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SYMPOSIUM ARTICLE

Weak Relationships Between Swimming Morphology and Water Depth in Wrasses and Parrotfish Belie Multiple Selective Demands on Form–Function Evolution

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Synopsis Mechanical tradeoffs in performance are predicted to sculpt macroevolutionary patterns of morphological diversity across environmental gradients. Water depth shapes the amount of wave energy organisms' experience, which should result in evolutionary tradeoffs between speed and maneuverability in fish swimming morphology. Here, we tested whether morphological evolution would reflect functional tradeoffs in swimming performance in 131 species of wrasses and parrotfish (Family: Labridae) across a water depth gradient. We found that maximum water depth predicts variation in pectoral fin aspect ratio (AR) in wrasses, but not in parrotfish. Shallow-water wrasses exhibit wing-like pectoral fins that help with "flapping," which allows more efficient swimming at faster speeds. Deeper water species, in contrast, exhibit more paddle-like pectoral fins associated with enhanced maneuverability at slower speeds. Functional morphology responds to a number of different, potentially contrasting selective pressures. Furthermore, many-to-one mapping may release some traits from selection on performance at the expense of others. As such, deciphering the signatures of mechanical tradeoffs on phenotypic evolution will require integrating multiple aspects of ecological and morphological variation. As the field of evolutionary biomechanics moves into the era of big data, we will be uniquely poised to disentangle the intrinsic and extrinsic predictors of functional diversity.

Introduction

Understanding the major environmental drivers that influence phenotypic variation is a core question in evolutionary biology (Arnold 1983; Schluter 2000). Form–function relationships influence the range of resources, such as food items and environmental space, that organisms can exploit (Garland and Losos 1994; Wainwright and Reilly 1994). These relationships simultaneously respond to numerous, potentially competing, performance demands imposed by abiotic and biotic selective pressures (Alexander 1985; Tanaka and Suzuki 1998; Langerhans 2009; Muñoz and Losos 2018), and these pressures can shape the direction and rate of morphological evolution in different traits (Walker 2007; Muñoz 2019). In the marine realm, organisms must contend with the physical characteristics of their habitats, such as water energy, and habitat complexity (Fulton et al. 2001, 2005; Beaugrand et al. 2002; Gray 2002). Across different marine environments, these physical features might vary in a way that results in different patterns of phenotypic adaptation (Fulton et al. 2005; Alben et al. 2013). These evolutionary differences might be further magnified when the associated morphological traits experience performance tradeoffs, such that no single phenotype can simultaneously optimize two functions (Ghalambor et al. 2003; Walker 2010; Holzman et al. 2012; Muñoz et al. 2017, 2018).

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Interactions with fluids shape organismal behavior and morphology (Vogel 1994), and variation in water flow plays a major role in the locomotor demands of aquatic organisms (Domenici 2003; Blake 2004; Fulton et al. 2005; Alben et al. 2013). In fishes, differences in body shape and fin morphology contribute to differences in swimming performance (Imre et al. 2002; Walker and Westneat 2002a; Langerhans and Reznick 2010; Walker 2010). For example, water velocity contributes to morphological differences that influence swimming performance among fishes (Alexander 1967; McLaughlin and Grant 1994). Studies centered on a few focal species largely support the idea that fin features respond to wave energy to optimize swimming performance (Imre et al. 2002; Thorsen and Westneat 2005; Fulton et al. 2013), but relatively little is known about how hydrodynamic forces like drag shape broad macroevolutionary patterns of swimming morphology (Bellwood and Wainwright 2001; Fulton et al. 2001, 2005).

Fishes in the family Labridae (which includes wrasses and parrotfish) are one of the most species-rich and ecologically diverse groups of fishes that inhabit coral reefs (Barber and Bellwood 2005; Cowman et al. 2009). Like many reef fishes, labrids move primarily by using both rowing and flapping motions of their pectoral appendage, as well as a variety of intermediate behaviors along this continuum (Webb 1994; Lauder and Jayne 1996; Walker and Westneat 2002b; Fulton 2007, 2010). In general, the shape of pectoral fins vary between those with higher aspect ratios (ARs) (more wing-like) used for flapping strokes to those with lower ARs (more paddle-like) used for rowing strokes (Walker and Westneat 2000, 2002a). Whereas wing-like pectoral fins (high AR) enable flapping for more efficient swimming at greater speeds, more paddle-like pectoral fins (lower AR) assist with rowing which generates more thrust for maneuverability at lower speeds (Walker and Westneat 2002b; Wainwright et al. 2002; Thorsen and Westneat 2005). Thrust is generated differently between flapping and rowing. High AR flapping generates enough lift to create a net forward thrust ideal for cruising speeds (Vogel 1994; Walker and Westneat 2002a). Low AR rowing is characterized by greater drag in the backward stroke but more forward thrust generated during the rearward stroke (Vogel 1996; Walker and Westneat 2002a). Given these features, the morphology of pectoral fins in wrasses should vary between habitats with different amounts of wave exposure (Fulton and Bellwood 2004; Fulton et al. 2005). Reef organisms from shallow environments experience greater water velocities due to greater wave action (Denny 1988). In a study of 43 wrasse species, Fulton et al. (2001) discovered that wrasses from shallower environments possess higher AR pectoral fins, which are associated with greater thrust for efficient, high-speed swimming in wave-swept environments (Bellwood and Wainwright 2001; Fulton and Bellwood 2004; Fulton et al. 2005). At depth, in contrast, wrasses experience less wave energy and possess lower AR pectoral fins, associated with greater maneuverability (Bellwood and Wainwright 2001; Fulton et al. 2001, 2004, 2005).

Here, we explore these patterns with an expanded dataset of 131 labrid species to address two specific aims. First, we ask whether relationships between pectoral fin AR and water depth hold when parrotfish (the other major lineage of labrids) are included. Parrotfish are typically high AR swimmers and are behaviorally different from wrasses (Wainwright et al. 2002). Whereas wrasses are predators to fish and more active invertebrates, parrotfish are considered grazers that primarily feed on coral, detritus, benthic infaunal invertebrates, and large fleshy algae (Bellwood and Choat 1990; Wainwright et al. 2002; Price et al. 2010, 2011). Parrotfish can cover large cruising distances between foraging sites (a behavior for which having a high AR for flapping is optimal) and will dive to deeper depths (where having a lower AR is optimal) to graze (Bellwood 1995a, 1995b). Thus, it remains unclear whether parrotfish should follow or break the expected depth–AR relationship. Second, we explored whether different measurements of AR between two labrid pectoral AR datasets (Wainwright et al. 2002; Aiello et al. 2017) impacted relationships with water depth. The AR is defined by the equation $AR = h^2/s$, where h is the height of the fin and s is the surface area of the fin. Wainwright et al. (2002) used fin leading edge to define h, whereas Aiello et al. (2017) defined h as the longest fin span (regardless of leading edge) (Fig. 1). While our general prediction was that both AR measures would be correlated with water depth, relative differences in the strengths of these relationships might illuminate whether evolutionary patterns vary among different aspects of fin shape.

Materials and methods

Morphological and water depth data

We gathered data for morphological traits from two previously published studies, resulting in a combined dataset of 131 labrid species, including 100 species of wrasses and 31 species of parrotfish (Fig. 2 and Supplementary Table S1). One of these datasets

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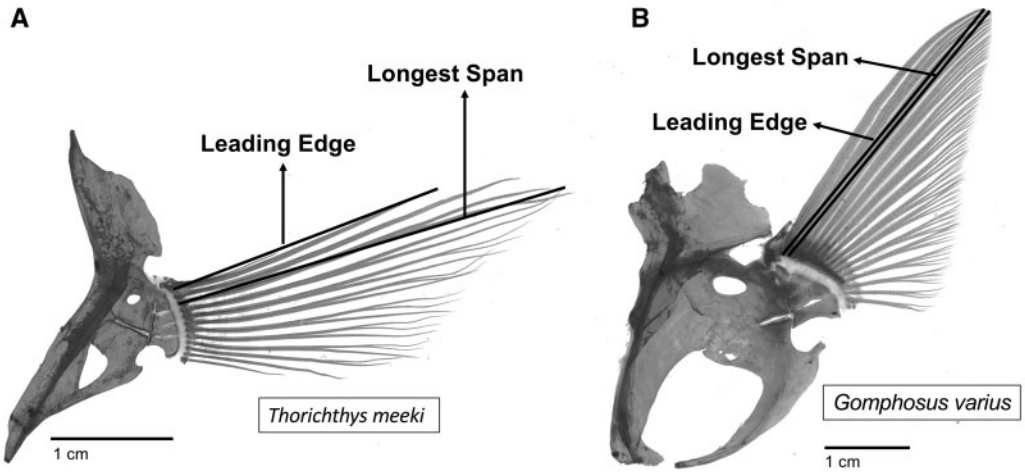

Fig. 1 Images of two pectoral fins illustrating differences in shape. (**A**) Leading edge is considerably smaller than longest span, whereas in panel **B** the lengths are nearly equivalent. Please note that the species in panel A, *Thorichthys meeki*, is a cichlid, not a labrid. We selected this species because it provides a visually clear example of a fin in which the longest span greatly exceeds the length of the leading edge. The species shown in panel B, *Gomphosus varius*, is a wrasse. Images were kindly supplied with permission by M. Westneat. The original images were enhanced for brightness to make fin edges clear.

came from Wainwright et al. (2002) and the other came from Aiello et al. (2017). In the Wainwright et al. (2002) dataset, pectoral fin AR was measured using the square of the leading edge length divided by the projected area of the fin (Fig. 1). Pectoral AR in the Aiello et al. (2017) dataset was measured as the square of the longest fin span (often, but not always, the leading edge) divided by the fin area (Fig. 1). The measurements from Wainwright et al. (2002) were divided by 2 so that they would reflect the AR of a single fin to ensure comparability to the Aiello et al. (2017) dataset. To categorize differences in habitat use, minimum and maximum depth data were collected from Fishbase (http://www.fishbase.org/) for each species (Froese and Pauly 2019). All statistical analyses were performed in the R environment (R Development Core Team 2018).

Evolutionary analyses

We used the recent time-calibrated phylogeny of Baliga and Law (2016). For this phylogenetic tree, the topology, branch lengths, and divergence times were estimated in a Bayesian framework using a relaxed-clock model approach, based on both mitochondrial and nuclear data, and with calibration points supplied by six fossils. We pruned down the tree of Baliga and Law (2016) to the 131 labrid species for which we had morphological and depth data. We visualized water depth and AR data with trait maps built using the *contMap* function in the phytools package (Revell 2012). We first estimated the phylogenetically-corrected correlation (Pearson's r) between the Wainwright and Aiello datasets using the *phyl.vcv* function in the phytools package (Revell 2012).

We then estimated the relationships between water depth and pectoral AR using phylogenetic generalized least-square regression (PGLS). The degree to which phylogeny impacts the covariance structure of the residuals can vary substantially (Felsenstein 1985; Revell 2010). To account for this variation in our PGLS analyses, we employed a model in which the maximum likelihood estimate of phylogenetic signal (λ) was simultaneously estimated with the regression parameters. This method outperforms most other approaches (including non-phylogenetic approaches) under a broad range of conditions (Revell 2010). We performed phylogenetic regressions using the *gls* function in the R package nlme (Pinheiro et al. 2020), with pectoral fin AR as response variables and minimum and maximum depth as the predictor variables.

Results

Species' pectoral fin ARs were correlated between datasets (phylogenetic correlation: $r = 0.466$, $P < 0.001$), with AR measurements often (but not always) higher in the Aiello et al. (2017) dataset than in the Wainwright et al. (2002) dataset (Fig. 3). Contrary to our expectations, we only found weak signatures connecting pectoral fin AR with minimum and maximum water depth. When data for wrasses and parrotfish were combined, we detected no relationships between water depth and pectoral AR for either dataset (Fig. 4 and Table 1).

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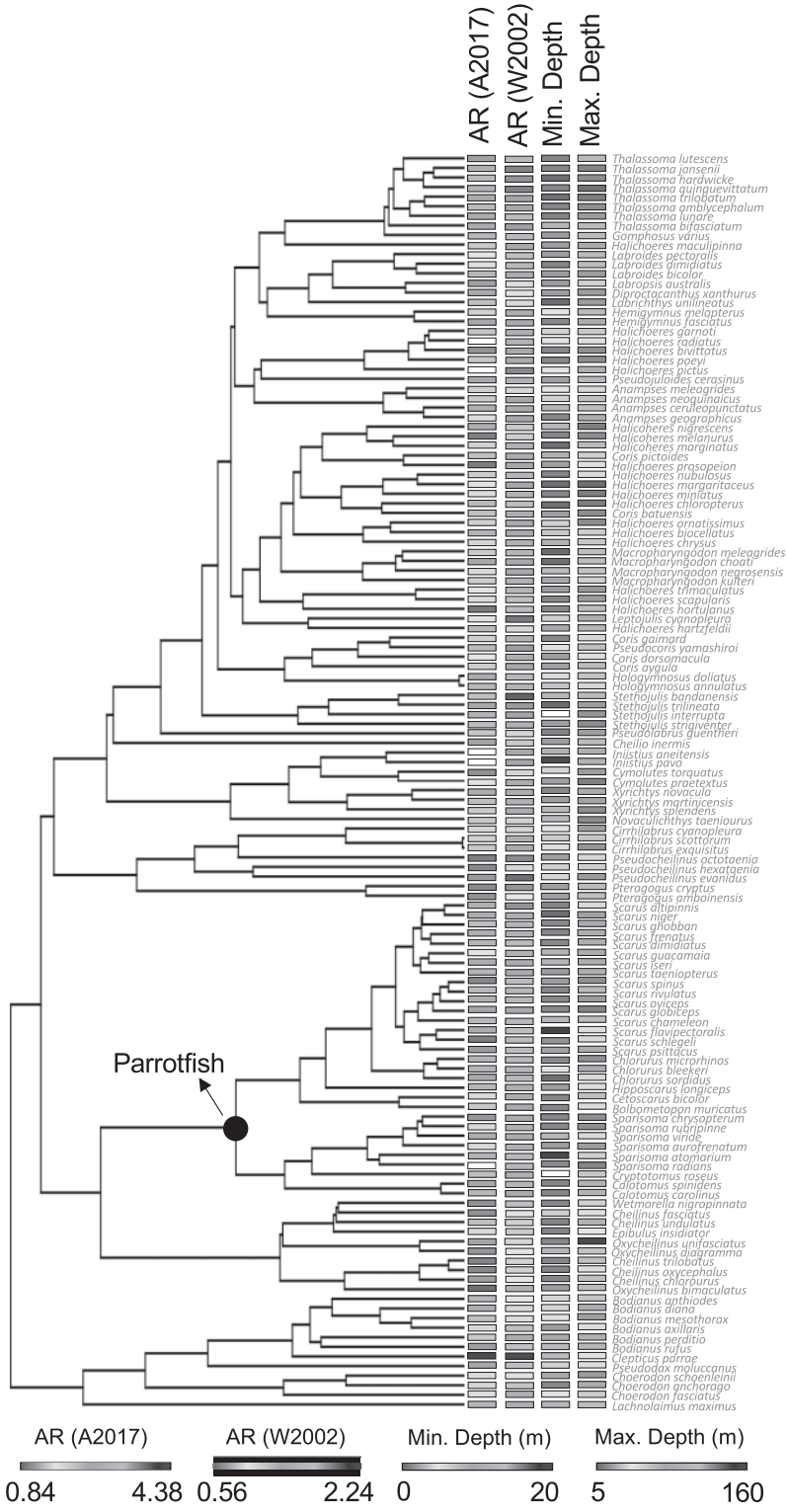

Fig. 2 Phylogeny showing the 131 species of labrids included in this study. Trait maps are provided for minimum depth (m), maximum depth (m), pectoral fin AR from the Wainwright et al. (2002) dataset (AR W2002), and pectoral fin AR from the Aiello et al. (2017) dataset (AR A2017). Legends below the tree indicate the value ranges for each trait.

When wrasses were analyzed separately, we detected an inverse relationship between maximum water depth and pectoral fin AR, but only in the Aiello et al. (2017) dataset (Fig. 5 and Table 1). When parrotfish were analyzed separately, we detected no relationships between water depth and AR in either

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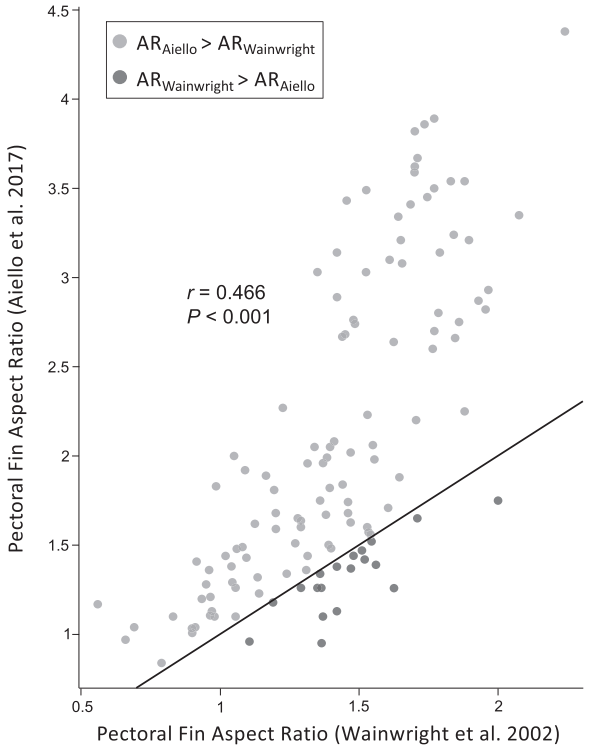

Fig. 3 Plot showing the relationship between pectoral aspect fin ratio measured by Wainwright et al. (2002) (*x*-axis) and Aiello et al. (2017) (*y*-axis). The black line shows a 1:1 relationship between datasets.

the Aiello et al. (2017) or Wainwright et al. (2002) datasets (Fig. 5 and Table 1).

Discussion

Performance tradeoffs are predicted to limit the range of phenotypes organisms exhibit, resulting in distinct macroevolutionary patterns across environmental gradients (Ghalambor et al. 2003, 2004; Holzman et al. 2012; Muñoz et al. 2017, 2018; Stayton 2019). In reef fishes, fin form shapes evolutionary patterns of hydrodynamic performance (Walker and Westneat 2000; Thorsen and Westneat 2005) and contributes to patterns of niche diversity (Bellwood and Wainwright 2001; Wainwright et al. 2002). However, across a relatively broad depth gradient (0–20 m minimum depth range and 5–160 m maximum depth range; Fig. 2 and Supplementary Table S1), we discovered weak, if any, macroevolutionary signatures of pectoral fin adaptation. We found that pectoral fin AR responds (albeit weakly) to water depth in a manner consistent with functional tradeoffs based on water column use (Fulton et al. 2001, 2005; Blake 2004). Specifically, wrasses from more wave-swept (shallow) environments exhibit more wing-like pectoral fins (with higher ARs), which is associated with more sustained swimming speeds (Fulton et al. 2001, 2005; Wainwright et al. 2002; Thorsen and Westneat 2005). In deeper habitats with less wave flow, wrasses exhibit more paddle-like pectoral fins (with lower ARs), associated with greater maneuverability (Fulton et al. 2001, 2002, 2005). This result fits into a broader picture of morphological adaptation to water depth in bony fishes: surface-based swimming is generally associated with more thrust-based propulsion, whereas deeper water fishes exhibit features associated with greater maneuverability and more undulatory swimming (e.g., Myers et al. 2020).

In contrast, we did not discover any depth-based signatures in parrotfish pectoral fin AR. Parrotfishes typically have high AR fins and are known to dive at deeper depths to graze on coral and macroalgae (Bruggemann et al. 1994; Bellwood 1995b; Rotjan and Lewis 2006; Hoey and Bellwood 2008). One interesting observation is that *Sparisoma* parrotfish tend to have relatively lower ARs. Feeding in this group is diverse and includes scraping detritivores and grazing herbivores (Randall 1967; Price et al. 2009). This larger variation in diet (for parrotfish) could result in less of a demand to cruise larger distances between feeding patches. The other clade within parrotfish includes fishes that scrape more on coral, which would create the demand to have to travel between coral patches (Bellwood and Choat 1990). Another possibility is that fishes aren't limited to "flapping" or "rowing" behaviors. Parrotfish might be versatile in how they use their pectoral appendages, exhibit intermediate behaviors along the flapping-rowing continuum (Lauder and Jayne 1996; Walker and Westneat 2002a), and dynamically shift their swimming during feeding (Rice and Westneat 2005). For example, Aiello et al. (2020) observed that the greenblotch parrotfish, *Scarus quoyi*, exhibits a fin stroke with plane angles intermediate between that of a drag-based rower, *Halichoeres bivittatus* (a wrasse with low AR pectoral fins), and a lift-based flapper, *Gomphosus varius* (a wrasse with high AR pectoral fins).

One major question that emerges from our results is why pectoral fin AR decreases with water depth when examined with the Aiello et al. (2017) dataset but not with the Wainwright et al. (2002) dataset. Both measurements are correlated with each other, although the strength of the correlation is not especially strong (Fig. 3). Although both measures provide clear and intuitive descriptions of fin shape, they differ in a few ways. Perhaps in part because the leading edge is not always the longest fin ray, estimates of AR were generally lower in the Wainwright et al. (2002) dataset than in the Aiello

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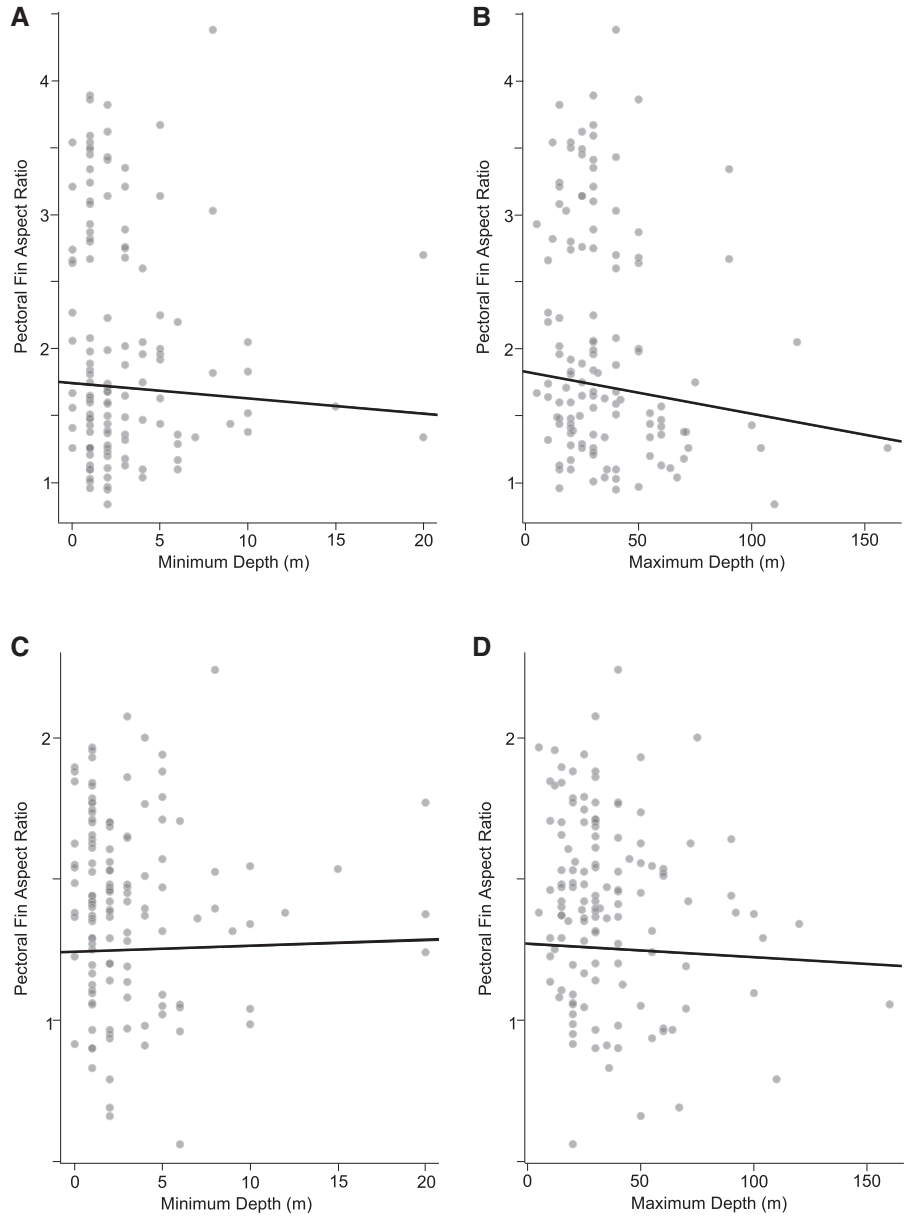

Fig. 4 Plots showing the relationships between pectoral AR and minimum (A + C) and maximum (B + D) water depth. Data from Aiello et al. (2017) are given in panels A + B and data from Wainwright et al. (2002) are given in panels C + D.

et al. (2017) dataset. Because AR is based off the square of fin span, the deviation between AR measurements can be particularly pronounced in high AR species. As an important caveat, however, the leading edge often is the longest fin ray in labrids (P. Wainwright, personal communication), so differences in longest span might not fully explain this pattern. Another possibility is that differences between datasets arise in the measurement of fin surface area, which varied a bit with regards to how specimens were handled for images (Wainwright et al. 2002; Aiello et al. 2017). Our general takeaway is that how morphological traits are measured might impact the trends we extract from macroevolutionary studies. Ideally, macroevolutionary relationships would be supported by independent datasets measured in equally valid but slightly different ways. In this case, however, we suspect the differences we observed arise because our environmental measures were not especially informative, rather than due to differences in how AR was measured.

Minimum and maximum water depth are overall weak predictors of AR. Fulton et al. (2001) described water column use via height above the substratum (rather than water depth), which was strongly correlated with pectoral fin AR in reef flat wrasses. Similarly, Bellwood and Wainwright (2001) found that labrids in more exposed areas of the reef have

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Table 1 Phylogenetic generalized least squares (PGLSs) regressions reveal an overall weak signal for morphological evolution in response to water depth

	Source	Data included	Coeff.±SE	λ	t	Number of species	P
I. Minimum depth	Aiello et al. (2017)	All Species	−0.011±0.013	0.900	−0.813	124	0.418
		Wrasses	0.020±0.018	0.931	1.109	95	0.270
		Parrotfish	−0.037±0.022	0.860	−1.63	29	0.113
	Wainwright et al. (2002)	All Species	0.002±0.004	0.965	0.446	129	0.656
		Wrasses	0.002±0.006	0.981	0.302	99	0.763
		Parrotfish	0.002±0.006	0.633	0.323	30	0.749
II. Maximum depth	Aiello et al. (2017)	All Species	−0.003±0.002	0.892	−1.590	124	0.114
		Wrasses	−0.004±0.002	0.932	−2.276	96	**0.025**
		Parrotfish	0.003±0.006	0.803	0.447	30	0.658
	Wainwright et al. (2002)	All species	−0.000±0.001	0.964	−0.697	131	0.487
		Wrasses	−0.001±0.001	0.982	−1.389	100	0.169
		Parrotfish	0.002±0.002	0.638	1.358	31	0.185

In each analysis, water depth (minimum or maximum depth, m) is the predictor variable and pectoral fin AR is the response variable. $P < 0.05$ are shown in bold.

pectoral fins with higher ARs (which were measured using fin leading edge). Together, these results suggest that it is possible that we did not observe a stronger pattern because minimum/maximum depth is a weak predictor of wave exposure. While many reef fishes tend to exhibit at least some fidelity to different reef habitat zones (Williams 1982; Green 1996), it is possible that relative use of different depths establishes stronger constraints on pectoral fin morphology than maximum or minimum depth. For example, several species of *Halichoeres* wrasses are primarily found at shallow depths above 16 m (Wainwright et al. 2018). Yet, these same species are recorded to go down as far as 60 m when using FishBase. The coarse, limit-based categories used in our analysis could be obscuring patterns between depth and pectoral fin morphology. Although such measures are more broadly available than fine-scale measurements of habitat use, the ability to accurately infer macroevolutionary trends might be correspondingly limited.

It is also important to consider how potential ontogenetic differences in morphology and habitat use may influence patterns observed in this study. Within labrids, there are some species that settle and recruit directly in adult habitats (Eckert 1984). There are also species that have ontogenetic migrations between habitat zones (Green 1996). Additionally, some labrid species experience more prominent changes in pectoral fin AR through ontogeny than others (Fulton and Bellwood 2002). These morphological differences indicate that juveniles in general employ more drag-based rowing (Fulton and Bellwood 2002). Variation in habitat usage and morphology throughout different stages of ontogeny makes it even more difficult to understand the macroevolutionary patterns associated with morphology and habitat in labrids.

Another issue worth considering is how much pectoral fin AR translates into functional differences in swimming performance. Although pectoral fin AR is strongly correlated with field-measured swimming speeds ($r = 0.63$; Table 1 in Fulton et al. 2005), much of the residual variation remains to be explained. For example, differences in the surrounding musculature contribute to differences in swimming performance (Weihs 1989; Thorsen and Westneat 2005). Similarly, differences in fin shape besides AR (Combes and Daniel 2001) and fin material properties such as Young's modulus (Lauder and Madden 2006; Aiello et al. 2018a) also influence swimming performance. In addition to the passive properties of fins, active sensory feedback also contributes to effective locomotion performance: fine-scale mechanosensory tuning can dynamically alter how fishes with different morphologies behaviorally interact with water (Williams et al. 2013; Aiello et al. 2017, 2018b). Thus, although AR was measured in a static fashion from splayed images in both studies, it can actually be dynamically modulated during fin strokes.

Weak correlations between environment and morphology can also arise when organisms can use different morphological traits to accomplish similar functions (many-to-one mapping). (Wainwright et al. 2005; Wainwright 2007; Muñoz 2019). By supplying multiple morphological pathways to a

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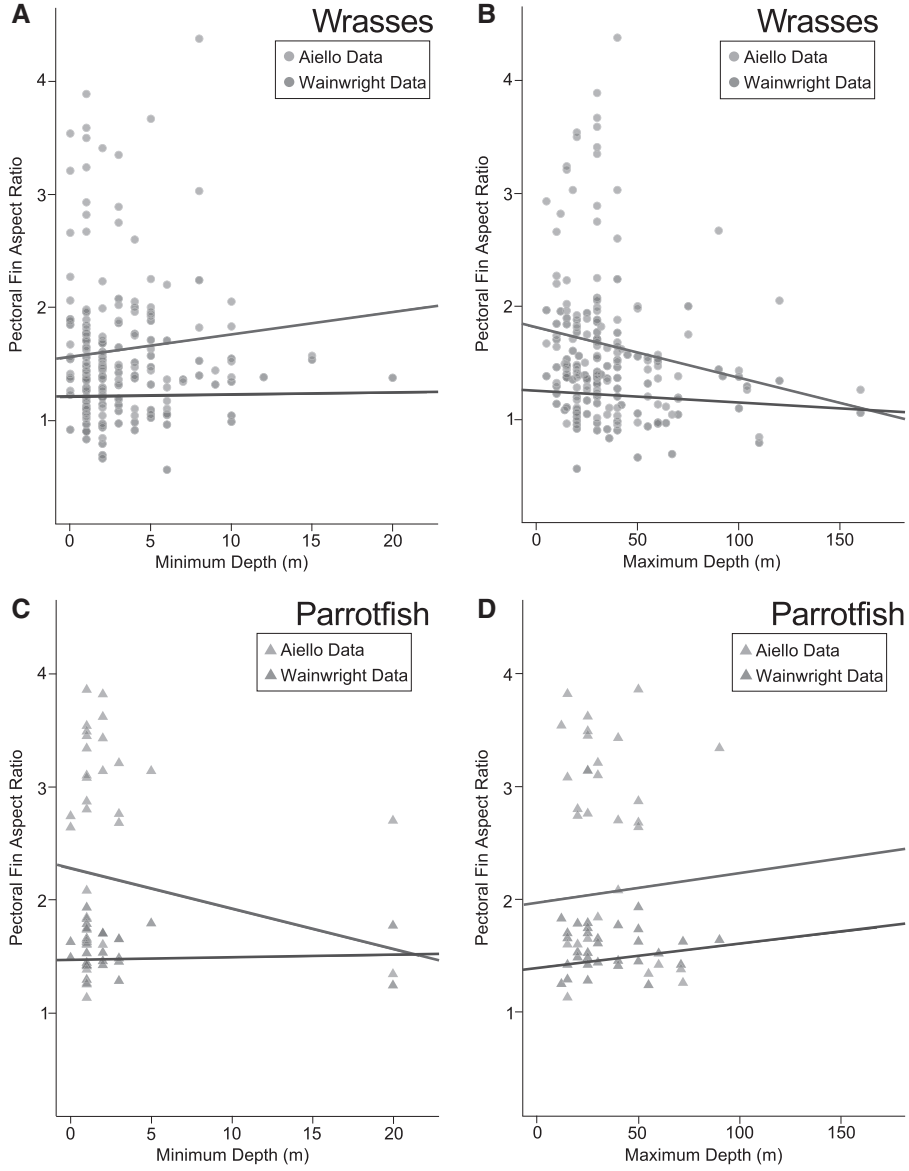

Fig. 5 Plots showing the relationships between water depth and pectoral AR in wrasses (panels A + B) and parrotfish (panels C + D). Point color refers to the data source. Each point represents a different species of fish.

common performance outcome, many-to-one mapping can release some aspects of morphology from selection on performance (Collar and Wainwright 2006; Muñoz et al. 2018). Swimming speed reflects the combination of many biomechanical and behavioral properties, which may weaken the correlation between morphology and performance, even when strong functional tradeoffs across ecological gradients are present (Alfaro et al. 2004, 2005). This may be especially true for morphological traits that experience strong genetic and developmental constraints (Wagner and Altenberg 1996; Albertson et al. 2005; Bright et al. 2016). It may also be the case that some aspects of functional morphology (e.g., musculature, skeletal traits, and shape) exhibit a stronger relationship with performance than other traits, reflecting an underlying mechanical sensitivity of some component of the system (Anderson and Patek 2015). Even in redundant systems, evolution will often target the mechanical pathway most strongly correlated with performance (Muñoz et al. 2017, 2018). In other words, functional redundancy, genetic constraints, and mechanical sensitivity can interact to decouple morphological and performance evolution in some traits (Muñoz 2019).

Fish morphology is influenced by a number of selective pressures besides wave energy. This milieu of diverse selective pressures contributes to

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exceptional phenotypic and species diversity of fishes (Rabosky et al. 2013; Friedman et al. 2019). For example, the temperature, salinity, and presence of toxins in water all impact patterns of body shape evolution in fishes (e.g., Pilakouta et al. 2019; Price et al. 2019; Styga et al. 2019; Camarillo et al. 2020). Fish swimming morphology also correlates with dietary niche; for example, trophic specialists exhibit high functional diversity and rapid rates of morphological evolution (Borstein et al. 2019). Sexual selection can promote evolution of body shape in fishes, even when those same features do not enhance swimming performance (Meyer et al. 1994). Predator-induced selection can result in morphological evolution that alters swimming performance (Ghalambor et al. 2004; Price et al. 2015). Functional trait variation almost certainly reflects a compromise in response to many different, potentially contrasting, selective pressures (Levins and Lewontin 1985; Huey et al. 2003; Muñoz and Losos 2018). By extension, disentangling the macroevolutionary signatures of different selective pressures on functional morphology will require a framework in which large-scale ecological, environmental, phenotypic, and phylogenetic data are simultaneously compared. Such approaches have been traditionally hindered by the rate-limiting step of data acquisition. As the field of evolutionary biomechanics rapidly transitions into the era of big data (Chang and Alfaro 2016; Muñoz and Price 2019), the ability to address fundamental questions about form–function evolution robustly is quickly becoming within our reach.

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Supplementary data

Supplementary data are available at *ICB* online.

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