sum_{i=1}^n \text{Eff}_i. \quad (4)$$

For a fish in which the propulsors of interest are the pectoral fins and the caudal fins, we can then think of gait as the series of inputs producing each speed:

$$U \propto \text{Eff}_{\text{pectoral}} + \text{Eff}_{\text{caudal}}. \quad (5)$$

This can be visually depicted as in Fig. 2. Note that this approach is modular, and easily modified to examine different output variables, different numbers of propulsors and different effort or input equations.

To demonstrate how this approach would work for more than two propulsors, including a term for body undulation, a simulated data set (see Supplementary Information 1 and Table S2) was created based on pectoral and caudal effort measures collected here, estimates of body undulations from observed midline kinematics, and manufactured data for median fin kinematics. A good candidate

for a metric describing body undulation can be defined as follows:

$$\text{Eff}_{\text{body}} \propto \frac{\int A dL}{L} \times f_{\text{body}}, \quad (6)$$

where $(\int A dL)/L$ is the average lateral amplitude along the length of the body from snout to posterior end of the caudal peduncle (excluding the tail), and f_{body} is the frequency of body undulation. This metric is similar to and has the same units as fin effort; and is similar in derivation to other measures of body undulation (Aleyev, 1977). Example values for this metric are included in Fig. 4 and used in Supplementary Information 1 with simulated data (included in Table S2). It is worth noting here that caudal fin effort and body undulation effort defined as above will be related, as caudal fin effort is a product of undulation of the body producing translation of the caudal fin base and the intrinsic movement of the caudal fin. However, if body undulation is measured, it is easy to distinguish independent caudal fin movement (body effort ≈ 0 , caudal fin effort > 0) from that caused by undulation of the body (body effort > 0 , caudal fin effort > 0).

If we restrict ourselves to the two-propulsor case, this framework also provides an easy means of visually characterizing and comparing gait in a quantitative framework, by plotting the output as a function of the propulsive inputs. In this context, gait is the trajectory through a 3D propulsive space, and a true ‘gait transition’ would be represented as a discontinuity in this trajectory. For example, Fig. 2 demonstrates three possible gait trajectories that one would expect of traditional swimming modes. A ‘perfectly labriform’ fish would increase steady swimming speed by

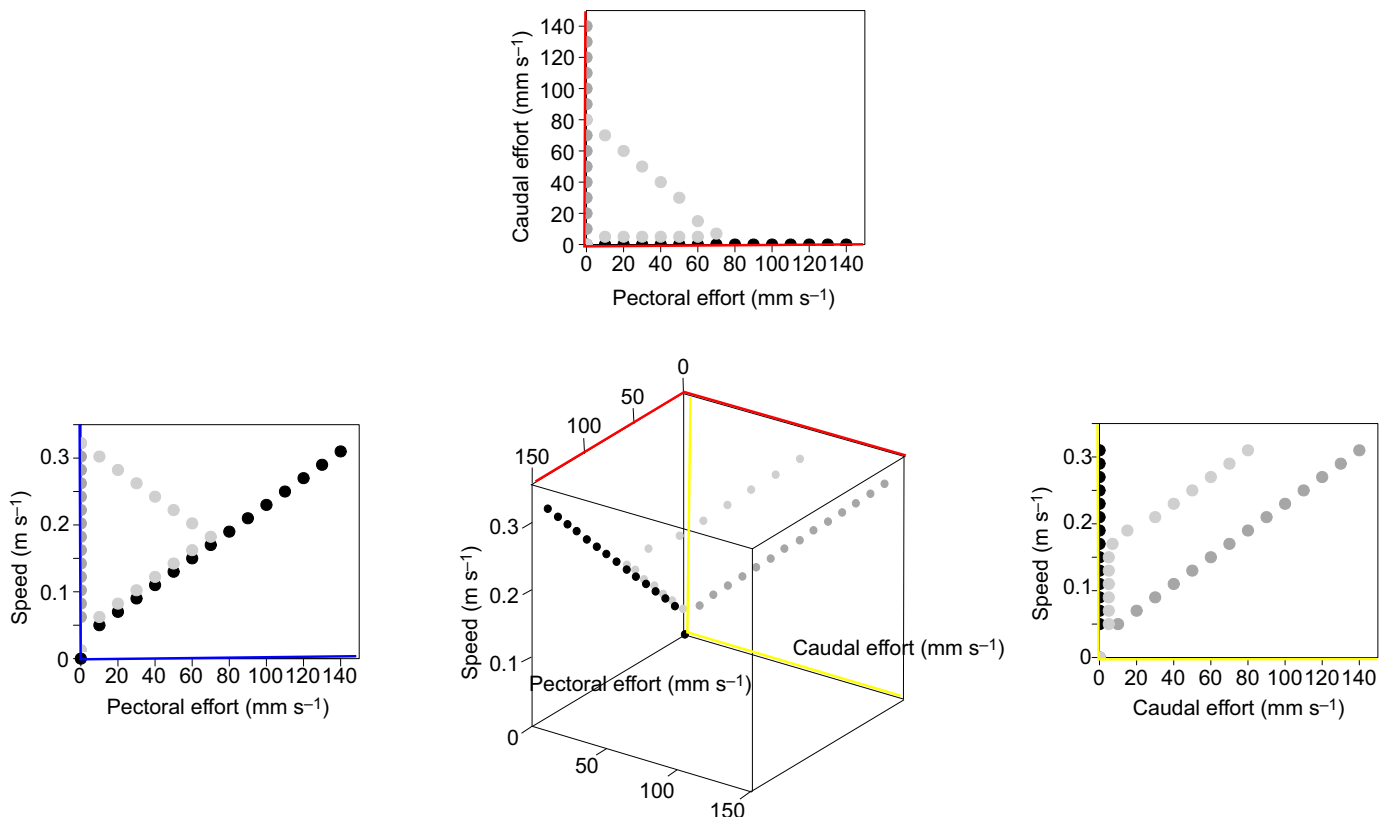


Fig. 2. Hypothetical ‘gait trajectories’ and 2-D isometric projections of three potential swimming ‘types’: perfectly labriform (black), perfectly carangiform (dark grey) and a type transitioning from labriform to body–caudal fin swimming (light grey). The projection on blue axes shows the contribution of the pectoral fins with speed. The projection on the yellow axes shows the contribution of the caudal fin with speed. The projection on the red axes can be considered the occupation of gait space, showing what combinations of propulsive movements are used by the fish. Note that the light grey trace has been shifted slightly in the y-axis to avoid overlap.

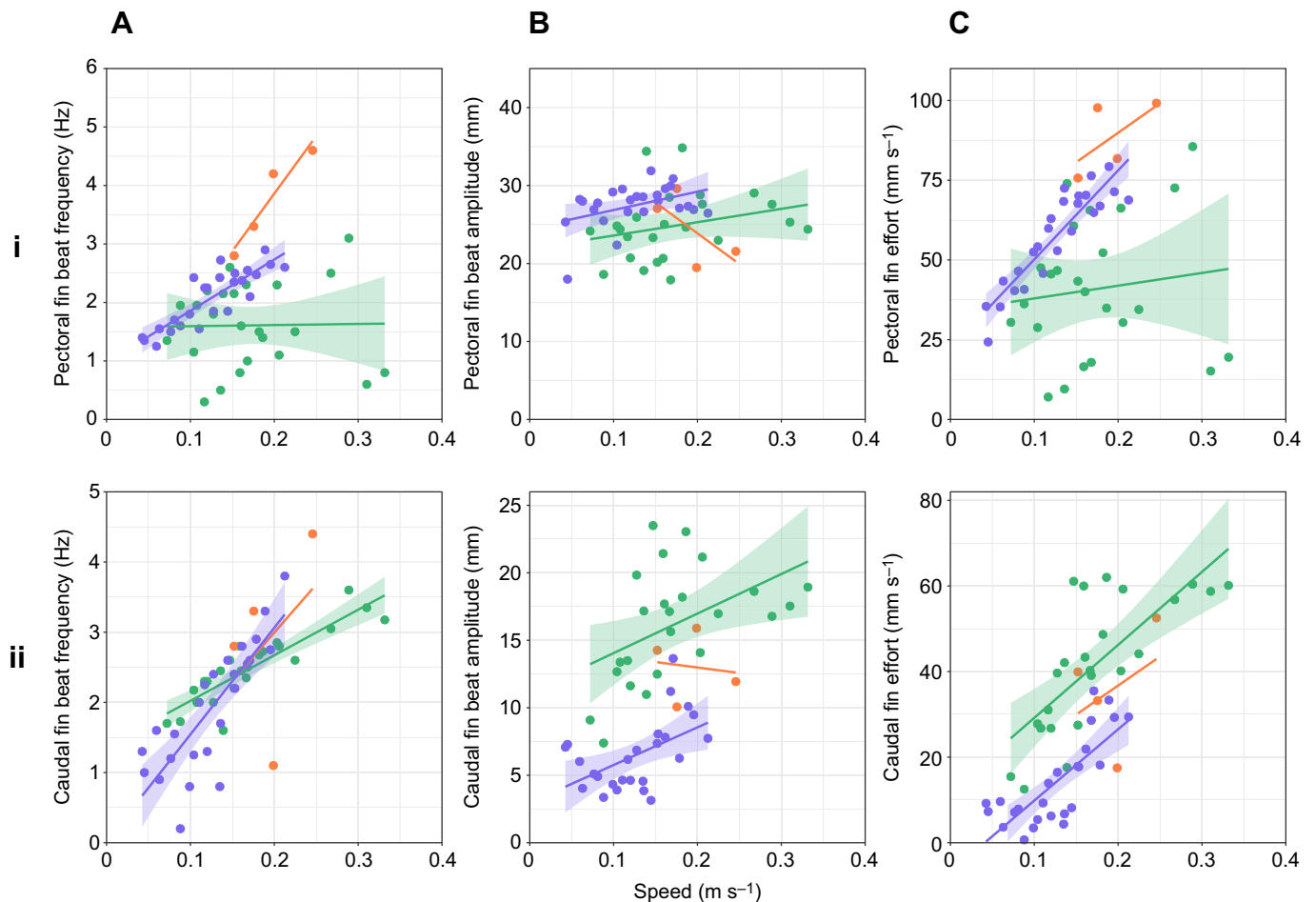


Fig. 3. Pectoral (i) and caudal (ii) fin beat frequency, amplitude and ‘effort’ as a function of steady swimming speed. (A) Fin beat frequency. (B) Fin beat amplitude. (C) Effort. Each point is the mean average of all trials at that speed for a given fish. Linear regressions for each species are shown with 95% confidence intervals shaded. There was insufficient sampling to calculate confidence intervals for *Crenicichla*. Species are indicated by color as in Fig. 1. Statistical comparisons are presented in Table 1. *Cichla* $n=4$; *Crenicichla* $n=2$; *Symphysodon* $n=3$.

increasing only pectoral input (black points); a ‘perfectly carangiform’ fish would increase speed by increasing only caudal input (dark grey points); and a fish with a typical paired-fin to body–caudal fin gait transition would have a bend in its trajectory through propulsive space, as it begins to favor the latter propulsive system (light grey points) (Fig. 2). When considering only the input axes, as in the top graph of Fig. 2, it is apparent that these hypothetical fish occupy different regions of gait space.

The above proportionality and graphing scheme was used to visually compare the trajectory through propulsor space (gait) of the three species examined here. Note that this approach still holds for more than two propulsors, but visualization of more than two propulsors requires multiple plots or application of dimension reduction techniques (see Supplementary Information 1 for demonstration).

Note on body size and scaling

There are some problems with methods accounting for the effects of scaling by simply dividing swimming speed by body length (Drucker and Jensen, 1996). While the individuals used in this study were all of very similar length, *Crenicichla* individuals were slightly larger than the others, and did not overlap with the other two species along the size domain, precluding their inclusion in a regression-based analysis with size as a covariate. Therefore, I chose to

compare midline kinematics, gait transition speed and maximum prolonged speed by normalizing swimming speed to standard length. Gait transition speed and maximum prolonged swimming speed are also given without normalization, but these values were not considered comparable for statistical testing. Kinematic parameters (i.e. frequency, amplitude, ‘effort’ as defined) and gait trajectories were compared and plotted without normalization, as there was no *a priori* expectation of how they will scale. That being said, use of this approach in the future can explicitly test for allometric effects on gait, given appropriate experimental design.

RESULTS

Differences in kinematic strategy

The three species of cichlids used different kinematic strategies to propel themselves at increasing speeds. Generally, all three species changed caudal fin beat frequency rather than caudal fin beat amplitude at different speeds, but varied both pectoral fin beat frequency and pectoral fin amplitude (Fig. 3, Table 1). Speed and species had interacting effects on all measures of pectoral fin use but independent effects on caudal fin use, i.e. different species had similar slopes of the curves of caudal fin kinematics against speed, but different intercepts (Table 1, Fig. 3). The changes across species typically involved which fins were being used at any given speed. At low speeds, *Cichla* used the pectoral fins as the primary

Table 1. Linear mixed-effects models to determine variation in fin beat frequency, amplitude and ‘effort’ with respect to speed and species (fixed effects) while accounting for individual variation (random effect)

Response variable	Speed:species (d.f.=2)	Speed (d.f.=1)	Species (d.f.=2)
Pectoral fin frequency	$\chi^2=19.78$, $P<0.001$	–	–
Pectoral fin amplitude	$\chi^2=8.18$, $P=0.017$	–	–
Pectoral fin effort	$\chi^2=28.20$, $P=0.003$	–	–
Caudal fin frequency	$\chi^2=3.17$, $P=0.205$	$\chi^2=58.08$, $P<0.001$	$\chi^2=6.33$, $P=0.042$
Caudal fin amplitude	$\chi^2=1.73$, $P=0.421$	$\chi^2=16.59$, $P<0.001$	$\chi^2=19.96$, $P<0.001$
Caudal fin effort	$\chi^2=0.76$, $P=0.685$	$\chi^2=55.98$, $P<0.001$	$\chi^2=15.10$, $P<0.001$

Data correspond with those depicted in Fig. 3. Where there was a significant interaction effect, single-factor effects are not reported. Statistics are reported from Type II Wald Chi-square tests of linear mixed-effects models.

propulsors, increasing pectoral fin beat frequency to speed up. At the gait-transition speed, *Cichla* began to use body–caudal fin propulsion, increasing caudal fin beat frequency while reducing pectoral fin beat frequency (Fig. 3, Table 1). *Symphysodon* used an alternative kinematic strategy, increasing both pectoral fin beat frequency and pectoral fin beat amplitude, and eventually employing the caudal fin to increase speed. *Crenicichla*, when it swam at all, increased pectoral fin beat frequency with increasing speed (Fig. 3, Table 1). Data from *Crenicichla*, however, may be unreliable, as the fish tended to ‘swim’ in contact with the bottom of the flume. The inability to elicit reliable steady swimming in *Crenicichla* raises the question as to whether this species has the physiological capacity for steady swimming at all.

Patterns of body undulation also varied across species (Fig. 4), and in the case of *Cichla* also varied with speed. Neither *Symphysodon* nor *Crenicichla* had any observable body bending during steady swimming at any speed. This was notable in *Crenicichla*, which has both the most elongate, anguilliform body shape and can bend with very low radius of curvature when maneuvering (K.F., personal observation). If *Crenicichla* swam steadily according to predictions based on its morphology, it would have used a more anguilliform gait (Webb, 1973). Instead, when it swam, it did so with a gait very similar to that of *Symphysodon* (Figs 3 and 4). *Cichla* used no body bending at low speeds, but increased its body bending as speed increased, maintaining almost a full sinusoidal wavelength along its body at the fastest speeds measured (Fig. 4).

Differences in morphology do not necessarily impose differences in performance

Despite the marked differences in morphology and, in some cases, kinematics across the three species, differences in steady swimming performance were small to negligible (Fig. 5). There was a significant effect of species on both normalized gait transition speed and normalized maximum prolonged swimming speed (U_{trans} : Type II Wold $\chi^2=6.33$, d.f.=2, $P=0.042$; U_{max} : Type II Wold $\chi^2=8.66$, d.f.=2, $P=0.013$). *Post hoc* testing did not reveal significant pairwise differences among gait transition speeds (Tukey contrasts: *Crenicichla*–*Cichla*: $P=0.083$; *Symphysodon*–*Cichla*: $P=0.093$; *Symphysodon*–*Crenicichla*: $P=0.897$). The only significant difference across species was between the maximum prolonged swimming speed of *Cichla* and *Symphysodon*, with *Cichla* having a significantly higher maximum prolonged speed (Fig. 5; Tukey contrasts: *Crenicichla*–*Cichla*: $P=0.234$; *Symphysodon*–*Cichla*: $P=0.011$; *Symphysodon*–*Crenicichla*: $P=0.934$). When this result is considered in conjunction with gait transition speed (defined as the speed at onset of caudal fin use), it shows that *Cichla* uses caudal fin-based propulsion for a broader speed range than *Symphysodon*, which may contribute to its steady swimming performance.

High variation in use of the non-primary propulsor

For the two species that swam consistently, the gait trajectories reveal that one propulsor had a much noisier relationship with speed than the other (Fig. 6). For *Cichla*, the pectoral fins were used

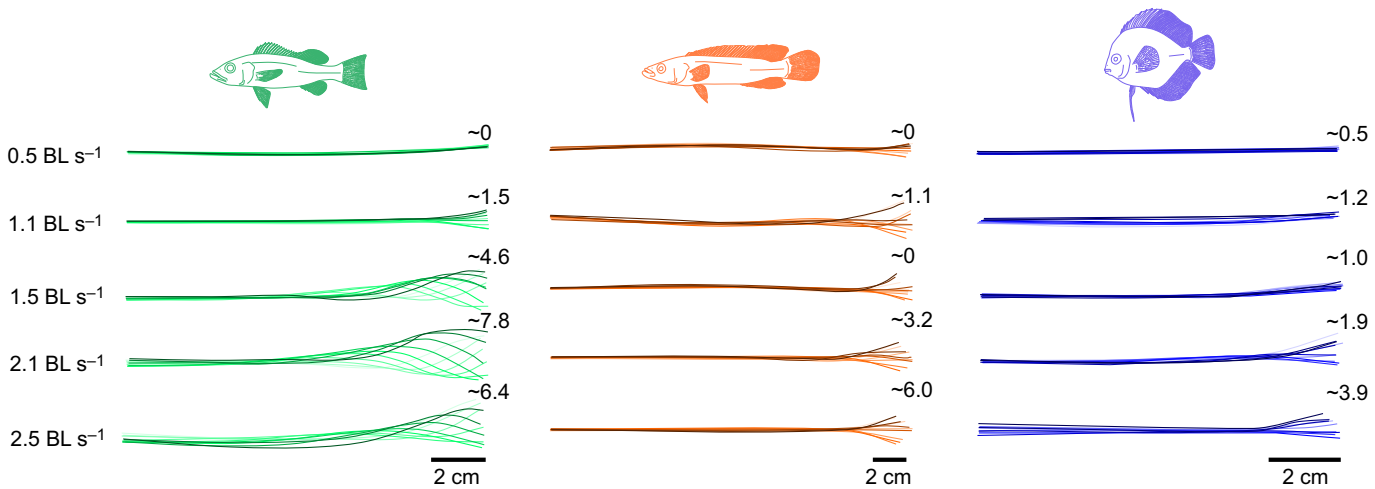


Fig. 4. Representative midline kinematics of each species at 0.5, 1.1, 1.5, 2.1 and 2.5 BL s^{−1}. Species are indicated by color as in Fig. 1: 0% of caudal fin beat cycle is shown in the lightest hue and 90% is shown in the darkest hue for each kinematic envelope. Numbers (top right) indicate body undulation effort, calculated as described in Materials and methods, in mm s^{−1}. Note that these tend to be higher in *Crenicichla* because of its size: the *Crenicichla* presented here was a larger fish. Midlines are scaled to unit body length across species; actual scale bars are presented for each species.

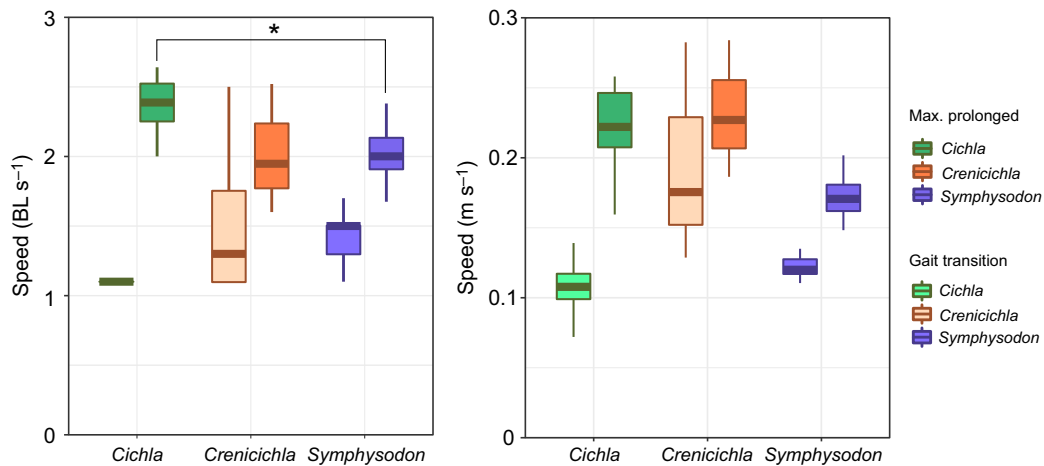


Fig. 5. Pectoral–caudal gait transition speed and maximum prolonged swimming speed. Note that gait transition speed is defined as the onset of caudal fin use; almost all fishes continued to use their pectoral fins in addition to the caudal fin after the gait transition. Left: speed normalized to body length. Right: raw speed. Within each panel, U_{trans} is plotted to the left of U_{max} for each species. Note that statistical comparisons were only conducted for normalized speed. *Significant differences with $P < 0.05$ following mixed factor modeling and *post hoc* Tukey HSD. Bars indicate mean, 25% and 75% quartiles, and lines indicate the range of the data. Sample sizes for these data are presented as $n = U_{\text{trans}}, U_{\text{max}}$: *Cichla* $n = 5, 5$; *Crenicichla* $n = 3, 2$; *Symphysodon* $n = 5, 5$.

inconsistently with increasing speed, and for *Symphysodon*, caudal fin use was inconsistent, though less variable than the use of the pectoral fins of *Cichla*. This likely reflects the contribution of each system to propulsion overall, with the non-primary propulsors having more variability. In most of the fishes studied, however, even

the non-primary propulsor was almost always being used, often substantially, and probably played an important role in swimming. The median species trajectories also suggest that *Cichla* used the typical paired-fin to body–caudal fin gait transition (the curve in the median trajectory), but *Symphysodon* did not (Fig. 6). In contrast to

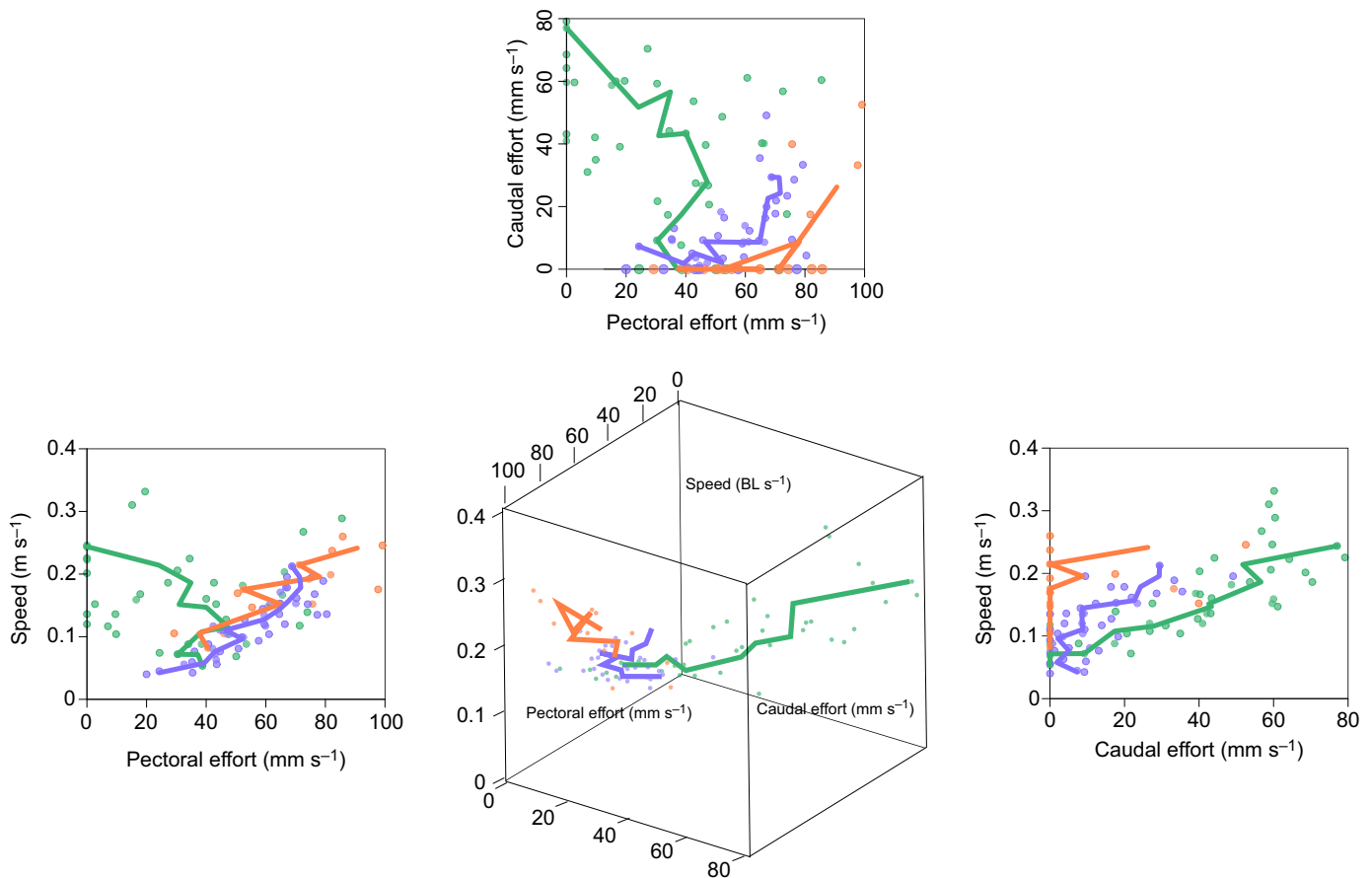


Fig. 6. Gait trajectories and gait space occupation for the three species used in this study. Points show the average of five fin beats for each of caudal effort and pectoral effort for a given fish trial. For each species, the median values for each speed are connected by straight-line segments. Species are indicated by color as in Fig. 1. *Cichla* $n = 4$; *Crenicichla* $n = 2$; *Symphysodon* $n = 3$.

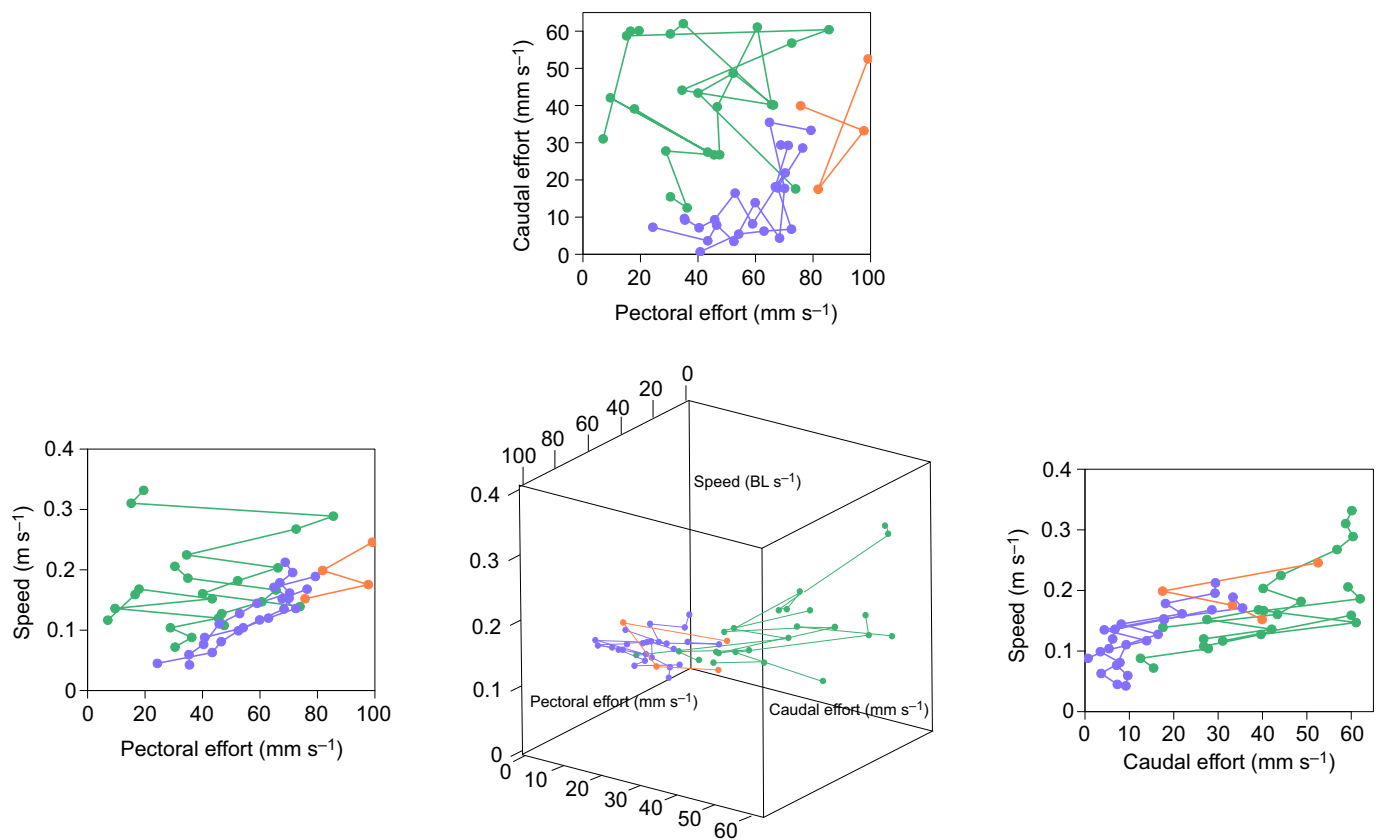


Fig. 7. Average gait trajectories and gait space occupation for individual fish of the three species used in this study. Lines connect average values for an individual fish at different speeds. Species are indicated by color as in Fig. 1. *Cichla* $n=4$; *Crenicichla* $n=2$; *Symphysodon* $n=3$.

trading one propulsor for another, once *Symphysodon* began to use its caudal fin, it increased both pectoral and caudal fin effort with increasing speed – less a ‘transition’ than an augmentation (Fig. 6). In addition, the projection of these gait trajectories can be used as an analog to Hildebrand-type tetrapod ‘gait spaces’ (Hildebrand, 1976) – showing that *Cichla* and *Symphysodon* occupy distinct areas of gait space (Fig. 6).

Differences in individual patterns of steady swimming kinematics are further highlighted and reinforced by the depiction of each individual fish’s gait trajectory (Fig. 7). All of the *Symphysodon* individuals followed almost the exact same path through gait space, indicating consistency across individuals in the use of both pectoral and caudal propulsion to increase speed. *Cichla* individuals, however, had more erratic, zig-zagging trajectories through gait space (Fig. 7). This suggests that, perhaps, *Cichla* are capable of using multiple kinematic patterns to achieve the same or similar speeds, supplementing low caudal fin use with pectoral fin use or vice versa.

DISCUSSION

Context for comparison of propulsive gaits

Despite the widespread use of swimming gait categories in the fish biomechanics literature, their application has two fundamental limitations, discussed further below. First, existing swimming gait categories are incapable of accommodating swimmers that use multiple, potentially independent, propulsors simultaneously. Second, they fail to provide a framework for using experimental data – including many data that have already been collected – to address comparative questions about fishes that use either multiple or non-standard swimming modes. These limitations are reduced in

the gait trajectory framework defined herein, though this approach is not without its own limitations.

Gait studies that have examined the kinematics of more than one propulsor often demonstrate that fishes are not constrained to any one category, and can use aspects of multiple categories at any given speed (Lauder, 2006). For example, fishes using body–caudal fin undulations may use pectoral fin movements at the same time. The median fins can also, simultaneously, contribute to steady swimming propulsion, though their roles are comparatively understudied (Lauder, 2006). Existing gait categories can only treat multiple propulsors if they are used in series – in which case, they are invoked as a gait transition (e.g. transition from labriform to subcarangiform with increasing speed; Drucker, 1996). In the case of simultaneous use of multiple propulsors, existing gait categories ignore the non-dominant propulsor, with the unfortunate side effect that there are little data (or research) on what these additional propulsors are doing. Nor can the issue of simultaneous multiple independent propulsors in swimmers be adequately addressed by gait definitions applied to terrestrial mechanics. Although comparative methods of addressing the latter have informed the approach taken here (Hildebrand, 1965, 1976), they cannot be applied to fish swimming as is. Terrestrial gait metrics such as duty factor cannot be readily defined in fishes given existing experimental techniques (though these data are starting to become available, e.g. Lucas et al., 2015). In addition, terrestrial gait metrics by and large focus on patterns of weight support, which is not an issue for most fishes. Thus, questions of how multiple propulsive elements can contribute and interact during steady swimming have remained understudied, in part as a result of the absence of a framework in which to study them.

Historically, the lack of a quantitative framework to explore the diversity of ‘non-standard’ swimming modes has also restricted the use of existing data to address comparative questions about fishes using different swimming modes. Within the context of a single gait category, one might measure different contributions of the dominant propulsor, but to do so across categories would require a quantitative means of comparison. The quantitative framework established by Hildebrand (1965, 1976) and Gambaryan (1974) for terrestrial gaits has been used successfully to ask questions about gait variability, the extent of hypothetical gait diversity, and how variables of interest (development, allometry, etc.) affect gait (e.g. Hildebrand, 1976; Peters, 1983; Lemelin et al., 2003). Because of the lack of a means to quantify variation within and across fish gait categories, asking similar questions in aquatic systems has been restricted to only those groups that remain within a similar category (and typically, only single species).

The main goal of this study was to test a new method of defining and characterizing fish gaits that both provides for quantitative inclusion of combinations of multiple propulsors and allows for standardized comparisons of the many diverse swimming gaits. This method was used to compare the gaits and steady swimming performance of three species of cichlid with body shapes associated with swimming specializations.

The existing literature on fish swimming provided likely candidates for incorporation into a fish ‘gait formula’. During steady swimming at any given speed, virtually every fish propulsor operates with some preferred (near-constant) frequency and some (near-constant) amplitude (Bainbridge, 1958). This consistency makes these metrics reasonably reproducible and meaningful for categorizing fish gaits. Values for fin beat frequency in particular are reported in almost every study of steady swimming, though usually only for one propulsor of interest. These data are readily available, and much easier to collect at present than more sophisticated hydrodynamic information. Combined, these two parameters can summarize the movement of a given swimming propulsor reasonably effectively (Webb, 1973).

Quantifying kinematic strategy provides a means of isolating and comparing gaits

As swimming performance (or, in fact, all locomotor performance) is the product of the combined and interacting effects of morphology, kinematics and physiology, it is impossible to understand how each of these factors individually affects performance without having some way of isolating the variation in each (Arnold, 1983). By parameterizing gait kinematics, it is possible to explicitly measure the association between kinematics and other variables of interest, such as co-occurring morphology and muscle physiology, and compare kinematics across a range of species and conditions. The three species in this study have fairly archetypal body morphologies with respect to hypotheses of swimming eco-morphology, but any attempt to attribute differences in their swimming performance to shape would be confounded without knowledge of any variation in their steady swimming gait (and physiology, but that is beyond the scope of this study).

The gait trajectory analysis defined and used here largely isolates movement patterns from gross morphology (though see below for concerns and possible future approaches). For instance, even though *Crenicichla* and *Symphysodon* have different body shapes, their kinematic gaits are similar (Figs 3 and 4). And although the maximum prolonged speed in *Crenicichla* is similar to that of *Cichla* (when body size is unaccounted for), their kinematics are different. In fact, the kinematics for *Crenicichla* were in contrast with what was

hypothesized based on body form alone: when *Crenicichla* did swim, it did so using a more stereotypically labriform gait than undulatory. This may be a product of life history and muscle physiology. As a burst-and-coast predator, a fish may not have much slow twitch muscle fiber to support prolonged periods of body undulation, and therefore favor a more labriform gait. The fact that *Crenicichla* is an ambush predator makes it an interesting test case for a steady swimming gait framework, in that it highlights that methods comparing steady gaits are likely to be most applicable to fishes for which steady swimming is an important behavior.

Potential for many-to-one mapping of morphology and kinematics on performance

If species differ in both morphology and gait, these factors will confound the effects of one another on performance. In this case, the higher steady swimming performance of *Cichla* in terms of maximum sustainable speed may be the product of its ‘cruising’ morphology, its body undulating kinematics, its muscle physiology or some combination of the three – the contributions of any to performance and the interaction among them is confounded. While the gait trajectory approach successfully described variation in movement patterns, its application to these three species highlighted the potential for many-to-one mappings of morphological and kinematic traits on swimming performance. These three species, with three different morphologies, used two kinematic strategies. Despite these differences, there was surprisingly little variation in steady swimming capacity among the three species. Two species (*Cichla* and *Crenicichla*) obtained remarkably similar maximum prolonged swimming speeds, despite having different morphology and different kinematics. This demonstrates how tenuous the links between morphology, kinematics and performance can be in the case of a function as multifaceted as steady swimming capacity, which is as much governed by underlying physiology as outwardly visible traits. Without direct observation and measurement of function, these results suggest caution in the application of swimming mode assumptions based on morphology.

Choices and refinement of the gait trajectory approach

The gait trajectory approach as tested here successfully described the kinematic patterns of the species tested, depicting the changing and variable use of two distinct propulsive structures with speed. It successfully demonstrated how some variation in performance as defined can be attributable to differences in gait and morphology, and also how performance can be similar in the face of distinctly different gait and morphology (suggestive of underlying physiological variation). The approach can be extended to incorporate additional propulsive elements with little modification. Any fish that swims steadily can be plotted in this multi-dimensional gait space. The incorporation of additional propulsors, such as the dorsal fin or anal fin, merely requires the addition of more axes, which can be analyzed quantitatively with no change in approach. While these cannot all be visualized in three dimensions, projections of the multiple axes into lower dimensional space, or dimension reduction techniques can be applied for visualization. For example, a gymnotiform swimmer would probably fall largely on an anal fin axis, with little to no caudal input.

That being said, there are several choices and refinements of the method that can be made going forward. First, the choice of propulsive input function (‘effort’, here) can be modified based on the researcher’s intent. A researcher interested in variation across pectoral fin propulsion, for instance, may want to incorporate some measure of angle of attack into his or her effort function.

An additional challenge is how to account for the effects of allometry on both amplitude and frequency, aside from differences in morphological configuration. When the fish being compared are of similar size, this is not an issue, but there are likely non-linear allometric relationships between frequency, amplitude and body size. Perhaps the best way of accounting for this variation is to measure it empirically, and thereby experimentally determine the nature of such allometric relationships for a number of individual species. Then it may be possible to derive a general relationship (or series of relationships) between size and gait.

Finally, it is worth noting that the gait trajectory approach as defined here does not account for differences in propulsive phase relationships (e.g. phase differences between the pectoral and caudal fins, or between pectoral fins; Hale et al., 2006). These can be described categorically and plotted on top of a trajectory, or treated separately from the trajectory itself.

Future directions for the study of swimming gaits

Given the ability to quantitatively compare swimming gait trajectories, there are many questions about swimming gait that can be addressed. The gait trajectory approach can be applied to treat gait as a response variable, and determine the effects of other important biological factors such as size, fatigue or flow conditions on gait itself. The explicit measurement of multiple propulsor movements can be incorporated into metabolic studies and hydrodynamic studies, determining the economy of a particular gait or a particular propulsor. In conjunction with dimension reduction techniques, gait trajectories may also assist in the identification of kinematic parameters that covary or that may have otherwise been considered unimportant. The isolation of kinematic variables as presented here is another step towards understanding how morphology, kinematics and physiology interact to produce performance.

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Competing interests

The author declares no competing or financial interests.

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Data availability

Data from this study are archived and publically available under a Creative Commons CC BY Attribution 4.0 International license, and can be accessed from an Open Science Framework project at <https://osf.io/mw5qx> (doi:10.17605/OSF.IO/MW5QX; Feilich, 2017).

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.157180.supplemental>

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Table S1. Individuals and trials included in each analysis. All trials meeting the requirements for a given analysis were included. Species is indicated in the Fish code (Cicoce = *Cichla ocellaris*, Cresax = *Crenicichla saxatilis*, Symaeq = *Symphysodon aequifasciatus*).

Numerical column entries are the number of trials for that individual included, with ‘-’ when no trials were available. Avg. Gait Trajectory indicates whether (Y) or not (N) a given fish had sufficient data to be included in Figure 7. Species Gait Trajectory indicates whether the data for a given fish were included in the calculation of the species average trajectory.

Fish (Total Trials Attempted)	Trans. Speed	Max. Speed	Freq. and Amp.	Avg Gait Trajectory	Species Gait Trajectory
Cicoce1 (3)	3	3	1	Y	Y
Cicoce2 (3)	3	3	1	Y	Y
Cicoce3 (3)	3	3	2	Y	Y
Cicoce4 (4)	3	3	2	Y	Y
Cicoce5 (3)	3	3	-	N	N
Cresax1 (6)	2	2	2	Y	Y
Cresax2 (4)	1	1	1	Y	Y
Cresax3 (4)	1	-	-	N	N
Symaeq1 (3)	3	3	2	Y	Y
Symaeq2 (3)	3	3	2	Y	Y
Symaeq4 (3)	1	1	-	N	N
Symaeq5 (3)	3	3	2	Y	Y
Symaeq10 (2)	2	2	-	N	N

Supplementary Information 1

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Table S2

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