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Size as a complex trait and the scaling relationships of its components across teleosts

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Abstract

Body size influences nearly every aspect of an organism's biology and ecology. When studying body size, researchers often focus on a single dimension, such as length, despite the fact that size can evolve by altering multiple body dimensions. The distinct ways organisms change their size can have profound consequences on evolutionary and ecological processes. Here, we investigate the evolution of size as a complex trait by exploring the interaction between body length, depth, and width across 42 orders of teleost fishes. Using Ornstein-Uhlenbeck models, we compare shifts in the adaptive landscapes of each of the three size components, and in the scaling relationships between them. We find that fishes change their size in a myriad of ways: changes in length, depth and width rarely co-occur on the phylogeny or in accordance with composite measures of size (body mass or the geometric mean). Body size diversity tends to accumulate along trajectories close to isometry but there is also some variation in the allometric regimes. Finally, orders with scaling shifts are more species rich than those without shifts, suggesting that body size diversity trajectories have the potential to be associated with distinct diversification scenarios in teleosts. Based on the evolutionary relationships we found between size components, we recommend that researchers treat body size as a complex trait to properly evaluate the patterns and processes of size variation in nature.

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Introduction

Size is of primary importance in shaping the role of organisms in nature. Most, if not all, organismal characteristics vary closely with body size. Consequently, organisms can change their ecological niche by simply changing their body size (Calder 1984; Bonner 2011). For example, large animals will also have large heads and jaws that allow them to feed on larger prey (e.g. King 2002). Species with different body sizes will also likely have distinct generation times (Purvis and Orme 2005) and metabolic rates (Kleiber 1932; Brown et al. 2004; Uyeda et al. 2017). In addition, changes in body size can have profound impacts on evolutionary and ecological processes occurring well beyond the individual organismal level. Increasing or decreasing body size can affect species extinction probability (Smith et al. 2018; Payne and Heim 2020), the macroevolutionary dynamics of a clade (Feldman et al. 2016; Amado et al. 2020), and the structure of ecological networks within biological communities (Woodward et al. 2005; Pinto-Coelho et al. 2021).

Despite body size being the focus of many studies, as well as a trait that is easy to measure and widely available in the literature, establishing general patterns of size evolution is challenging (Clarke 2021). Body size is a complex trait, not only because there are many selective pressures underlying its variation in nature but also because it encompasses different dimensions and thus the potential to be measured by distinct variables (Vea and Shingleton 2020). The multidimensional aspect of body size opens several possibilities by which organisms can change their size, and by altering body proportions (e.g. length, width, or depth) distinct shapes can be produced. Nevertheless, researchers often focus on one body size component (e.g. length) or metric (e.g. standard length) when investigating relationships between size and ecological or geographical aspects (e.g. Alencar et al. 2017; Womack and Bell 2020), or even to understand biological scaling (e.g. Tsuboi et al. 2018; Tonini et al. 2020). Moreover, the metric chosen often varies depending on the convention for a particular taxonomic group. Ichthyologists commonly use standard or total length as a measure of body size (e.g. Albert and Johnson 2012; Froese and Pauly 2021), while mammalogists frequently use body mass (e.g. Smith et al. 2003; Jones et al. 2009). However, to properly identify size patterns at broad scales and understand the underlying processes, we need approaches that take into account different body size metrics (Law et al. 2018; Clarke 2021).

Size usually accounts for most of the morphological variation we observe across organisms (e.g. Law 2020; Pigot et al. 2020). Therefore, assuming one-to-one mapping of morphological-to-ecological variation, ecological shifts might occur more frequently as a result of changes in organismal size rather than shape. Indeed, size has been suggested to be a "line of least evolutionary resistance" underlying morphological and ecological diversification (Schluter 1996; Marroig and Cheverud 2005, 2010). Under this scenario, body form diversity (by "body form" we mean a single unified unit comprising size and shape, Klingenberg 2016) would mostly comprise body size variants without large amounts of shape variation. These body size variants may arise as the result of genetic channeling or developmental bias (Brakefield 2006). In other words, body parts would frequently change isometrically, which means the relative proportions would be preserved with an allometric slope equal to one. At the macroevolutionary scale, body size diversity might be observed to primarily accumulate following trajectories close to isometry (species would tend to be larger or smaller copies of each other), especially because scaling relationships tend to remain relatively constant through time (e.g. Voje et al. 2013; Houle et al. 2019).

In this study, we explore the evolution of body size across teleost fishes by considering size as a complex trait. Teleosts exhibit a high diversity of body sizes and shapes (Albert and Johnson 2012; Floeter et al. 2018; Friedman et al. 2019; Price et al. 2019). Catfishes (order Siluriformes), for example, range from the tiny candirus (family Trichomycteridae) that measure approximately 3 centimeters in length to the Mekong giant catfish (*Pangasius gigas*) that can reach lengths of up to 3 meters (Froese and Pauly 2021). The incredible size diversity within teleosts relates to a variety of lifestyles and the occupation of distinct ecological niches, which relate to differential performance across these environments (e.g. Bernatchez & Dodson 1987; Steele and López-Fernández 2014; Bloom et al. 2018; Friedman et al. 2020; Rincon-Sandoval et al. 2020; Martinez et al. 2021; Clarke 2021). Deeper bodies, for example, can increase unsteady swimming performance in fishes, which has been observed as an adaptation to navigating structurally complex environments (e.g. Langerhans and Reznick 2010; Larouche et al. 2020).

As body size reflects the collective size of the body's component parts (Vea and Shingleton 2020), there are multiple evolutionary paths by which fishes and, organisms in general, can change their body size. We therefore investigate the evolution of three body size components (length, depth and width) and two composite metrics (body mass and the geometric mean of length, depth and width, *sensu* Price et al. 2019) within 42 orders of teleosts. First, by identifying shifts in phenotypic optima, we ask if changes in the three body size components co-occur on the phylogeny. We also explore the similarity between the phylogenetic position of the phenotypic optima of the different body size components and those estimated for body mass and the geometric mean. In the next step, we investigate how often the allometric regimes (relationships between length, depth and width) shifted during the radiation of the orders analyzed. If size is a line of least evolutionary resistance in teleosts, body form evolution should mostly comprise changes in size but not necessarily in shape and thus we would expect body size diversity to accumulate by predominantly following trajectories close to isometry. Additionally, we predict that allometric shifts in orders following trajectories close to isometry will be rarer, since selection would favor and maintain isometry over broad temporal scales. Our exploratory framework provides a general overview of how body size diversity accumulated within teleost fishes and enables us to identify parts of the teleost tree of life where unique processes might have played an important role in shaping body size evolution.

Materials and methods

Morphological data, phylogenetic information and focal clades

We used measurements of standard length, maximum body depth, maximum fish width (which could be on the head or body of the fish) and mass from a large morphological dataset generated for more than 6000 species of teleosts obtained from specimens deposited at the Smithsonian National Museum of Natural History (see Price et al. 2019). Although we endeavored to only include adult-sized specimens during data collection (Price et al. 2019), the absolute size of the specimens is limited by the size of the jars. Therefore, large species are likely represented by smaller specimens than their actual maximum size. It should also be noted that specimen body mass will be less accurate than those measured on fresh

specimens, as some were labeled with heavy tags and not all the specimens were intact; for example, internal organs had been excised from some specimens. We also calculated the geometric mean of standard length, maximum body depth and maximum fish width, as the cube root of the product of the three-size components (*sensu* Price et al. 2019) as an additional size metric. All five size traits were log-transformed prior to the analyses below.

Using the phylogenetic tree of ray-finned fishes generated by Rabosky et al. (2018), we first investigated which orders were monophyletic using the R package MonoPhy (Schwery and O'Meara 2016). MonoPhy takes a list of species with its corresponding orders and verifies if the species belonging to a given order all form a group, where all species descend from a common ancestor. We identified 60 monophyletic orders of teleosts and retained 42 of them, which had 10 or more species within our morphological dataset, for our subsequent analyses (see Table S1 for the number of species per order). For higher-level taxonomy (families and orders) we followed the molecular taxonomy of Betancur-R et al. (2017).

Shifts in size optima across teleosts

The Ornstein-Uhlenback (OU) process (described by the Eq. 1) is ideal for modeling changes in phenotypic regimes during the radiation of a lineage (Butler and King 2004; Beaulieu et al. 2012; Cooper et al. 2016). In summary, this equation describes the amount of change of a trait X over a given amount of time t; θ is the phenotypic optimum, which represent the hypothetical phenotypic value towards which populations are evolving; σ is the phenotypic rate, which measures the intensity of the random fluctuations in the evolutionary process; and α is the strength of selection, which indicates the attraction towards the phenotypic optimum. When α = 0, the OU process reduces to Brownian Motion (see Hansen 1997; Butler and King 2004; Beaulieu et al. 2012).

We used the R package ℓ1ou (Khabbazian et al. 2016) to detect shifts in the phenotypic optimum of each of the five size traits during the radiation of every order. ℓ1ou fits multi-optima OU models and uses the lasso (Least Absolute Shrinkage and Selection Operator, Tibshirani and Taylor 2011) method to identify an optimal set of phenotypic regimes on a phylogeny, given the trait values of the terminal taxa (Slater and Friscia, 2019). ℓ1ou identifies a set of phenotypic regimes by varying the phenotypic optimum and fixing α and σ parameters. An estimated shift in the phenotypic optimum of a trait can be interpreted as a shift in the value towards which the trait is evolving (with a fixed σ and α). It represents an adaptive zone around which the traits true value potentially fluctuates stochastically (Hansen 1997, Uyeda and Harmon 2014). ℓ1ou assumes that traits are evolving along branches according to an OU process but does not quantify whether they have reached the estimated optimal values. How quickly a lineage reaches the new optimum following a shift is quantified by the phylogenetic half-life (given by ln(2)/α), which is the average time it will take the trait to change half-way to the new optimal value. If the half-life exceeds the age of the order, it is clear that the adaptive process is relatively weak, as the clade will likely never reach the new optimum. For α we set an upper bound of five to help the models converge and the upper bound was reached in a few analyses (see Table S2). We set the maximum number of shifts in the phenotypic optimum as half of the total number of tips and performed model comparison using a phylogenetic Bayesian Information Criterion (BIC). We used the best estimated shift configuration (lowest BIC) to compare the adaptive landscapes (i.e. number and position of shifts) characterizing the evolution of each size component and

the additional composite metrics. However, as a way to quantify the uncertainty surrounding each of the shifts that we considered as valid (see below), we calculated the number of times each shift was sampled across all best shift configurations for each order and size trait. ℓ1ou outputs with the shifts and corresponding "support" values are provided as part of the supplementary material. We could not estimate these values for the two largest orders, Cypriniformes and Siluriformes, due to the lack of computational resources.

$$dX(t) = \alpha[\theta - X(t)]d(t) + \sigma dB(t) \qquad \text{(Eq. 1)}$$

After analyzing each size trait across the 42 orders, we extracted the estimated number of shifts in the phenotypic optima to assess: (1) which size component or metric were more or less likely to vary, (2) which orders have the most or fewest number of shifts, and (3) how the number of shifts varied across the size components within each order. To evaluate how similar the adaptive landscapes of the three size components are, we extracted the common shifts that occurred on the same branch of the phylogeny in each order. Common shifts can be interpreted as shifts in the tendency of evolution of multiple traits (toward new phenotypic optima). They do not indicate that trait evolution is correlated, as the optima could shift in different directions, with different magnitudes. Each trait continues to evolve according to an OU process with a constant σ and α, and may or may not be close to the estimated optimal value. We also compared how many shifts in the three size components co-occurred with those of the other two size metrics (body mass and the geometric mean). We evaluated whether common shifts occurred in the same direction (if the phenotypic optimum associated with each of these shifts increased or decreased compared to the corresponding ancestral regime). Finally, we compared the magnitude of change in the phenotypic optimum of each common shift relative to the estimated ancestral value. We did this by estimating the variance of the magnitudes of the common shifts among the three size components, or by calculating the difference in the magnitudes of common shifts between a given pair of size components (e.g. standard length and body depth). We considered as "valid shifts" only the shifts for which the corresponding regime encompassed at least two species.

Given that the proportion of species sampled within our morphological dataset varies widely across orders, we also investigated whether the number of shifts detected by ℓ1ou is related to the proportion of species sampled by fitting negative binomial generalized linear models (GLM) using the function glm.nb of the R package MASS (Venables and Ripley 2002). We chose to use negative binomial GLM to account for overdispersion, and performed this step using the number of shifts estimated for each size metric (standard length, body width, body depth, geometric mean and body mass).

Macroevolutionary dynamics of allometry: quantifying the relationship between length, width and depth

We used the R package bayou v 2.2.0 (Uyeda and Harmon 2014; Uyeda et al. 2020) to search for shifts in the phenotypic optima of the scaling relationships between each of the three size components (standard length, body depth and fish width) across 42 orders. Like ℓ1ou, bayou fits multi-optima OU models but using a Bayesian Reversible jump MCMC algorithm. In contrast to ℓ1ou, bayou searches for shifts in an allometric ridge, described by

the intercept and slope of the relationship between two traits, rather than a single value for the optimum (see Uyeda et al. 2017). We fixed the σ and α parameters, as we were primarily interested in the optima, and estimating σ and α would have substantially increased the runtime of the analyses.

For each of the three scaling relationships explored (standard length vs. body depth, standard length vs. body width, and body depth vs. body width), intercepts and slopes were allowed to vary during the radiation of each order. Therefore, shifts in the scaling relationships (or allometric regimes) can comprise shifts in slopes, intercepts or both. Prior distributions were set as the default and the prior for the maximum number of shifts as half of the number of tips of each order. Starting values for slopes were obtained by fitting linear models for each relationship in each order and we used the mean and standard deviation of empirical dependent variables as starting values for the intercept. We zero centered the distribution of independent variables prior to the analyses. We ran MCMC chains for each relationship for 500,000–15 million generations sampling every 1000 generations. We excluded the first 30% of generations as burn-in and assessed convergence by checking the tracer plot of the parameters and effect sample sizes. We considered only shifts with posterior probability greater than 0.9 and for which the corresponding allometric regime encompassed at least three species (see Uyeda et al. 2017).

To evaluate if body size diversity predominantly followed an isometric trajectory we explored whether the distribution of slopes associated with the allometric regimes across the 42 orders were centered around one. Specifically, we calculated the 95% highest density interval of the slopes across these allometric regimes using the R package HDInterval (Meredith and Kruschke 2020). We also provide the 95% highest density interval of the intercepts for comparison. Next, we used phylogenetic ANOVAs implemented in the R package Phytools (Revell 2012) to investigate whether the orders lacking allometric shifts were associated with background slopes closer to isometry compared to those orders where shifts occurred. We performed phylogenetic ANOVAs using mean slopes estimated across background regimes detected for each order (including the three scaling relationships) and an order-level phylogenetic tree extracted from the species-level tree provided by Rabosky et al. (2018). We did not repeat the GLM analyses that we performed on the ℓ1ou results to test the relationship between the proportion of species sampled and the number of shifts because we had no *a priori* expectations that decreasing the proportion of the species sampled would change the allometric regime and thus affect the probability of detecting an allometric shift.

Results

Shifts in size optima

Considering all shifts estimated for standard length, fish width, and body depth across 42 teleost orders, no size component or metric is more or less dynamic relative to the others. The average number of shifts when considering all orders together is generally similar among the three size components (length=4.1, depth=3.3, width=3.3; Fig. 1) and also when compared to the other size metrics analyzed herein (geometric mean=3.1, body mass=3.2, Fig. 1). However, one order (Siluriformes) has a much higher number of shifts

Fig. 1 Distribution of the number of shifts in the optima detected by the ℓ1ou analyses of standard length, body depth, fish width, geometric mean and body mass during the radiation of 42 teleost orders
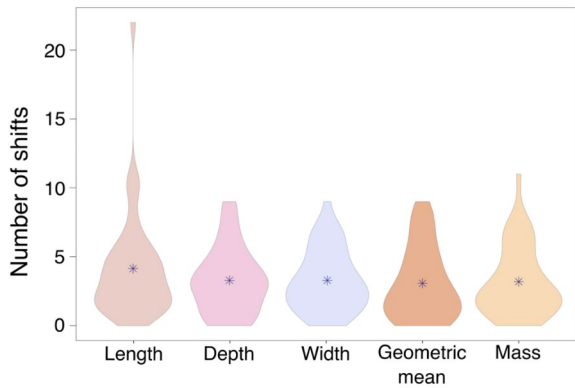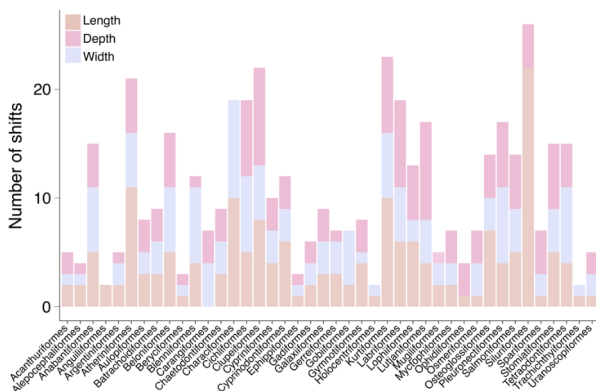

in standard length (22 shifts), increasing the maximum range for this variable relative to the others (Figs. 1 and 2).

Comparing orders enables us to identify clades with the highest and lowest total number of shifts in size optima relative to the overall trend. Anguilliformes, Beryciformes, Ephippiformes, Holocentriformes, and Trachichthyiformes have fewer shifts in their size components than 90% of all the orders analyzed (Table S1, Fig. 2). In contrast, Atheriniformes, Clupeiformes, Kurtiformes and Siluriformes have more shifts in their size components than 90% of the teleost orders analyzed (Table S1, Fig. 2). Within orders, the number of shifts in length, depth and width also varies (Table S1, Fig. 2). For example, depth and width did not change within Anguilliformes (eels) whereas length changed twice. During the radiation of Siluriformes (catfishes) we detected only four shifts in depth and no shifts for width compared to 22 shifts in length. In Characiformes, depth did not change but length and width changed 10 and 9 times, respectively. While Beryciformes, Chaetodontiformes, Ephippiformes, Gadiformes, Galaxiiformes show the exact same number of shifts for each of the size components.

By comparing common shifts between the size components, it becomes evident that size does not change in a consistent manner across teleosts (Fig. 3, Figs S1-3). Shifts in the primary optima of the three size components rarely occur on the same branch in most clades (see Fig. 3). In fact, there are no common shifts between length, depth, and width in 18 of

Fig. 2 Number of shifts in the optima detected by the ℓ1ou analyses of standard length, body depth and body width across each order

Fig. 3 Common shifts in the optima between the three size components (standard length, body depth and body width). Dark grey bars depict the total number of shifts detected by the ℓ1ou analyses for each order and light grey bars depict the number of these shifts that occur in the same phylogenetic position (i.e. same branch of the phylogeny) across the three size components

the 42 orders. The other 24 orders have at least one common shift between the three size components and they always involve changes in the same direction (Fig. 3, Table S1), with only a slight magnitude difference in most cases (Fig. S4). We did not find any evidence that one size component consistently changes more frequently with one of the other two components, although this varies greatly between orders (see Figures S1-3). Regardless of which size components change together, they always change in the same direction (Table S1) and only with a slight magnitude difference in most cases (Fig. S5-7).

The distribution of shifts (total and common shifts) was similar when comparing each size component to both the geometric mean and body mass (Figure S8-10). We did not find strong evidence that one size component has more shifts in common with either the geometric mean or body mass. Standard length has only slightly fewer common shifts with both body mass and geometric mean compared to width and depth (Fig. S8-10). This is illustrated by comparing the number of orders that share at least 80% of shifts between each trait and the composite measures of size (mass and geometric mean): 8 orders share at least 80% of their shifts between standard length and body mass and 9 orders share at least 80% of their shifts between standard length and geometric mean, compared to 9 orders that share at least 80% of their shifts between body width and body mass, 13 orders that share at least 80% of their shifts between body width and geometric mean, 12 orders that share at least 80% of their shifts between body depth and body mass, and 11 orders that share at least 80% of their shifts between body depth and geometric mean.

We detected a potential species sampling effect on the estimated number of shifts in standard length, as there was a tendency for the number of shifts to increase as the proportion of species sampled decreased (Table S3). However, this trend was not evident in any of the other variables explored here (body depth, fish width, body mass and geometric mean), suggesting that species sampling does not explain most of the trends that we found, although standard length may be sensitive to species sampling effects. A summary of parameter estimates (α, σ and phylogenetic half-life), number of shifts, and the direction of shifts detected by ℓ1ou for each size metric can be found in Tables S1 and S2. Most of the estimated phylogenetic half-lives are much smaller than the age of the orders suggesting that these lineages might have reached their phenotypic optima.

Macroevolutionary dynamics of allometry

We found shifts in allometric regimes (changes in slope and/or intercept) described by the relationships between length and depth for only 11 of the 42 teleost orders. This decreased to 9/42 when analyzing depth and width, and to 7/42 when analyzing length and width. The maximum number of shifts in allometric regimes was three (see Table S4), which occurred between length and depth within Anguilliformes and Cichliformes. No order had shifts across all three scaling relationships, however, almost half of the orders analyzed (45%, Table S4) experienced a shift between either length and depth, length and width or depth and width, at some point during their radiation (Table S4, Fig. 4 A). Shifts in these scaling relationships are widespread across the phylogeny (Fig. 4 A), with one exception; there were no shifts between length and width during the radiation of the clade that comprises Ovalentaria, Gobiiformes and Kurtiformes (Table S4, Fig. 4 A). Summary statistics, parameter estimates, and phylogenetic half-lives for each order and scaling relationship can be found in Table S5 and Table S6. As in the ℓ1ou analyses, phylogenetic half-lives are for the most part smaller than the age of the orders. Plots showing the shifts estimated across 42 orders for each scaling relationship are also provided in the supplementary material.

The optimal values for the scaling relationships between the three size components are associated with slopes concentrated close to one (density peaks: slope $_{length ~ depth}$ = 1.02, slope $_{length ~ width}$ = 0.94, slope $_{depth ~ width}$ = 0.92, see Fig. 4B), suggesting that body size
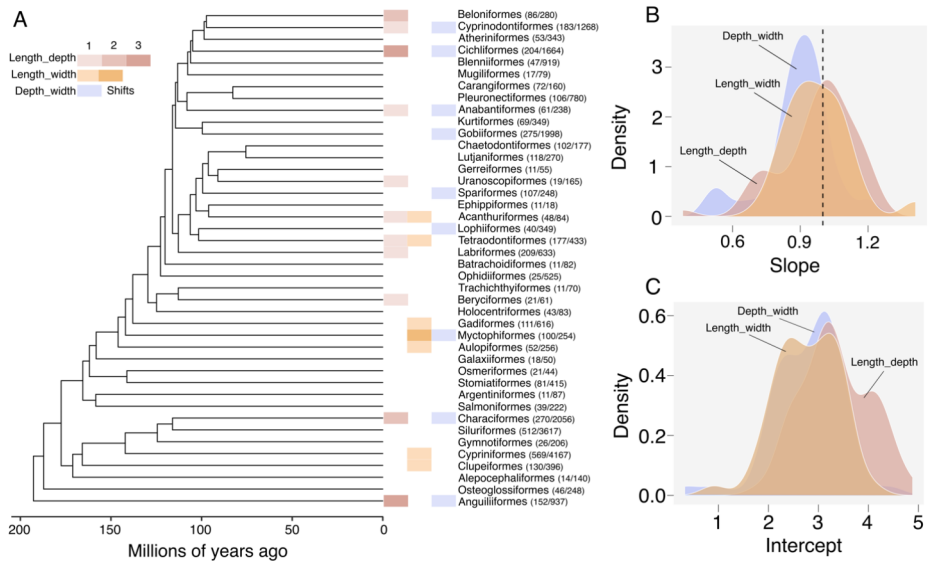
Fig. 4 A) Number of allometric shifts detected by bayou for the three allometric relationships explored: length vs. depth (red), length vs. width (orange), and depth vs. width (blue) across the order-level phylogeny of teleosts. Numbers in parentheses represent species sampling and richness respectively. B) Distribution of the estimated slopes of the allometric regimes detected across teleost orders for the three allometric relationships. Dashed line indicates a slope equal to one. Slopes estimated for each regime can be found in Table S6. C) Distribution of the estimated intercepts of the allometric regimes detected across teleost orders for the three allometric relationships. Intercepts estimated for each regime can be found in Table S6. Phylogenetic tree modified from Rabosky et al. 2018
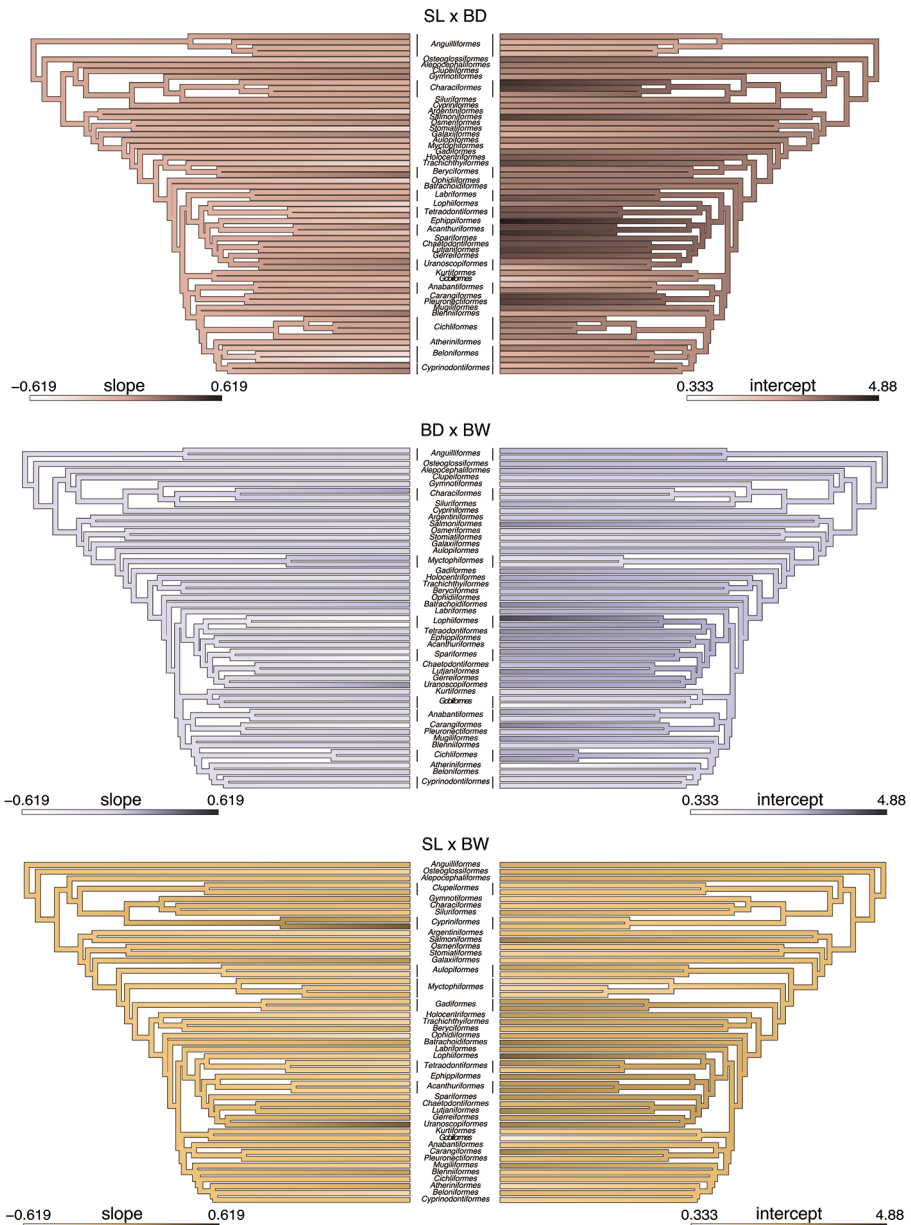
Fig. 5 Summary of the estimated slopes (left) and intercepts (right) of the allometric regimes (shifts and background regimes) detected by bayou across teleost orders for the three allometric relationships: length and depth, depth and width, and length and width. Each allometric regime corresponds to a branch in the phylogeny. For example, orders represented by one branch have no shifts and have one regime; orders represented by two branches have one shift and, therefore, are described by two regimes. Slopes are presented as the difference relative to isometry. SL = standard length; BD = body depth; BW = body width. Plots produced using the function CountMap in the R package Phytools (Revell 2012). Phylogenies modified from Rabosky et al. (2018)

diversity accumulates towards a trajectory close to isometry. However, there is some variation in slopes both within and among the different optimal scaling relationships estimated. The 95% highest density interval for slopes ranges from 0.68 to 1.25 for length and depth, 0.71 to 1.19 for length and width, and 0.48 to 1.10 for depth and width (see also Fig. 4B). We found no evidence that an absence of shifts was associated with background slopes closer to isometry ($F_{phylo\_anova} = 1.23$, $P_{phylo\_anova} = 0.24$). The density curves around the intercepts were broader relative to those estimated for the slopes (Fig. 4 C). The 95% highest density interval for the intercepts ranges from 2.34 to 4.54 for length and depth, 1.71 to 3.64 for length and width, and 1.93 to 4.43 for depth and width (Fig. 4 C). Slope and intercept estimates of each allometric regime detected across the 42 orders for the three scaling relationships can be found in Table S6 and visualized in Fig. 5.

Discussion

Our goal was to investigate the adaptive landscapes associated with the evolution of body size in teleosts by comparing three different size components: body length, depth, and width. We found that the adaptive landscapes estimated can be very distinct for length, depth and width when analyzing the same order. These adaptive landscapes also differ greatly from those estimated for other size metrics, such as body mass and the geometric mean. We also found that allometric regimes rarely changed during the radiation of teleosts and that most orders are evolving under allometric regimes that are close to isometry.

Our analyses of shifts in the phenotypic optima of the individual size components reveal that fishes can change their size in a multitude of ways. Shifts in fish length, depth and width optima rarely occurred on the same branch in most clades. This agrees with previous findings that teleosts changed their body form (size and shape) frequently during their radiation (e.g. Price et al. 2019; Kolmann et al. 2020; Rincon-Sandoval et al. 2020; Collar et al. 2021; Martinez et al. 2021). These shifts in body form were potentially driven by a variety of different ecological processes. Previous work has shown that intra- and interspecific competition (Schluter and McPhail 1992; Svänback et al. 2008) and predation pressure can lead to changes in body shape and size in fishes (e.g. Brönmark and Miner 1992; Andersson et al. 2006; Langerhans and Reznick 2010; Price et al. 2015; Hodge et al. 2018). Transitions between habitats, such as riverine, lacustrine, marine and freshwater environments (Griffiths 2010; Clarke 2021) as well as the evolution of migratory behavior (Griffiths 2010; Bloom et al. 2018; Burns and Bloom 2020) are also well known drivers of body size evolution in fishes. Changes in migratory behavior, for example, may explain several of the shifts in Clupeiformes (Bloom et al. 2018), one of the orders with the highest number of shifts. However, these ecological drivers of body size evolution have mostly been assessed using body length, the most common measure of fish size in the literature. As emphasized by our results, changes in size optima do not only occur by changing body length. Indeed, predictions concerning the occupation of distinct trophic-levels benefit from including other body size metrics and dimensions other than only length (see Akin and Winemiller 2008; Keppeler et al. 2020). Additionally, the variety of potential evolutionary paths taken by teleosts when changing their body form could reflect consequences of lineage-specific genetics and developmental constraints. As an example, Kolmann et al. (2020) found that body size

decreased in two lineages of needlefishes (Belonidae) but was followed by a decrease in the number of vertebrae in only one of them.

Mismatches between the adaptive landscapes of the three body size components (length, depth and width) could potentially reflect divergent processes acting on the different components. Transitions between benthic-pelagic lifestyles have frequently been shown to be an important driver of body shape shifts (Ribeiro et al. 2018; Rincon-Sandoval et al. 2020; Friedman et al. 2020, 2021), and transitions between marine and freshwater environments have altered body proportions in needlefishes (Kolmann et al. 2020). Alternatively, mismatches could simply reflect chronological asynchrony in the evolution of the size components and may not mean that these traits are evolutionary decoupled. In other words, part of the mismatches between the adaptive landscapes could be explained as delays in the evolution of one size component relative to the other. Also, we cannot discount the possibility that mismatches between the adaptive landscapes are the result of uncertainty in the phylogenetic position of the estimated optima. However, we found that most of the phylogenetic positions of shifts are quite consistent at least across the different shift configurations sampled (see ℓ1ou plots provided in the supplementary material).

Adaptive landscapes also differ between the size components and the two composite body size metrics (body mass and geometric mean). Therefore, different size metrics can show distinct patterns, which will potentially affect any subsequent biological interpretations. For example, several comparative studies have drawn different conclusions depending on which measure of size is used. Welch (2009) showed that the use of different size metrics influenced his conclusions concerning whether or not the widely known Island rule (i.e. species change their size on islands, Foster 1964; Van Valen 1973) applied to primates. Similarly, body temperature of insects living at the leaf surface are correlated with different body size metrics (length, width and height) but it is body height that best explains body temperature variability (see Pincebourde et al. 2021). Further, Law et al. (2018) found that body length and mass show completely distinct patterns of phenotypic evolution in mustelids.

Although the optima of the different body size components have frequently changed across teleosts, these shifts can still be part of a broader allometric regime where body form diversity accumulates along either an isometric or non-isometric trajectory. For example, within Siluriformes (catfishes) we detected distinct adaptive landscapes for the separate size components using ℓ1ou, meaning that shifts in length, depth and width never occurred on the same branch in the phylogeny (Fig. 3). However, our bayou analyses suggested that these body size components have been evolving under a broader allometric regime towards a trajectory close to isometry (mean slope=0.96, Table S4). Similarly, Stomiatiformes (dragonfishes, lightfishes and others) shifted length, depth or width several times throughout their evolutionary history but belong to a single broader allometric regime which, in contrast to Siluriformes, follows towards an evolutionary trajectory that is quite far from isometry (mean slope=0.77, Table S4). It is important to bear in mind that ℓ1ou and bayou infer adaptive landscapes in distinct ways. Bayou infers hypothetical regimes under which the relationship between two size components is evolving, and whether a given regime has shifted during the radiation of a clade. ℓ1ou models hypothetical regimes under which a single trait is evolving, without dependency on any other trait, and also infers whether a given regime has shifted during the radiation of a clade.

We predicted that if size acts as a line of least evolutionary resistance in teleosts, most allometric regimes would be close to isometry. Indeed, our results reveal that the slopes

associated with allometric regimes are concentrated close to one (Fig. 4B) in the majority of the clades. The body size diversity of a few clades appears to have been accumulating under trajectories more distant from isometry (Fig. 4B, Table S4) and several of these have unusual body shapes, and a few have very particular life-history strategies, diets or habits. This includes, Uranoscopiformes, which comprises the Sandperches, Torrentfishes, and Stargazers, along with Lophiiformes (anglerfishes), Stomiatiformes (dragonfishes, lightfishes and others) and the elongated Ophidiiformes (cusk-eels, pearlfishes and others), which together include several deep-sea lineages.

Isometric or not, changes in the trajectories of body size diversity are uncommon within orders. We detected shifts in slightly less than half of the 42 orders analyzed, and even then, only one or two shifts in the allometric regime were detected in most of these clades. Therefore, our results suggest that allometric regimes have been relatively stable during the radiation of the vast majority of teleostean orders. Scaling relationships are similarly conserved among ontogenetic allometries across species from distinct teleost orders (Castro et al. 2018). Combined, these results agree with the widely suggested pattern that scaling relationships tend to be conserved over long time scales (Voje et al. 2013; Pélabon et al. 2014; Houle et al. 2019). We hypothesize that changes in allometric regimes might be more commonly detected deeper in the teleostean phylogeny, giving rise to the diversity of body plans that we currently observe between orders, such as the highly elongated Anguilliformes (eels) or the laterally flattened Pleuronectiformes (flatfishes). These clades might have reached evolutionarily successful allometric relationships, which would rarely require further changes in the broad allometric relationships between the size components. This seems especially true for species-rich orders such as the Siluriformes, which showed no shifts in their scaling relationships, despite changing length several times during their radiation (see Fig. 2). Therefore, analyzing the adaptive landscape of the whole teleost clade represents a fruitful avenue in the investigation of body form evolution in fishes, but also creates challenges for the computationally intensive analyses performed here.

Contrary to our expectation that shifts in the scaling relationships (i.e. allometric regimes) would be rarer in orders evolving toward trajectories close to isometry, we found that shifts occurred independent of whether body size diversity was evolving under an isometric or non-isometric regime. Interestingly, clades with shifts are also more species-rich than the clades without shifts ($F_{phylo\_anova} = 7.54$, $P_{phylo\_anova} < 0.05$, Table S4). While this relationship may simply reflect a higher likelihood of detecting shifts in more speciose clades, mechanistic explanations also exist. More shifts within species-rich clades may reflect external pressures on lineages to change their evolutionary trajectory, allowing further diversification under a new regime. This could happen as a result of diversity-dependent processes, such as an increase in the number of species and more intense competition forcing lineages to explore distinct parts of the morphospace.

In conclusion, we show that the evolution of body size in teleosts is a complex process that is hard to predict based on a single measure of size. This has important implications for studies using teleost body size to investigate ecological and evolutionary questions, as conclusions may change depending on how size is measured. It is therefore necessary to take into account the limitations and specificity of the size variables used. Ideally, one should consider more than one size metric or investigate "body size" by considering it as a complex trait under a multivariate framework. The patterns we recover also raise several questions that deserve further investigation. For example, would we get similar results when apply-

ing a hypothesis-driven OU framework, such as OUwie (Beualieu et al. 2012), to analyze body size convergence across ecological regimes but using non-size-corrected body depth or width as the size metric? Or, why do Siluriformes have many more shifts in their length optima than the optima associated with width or depth? Shifts in habitat use and biogeographic processes have been suggested to potentially underlie body length evolution within catfishes (e.g. Hardman & Hardman 2008; Roxo et al. 2017) but it would be interesting to know why depth and width seem to be less labile in this order. Finally, our results also highlight that variation in allometric trajectories have potential macroevolutionary implications, as shifts in allometric regimes tend to occur in lineages with greater species richness. Further investigation is needed to understand whether this pattern is due to differences in rates of diversification or clade age and to explore the subsequent impact of these body size trajectories on the morphological and ecological diversification of fishes.

Code Availability Not applicable.

Availability of data and material The morphological dataset analyzed in this study is currently under consideration as a data paper at Ecology, prior to publication it is available from SAP on request. Other datasets generated during this study are available as part of the supplemental material.

Declarations

Conflicts of interest/Competing interests The authors declare to have no competing interests.

Ethics approval Not applicable.

Consent to participate All authors agreed to participate in this study.

Consent for publication All authors gave consent to the publication of this study.

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