

RESEARCH ARTICLE

Functional morphology of endurance swimming performance and gait transition strategies in balistoid fishes

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ABSTRACT

Triggerfishes and filefishes (Balistoidea) use balistiform locomotion to power steady swimming with their dorsal and anal fins, and transition to a gait dominated by body and caudal fin (BCF) kinematics at high speeds. Fin and body shapes are predicted to be strong determinants of swimming performance and gait transitions. The goal of this study was to combine morphometrics and critical swimming tests to explore the relationships between fin and body shapes and swimming performance in a phylogenetic context in order to understand the evolution of balistiform swimming. Among 13 species of balistoid fishes, those with high aspect ratio fins tended to achieve higher critical swimming speeds than fishes with low aspect ratio fins. Species with long, large median fins and wide caudal peduncles used the balistiform gait alone for a larger percentage of their total critical swimming speed than fishes with short, small median fins and narrow caudal peduncles. Although analyses revealed overall positive relationships between median fin aspect ratios and gait transition speeds, fishes on both ends of the aspect ratio spectrum achieved higher swimming speeds using the balistiform gait alone than fishes with median fins of intermediate aspect ratios. Each species is specialized for taking advantage of one gait, with balistiform specialists possessing long, large median fins capable of the large power requirements of high-speed swimming using the median fins alone, while BCF specialists possess short, small median fins, ill-suited for powering high-speed balistiform locomotion, but narrow caudal peduncles capable of efficient caudal fin oscillations to power high-speed locomotion.

KEY WORDS: Balistiform locomotion, Fins, Aspect ratio, U_{crit} , Body/caudal fin

INTRODUCTION

Fishes employ a wide variety of biomechanically distinct swimming modes to power aquatic locomotion, and this functional diversity is often reflected in the morphology of the fins and body. Accordingly, fish swimming modes are defined based on the parts of the body involved in thrust production during steady swimming (Breder, 1926; Webb, 1984; reviewed in Sfakiotakis et al., 1999). The two major categories of classically defined swimming modes are body/caudal fin (BCF) and median/paired fin (MPF) locomotion. BCF swimmers undulate sinusoidal body bending waves along the body, or oscillate their caudal fins. Conversely, MPF swimmers rely on undulations or oscillations of their median or paired fins for propulsion, while holding their bodies and caudal fins steady at most speeds.

The reliance of fishes on particular anatomical features for locomotion has led to extensive research aimed at understanding important trends among fin shape, body shape and swimming performance (Nursall, 1958; Walker and Westneat, 2002; Wainwright et al., 2002; Rouleau et al., 2010; Xin and Wu, 2013). These studies have revealed a widespread correlation between increasing aspect ratio (AR) of fins involved in propulsion and increasing steady swimming performance across a variety of swimming modes. AR is a measure of how ‘wing-like’ an airfoil is, and in the context of fish fins it is typically defined as the span of the fin squared, divided by the surface area of the fin (Nursall, 1958; Lighthill, 1970). The theory behind high AR fins leading to high-endurance swimming performance is based on hydrodynamic efficiency. High AR fins reduce the production of destabilizing tip vortices and experience decreased drag due to lift along their edges (Bushnell and Moore, 1991; Vogel, 1994). However, relationships between fin ARs and fish swimming hydrodynamics and performance have generally been examined theoretically (Lighthill, 1970; Karpouzian et al., 1990; Xin and Wu, 2013) or experimentally (Drucker and Jensen, 1996; Walker and Westneat, 2002; Wainwright et al., 2002; Fulton and Bellwood, 2004) in fishes that power locomotion with oscillatory fin kinematics, leaving these relationships largely unexplored in the context of undulatory fins.

An important characteristic of MPF swimmers, and a central focus of this study, is the fact that they undergo a gait transition with increasing speed from their respective steady MPF gait to an unsteady burst-and-glide BCF gait (Whoriskey and Wootton, 1987; Wright, 2000; Korsmeyer et al., 2002; Walker and Westneat, 2002; Cannas et al., 2006; Hale et al., 2006; Svendsen et al., 2010; Feilich, 2017). The gait transition from MPF to BCF propulsion requires recruitment of axial body musculature and caudal fin oscillations, suggesting that body and caudal fin shape might play an important role in determining swimming efficiency and performance of MPF swimmers. Despite extensive research on pectoral fin shape and gait transitions in fishes (Drucker and Jensen, 1996; Walker and Westneat, 2002), relationships among body and caudal fin morphometrics and endurance swimming performance of MPF swimmers have not previously been explored. Thus, a central goal of this study was to explore patterns of fish lateral profile morphometrics, including the dorsal, anal and caudal fins as well as body shape, and their associations with swimming performance and gait transitions.

Fishes in the superfamily Balistoidea are an ideal system in which to test hypotheses about morphology and swimming performance across a range of MPF kinematic patterns and gait transition strategies. This monophyletic superfamily is made up of 42 triggerfish species (Balistidae) and 107 filefish species (Monacanthidae), all of which power slow forward locomotion using their dorsal and anal fins while holding their bodies and caudal fins steady in the balistiform swimming mode. Despite this shared swimming mode, balistoid fishes possess a wide range of morphologies from deep-bodied *Balistes* and *Brachaluteres* genera to elongate *Oxymonacanthus* and

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Anacanthus genera (Dornburg et al., 2011; Hutchins and Swainston, 1985). Additionally, balistoid fishes possess median fins spanning a morphological continuum from high AR, posteriorly tapering fins of *Odonus niger* and *Canthidermis sufflamen* to low AR, rectangular fins of *Oxymonacanthus* and *Aluterus* species (Wright, 2000; Dornburg et al., 2011). Coupled with this morphological diversity, balistoid fishes lie on a kinematic continuum from swimming powered by highly oscillatory, flapping median fin kinematics to highly undulatory, wave-like median fin kinematics (Wright, 2000; Lighthill and Blake, 1990). Balistoid fishes with high AR median fins use oscillatory fin kinematics, while fishes with low AR median fins utilize more undulatory fin kinematics (Wright, 2000). Balistoid fishes undergo a gradual gait transition with increasing speed from balistiform locomotion alone at low speeds, to a gait involving both balistiform locomotion and a small BCF contribution at intermediate speeds, and finally to a gait dominated by burst-and-glide BCF locomotion at their fastest speeds (Wright, 2000; Korsmeyer et al., 2002). Wright (2000) examined relationships between morphology and swimming performance of balistoid fishes, and discovered that triggerfishes with higher AR median fins were capable of increased endurance swimming performance and higher gait transition speeds compared with triggerfishes with lower AR fins. To build on this prior work, a second major goal of the present study was to increase the sampling of triggerfishes, add a set of filefishes, and interpret morphometrics and swimming performance datasets within a well-resolved phylogeny of the Balistoidea.

Recent advances in our understanding of balistoid phylogenetics (Dornburg et al., 2008, 2011; Santini et al., 2013; McCord and Westneat, 2016) and the development of rigorous phylogenetic comparative methods have allowed us to account for phylogenetic structure in analyses of balistoid functional morphology. Additionally, the advancement of geometric morphometric techniques now allows for fine-scale analyses of morphological diversity (Dornburg et al., 2011; Feilich, 2016) beyond linear measurements and ratio calculations (Wright, 2000). Using these methods, we set out to quantify important axes of shape variation within balistoid fishes in a phylogenetic context.

The primary goals of this study were thus to use endurance swimming performance tests, geometric morphometrics and phylogenetic comparative methods to test functional hypotheses between balistoid fin and body shapes and swimming performance in order to better understand the evolution and subsequent functional diversification of the unique balistiform swimming mode.

MATERIALS AND METHODS

Species selection and care

Swimming performance data were analyzed for eight triggerfish and five filefish species (Fig. 1). We combined swimming performance data for seven triggerfish species [*Balistapus undulatus* (Park 1797), *Balistoides conspicillum* (Bloch and Schneider 1801), *Melichthys vidua* (Richardson 1845), *Odonus niger* (Rüppell 1836), *Rhinecanthus aculeatus* (Linnaeus 1758), *Sufflamen chrysoternum* (Bloch and Schneider 1801) and *Xanthichthys auromarginatus* (Bennett 1832)] and one filefish species [*Cantherhines macrocerus* (Hollard 1853)] from Wright (2000), with new performance measures from one additional triggerfish species [*Sufflamen bursa* (Bloch and Schneider 1801)] and four additional filefish species [*Acreichthys tomentosus* (Linnaeus 1758), *Oxymonacanthus longirostris* (Bloch and Schneider 1801), *Paraluteres prionurus* (Bleeker 1851) and *Pervagor janthinosoma* (Bleeker 1854)]. Data from *Pseudobalistes fuscus* (Bloch and Schneider 1801) (Wright, 2000) were not included

in our analyses, as swimming data were only available for two individuals. Swimming data from a total of 54 individuals were included in this study with an average of 4.2 individuals per species (range: 3–5). All individuals were post-juveniles with total lengths ranging from 6.04 to 12.31 cm (mean 9.02 cm).

Prior to swimming performance tests, all fishes were housed in separate tanks connected through a 1200 l saltwater flow-through system. The artificial seawater in this system was maintained at a temperature of $24 \pm 1^\circ\text{C}$ and a specific gravity of 1.024 ± 0.001 . All fishes were fed freeze-dried krill, fish flakes and pellets with the exception of corallivorous *O. longirostris*, which were provided with live brown *Acropora* spp. coral. All fishes were deprived of food for 24 h before swimming tests in order to control for metabolism (Alsop and Wood, 1997). All animal care protocols were approved by University of Chicago IACUC 72365.

Endurance swimming performance tests

Fish swimming performance is typically measured using a flow tank, in which fishes are forced to swim against a controlled flow. The standard metric for assessing a fish's endurance swimming performance is critical swimming speed (U_{crit}), defined as:

$$U_{\text{crit}} = u_i + \left(\frac{t_i}{t_{ii}} \times u_{ii} \right), \quad (1)$$

where u_i is the penultimate velocity (in cm s^{-1}) reached by the fish, t_i is the time (in minutes) that the fish swam at the highest reached velocity before exhaustion, t_{ii} is the length (in minutes) of each velocity increment, and u_{ii} is the prescribed velocity step increment (in cm s^{-1}) (Brett, 1964). The results of critical swimming performance tests in fishes are dependent on the chosen magnitude and timing of the velocity step increment (u_{ii} and t_{ii} , respectively), complicating direct comparisons of critical swimming performance among studies (Farlinger and Beamish, 1977; reviewed in Kolok, 1999). In order to ensure reliable comparisons between balistoid U_{crit} data gathered from the literature (Wright, 2000) and those measured in this study, we followed the critical swimming protocol of Wright (2000) exactly. Specifically, the length of each fish was quickly measured and recorded during transfer of the fish from their holding tanks to the flow tank. This measurement was used to calculate the length-specific velocity increments (u_{ii}) used in the swimming tests. All fishes then performed a critical swimming test consisting of a 2 h acclimation period in which fishes swam in the flow tank at a low velocity of $0.5\text{--}1$ total lengths (TL) s^{-1} , followed by a stepwise increase in flow velocity of approximately 0.5 TL s^{-1} (u_{ii}) (fork lengths for *O. niger*) every 15 min (t_{ii}) until the fishes were exhausted, as evidenced by their inability to remove themselves from the downstream grate for greater than 30 s (Wright, 2000). All swimming tests were conducted in the same custom-made flow tank used by Wright (2000), with a working section with dimensions $25 \text{ cm} \times 33 \text{ cm} \times 104 \text{ cm}$. The working section was subdivided length-wise into three equal partitions ($25 \text{ cm} \times 33 \text{ cm} \times 32 \text{ cm}$) using plastic 'egg-crate' barriers as collimators between partitions. A thin sheet of acrylic was bent into a half-pipe shape and inserted into each subdivision of the working section in order to prevent the fishes from avoiding swimming by wedging themselves into corners using their erectable dorsal spines and ventral keels. In a few cases, the critical swimming performance of two or three individuals was determined at the same time by restricting each individual to its own separate partition of the flow tank. In such cases, exhausted fish were quickly removed from their partition using a dipnet, and the remaining fish continued the

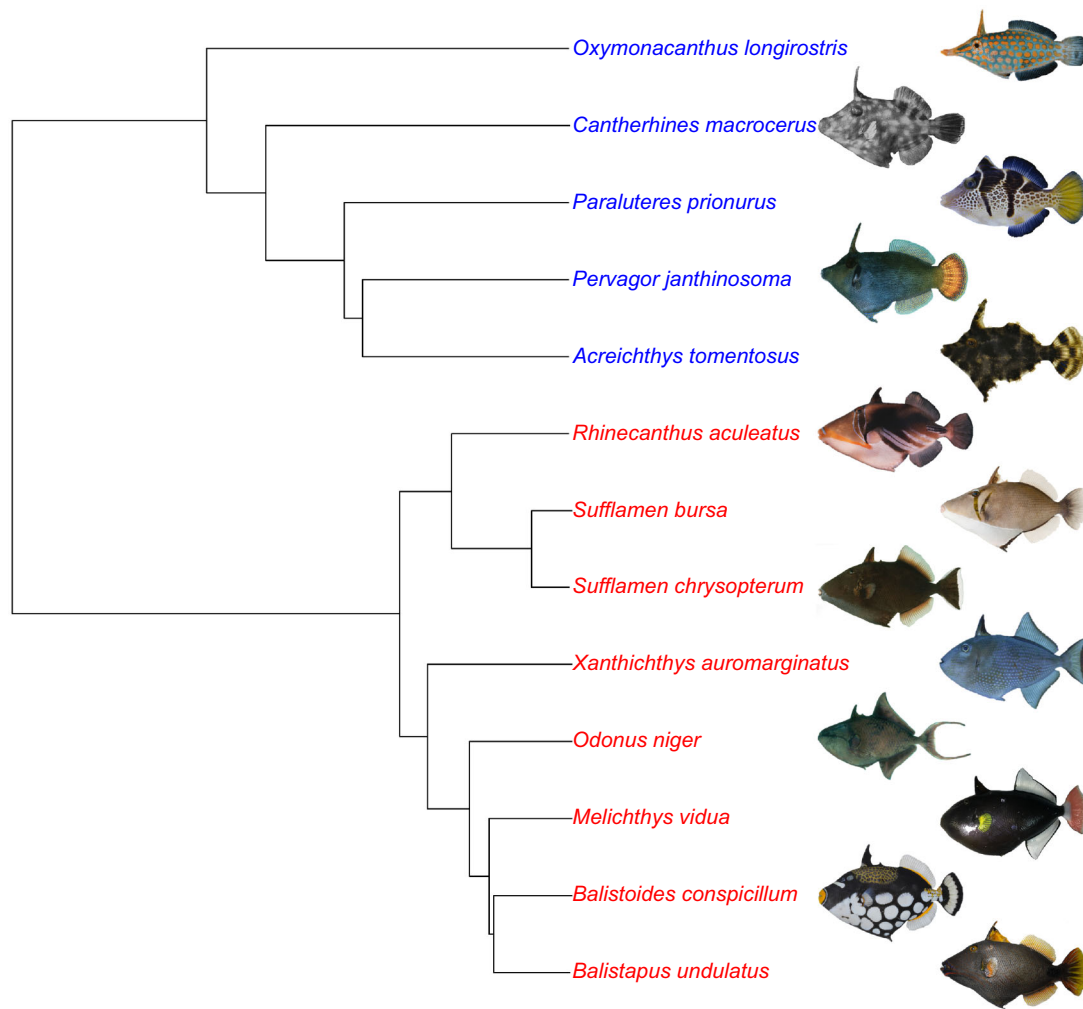


Fig. 1. Phylogeny of the 13 balistoid species used in this study. Species are color coded, with triggerfishes (Balistidae) in red and filefishes (Monacanthidae) in blue. Photo credits: *A. tomentosus*, *B. conspicillum*, *P. prionurus* (KPM-NR 53324, KPM-NR 45205, KPM-NR 57283; Hiroshi Senou); *B. undulatus*, *M. vidua* (A.B.G and M.W.W.); *C. macrocerus*, *O. longirostris*, *P. janthinosoma*, *R. aculeatus*, *S. chrysopteron* (John E. Randall); *O. niger* (Rick Winterbottom); *X. auromarginatus* (ROM 40935; Rick Winterbottom); *S. bursa* (USNM 439728; Jeffrey T. Williams. Copyright 2006 Moorea Biocode, Smithsonian Institute). Phylogeny trimmed from McCord and Westneat (2016).

swimming test uninterrupted. Wright (2000) calibrated the flow tank velocity before the swimming trials by filming and digitizing the downstream motion of suspended particles over a range of speeds. In this study, flow speed was measured and adjusted during each swimming trial in real-time using a Höntzsch Instruments flow sensing probe (HFA serial no: 843, Waiblingen, Germany).

U_{crit} provides a measure of the total sustained swimming performance limits regardless of the swimming gait used. In order to investigate the endurance swimming limits of balistiform locomotion alone (swimming powered by median fins only), gait transition data were recorded for each fish during the critical swimming trials. Because of the gradual nature of gait transitions from balistiform locomotion to BCF locomotion, Wright (2000) defined two gait transition speeds: $U_{t,low}$ and $U_{t,high}$. $U_{t,low}$ was defined as the speed interval during which the first signs of gait transition are evident, as indicated by occasional use of the caudal fin. This gait is characterized by steady balistiform locomotion plus occasional short BCF-powered bursts (balistiform+BCF). As $U_{t,low}$ is the speed at which fish no longer power locomotion using the median fins alone, this speed

can be considered the upper limit of swimming speed accomplished using balistiform locomotion alone. $U_{t,high}$ is defined as the speed interval during which the fish is no longer able to maintain a steady position in the flow tank using the median fins alone, as evidenced by use of the caudal fin every 10 s or less. This gait is characterized by frequent, large BCF-powered bursts followed by unsteady median fin-powered locomotion as the fish glides downstream and prepares for the next BCF burst. Using this definition, it is possible for $U_{t,high}$ to be greater than U_{crit} if this gait transition occurs during the same velocity increment in which the fish becomes exhausted.

Following swimming performance tests, U_{crit} , $U_{t,low}$ and $U_{t,high}$ were calculated for each individual. In order to control for the effect of fish size on swimming performance, these swimming performance metrics were expressed in terms of total lengths per second ($TL\ s^{-1}$) rather than raw speed ($cm\ s^{-1}$) for subsequent analyses. Because of the presence of elongate fin extensions at the dorsal and ventral margins of *O. niger* caudal fins, the total length of *O. niger* individuals was measured as the length from the anterior-most point of the head to the distal edge of the center of

the caudal fin (similar to fork length). Finally, we calculated the percentage of the total critical swimming speed in which each fish swam using its median dorsal and anal fins only (percent balistiform locomotion) as:

$$\% \text{ Balistiform locomotion} = \frac{U_{t,low}}{U_{crit}} \times 100\%. \quad (2)$$

Quantifying morphology

Following swimming experiments, fishes were killed with tricaine sulfonate salt (MS-222) and photographed for morphometric analyses. All specimens included in Wright's (2000) swimming performance study were fixed in formalin and stored in 70% ethanol at the Field Museum of Natural History (FMNH) in 2000. As a result of the fixation process, the fins of many of these specimens had become rigid in an unnatural position, but were otherwise in good condition. In order to spread the fins out to their natural positions for morphometric analyses, we soaked the preserved fish in a trypsin solution for 72 h. These fishes, along with the individuals tested in our swimming trials, were laid flat on their sides, pinned out with their fins fully extended and photographed with a ruler for morphometric analyses. In order to increase the sample size for morphometric analyses, photographs of museum and aquarium trade specimens within 25% of the length range of the individuals used in the swimming experiments were included, resulting in a total of 102 individuals included in morphometric analyses (see Table S1 for sample sizes of individual morphological datasets).

In order to quantify the morphological diversity of fin and body shapes, a total of 109 digital landmarks were placed along the fins and bodies of the fishes using the R package StereoMorph (Olsen and Westneat, 2015) (Fig. 2). Twenty-six landmarks were manually placed along the fins and bodies of each fish using the *landmarks* function in StereoMorph (white circles and blue triangles in Fig. 2), and the dorsal, anal and caudal fins were outlined using the *curves*

function in StereoMorph (blue lines in Fig. 2). The *curves* function interprets and returns the position of landmarks along a digitized Bezier curve. Curves were digitized along the anterior, dorsal, posterior and ventral surface of each fin, resulting in four independent curves along each fin. Following digitization, landmarks placed along the fins using the *curves* function were subsampled and evenly spaced, resulting in 34, 34 and 27 landmarks along the dorsal, anal and caudal fins, respectively (blue circles in Fig. 2). If any structures of a specimen were visibly damaged, those structures were not digitized or included in subsequent analysis. A few dorsal and anal fins ($n=4$ and 7, respectively) in otherwise good condition had preservation artifacts in the positions of one or more fin rays. In order to include these fins in subsequent analyses, we developed and utilized a Mac application FinRotate (<https://github.com/mwestneat/FinRotate>), capable of rotating individual fin rays about their base to digitally spread the fin membrane a small amount, while retaining the fin ray lengths and leaving the base positions unchanged. We ensured that the area of each fin changed less than 6.5% during these adjustments. These fins are indicated in Table S2 and the details of each fin adjustment are given in Table S3. Most balistoid fishes possess a mobile ventral keel that can be extended and retracted. For photographs in which the ventral keel was not positioned in its fully extended position (indicated with an asterisk in Table S2), the *estimate.missing* function in the R package geomorph (<https://cran.r-project.org/package=geomorph>) was used to estimate the position of the pelvic fin rudiment at the ventral tip of the extended ventral keel. The missing landmark positions were estimated for individuals of each species separately using all correctly positioned individuals of the same species as reference specimens. As all *C. macrocerus* individuals within the size range of the those included in the swimming trials were formalin fixed with the ventral keel depressed, a photograph of one slightly smaller, but correctly positioned, *C. macrocerus* individual was identified in the literature (Randall, 1964) and used to estimate the position of the extended ventral keel for this species. This reference specimen was not used in subsequent morphometric analyses.

The digitized landmark data were subdivided into five separate datasets for geometric morphometric analyses: full shape (all landmarks), body only, dorsal fin only, anal fin only and caudal fin only. Next, each landmark was designated as either a functionally homologous 'landmark' (white circles in Fig. 2) or a geometrically relative 'semi-landmark' (blue shapes in Fig. 2). The landmarks and semi-landmarks included in each morphological dataset were then projected into tangent space using generalized Procrustes analysis (GPA) in order to remove variation in landmark position due only to rotation, translation and scaling using the *gpa* function in geomorph. During Procrustes superimposition, each semi-landmark was allowed to slide relative to neighboring static landmarks using a method that minimizes the bending energy among specimens. In addition to translating, rotating and scaling the relative landmark positions of each specimen while preserving the important shape information, the *gpa* function also calculates the centroid size (a measure of relative size) for each specimen. Each morphological dataset (full shape, body shape, dorsal fin shape, anal fin shape and caudal fin shape) underwent GPA independently, so that Procrustes-transformed shapes and centroid sizes of each morphological unit could be analyzed separately.

Following GPA, we calculated species means of Procrustes-transformed landmark coordinates and centroid sizes for each morphological dataset. Principal components analyses (PCA) were then performed on the species-averaged, Procrustes-aligned landmark coordinates of each morphological dataset in order to

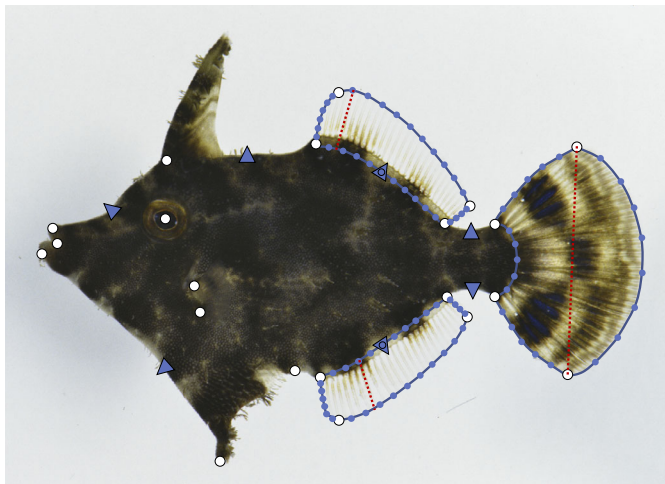


Fig. 2. Geometric morphometrics digitization scheme demonstrated for the filefish *Acreichthys tomentosus* (KPM-NR 53324). White circles represent functionally homologous non-sliding landmarks. Blue triangles represent sliding semi-landmarks included in only the full-shape and body-only datasets. Blue curves outlining the dorsal, anal and caudal fins were used for area calculations, and points along these curves (blue circles) were subsampled and treated as sliding semi-landmarks in geometric morphometric analyses. Red dotted lines represent the span measurements used for aspect ratio (AR) calculations. Photo credit: Hiroshi Senou.

identify, describe and quantify major axes of shape variation within the 13 species examined in this study using the *PlotTangentSpace* function in geomorph.

The shape changes described by the two most significant axes of morphological variation [principal component (PC)1 and 2] of each dataset were then visualized using backtransform morphospaces (MacLeod, 2009; Olsen, 2017). We used this backtransformation method to visualize the theoretical fin and body shapes of each species as described only by morphological characteristics relevant to the two most significant axes of shape variation. We then plotted these shapes in their relative positions of morphospace for each morphological dataset. In order to visualize the full range of theoretical shapes in this PC1–PC2 morphospace, we generated evenly spaced PC scores along the observed ranges of the first two axes of shape variation (PC1 and 2) for each dataset and plotted the corresponding shapes in their respective position in each morphospace. Finally, we projected a phylogeny (McCord and Westneat, 2016) into each morphospace using the *phylo-morphospace* function in the R package phytools (Revell, 2012) in order to assess evolutionary directionality of shape changes within and between each family.

In addition to the geometric–morphometric datasets described above, five morphological ratios were calculated for each species. First, we calculated the ARs of the dorsal, anal and caudal fins. AR was calculated as:

$$AR = \frac{b^2}{A}, \quad (3)$$

where b is the maximum span of the fin perpendicular to the direction of forward motion (dotted red lines in Fig. 2) and A is the surface area of the fin. For the dorsal and anal fins, span was measured as the Euclidian distance from base to tip of the longest fin ray of each fin independently. Caudal fin span was measured as the Euclidian distance from the dorsal-most point of the fin to the ventral-most point of the fin when the caudal fin was fully spread open. Span and area measurements were calculated using the photos digitized in StereoMorph. Finally, in order to assess variation in relative fin sizes among species, we calculated two area ratios. The first area ratio (median fin:BCF area ratio) provides a measure of relative combined dorsal and anal fin area compared with the combined body and caudal fin area. The second area ratio (caudal fin:body area) provides a measure of relative caudal fin size.

Statistical analyses

All statistical analyses were carried out in a phylogenetic context, using a pruned time-calibrated phylogeny based on four mitochondrial and five nuclear gene sequences from 80 balistoid species and six outgroup taxa from the families Diodontidae, Ostraciidae and Tetraodontidae (McCord and Westneat, 2016). In order to account for numerical imprecision due to small rounding errors when reading this phylogeny into R, we used the *nmls* method in the *force.ultrametric* function within phytools (Revell, 2012) to force the tree to conform to the strict ultrametric requirements of R packages used in downstream analyses. In order to assess relationships between fish size and size-adjusted swimming metrics (in TL s^{-1}), univariate phylogenetic generalized least squared (PGLS) regressions were conducted between species-averaged fish total length and species-averaged, size-adjusted swimming performance metrics (U_{crit} , $U_{\text{t,low}}$, $U_{\text{t,high}}$ and percent balistiform locomotion) using the *pgls* function in the R package caper (<https://CRAN.R-project.org/package=caper>). PGLS regressions were also

conducted among all swimming performance metrics in order to identify correlations between swimming metrics. PGLS regressions between species-averaged centroid sizes and GPA-transformed coordinates of each geometric–morphologic dataset were conducted in order to assess lingering allometric relationships between size and shape of each structure following GPA. Only the anal fin dataset exhibited a significant allometric correlation between centroid size and GPA-transformed shape (PGLS: $P=0.015$), so centroid size was used as a covariate in all subsequent geometric–morphometric functional morphology PGLS regressions for the anal fin. Spearman's rank correlations were used to assess correlations between geometric–morphometric PC scores and fin aspect and area ratios.

Functional morphology hypotheses were tested using univariate PGLS regressions between the species-averaged fin ratios and PC scores of the first two axes of shape variation for each geometric–morphometric dataset versus size-adjusted (TL s^{-1}), species-averaged swimming performance metrics (U_{crit} , $U_{\text{t,low}}$, $U_{\text{t,high}}$ and percent balistiform locomotion). The multiple R^2 values for each relationship given by the *pgls* function in caper are provided below and in Table 1. In order to account for multiple statistical tests being conducted on the same dataset, all functional morphology P -values were adjusted to control for false-discovery rate using the Benjamini–Hochberg (BH) method (Benjamini and Hochberg, 1995) with the *P.adjust* function in the R package stats (<http://www.R-project.org/>). All functional morphology trends were nearly identical between $U_{\text{t,low}}$ and $U_{\text{t,high}}$ (see Table S4), so $U_{\text{t,high}}$ functional morphology relationships are not discussed below or included in the BH *P.adjust* method, resulting in a total of 45 functional morphology statistical tests input into the BH p -adjust function. The BH-adjusted P -values for functional morphology relationships are reported below, and raw P -values can be found in Table S4. Results were considered significant when the BH-adjusted P -values were less than 0.05. All other statistical tests (correlations between measured swimming variables, allometric relationships between size and shape, and correlations between fin ratios and geometric–morphometric PC scores) were undertaken prior to hypothesis testing in order to ensure that subsequent functional morphology analyses controlled for any confounding correlations between variables, and thus the P -values of these tests were not adjusted using the BH method. In order to further explore and account for any non-isometric relationships between fish length and swimming performance, residuals from linear regressions between species-averaged fish TL and species-averaged raw (cm s^{-1}) swimming performance metrics (U_{crit} , $U_{\text{t,low}}$ and $U_{\text{t,high}}$) were used in additional PGLS regressions of swimming performance metrics (residuals) against morphology datasets as recommended by Kolok (1999). The P -values from these additional PGLS regressions were adjusted using the BH *P.adjust* method and subsequently compared with those of the original (swimming metrics expressed in TL s^{-1}) functional morphology tests. All statistical analyses were performed using R software version 3.3.2 (<http://www.R-project.org/>).

RESULTS

Swimming performance

Critical swimming performance (U_{crit}) of the 13 balistoid species examined ranged from 3.58 TL s^{-1} in the triggerfish *B. conspicillum* to 6.41 TL s^{-1} in the triggerfish *O. niger* with an average of 4.67 TL s^{-1} (Table S5). Five individuals (one *O. niger*, two *R. aculeatus* and two *X. auromarginatus*) reached the maximum speed of the flow tank before exhaustion, so these species' U_{crit}

Table 1. Results of functional morphology phylogenetic generalized least squared (PGLS) regressions

PGLS relationship	Directionality	Multiple R^2 (Balistoidea)	Benjamini–Hochberg-adjusted P -value		
			Balistoidea	Balistidae	Monacanthidae
Dorsal fin AR vs U_{crit}	Positive	0.591	0.0107	0.0478	0.975
Anal fin AR vs U_{crit}	Positive	0.605	0.0107	0.0416	0.975
Caudal fin AR vs U_{crit}	Positive	0.488	0.0240	0.0416	0.553
Median fin:BCF area ratio vs U_{crit}	Positive	0.461	0.0268	0.0833	0.975
Dorsal fin AR vs $U_{t,low}$	Positive	0.653	0.00746	0.0202	0.994
Anal fin AR vs $U_{t,low}$	Positive	0.657	0.00746	0.0202	0.994
Caudal fin AR vs $U_{t,low}$	Positive	0.421	0.0351	0.0400	0.713
Median fin:BCF area ratio vs $U_{t,low}$	Positive	0.797	0.00179	0.0202	0.925
Median fin:BCF area ratio vs % Bal	Positive	0.487	0.0240	0.0833	0.465
Full shape PC2 vs U_{crit}	Positive	0.444	0.0307	0.0638	0.465
Body shape PC1 vs U_{crit}	Negative	0.423	0.0351	0.0521	0.975
Dorsal fin shape PC1 vs U_{crit}	Positive	0.548	0.0162	0.0521	0.975
Dorsal fin shape PC2 vs U_{crit}	Positive	0.532	0.0162	0.0416	0.975
Caudal fin shape PC1 vs U_{crit}	Positive	0.497	0.0268	0.351	0.540
Full shape PC1 vs $U_{t,low}$	Negative	0.604	0.0107	0.0322	0.975
Full shape PC2 vs $U_{t,low}$	Positive	0.543	0.0162	0.0202	0.540
Body shape PC1 vs $U_{t,low}$	Negative	0.692	0.00746	0.0202	0.975
Dorsal fin shape PC1 vs $U_{t,low}$	Positive	0.592	0.0107	0.0202	0.975
Dorsal fin shape PC2 vs $U_{t,low}$	Positive	0.668	0.00746	0.0202	0.975
Anal fin shape PC2 vs $U_{t,low}$	Positive	0.717	0.0162	0.0416	0.925
Caudal fin shape PC1 vs $U_{t,low}$	Positive	0.507	0.0265	0.0833	0.811
Full shape PC1 vs % Bal	Negative	0.414	0.0358	0.134	0.975
Body shape PC1 vs % Bal	Negative	0.411	0.0358	0.125	0.975

Results correspond to PGLS regressions using critical swimming speed (U_{crit}) and the first gait transition speed ($U_{t,low}$) values measured in total length per second ($TL s^{-1}$). AR, aspect ratio; % Bal, percent balistiform locomotion. Bold values indicate statistically significant trends ($P < 0.05$).

values should be considered conservative estimates. The U_{crit} family averages were 5.04 and 4.09 $TL s^{-1}$ for the triggerfishes and filefishes, respectively. The initial gait transition speed ($U_{t,low}$) ranged from 2.14 $TL s^{-1}$ in *B. conspicillum* to 4.94 $TL s^{-1}$ in *O. niger*, with an average of 3.40 $TL s^{-1}$ (Table S5). The $U_{t,low}$ family averages were 3.28 and 3.59 $TL s^{-1}$ for the triggerfishes and filefishes, respectively. Two filefishes, one *P. prionurus* and one *O. longirostris*, never fully transitioned to the unsteady BCF gait ($U_{t,high}$). Among fishes that did make the second gait transition, $U_{t,high}$ ranged from 2.94 $TL s^{-1}$ in the triggerfish *R. aculeatus* to 5.56 $TL s^{-1}$ in *O. niger* (Table S5), with an average of 3.99 $TL s^{-1}$. The $U_{t,high}$ family averages were 3.87 and 4.18 $TL s^{-1}$ for the triggerfishes and filefishes, respectively. The percentage of the critical swimming trial in which the fishes swam using their median fins only (percent balistiform locomotion) ranged from 45.3% in *R. aculeatus* to 93.9% in *P. prionurus* (Table S5). All filefish species used balistiform locomotion exclusively (with no caudal fin contribution) for greater than 75% of their critical swimming tests, with a family average of 88%. Conversely, all triggerfish species used balistiform locomotion alone for less than 78% of their swimming tests, with a family average of 66%.

PGLS regressions revealed no significant relationships between size-adjusted ($TL s^{-1}$) swimming performance metrics and fish TL (U_{crit} : $P=0.41$, multiple $R^2=0.0627$; $U_{t,low}$: $P=0.22$, multiple $R^2=0.131$; $U_{t,high}$: $P=0.29$, multiple $R^2=0.102$; percent balistiform locomotion: $P=0.23$, multiple $R^2=0.126$). U_{crit} was significantly correlated with $U_{t,low}$ ($P=0.00064$, multiple $R^2=0.668$) and $U_{t,high}$ ($P=0.0037$, multiple $R^2=0.550$), but not with percent balistiform locomotion ($P=0.46$, multiple $R^2=0.050$). Percent balistiform locomotion was significantly correlated with $U_{t,low}$ ($P=0.0043$, multiple $R^2=0.538$) and $U_{t,high}$ ($P=0.0085$, multiple $R^2=0.482$). Finally, a PGLS regression revealed a highly significant correlation between $U_{t,low}$ and $U_{t,high}$ ($P=1.0e^{-6}$, multiple $R^2=0.895$). Nearly all trends between morphology and gait transition speeds were the same regardless of which gait transition speed was used

(Table S4), so subsequent results include only $U_{t,low}$, U_{crit} and percent balistiform locomotion.

Fin ratios

Anal fin ARs ranged from 0.32 in *O. longirostris* to 1.24 in *O. niger*, with an average of 0.62. Triggerfishes tend to have higher anal fin ARs (range 0.52–1.24, mean 0.73) than filefishes (range 0.32–0.62, mean 0.43). Dorsal fin AR ranged from 0.31 in *O. longirostris* to 1.16 in *O. niger*, with an average of 0.60. Triggerfishes also tend to have higher dorsal fin ARs (range 0.46–1.16, mean 0.72) than filefishes (range 0.31–0.53, mean 0.41). Caudal fin AR ranged from 1.57 in *C. macrocerus* to 3.05 in *X. auromarginatus* with an average of 2.51. Triggerfishes tend to have higher caudal fin ARs (range 2.46–3.05, mean 2.73) than filefishes (range 1.57–2.70, mean 2.16). Median fin: BCF area ratio ranged from 0.15 in *R. aculeatus* and *A. tomentosus* to 0.32 in *O. niger*, with an average of 0.21. There was no difference between triggerfish and filefish family means for this metric. Caudal fin:body area ratio ranged from 0.13 in *B. conspicillum* to 0.32 in *P. prionurus* with an average of 0.18. Filefishes have larger caudal fins relative to their bodies (range 0.20–0.32, mean 0.25) than triggerfishes (range 0.13–0.16, mean 0.14).

Geometric morphometrics

Full shape

The primary axis of variation (PC1: 46%) for this dataset, including all parts of the fish, describes the length and position of the dorsal and anal fins and caudal peduncle depth (Fig. 3A). High PC1 scores are associated with narrow caudal peduncles, deep bodies and short, posteriorly positioned dorsal and anal fins. The second axis of variation (PC2: 24%) differentiates fishes primarily based on fin shape. High PC2 morphospace is occupied by fishes with concave or truncated caudal fins and high AR median fins with long leading edges and short trailing edges. Conversely, low PC2 morphospace is occupied by fishes with highly convex caudal fins and low AR median fins with

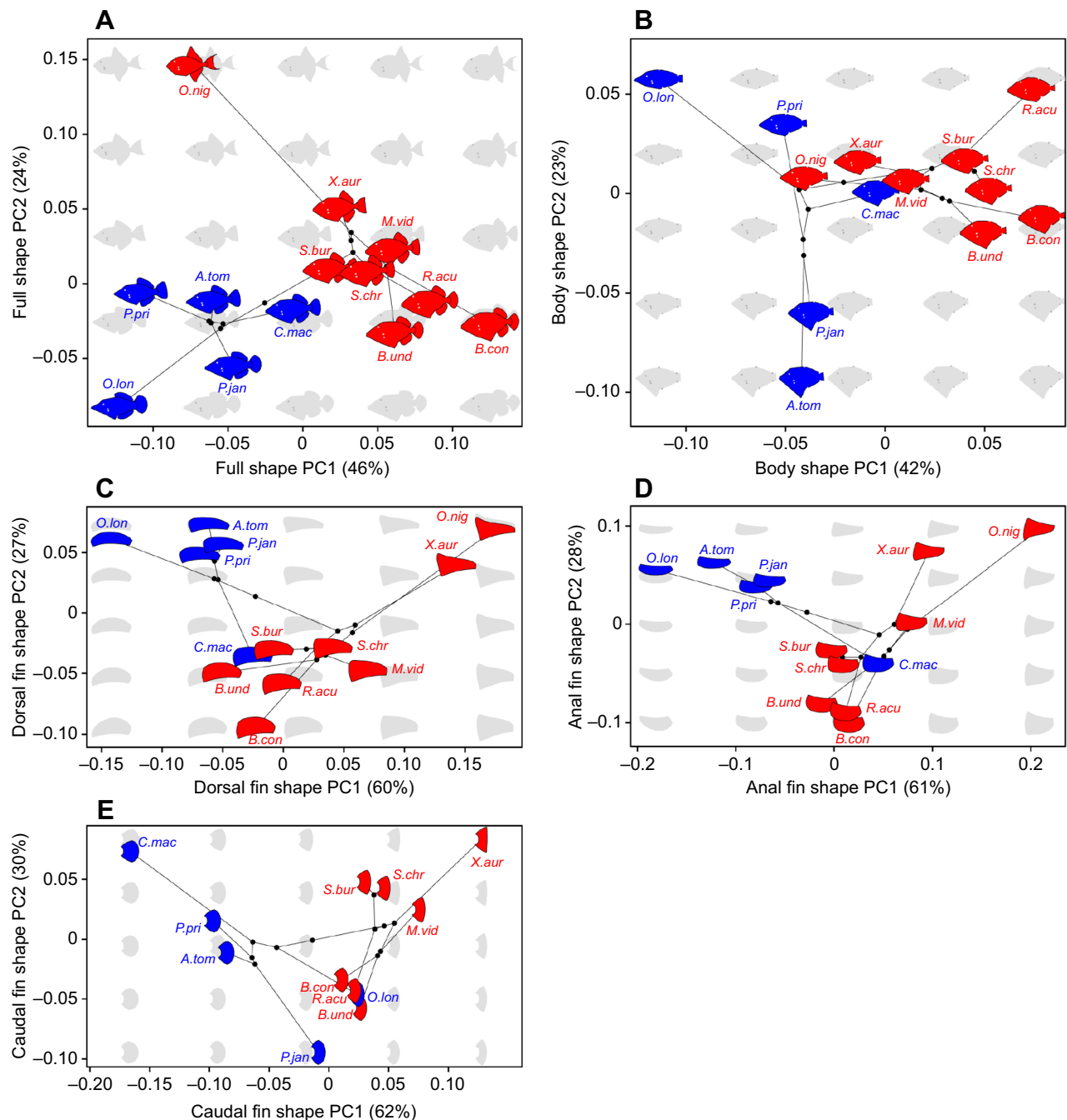


Fig. 3. Phylomorphospaces depicting backtransformed shapes along the two most significant axes of shape variation for each morphological dataset. Red (Balistidae) and blue (Monacanthidae) shapes represent the backtransformed shapes of each species included in this study. Gray shapes represent theoretical backtransformed shapes corresponding to each location in morphospace. Black lines represent the phylogeny from Fig. 1 transformed into each morphospace. Black dots along these lines represent theoretical positions of each ancestral node. (A) Full shape. (B) Body shape. (C) Dorsal fin shape. (D) Anal fin shape. (E) Caudal fin shape. Sample sizes for each morphometric dataset are reported in Table S1.

leading and trailing edges of similar lengths. Filefishes cluster in the area of morphospace defined by shallow bodies, wide caudal peduncles and long median fins (low PC1) as well as convex caudal fins and low AR median fins (low PC2). Triggerfishes occupy the area of morphospace defined by deep bodies, narrow caudal peduncles and short median fins (high PC1) as well as convex or truncate caudal fins and mid to low AR median fins (low to mid PC2), with the exception of *O. niger*, which sits in a largely unoccupied area of morphospace (low PC1 and high PC2).

Body only

The primary axis of variation (PC1: 42%) describes the ratio of anterior body depth to posterior body depth, the slope of the head profile and median fin length (Fig. 3B). Fishes with high PC1 scores are deep-bodied anteriorly with narrow caudal peduncles, short median fins and convex forehead profiles. Conversely, fishes with low PC1 scores are shallow-bodied anteriorly with wide caudal peduncles, long median fins and concave forehead profiles. PC2 (23%) describes ventral keel depth. Fishes with deep ventral keels occupy areas of low PC2 morphospace. Most triggerfishes cluster in

areas of morphospace defined by deep bodies, narrow caudal peduncles, convex forehead profiles (mid to high PC1) and ventral keels of moderate to shallow depth (mid to high PC2). Filefishes generally occupy areas of morphospace defined by narrow bodies, wide caudal peduncles and concave forehead profiles (mid to low PC1) and span the full range of PC2 morphospace. The filefish *C. macrocerus* appears to have converged upon an area of body morphospace primarily occupied by triggerfishes.

Dorsal fin

The primary axis of variation (PC1: 60%) describes the length ratio of the leading edge to the trailing edge of the fin (Fig. 3C). Low PC1 regions of morphospace are occupied by fins with leading and trailing edges of similar lengths, while high PC1 regions are occupied by fins with long leading edges and short trailing edges. Dorsal fin PC1 scores are positively correlated with dorsal fin ARs (Spearman's rank correlation $\rho=0.97$, $P<0.0001$). PC2 (27%) describes overall length:depth ratio, with long, shallow fins occupying areas of higher PC2 morphospace, and short, deep fins occupying areas of low PC2 morphospace. Dorsal fin PC2 is not correlated with dorsal fin AR (Spearman's rank correlation $\rho=-0.30$, $P=0.32$). Filefishes cluster in morphospace defined by low AR, shallow and elongate fins (low PC1, high PC2) with the exception of *C. macrocerus*, which groups with most triggerfishes in the area of morphospace defined by short, deep dorsal fins of intermediate AR (mid PC1, low PC2). *Odonus niger* and *X. auromarginatus* diverged from the rest of the Balistidae to occupy the area of morphospace defined by high AR, elongate dorsal fins (high PC1 and high PC2).

Anal fin

The primary axis of variation (PC1: 61%) describes the overall length–depth ratio of the fin as well as the orientation and length ratio of the leading edge to the trailing edge of the fin (Fig. 3D). Low PC1 regions of morphospace are occupied by elongate, shallow fins, with leading and trailing edges of nearly equal length. Conversely, high PC1 morphospace is occupied by short, deep anal fins with anteriorly oriented leading edges that are significantly longer than their trailing edges. Anal fin PC1 scores are positively correlated with anal fin ARs (Spearman's rank correlation $\rho=0.97$, $P<0.0001$). PC2 (28%) differentiates anal fins primarily by the length of the leading edge and shape of the distal edge. Anal fins with high PC2 scores have anteriorly oriented, straight leading edges with posteriorly tapering distal edges, while fins with low PC2 scores have posteriorly curved leading edges and deep, convexly rounded distal edges. Anal fin PC2 is not correlated with anal fin AR (Spearman's rank correlation $\rho=0.011$, $P=0.98$). Filefishes cluster in morphospace defined by shallow, elongate anal fins (low PC1) with anteriorly oriented leading edges and slightly tapering distal edges (high PC2), with the exception of *C. macrocerus*, which groups with most triggerfishes in the area of morphospace defined by deep, rounded anal fins (low PC2) of intermediate length and AR (mid PC1). *Odonus niger* and *X. auromarginatus* occupy the area defined by elongate, posteriorly tapering, high AR anal fins (high PC1 and high PC2).

Caudal fin

The forked caudal fin of *O. niger* is a major outlier along caudal fin PC1 according to a Rosner's generalized extreme studentized deviate test conducted with the *rosnerTest* function in R (Millard, 2013), so this species was removed from all caudal fin geometric–morphometric analyses and the caudal fin PCA was rerun without

O. niger. Among the remaining 12 species, the primary axis of variation (PC1: 62%) describes changes in overall length:depth ratios and the shape of the posterior edge of the caudal fin (Fig. 3E). Caudal fins occupying areas of low PC1 morphospace are elongate and narrow with highly convex posterior edges, while caudal fins occupying areas of high PC1 morphospace are short and deep with truncate posterior edges. Caudal fin PC1 is positively correlated with caudal fin AR (Spearman's rank correlation $\rho=0.94$, $P<0.0001$). Caudal fin PC2 describes the length of the dorsal and ventral edges of the fin. Fins with low PC2 scores have short dorsal and ventral edges, while fins with high PC2 scores have long dorsal and ventral edges. Triggerfishes possess fairly deep caudal fins with slightly convex or truncate distal edges (mid to high PC1). Most filefishes possess fairly narrow caudal fins with more convex distal edges (mid to low PC1). Fishes from both families span the entirety of PC2.

Functional morphology

Analyses revealed significant relationships among several aspects of balistoid fin and body shape variation, endurance swimming performance and gait transition strategies. As expected, median fin size and many aspects of median fin shape were found to be strong predictors of critical swimming performance and gait transition speeds. Several aspects of body and caudal fin shape were also found to be significantly correlated with swimming performance. Functional morphology results were quite similar between the two size-adjustment methods (Table S4), so subsequent statistics, results and discussion are based on performance metrics measured in $TL\ s^{-1}$ only.

Fin ratios and performance

Univariate PGLS regressions revealed significant positive correlations between U_{crit} and dorsal, anal and caudal fin ARs (see Table 1 for statistical significance) (Fig. 4A–C). Additionally, increasing the area ratio of the median fins to the body and caudal fin (median fins:BCF area ratio) is associated with increased U_{crit} (PGLS: $P=0.0268$) (Fig. 4D). Higher dorsal, anal and caudal fin ARs and increased median fins:BCF area ratio are also associated with increased gait transition speed ($U_{t,low}$) (Table 1) (Fig. 5). Although not detected as outliers in these relationships by Rosner's generalized extreme studentized deviate tests, three triggerfish species with median fins of especially high ARs, *O. niger*, *X. auromarginatus* and *M. vidua*, clearly contribute substantially to the observed trends between fin ARs and both U_{crit} and $U_{t,low}$. Finally, median fin:BCF area ratio is positively correlated with percent balistiform locomotion (PGLS: $P=0.0240$) (Fig. 6).

Geometric morphometrics and performance

Univariate PGLS regressions of PC scores against swimming performance metrics revealed 14 significant functional morphology trends within the superfamily Balistoidea (Table 1). Fishes with deeper bodies and less convex caudal fins (high full shape PC2, high caudal fin PC1) and fishes with elongate (high dorsal fin PC2), posteriorly tapering (high dorsal fin PC1) dorsal fins are associated with increased U_{crit} (Fig. 7). Many aspects of balistoid fin and body shape are also associated with $U_{t,low}$ (Fig. 8) (Table 1). Interestingly, the most significant axes of median fin shape correlated with $U_{t,low}$ are not correlated with fin ARs. Specifically, elongate dorsal and anal fins, regardless of AR (high dorsal and anal fin PC2s) are associated with higher $U_{t,low}$ (Fig. 8C,D). Balistoid fishes with narrow caudal peduncles (high full shape PC1) and highly convex caudal fins (low full shape PC2, low caudal fin PC1) tend to recruit

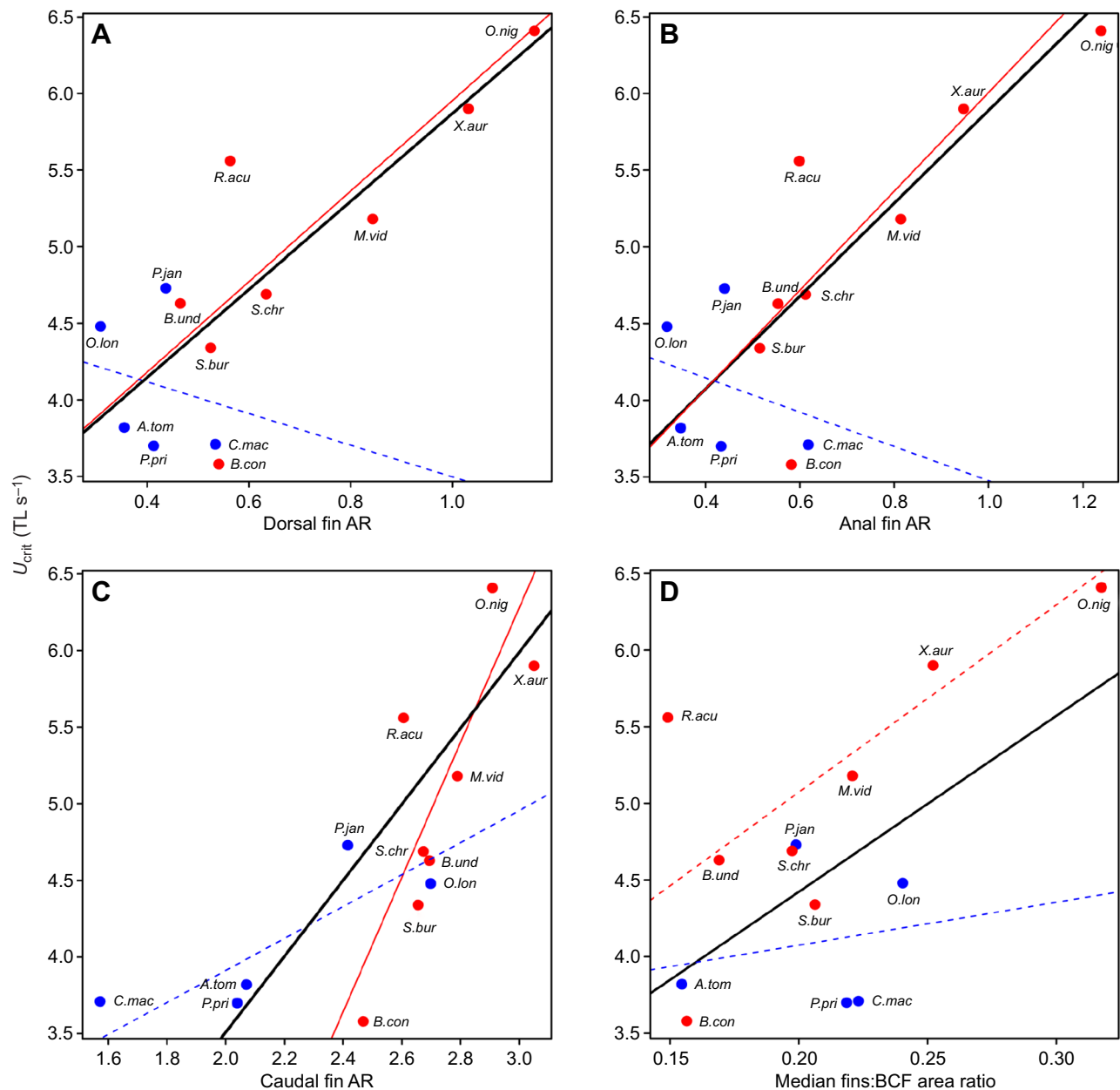


Fig. 4. Relationships between fin ratios and critical swimming performance (U_{crit}). U_{crit} data are given in total lengths per second ($TL\ s^{-1}$). (A) Dorsal fin AR. (B) Anal fin AR. (C) Caudal fin AR. (D) Ratio of median fins area to combined body and caudal fin (BCF) area. All points represent species means. Red and blue points indicate triggerfishes and filefishes, respectively. Black lines depict the phylogenetic generalized least squared (PGLS) regression lines for all 13 balistoid species included in this study. Red and blue lines depict independent PGLS regression lines for the triggerfishes and filefishes, respectively. Solid and dashed lines indicate significant ($P < 0.05$) and non-significant ($P > 0.05$) trends, respectively. Sample sizes for U_{crit} and morphometric datasets are reported in Tables S5 and S1, respectively.

the caudal fin at slower speeds (lower $U_{t,low}$) than fishes with wide caudal peduncles and less convex caudal fins (Fig. 8A). Finally, fishes with elongate median fins and wide caudal peduncles (low full shape and body PC1s) use balistiform locomotion alone for a higher percentage of their overall U_{crit} (high percent balistiform locomotion) than fishes with short median fins and narrow caudal peduncles (high full shape and body PC1s) (Fig. 9).

Family trends

Many of the trends in functional morphology remain significant when assessed among the eight triggerfish species alone, but many filefish species do not follow the overall balistoid functional

morphology trends (Table 1). In fact, among the five filefish species examined in this study alone, no axes of body or fin shape variation are associated with U_{crit} , $U_{t,low}$ or percent balistiform locomotion (Table 1; Table S4).

DISCUSSION

Triggerfishes and filefishes are capable of relatively high critical swimming performance compared with median and paired fin locomotor specialists from other fish families. The hypotheses that high fin ARs are associated with higher endurance swimming performance and higher gait transition speeds were strongly supported in our analysis. However, triggerfishes and filefishes

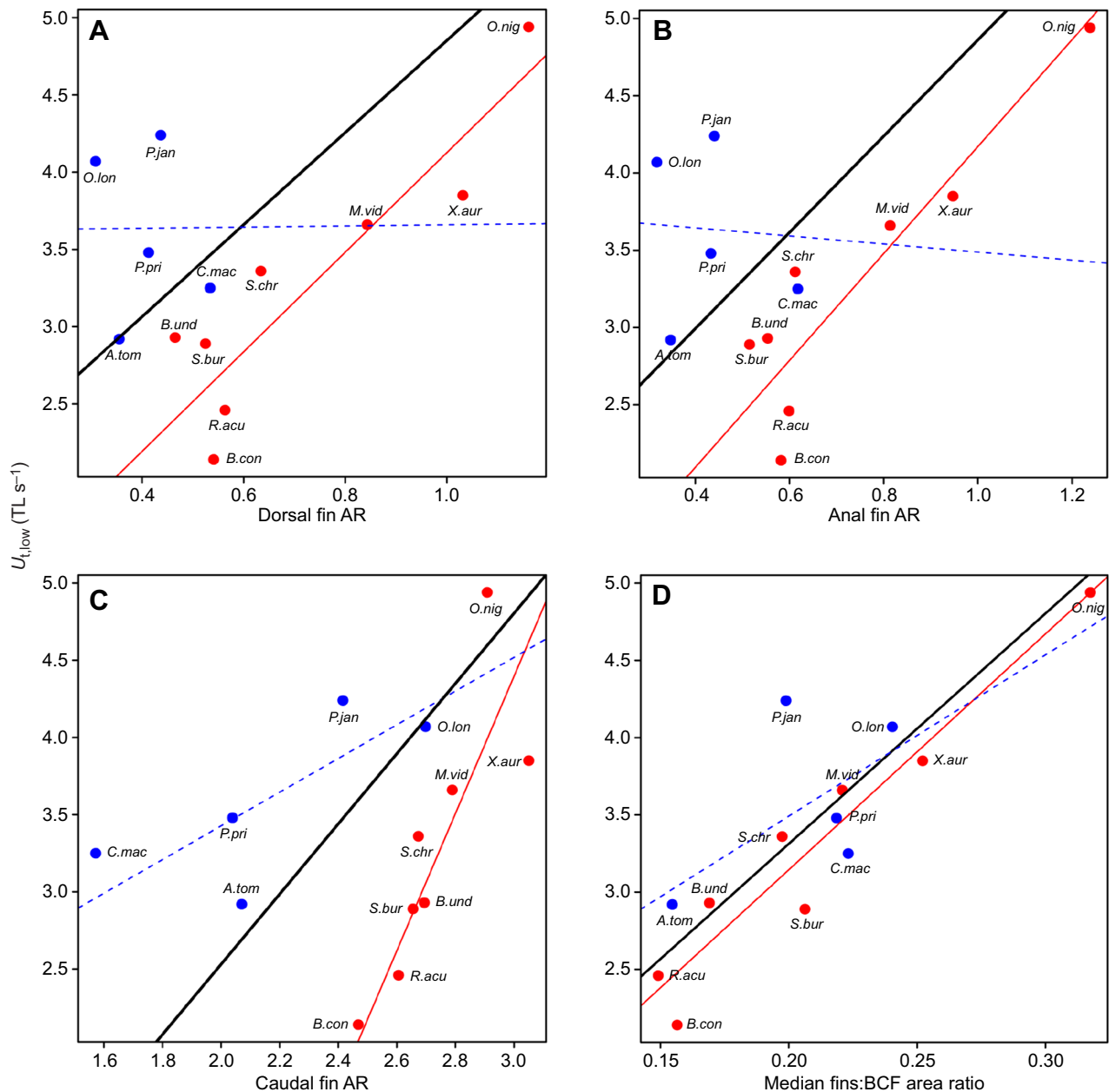


Fig. 5. Relationships between fin ratios and the first gait transition speed ($U_{t,low}$). $U_{t,low}$ data are given in total lengths per second ($TL s^{-1}$). (A) Dorsal fin AR. (B) Anal fin AR. (C) Caudal fin AR. (D) Ratio of median fins area to combined BCF area. All points represent species means. Family association and statistical significance are indicated by color and line type, respectively, as in Fig. 4. Sample sizes for $U_{t,low}$ and morphometric datasets are reported in Tables S5 and S1, respectively.

showed different endurance swimming strategies and gait transition behaviors, with filefishes showing a strikingly high performance using pure balistiform locomotion. The central conclusions of this study are (1) fin and body shapes are good predictors of overall critical swimming performance in balistoid fishes, (2) balistoid fishes exhibit a variety of gait transition strategies to achieve high-speed endurance swimming performance and (3) each species appears to be morphologically specialized to take advantage of one of these gait transition strategies.

Swimming performance

The results of this study indicate that balistoid fishes are capable of strong endurance swimming performance. All 13 balistoid species in this study achieved U_{crit} values above $3.5 TL s^{-1}$. The nine fastest

species achieved U_{crit} values above $4 TL s^{-1}$, indicating that balistoid fishes are capable of higher critical swimming performance than other MPF swimmers such as the knifefish *Gymnotus carapo* (mean $U_{crit}=2.1 TL s^{-1}$; McKenzie et al., 2012), parrotfish *Scarus schlegeli* (mean $U_{crit}=3.2 TL s^{-1}$; Korschmeier et al., 2002), pufferfish *Takifugu rubripes* (mean $U_{crit}=3.22$ body lengths s^{-1} ; Yu et al., 2015), burrfish *Diodon holocanthus* (mean $U_{crit}=3.6 TL s^{-1}$; Wiktorowicz et al., 2010) and boxfish *Ostracion meleagris* (mean $U_{crit}=3.8 TL s^{-1}$; Gordon et al., 2000). The fastest species in this study, *O. niger*, achieved an average U_{crit} of $6.41 TL s^{-1}$, comparable to high-performance MPF endurance swimmers of similar length such as the wrasses *Gomphosus varius* and *Cirrhilabrus rubripinnis* (mean $U_{crit}=5.26$ and $6.05 TL s^{-1}$, respectively; Walker and Westneat, 2002). Previously reported

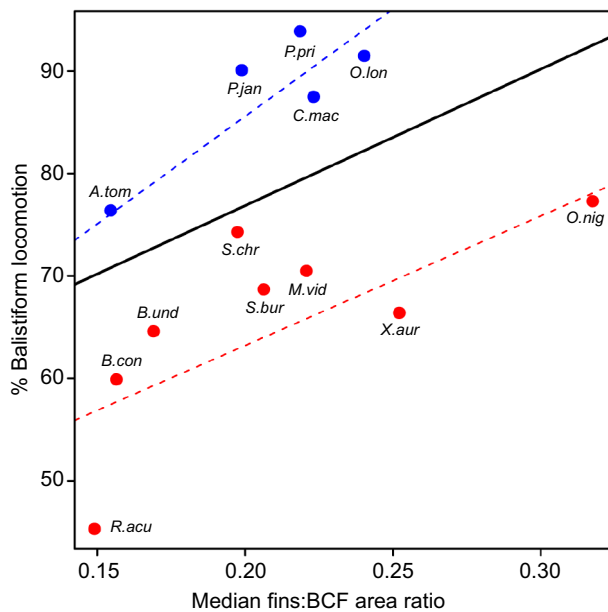


Fig. 6. Relationship between median fins:BCF area ratio and the percentage of U_{crit} achieved using the balistiform gait alone. All points represent species means. Family association and statistical significance are indicated by color and line type, respectively, as in Fig. 4. Sample sizes for percent balistiform locomotion and median fins:BCF area ratio are reported in Tables S5 and S1, respectively.

MPF-to-BCF gait transition speeds range from 1.75 fork lengths (FL) s^{-1} (Cannas et al., 2006) and 2.3 FL s^{-1} (Svendsen et al., 2010) in the surfperch labriform swimmer *Embiotoca lateralis* to 3.5 TL s^{-1} in the parrotfish labriform swimmer *Scarus schlegeli* (Korsmeyer et al., 2002) and over 5 TL s^{-1} in the boxfish ostraciiform swimmer *Ostracion meleagris* (Hove et al., 2001). Thus, the triggerfishes and filefishes in this study achieved fairly high swimming speeds using their MPF gait alone ($U_{t,low}$ range 2.14–4.94 TL s^{-1} , mean 3.40 TL s^{-1}) compared with MPF swimmers from other fish families.

The swimming performance results from this study also reveal interesting trends between balistoid families. Triggerfishes tend to achieve faster overall U_{crit} than filefishes (5.04 and 4.09 TL s^{-1} , respectively). However, triggerfishes recruit body and caudal fin musculature ($U_{t,low}$) at lower speeds than do filefishes (3.28 and 3.59 TL s^{-1} , respectively) and power swimming with balistiform locomotion alone for a lower percentage of their overall endurance swimming performance than do filefishes (66% and 88%, respectively). This means that, on average, filefishes achieved faster swimming speeds than triggerfishes using balistiform locomotion alone (higher $U_{t,low}$). Furthermore, this suggests that although nearly all past studies concerning the evolution (Dornburg et al., 2011), biomechanics (Blake, 1978; Wright, 2000; Korsmeyer et al., 2002; Hu et al., 2006; Loofbourrow, 2009), energetics (Korsmeyer et al., 2002) and performance (Wright, 2000; Korsmeyer et al., 2002) of balistiform locomotion have used triggerfishes as their balistiform swimming models, filefishes are likely a better system for studying high-speed balistiform locomotion because of their heavy reliance on the balistiform gait alone throughout much of their swimming speed range. Many past studies concerning balistiform locomotion (Korsmeyer et al., 2002; Hu et al., 2006; Loofbourrow, 2009) focused solely on *R. aculeatus*, the species that used balistiform locomotion for the smallest percentage of its U_{crit} in this study (45%), so the biomechanical and

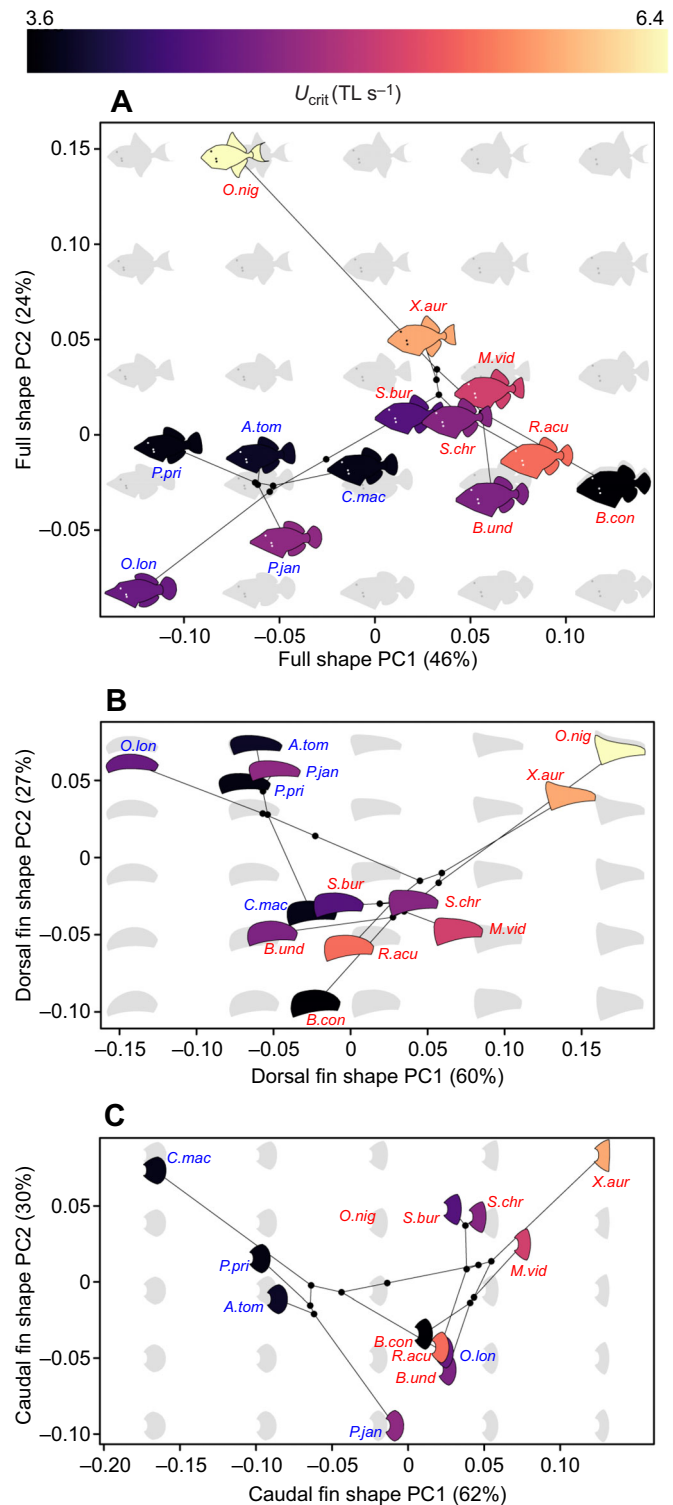


Fig. 7. Backtransformation phylomorphospace plots color coded for U_{crit} . See Fig. 3 for a description of backtransformation phylomorphospace plots. Shapes affiliated with each species are color coded according to mean U_{crit} measured in TL s^{-1} , as indicated by the color bar. (A) Full shape. (B) Dorsal fin shape. (C) Caudal fin shape. Species abbreviations are color coded by family, with triggerfishes in red and filefishes in blue. Sample sizes for U_{crit} and morphometric datasets are reported in Tables S5 and S1, respectively.

energetic trends observed in these studies may not be broadly applicable to all balistoid fishes. Keeping this in mind, it is important to note that previous research has indicated that



R. aculeatus actually incurs a significant energetic cost when transitioning from balistiform locomotion to a combined balistiform plus BCF gait ($U_{t,low}$), suggesting that balistoid fishes might undergo gait transitions in order to meet the power requirements of swimming faster in a highly viscous aquatic environment (Korsmeyer et al., 2002). This is in stark contrast to gait transitions of terrestrial animals, which are typically undergone to maximize mechanical efficiency at each speed (reviewed in Alexander, 1989). This power-requirement, rather than mechanical efficiency, energetics pattern described in *R. aculeatus* suggests that our $U_{t,low}$ measurement may be a good estimate of the upper speed limit of the balistiform gait for each species. However, this energetics pattern might not apply to all balistoid species, especially those with different morphologies and fin kinematics. Either way, it is clear from our results and those of Korsmeyer et al. (2002) and Wright (2000) that not all balistoid fishes power aerobic endurance swimming using the balistiform gait alone; rather, they are capable of long-term aerobic locomotion using the combined balistiform and BCF gait.

Critical swimming performance of balistoid fishes is highly correlated with fin ARs and area ratios. Fishes with high AR dorsal, anal and caudal fins and fishes with relatively large median fins tend to achieve higher U_{crit} . These trends support previous findings that balistoid fishes benefit from hydrodynamically efficient (high AR) and powerful (relatively large) dorsal and anal fins during endurance swimming (Wright, 2000). By expanding the scope of performance measures and fin metrics to additional species, this trend is expanded to include filefishes. The relationships between increasing median fin ARs and increasing U_{crit} are not surprising, given the hydrodynamic benefits of high AR fins (Lighthill, 1970; Bushnell and Moore, 1991) and the fact that the median fins are significantly involved in thrust production throughout the majority of the critical swimming tests (through $U_{t,high}$). The relationship between caudal fin AR and overall critical swimming performance reflects the fact that, on average, these balistoid fishes started recruiting occasional caudal fin oscillations ($U_{t,low}$) at speeds only 74% of the way to their respective critical swimming limits.

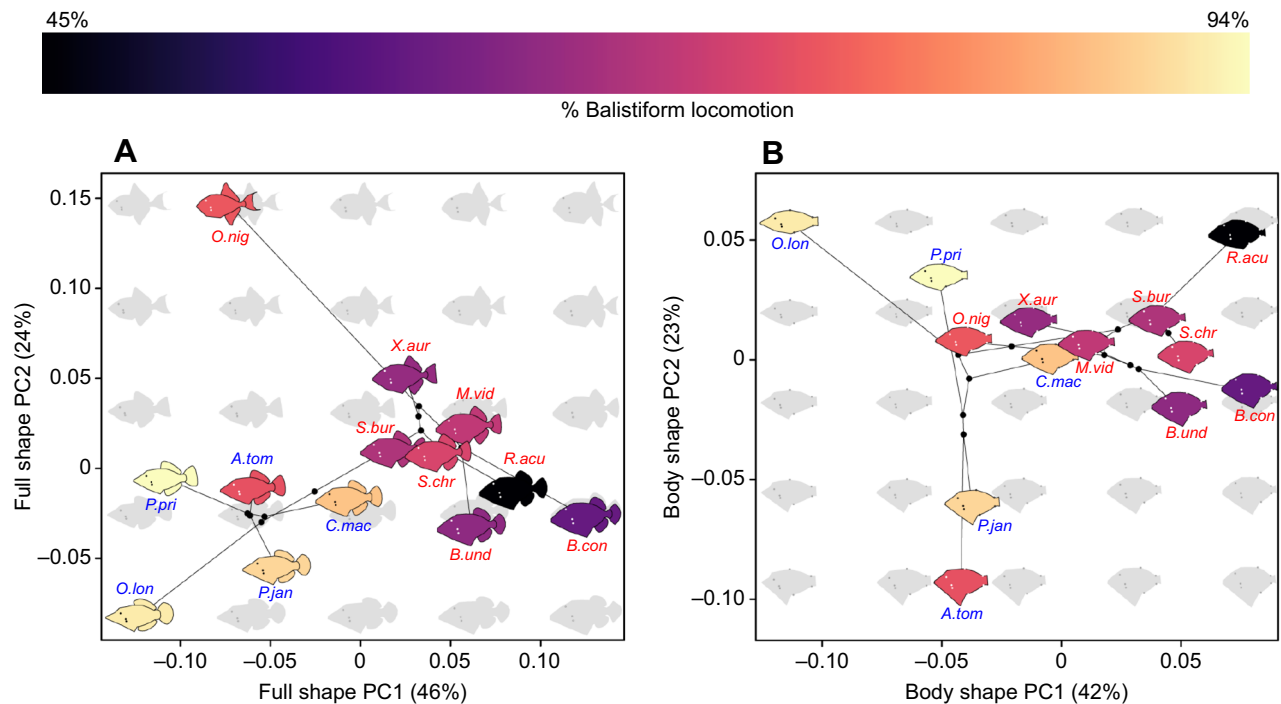


Fig. 9. Backtransformation phylomorphospace plots color coded for the percentage of U_{crit} achieved using the balistiform gait alone. See Fig. 3 for a description of backtransformation phylomorphospace plots. Shapes affiliated with each species are color coded according to mean percent balistiform locomotion, as indicated by the color bar. (A) Full shape. (B) Body shape. Species abbreviations are color coded by family, with triggerfishes in red and filefishes in blue. Sample sizes for percent balistiform locomotion and morphometric datasets are reported in Tables S5 and S1, respectively.

Triggerfishes were especially reliant on the caudal fin contribution, with a percent balistiform locomotion family average of only 66%. Theoretical work has demonstrated many hydrodynamic advantages of high AR fins, including decreased drag and decreased production of destabilizing tip vortices (Bushnell and Moore, 1991; Lighthill, 1970; Xin and Wu, 2013). These hydrodynamic advantages likely make balistoid fishes with high AR median and caudal fins capable of more energetically efficient propulsion using the balistiform and BCF gaits, respectively.

The strongest trends between morphology and swimming performance measured in this study were associated with gait transition speed ($U_{t,low}$), rather than overall critical swimming performance. Specifically, fishes with large median fins, high AR median fins, long median fins (regardless of AR) and wide caudal peduncles recruited axial musculature and the caudal fin ($U_{t,low}$) at higher speeds than fishes with small, short and rounded median fins and narrow caudal peduncles. It is important to note that the filefishes in this study do not conform to the trends between increasing median fin ARs and increasing $U_{t,low}$. In fact, close examination of these trends (Figs 5A,B and 8C,D) actually suggests that possessing median fins at either extreme of the AR continuum or median fin PC1 range (significantly associated with AR) results in improved swimming performance while using the balistiform gait alone ($U_{t,low}$) compared with median fins of intermediate ARs. Specifically, the species with the second and third fastest $U_{t,low}$ speeds (*P. janthinosoma* and *O. longirostris*) actually possess some of the lowest AR median fins measured in this study. In other words, it appears that two optima may exist between median fin AR and swimming performance powered by the balistiform gait alone ($U_{t,low}$), with the fastest balistiform locomotion speeds ($U_{t,low}$) achieved by fishes with the highest and lowest AR median fins, and the slowest maximum balistiform swimming speeds ($U_{t,low}$) achieved by fishes with median fins of intermediate ARs.

The multiple optima discovered between median fin ARs and $U_{t,low}$ can likely be explained by the fin kinematics used to achieve these balistiform locomotion speeds. Kinematics research has shown that high AR median fins are associated with oscillatory, flapping balistiform fin kinematics, while low AR median fins are associated with more wave-like, undulatory median fin kinematics (Wright, 2000). All filefishes added to this study (*A. tomentosus*, *O. longirostris*, *P. prionurus* and *P. janthinosoma*) have lower AR median fins than the fishes included in the Wright (2000) study, suggesting that these filefishes may possess even more undulatory fin kinematics than previously described for the group, although fin kinematics must be experimentally confirmed. The different median fin kinematics used by balistiform swimmers at either end of the median fin AR spectrum likely place different hydrodynamic pressures on the fishes (Wright, 2000; Sprinkle et al., 2017), and each fin shape may be hydrodynamically optimized for its respective kinematics. Specifically, low AR filefish fins may be optimized for high-speed endurance swimming using undulatory median fin kinematics, while the high AR fins of our three most influential species (*O. niger*, *X. auromarginatus* and *M. vidua*) may be optimized for high-speed endurance swimming using oscillatory median fin kinematics. The short, intermediate AR fins of species exhibiting the slowest $U_{t,low}$ speeds might not be optimized for high-speed endurance swimming using undulatory or oscillatory median fin kinematics, but these species appear to have evolved body and caudal fin shapes better suited for high-speed BCF swimming. Detailed research regarding dorsal, anal and caudal fin kinematics of morphologically diverse balistiform swimmers across multiple speeds and gait transitions could further clarify relationships between fin shapes and endurance swimming performance of balistoid fishes.

Associations among body and caudal fin shape and gait transition speed can also be explained by hydrodynamic principles. Balistoid fishes with high AR caudal fins and narrow caudal peduncles recruit

their caudal fins ($U_{t,low}$) at lower speeds than do balistoid fishes with low AR caudal fins and wide caudal peduncles. These relationships are best understood by considering $U_{t,low}$ to represent the speed at which caudal fin recruitment is beneficial, rather than the limit of median fin propulsion. Modeling studies have shown that narrow caudal peduncles and high AR caudal fins are more hydrodynamically efficient than wide caudal peduncles and convex caudal fins (Lighthill, 1969, 1970; reviewed in Webb, 1982). Triggerfishes, on average, were aided by caudal fin contribution during the upper 34% of their critical swimming performance, suggesting that caudal fin shape may be especially important for the endurance swimming performance of these triggerfishes at high speeds. Conversely, filefishes only recruited the caudal fin for an average of 12% of their critical swimming performance, suggesting that caudal fin shape is unlikely to be evolutionarily specialized for efficient endurance swimming performance in filefishes. This explains why triggerfishes tend to possess higher AR caudal fins than do filefishes (AR of 2.73 and 2.16, respectively). The low AR filefish caudal fins are likely to be more useful for short bursts of speed than for sustained swimming bouts (Weihs, 1973; Webb, 1982). These body, median fin and caudal fin traits come together in the full shape dataset, where we find strong correlations between $U_{t,low}$ and full shape PC1 and PC2. Fishes with long median fins and wide caudal peduncles (low PC1) and fishes with concave, high AR caudal fins (high PC2) exhibited higher gait transition speeds than did fishes with short median fins and narrow caudal peduncles (high PC1) and highly convex caudal fins (low PC2) (Fig. 8A).

Finally, some swimming performance trends are best explained by the percent balistiform locomotion data. Fishes with long and large median fins (regardless of their shape) and fishes with wide caudal peduncles used the balistiform gait alone for a larger percentage of their U_{crit} tests. This trend can be explained by the higher maximum power output made possible by large median fins (regardless of fin kinematics) while using the balistiform gait versus increased hydrodynamic efficiency of caudal fin oscillations provided by narrow caudal peduncles. Each species appears to be fairly specialized for taking advantage of one of these gaits, with balistiform specialists possessing elongate, large median fins, capable of overcoming the large power requirements of swimming at high speeds using the median fins alone, while BCF specialists possess short, small median fins, incapable of powering high-speed balistiform locomotion, but narrow caudal peduncles capable of facilitating efficient caudal fin oscillations to power high-speed endurance swimming. In order to better understand these functional morphology trends, more work is needed on the energetics and kinematics of each swimming gait across a broad taxonomic balistoid sample.

Ecomorphology

The wide range of endurance swimming abilities and gait transition strategies observed among the balistoid species in this study likely has implications for the ecologies of these fishes. All species in this study are reef associated (Randall et al., 1997), but they do not all use the reef in the same way. As noted by Wright (2000), *O. niger* and *X. auromarginatus* are largely planktivorous (Fricke, 1980; Randall et al., 1978) and spend large amounts of time swimming well above the reef while picking plankton from the water column (Fricke, 1980; Meyers, 1991), which explains why these two species have evolved fin and body morphologies suited for providing the highest critical swimming speeds measured in this study. The remaining 11 species can be classified as benthic grazers, as a large portion of their diet is composed of sessile or slow-moving benthic organisms (Peristiwady

and Geistdoerfer, 1991; Randall, 1955, 2007; Randall and Hartman, 1968; Hiatt and Strasburg, 1960; Meyer, 1985). Most of these species remain close to the shelter of the reef as they nip at algae, crustaceans, sponges, bivalves or the coral itself. All filefishes in the present study fall into this category, and this lifestyle likely does not require high-endurance swimming performance. However, these fishes probably do require large bursts of speed to escape predation into nearby holes in the reef, a behavior likely facilitated by their wide caudal peduncles and large, low AR caudal fins (Weihs, 1973; Webb, 1982). Other benthic grazing species (*B. undulatus*, *B. conspicillum*, *R. aculeatus*, *S. bursa* and *S. chrysopteron*) spend much of their time farther from the cover of the reef as they swim along open coral rubble lagoons and feed on more evasive prey such as crabs and even small fishes (Hiatt and Strasburg, 1960; Meyers, 1991; Sano et al., 1984; Randall, 1985; Randall et al., 1997; Vijay Anand and Pillai, 2005). These species likely require some combination of fast, aerobic bursts of speed to catch prey and escape predators over long distances on open sandy bottoms as well as efficient slow swimming performance to sustain long bouts of searching for benthic prey. These species group in body morphospace defined by narrow caudal peduncles and short median fins and exhibit some of the slowest gait transition speeds ($U_{t,low}$) measured in this study (Fig. 8), indicating that they rely heavily on caudal fin contribution to achieve high-speed locomotion. Furthermore, research has shown (Korsmeyer et al., 2002) that one species with this body type and lifestyle, *R. aculeatus*, is capable of highly efficient slow swimming using the balistiform gait, as well as sustainable, aerobic BCF-supplemented locomotion at higher speeds. Combined, these trends suggest that the small, short median fins of *R. aculeatus* are sufficient for slow grazing using balistiform locomotion, while the narrow caudal peduncle facilitates efficient, high-speed, aerobic BCF swimming used to escape predators and chase down elusive prey over expansive sandy lagoons. In order to determine how well these ecomorphological trends apply to balistoid fishes as a whole, more research is required on the morphometrics and ecologies of a larger, phylogenetically informed sample of the superfamily Balistoidea.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.B.G., M.W.W.; Methodology: A.B.G., M.W.W.; Software: A.B.G., M.W.W.; Validation: A.B.G.; Formal analysis: A.B.G.; Investigation: A.B.G.; Resources: M.W.W.; Data curation: A.B.G., M.W.W.; Writing - original draft: A.B.G., M.W.W.; Writing - review & editing: A.B.G., M.W.W.; Visualization: A.B.G.; Supervision: M.W.W.; Project administration: A.B.G., M.W.W.; Funding acquisition: A.B.G., M.W.W.

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Supplementary information

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