LETTER

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The deep sea is a hot spot of fish body shape evolution

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Abstract

Deep-sea fishes have long captured our imagination with striking adaptations to life in the mysterious abyss, raising the possibility that this cold, dark ocean region may be a key hub for physiological and functional diversification. We explore this idea through an analysis of body shape evolution across ocean depth zones in over 3000 species of marine teleost fishes. We find that the deep ocean contains twice the body shape disparity of shallow waters, driven by elevated rates of evolution in traits associated with locomotion. Deep-sea fishes display more frequent adoption of forms suited to slow and periodic swimming, whereas shallow living species are concentrated around shapes conferring strong, sustained swimming capacity and manoeuvrability. Our results support long-standing impressions of the deep sea as an evolutionary hotspot for fish body shape evolution and highlight that factors like habitat complexity and ecological interactions are potential drivers of this adaptive diversification.

KEYWORDS

body shape, deep sea, disparity, evolution, fish, linear morphometrics, marine, ocean depth, rate of evolution, teleost

INTRODUCTION

Ocean depth is among the most biologically consequential dimensions in marine ecosystems, along which numerous environmental factors vary that are relevant to living organisms. Among these are hydrostatic pressure, impacting solubilities of important compounds and the ability of organisms to incorporate carbon into calcified skeletal structures (Angel, 1997), dissolved oxygen needed for aerobic metabolism (Childress & Seibel, 1998), and light, which, along with nutrients, sets limits on primary production (Bienfang & Gundersen, 1977; Lalli & Parsons, 1997). Associated with these environmental gradients are broad shifts in the vertical structure of marine communities (Angel, 1989; Cook et al., 2013) as well as depth-specific adaptations for vision (Crescitelli, 1991; Hope et al., 1997), buoyancy control (Alexander, 1990; Pelster, 1997), and intraspecific communication (Haddock et al., 2010; Widder, 2010), to name a few. Clearly, environmental changes occurring with ocean depth have profound implications for phenotypic variation in marine organisms. Still, it is largely unknown how depth-dependent factors influence broad macroevolutionary patterns of phenotypic diversity.

Teleost fishes, with over 15,000 marine species, are distributed broadly across ocean habitats and depths (Helfman et al., 1997) and display an incredible degree of morphological diversity. Body shape is particularly variable across fishes and is often associated with factors like the hydrodynamic conditions that species typically encounter (Bejarano et al., 2017; Langerhans, 2008; Webb, 2006) and structural complexity of the habitats they occupy (Claverie & Wainwright, 2014; Friedman et al., 2020; Larouche et al., 2020). One reason for this is that body shape is thought to be associated with locomotor ability and therefore impacts how organisms capture prey and avoid predators (Mihalitsis & Bellwood, 2019; Webb, 1984), undertake large-scale migratory movements (Kipanyula & Maina, 2016; Riddel & Leggett, 1981), and navigate structured environments (Larouche

et al., 2020; Webb, 2006). To the extent that the nature of these and other swimming-related activities vary with respect to ocean depth, morphological traits associated with locomotion may also change accordingly.

Nearly all of our understanding of locomotor diversity and the role that swimming plays in the lives of fishes comes from observations of shallow-water inhabitants, but many factors that affect locomotion change with ocean depth. For example, turbulence is a common feature of shorelines and the ocean's surface that impacts swimming performance (Liao, 2007; Lupandin, 2005; Roche et al., 2014) and favours body shapes that can overcome the destabilizing consequences of unsteady flow (Webb, 2006; Webb & Cotel, 2010), but it also decreases rapidly with depth (de Boyer Montégut et al., 2004). Habitat complexity is another important factor for fish locomotion. Shallow sea environments include a number of structured habitats, many nearshore (e.g., coral and rocky reefs), that harbour large numbers of species with body plans specialized for manoeuvrability and navigation of complex surroundings (Larouche et al., 2020). Structured environments exist in the deep sea (e.g., sea mounts and hydrothermal vents) but are highly dispersed across vast expanses of relatively featureless benthic environments, like the abyssal plains (e.g., Won et al., 2003).

In addition to the abiotic environment, many ecological interactions involving extended or powerful swimming in shallow oceans also play out differently in the deep sea. One of the most consequential of these for the evolution of locomotor mechanics is predation (Webb, 1984). The visual interactions hypothesis posits that in sunlit surface waters, fishes can pursue prey (or avoid predators) over relatively large spatial distances (Childress & Mickel, 1985). As light levels diminish with depth, interaction distances are reduced, likely to the immediate vicinity of the organism, precluding prolonged pursuit. This interaction between light, vision, and locomotion is supported by observations in distantly related groups with image-forming eyes (fishes, cephalopods, and crustaceans), which consistently display decreasing metabolic rates with depth, in association with lower muscle enzyme levels and locomotor capacity (Childress, 1995; Childress & Somero, 1979; Seibel & Drazen, 2007; Seibel et al., 1997). Such trends are highly reduced or altogether nonexistent in organisms with less developed visual systems, like chaetognaths and cnidarians (Childress et al., 2008), further supporting the role of vision.

The above examples suggest that environmental and ecological features of shallow seas favour a diversity of swimming profiles differing from those expected in deeper waters. If true, we would expect differences in the diversification of body plans and manner of morphological variation across ocean depth regions. Specifically, the shallow water landscape provides a pervasive advantage for sustained cruising in the open water and

manoeuvrability near reef structures. These overarching themes likely result in repeated evolution of strong swimming forms to meet locomotor needs specific to shallow water environments (e.g., fish with comparatively large and robust caudal peduncles; Webb, 1982; Webb, 1984) and may even manifest as a constraint on overall body plan evolution. In contrast, strong swimming abilities and high manoeuvrability are thought to be less important in the deep ocean due to a reduction in vision-mediated predation and the relative scarcity of physically and biologically complex reef environments, respectively. These regions may therefore favour energetically efficient, slow sustained swimming styles. Here, more weakly muscularized and smaller caudal peduncles would be expected, but these features may also display greater morphological diversity due to reduced constraint on locomotion.

In this study, we evaluate patterns of body shape diversity and evolution in teleost fishes across ocean depth zones. Morphological trends with depth are potentially substantial due to the implications for locomotor performance resulting from differences in factors like turbulence, habitat complexity, and ambient light levels that occur along this axis. We characterized morphological changes between depth categories designed to capture broad differences in these environmental conditions. Morphological means, disparities, and rates of evolution were compared among ocean depths. The expectation is that some environments stimulate greater rates of body shape evolution than others, resulting in differences in standing morphological diversity when observed at macroevolutionary scales. Specifically, we predicted that overall disparity of fish body shapes and rates of morphological evolution would gradually increase with depth, reflecting constraints placed by the relative importance of strong swimming abilities in shallow environments and a progressive shift in deeper waters to locomotor profiles and morphologies suited to low activity lifestyles, potentially as a release of those constraints. Under this framework, we expected that morphological traits most impacted would be those associated with swimming performance.

MATERIALS AND METHODS

Data acquisition

This study makes use of a large morphological dataset for teleost fishes, collected collaboratively by the authors and a team of undergraduate researchers (see Price et al., 2020, for details on student involvement) on museum specimens from the Smithsonian National Museum of Natural History. Here, we use a subset of these data consisting of marine species with documented depth of occurrence. In total, we included 8362 specimens from 3033 species across 263 families and 34 orders. Eight linear

traits were measured on each specimen (Figure 1b), capturing major dimensions of body shape, with an emphasis on functional importance. A full account of collection procedures can be found in Price et al., (2019). Prior to analyses, measurements were averaged by species and matched to a published molecular phylogeny of teleost fishes (Rabosky, Chang, Title *al et* Alfaro 2018), trimmed to our dataset.

To account for the effect of size on morphological traits (allometry), we performed phylogenetic generalized least-squares (PGLS) regressions of the natural logarithm of linear measurements on the natural logarithm of body size. For this, we used the "procD.pgls" function in the R package, *geomorph* version 3.2.0 (Adams et al., 2019; R Core Team, 2020), which implements a residual randomization permutation procedure ($n = 10,000$ iterations) from the *RRPP* package, version 0.4.3 (Collyer & Adams, 2018; Collyer & Adams, 2019). Residuals from regressions were used as allometrically adjusted morphological data. Body size was measured as the cube-root of the product of length, depth, and width (Price et al., 2019). This metric was chosen to provide a more comprehensive measure of fish size, accommodating the full range of body shapes found in the data set, including very deep (e.g., butterflyfishes, Chaetodontidae), wide (e.g., goosefishes, Lophiidae), and elongate body plans (e.g., snake eels, Ophichthidae).

Depth zone categories

Species were grouped into one of three depth categories designed to capture the broadest possible differences in environmental conditions (light, turbulence, and habitat structure) relevant to fish locomotion. The "shallow" depth category is coincident with the epipelagic zone (0–200 m; $n = 1951$ species) and includes well-lit, wave-dominated regions and many structured nearshore habitats. The "intermediate" category (200–1000 m; $n = 692$ species) is equivalent to the mesopelagic or twilight zone, which often contains the transition from low downwelling light to no light at all (aphotic) and stable hydrodynamic conditions compared with the surface. Finally, the "deep" ocean is the completely aphotic region below 1000 m ($n = 333$ species), encompassing both the bathypelagic (1000–4000 m), and abyssopelagic (4000–6000 m). At these depths, the only source of light is bioluminescence and large expanses of benthic environments lack structural complexity. Depth zones included fishes from all marine habitats within the defined ranges, not only pelagic (Table S1). Species' maximum depth of occurrence was extracted from Fishbase (Froese & Pauly, 2019) using the "DepthRangeDeep" field with the "species" function in the R package, *rfishbase* (Boettiger et al., 2012), with values based on documented observations. We reviewed depths for egregious errors but were mindful not to let our own biases drive data editing, ultimately removing a
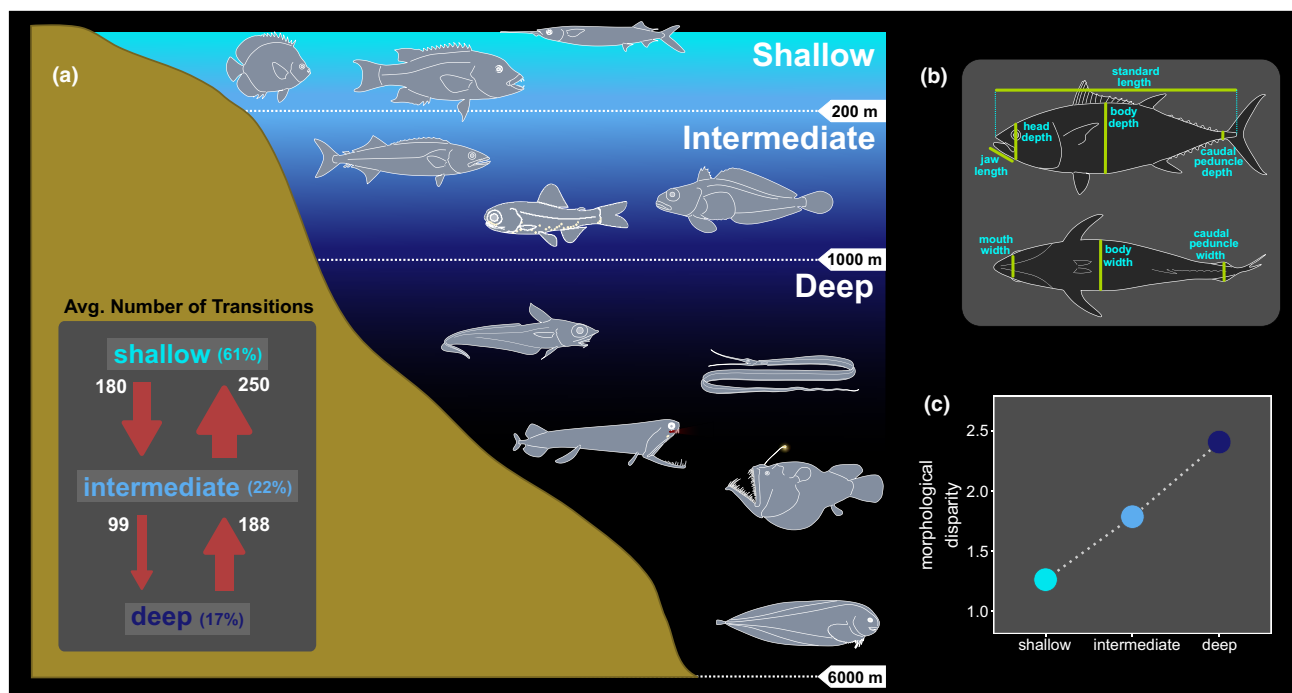

FIGURE 1 (a) Depth zone categories used in this study included shallow (0–200 m), intermediate (200–1000 m), and deep (1000–6000 m) marine habitats (illustration not to scale). An inset presents a summary of average numbers of evolutionary transitions between depth zones (white numbers with associated arrows indicating direction) and the percentage of time spent in each, based on 100 stochastic character maps on the phylogeny of the study species. (b) Eight linear morphological traits were measured, capturing functionally relevant dimensions of fish body plans. (c) Morphological disparity of 3033 teleost species (across all traits, simultaneously) increased incrementally as a function of ocean depth

single species from the study (the flying fish *Hirundichthys speculiger*, listed at 10,400 m, making it the deepest living fish—it is not). Binning species into broad depth categories was expected to largely mitigate issues with inaccurate maximum depth values, but we acknowledge that any approach, including our own, is vulnerable to sampling error in rare species and those near depth zone boundaries.

Morphological differences with ocean depth

To visualize major axes of body shape variation across fishes, we performed a nonphylogenetic principal component analysis (PCA) on all morphological traits. We used a PCA on the correlation matrix, not covariance, so that measurement scale (standard length was often an order of magnitude larger than other traits) would not impact our ability to visualize unique trait combinations. Additionally, we statistically tested whether overall body morphology (i.e., all traits in a multivariate framework) and mean values of each linear trait, individually, differed by depth zone. For this, we used the "procD.pgls" function in *geomorph* and the "pairwise" function in *RRPP* to perform a phylogenetic analysis of variance (ANOVA) and pairwise comparisons, respectively, based on 10,000 permutations.

Body shape disparity across depth zones

We measured morphological disparity within each of three ocean depth zones in both a multivariate framework across all traits as well as univariate, trait by trait. We used the "morphol.disparity" function in *geomorph*, calculating disparity within each zone as either the sum of diagonal elements of the covariance matrix for all traits divided by the number of species (multivariate data), or as a series of univariate variance estimates (trait by trait). This function performs pairwise comparisons of disparity between groups and implements a permutation routine for assigning statistical significance ($n = 10,000$ iterations). We also compared overall morphological disparity between four traditional oceanic depth zones (epipelagic, mesopelagic, bathypelagic, and abyssopelagic) but recovered similar values in the bathypelagic and abyssopelagic (both aphotic) that were not significantly different (Table S2). Given our initial predictions, we expected similar disparities as environmental factors relating to locomotion do not change markedly between these depth categories. Therefore, we opted for a three-depth-zone grouping scheme for the study.

Mode and tempo of trait evolution

We used the *OUwie* package (Beaulieu & O'Meara, 2016) in R, taking an evolutionary model-fitting approach to

test whether rates of evolution for each univariate trait varied by depth zone (also see Table S3). Reconstructions of character histories for depth groups were generated with the "make.simmap" function in *phytools* (Revell, 2012). We produced 100 stochastic character maps of depth categories across the phylogeny for our study species, with "ARD" (all rates different) to model transition probabilities between states based on an initial log-likelihood comparison from a sample of reconstructions.

We considered five models of varying complexity, under Brownian motion (BM) and Ornstein–Uhlenbeck (OU) models of trait evolution. BM1 models a single rate of evolution (σ^2), whereas BMS includes separate rates for each group of a categorical variable (shallow, intermediate, and deep). In contrast, OU models contain three parameters, including the location of the primary optima (θ), the strength of selection or "pull" toward the optima (α), and the rate of trait evolution (σ^2). We considered three OU models, OU1 where all three parameters (θ, α, and σ^2) are constant across categorical groups, OUM where the locations of trait optima (θ) differ between groups, and finally OUMV where both the optima and rates of trait evolution (θ and σ^2, respectively) differ between groups. We did not include OU models in which the α parameter varies. Our rationale was that we were most interested in the rates of trait evolution by depth and when α is allowed to vary, interpretation of the rate parameter (σ^2) cannot be isolated from the strength of selection, α (Cooper et al., 2016; Ho & Ané, 2014). Model fit was determined based on Akaike's information criterion adjusted for sample size (AICc) and AICc weights. Parameter estimates were retained for the preferred model.

RESULTS

Patterns of morphospace occupation

Across all species, the largest axis of morphological variation (PC 1, 43.5% of total variation) was most strongly associated with body elongation (Figure 2a; Table S4). PC 2 contained an additional 25.9% and largely characterized differences in body and mouth width. PC 3 (12.7% of variation) and PC 4 (9.3% of variation) were closely related to variation in jaw length, head depth, and caudal peduncle morphology.

Species' occupation of morphospace displayed important differences by depth, with an overall trend of body shape diversity becoming more evenly distributed from shallow to deep (Figure 2b–d; note incremental expansion of data ellipses). Fishes in the shallow depth zone had a large overall range in body shapes, but a majority of species were found in high density within a small region of morphospace. These species were centred on a fusiform or spindle-shaped body, typified by snappers (Lutjanidae). Additionally, two morphotypes were common in shallow environments but sparsely represented elsewhere. The
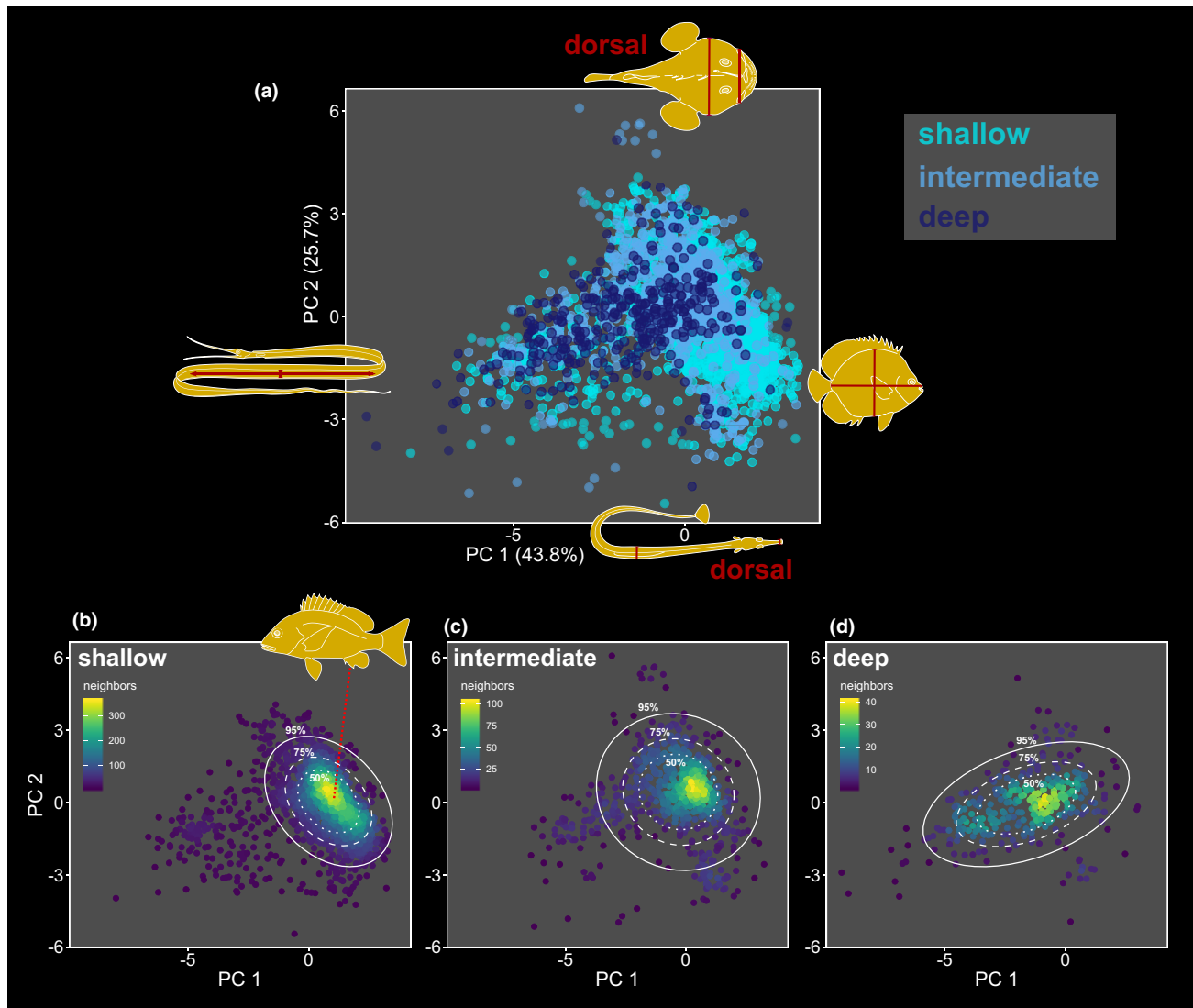
FIGURE 2 (a) Major axes of body plan variation in 3033 species of teleost fishes, represented by the first two principal component axes (PCs) from a PCA on eight linear traits. Each point is the average shape of a species, coloured by ocean depth zone. Drawings show representative species illustrating morphological variation across the plot. The percent of total variation explained by each axis is provided. (b–d) Points (species) are now coloured by the density of species in morphospace (purple =low density, yellow =high density), and ellipses represent areas within which 50%, 75%, and 95% of observations occur. A drawing of a representative species, *Lutjanus fulvus*, is shown in the "shallow" panel (b) at the centre of a dense aggregation of fusiform body plans

first were deep-bodied, laterally compressed forms, common in highly manoeuvrable species like butterflyfishes (Chaetodontidae; Figure 2a lower right of plot), and the second were species with small mouths (Figure 3a, bottom half of plot). These features are not mutually exclusive, as many deep-bodied species with small mouths are found in shallow habitats.

In the intermediate depth zone, there remains a large concentration of species with fusiform bodies, but body shape variation was more evenly dispersed compared with shallow seas. It is at these intermediate depths that a body plan almost nonexistent in shallow waters begins to appear, species with elongate and tapered tails (Figure 3a, top right of plot). Finally, in the deep sea, there is further dispersion of morphologies, with a strong propensity for variation along an axis of body elongation. At one

extreme are the most slender species in our dataset, snipe eels (Nemichthyidae), and at the other are globe-shaped species like oceanic anglerfishes (e.g., Melanocetidae and Oneirodidae). Fishes in deep waters also tended to have larger mouths (Figure 3, top half of plot), and groups like grenadiers (Macrouridae) and snailfishes (Liparidae) continued to occupy the tapered tail region of morphospace also found at intermediate depths.

Morphological differences with ocean depth

Phylogenetic multivariate analysis of variance (MANOVA) revealed significant differences in average body shape by depth ($F_{2,3030}$ = 6.69; p = 0.0002), with all pairwise comparisons between the three depth
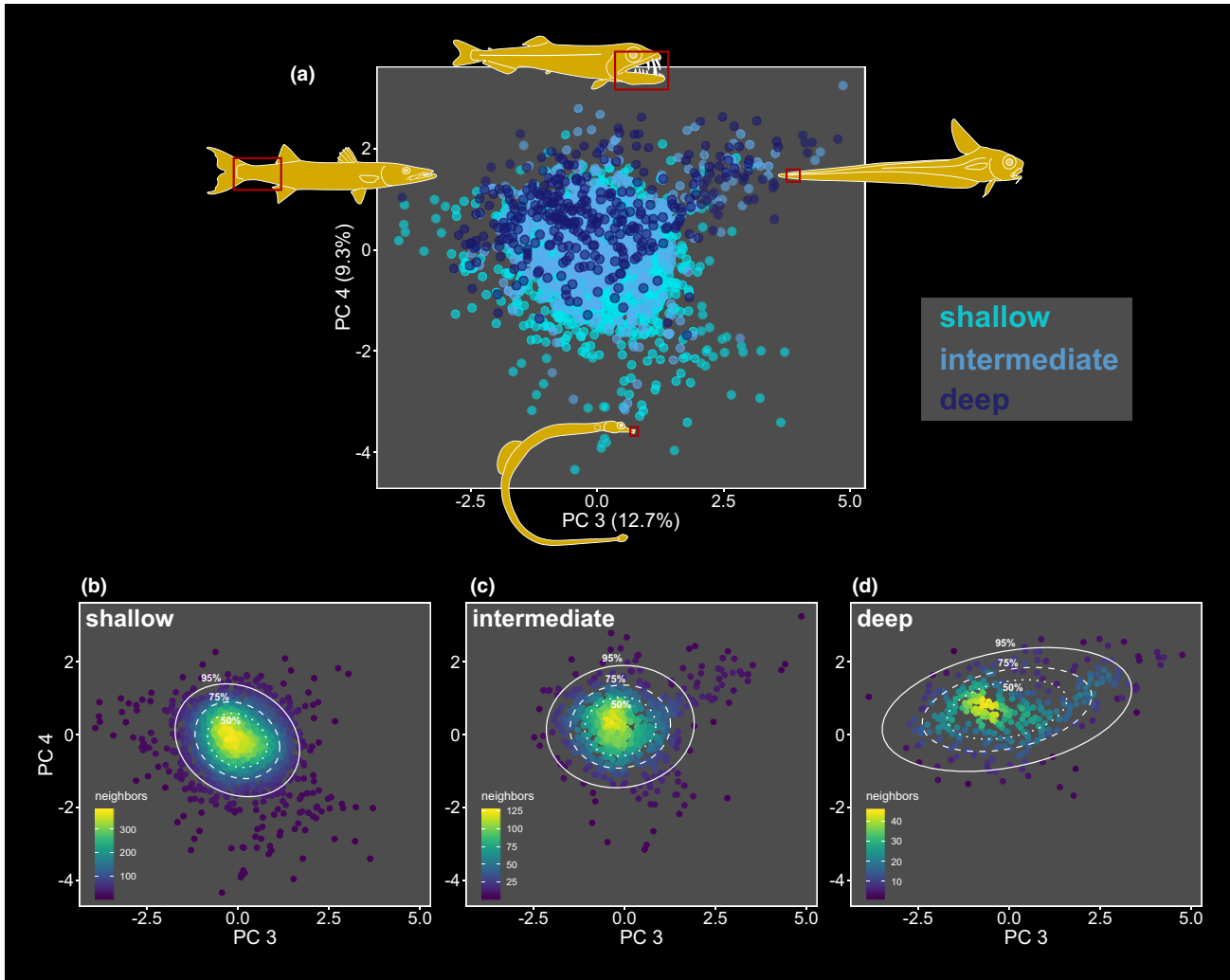
FIGURE 3 (a) Third and fourth principal component axes (PCs) from a PCA on eight linear traits in 3033 teleost species. Each point is the average shape of a species, coloured by ocean depth zone. Drawings show representative species illustrating morphological variation across the plot. The percent of total variation explained by each axis is provided. (b–d) PC plots are also presented with each depth zone plotted separately. Points (species) are now coloured by the density of species within morphospace, and ellipses represent areas within which 50%, 75%, and 95% of observations occur

zones significant at the $p < 0.05$ threshold (Tables S5 and S6). Several, but not all, of the individual traits differed between depth categories, as indicated by a series of phylogenetic ANOVAs (Figure 4; Tables S7 and S8). Lower jaw length was significantly greater in the intermediate and deep-sea zones compared with the shallow zone. Opposite patterns were observed for standard body length and body depth, which displayed ordered increasing and decreasing trends with ocean depth, respectively. Head depth was also significantly smaller in the deep sea than in the intermediate and shallow ocean, and caudal peduncle depth displayed statistically significant differences, generally decreasing from shallow to deep waters. Across all statistically significant phylogenetic ANOVAs and an overall MANOVA, the power of the ocean depth category to explain variation in traits was low (R^2 between 0.0047 and 0.017; Table S7), indicating that while there are differences in average trait

values, each depth zone harbours high body shape diversity accounted for by unmeasured factors.

Body shape disparity across depth zones

Morphological disparity of teleosts increased with ocean depth (Figure 1c; Table S9). Across all traits, variance is smallest in the shallow depth zone ($s^2 = 1.26$), larger in the intermediate ($s^2 = 1.79$), and greatest in the deep ($s^2 = 2.41$). Thus, the intermediate and deep zones contained 1.42 and 1.91 times greater morphological disparity, respectively, than surface waters. All pairwise comparisons of morphological disparity between depth zones were statistically significant ($p = 0.0001$ for each). This trend of increasing disparity with depth was consistent with observations of relative dispersion of species across morphospace (Figures 2 and 3b–d).
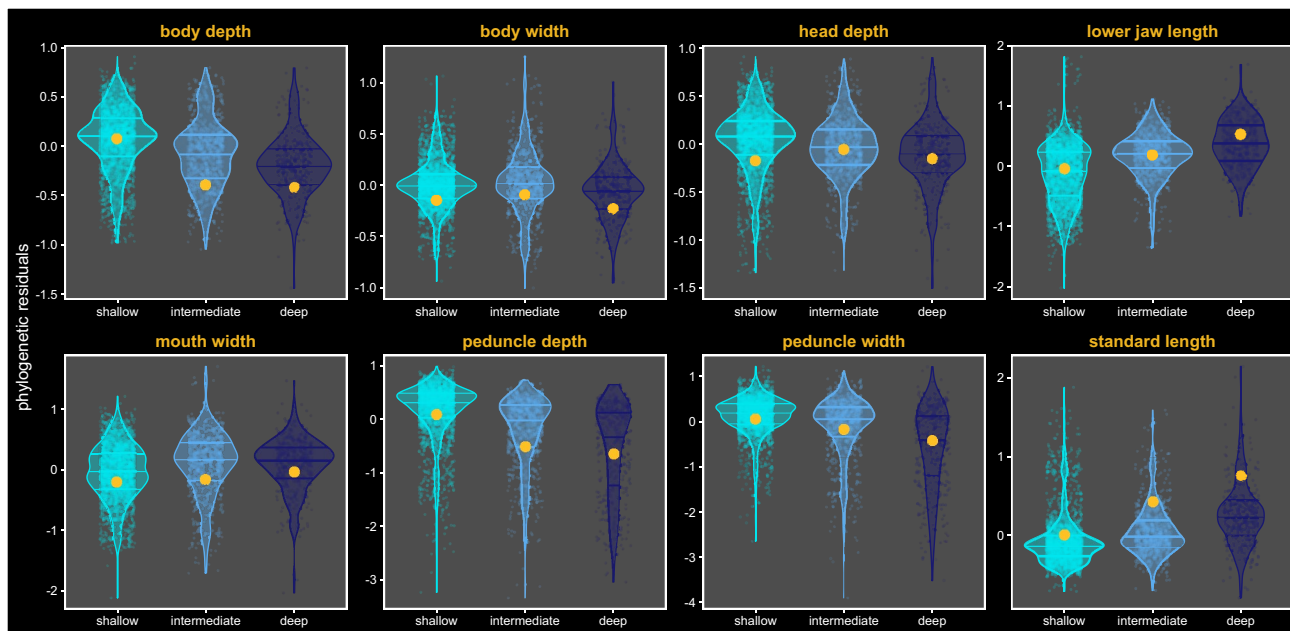
FIGURE 4 Distributions of eight linear morphological traits (residuals of phylogenetic regressions) in teleost species (points) across ocean depth zones. Average evolutionary optima (θ) estimated from the favoured model of trait evolution in this study, Ornstein–Uhlenbeck model with depth-specific optima and evolutionary rates (OUMV), plotted as large yellow points

Differences in overall morphological disparity between depth zones resulted from disparate, and sometimes opposite, variance patterns in individual traits (Tables S9 and S10). Additionally, a strong multivariate pattern observed at shallow depths—high density around fusiform shapes despite a large overall range (Figure 2)—was also evident in plots of univariate traits, but most strongly for the caudal peduncle, standard length, and body width (Figure 4). Variance in standard length was significantly greater in the deep sea ($s^2 = 0.17$), compared with intermediate ($s^2 = 0.11$; $p = 0.0053$) and shallow depths ($s^2 = 0.11$; $p = 0.0013$). In contrast, lower jaw length was more variable in the shallow ocean ($s^2 = 0.24$), than it was in either the intermediate depth zone ($s^2 = 0.14$, $p = 0.0001$) or the deep sea ($s^2 = 0.16$, $p = 0.0005$). Mouth width and maximum body width variances were significantly higher ($p < 0.05$) at intermediate depths than at others. Traits related to caudal peduncle shape displayed the greatest differences in variance, each incrementally increasing from shallow to deep-sea regions. All pairwise comparisons of peduncle traits were significantly different between regions ($p < 0.05$), where variance in peduncle depth and width were 2.81 and 4.56 times greater, respectively, in the deep sea compared with in the shallow depth zone. There were no differences in variances for body depth and head depth between the three ocean zones.

Mode and tempo of trait evolution

Reconstructions based on stochastic character mapping suggest that teleosts have spent a majority (61%) of their evolutionary history in the shallow depth zone, versus 22% and 17% in intermediate and deep zones, respectively (Figure 1a). The average number of transitions from deeper regions to shallow was greater than the reverse (Figure 1a). Transitions from deep to intermediate were 1.9 times more common than intermediate to deep, whereas intermediate-to-shallow transitions were about 1.4 times greater than shallow-to-intermediate transitions. Reconstructions also suggest that spiny-rayed fishes (Acanthomorpha), the most diverse radiation of teleost fishes and 83% of species in this study, are of deep-sea origin (Figure S1). Of 100 simmaps, 96 recovered the root node of acanthomorphs as "deep," and the rest as "intermediate".

For every trait, an OU model was favoured in which depth zones had different optima and rates of evolution (OUMV; Table S11). For all but one trait, the fastest evolutionary rates (σ^2) occurred at either intermediate depths (body depth, body width, and mouth width) or in the deep sea (head depth, caudal peduncle depth, caudal peduncle width, and standard length) (Figure 5; Table S12). Moderately large rate differences between depth zones were observed for body width (σ^2-intermediate/σ^2-shallow = 2.35) and standard length (σ^2-deep/σ^2-shallow = 2.85), but the largest were found for caudal peduncle width (σ^2-deep/σ^2-shallow = 4.73) and depth (σ^2-deep/σ^2-shallow = 8.65). The only trait that evolved fastest within the shallow ocean was lower jaw length, with σ^2 approximately 1.5 times greater than either of the two deeper regions.

Trait optima (θ) showed a marked increase for standard length and a corresponding decrease in body depth (Figure 4; Table S13), representing overall elongation of
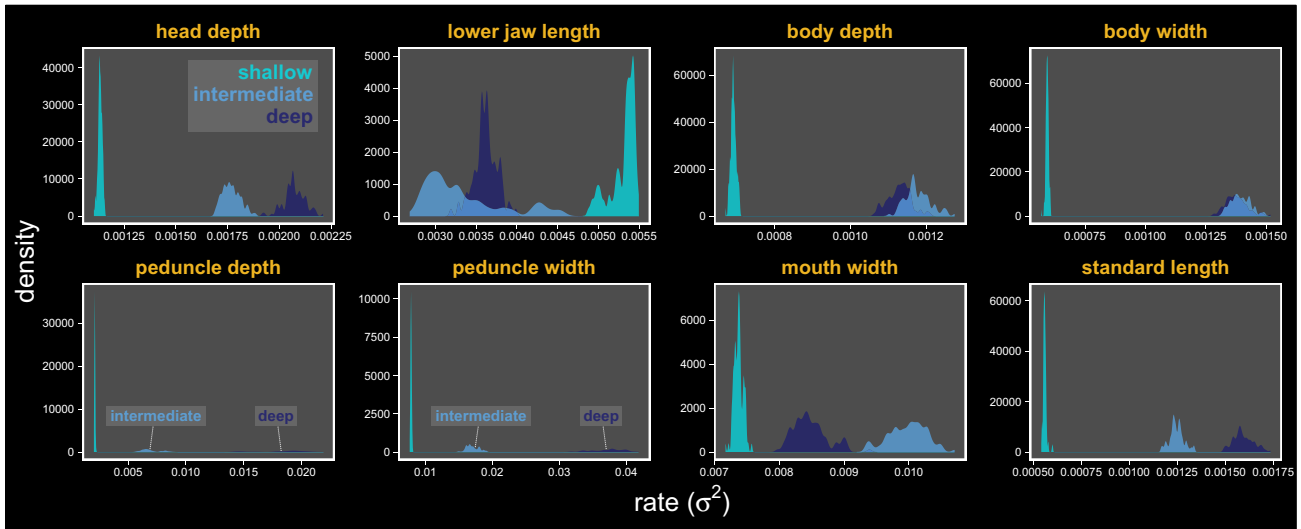
FIGURE 5 Density distributions for evolutionary rates (σ^2) by ocean depth zone, estimated from the favoured model of trait evolution in this study (OUMV)

body plans with ocean depth. Additionally, both caudal peduncle traits decreased in size from shallow to deep regions, while lower jaw length displayed the inverse pattern, increasing with depth.

DISCUSSION

Morphological disparity of marine fish body plans incrementally increases nearly twofold from ocean surface layers to the deep sea, as observed in over 3000 teleost species (Figure 1c). This trend is fuelled by faster rates of evolution in deeper habitats for a majority of traits considered (Figure 5). These patterns are consistent with the idea that environmental features associated with the ocean depth gradient alter the adaptive landscape in a way that changes both average body shapes of fishes and the dynamics of evolutionary change. While the sheer diversity of marine teleosts makes it difficult to draw generalizations about implications of the depth gradient for body plans, we emphasize two major distinctions between life in surface waters versus the deep ocean that may play a significant role. First, decreasing light availability in the deep ocean is expected to impact activity patterns of fishes as well as vision-based interactions. Second, shallow seas harbour an abundance of complex coral and rocky reef habitats that are home to a large fraction (roughly half) of the species captured in our shallow depth zone (Larouche et al., 2020). Life for fishes in these physically and biologically complex habitats likely places different demands on both swimming capabilities and feeding strategies than is experienced by fishes in the deep ocean.

We found shifts in average body shape and increasing rates of morphological evolution at greater ocean

depths, with the largest effects seen in traits that are important for locomotion. We interpret the trends as a reflection of environmental variation across the ocean depth gradient that changes the adaptive landscape for swimming performance. Shallow living species exist in a vision-dominated world where predatory encounters are largely mediated by vision, a sensory system that permits detection at considerable distances and facilitates behaviours like stalking and chasing prey. This distinction likely magnifies the importance of strong locomotor skills for fishes in well-lit seas, underscoring the impact of illumination on the nature and intensity of swimming activity. Among the most striking differences in morphospace occupation is the abundance of deep-bodied, laterally compressed body shapes in shallow seas (Figure 2a, lower right of plot), but their near absence in the deep sea. This body shape conforms closely to the archetypical manoeuvring specialist (Blake, 2004; Webb, 1984b) and includes groups like chaetodontids, acanthurids, and pomacentrids, taxa with intimate relationships with reef habitats. The scarcity of this body shape in the deep sea suggests that a premium on manoeuvrability is much less common for species that live in these habitats. The aphotic deep sea may, therefore, present favourable conditions for slow-speed, high-efficiency swimming conferred by long slender body shapes (Neat & Campbell, 2013; Tytell et al., 2010).

The idea that the deep sea offers a haven for the diversification of fishes with weak, energetically efficient swimming modes is supported by observations that many deep-living species have low density or "watery" muscles and tissues, possibly an adaptation for maintaining neutral buoyancy (Pelster, 1997), as well as reduced muscle enzymes (Childress & Somero, 1979; Seibel & Drazen, 2007; Seibel et al., 1997). Greater hydrostatic pressure may further facilitate efficient swimming in the

deep sea. In laboratory settings, European eels (*Anguilla anguilla*) experienced approximately 60% lower cost of transport under high-pressure conditions (Sébert et al., 2009). Elevated rates of evolution for locomotor traits in the deep ocean may therefore reflect the relaxation of strong selection for some aspects of locomotor performance such as manoeuvrability and high-speed cruising.

Given the wide range of morphologies and large number of species in the shallow depth zone, it may seem counterintuitive that it contained the lowest disparity in body plans. This paradox of low shallow sea diversity can be explained by contrasting the distribution and density of body shapes within morphospace. Low body shape disparity in shallow seas reflects the fact that a majority of species in that region are densely packed into a small range of morphologies that contains both fusiform body plans and laterally compressed, deep-bodied fishes (Figure 2b) expected to perform well during sustained cruising (Webb, 1984b) and unsteady flow (Webb & Cotel, 2010).

Despite the above example and other depth-restricted morphotypes (e.g., small mouths in the shallow ocean and long tapering tails in deeper regions), there was substantial morphological overlap across ocean depth zones for the primary axes of variation (Figures 2 and 3). This underlies the important observation that for all of the strange and unique morphological features in deep-sea fishes, they also displayed greater dispersion across primary dimensions of body shape variation common to all marine teleosts. In other words, although novel morphologies abound in the deep, it is not the sole driver of their elevated diversity.

Nature and implications of morphological trends

Differences in morphological diversity and evolution across ocean depth zones were largely associated with features relevant to locomotion. Relative body length is recovered here and in other studies as a primary axis of morphological variation in fishes (Claverie & Wainwright, 2014; Price et al., 2019), but it also increases with respect to its mean (Table S6), evolutionary optimum (θ; Figure 4), and rate of evolution (σ^2; Figure 5) at greater depths. Body elongation is a functionally consequential morphological transformation, resulting in more eel-like or "anguilliform" locomotion, whereby swimming is achieved with axial undulation along much of the body length (Lauder & Tytell, 2006). This swimming style has unique hydrodynamic implications (Gillis, 1996; Tytell & Lauder, 2004) and can increase locomotor efficiency by reducing the cost of transport, particularly at slow swimming speeds (e.g., van Ginneken et al., 2005). It is likely that elongate deep-water species with tapered bodies utilize an undulatory motion as a means of slow, steady propulsion suited to less muscularized bodies.

In addition to body length, caudal peduncle morphology displayed some of the strongest trends with ocean depth. There was a general reduction in size for the two peduncle traits in deeper ocean regions (Figure 4), but increasing variances (Table S10), and as much as an eight-fold faster rate of evolution compared with shallow seas (Figure 5). The caudal peduncle plays a vital role in high-powered undulatory swimming during predation and evading predators (Webb, 1982) and manoeuvrability in structured environments during unsteady swimming (Flammang & Lauder, 2009). That these activities are much more prevalent in well-lit, shallow environments likely explains the higher density of species centred on larger caudal peduncles (Figure 4). Conversely, the rarity of strong or manoeuvrable swimming behaviours in deeper waters is consistent with smaller caudal peduncles, but also greater variance and more rapid evolution due to relaxed constraint on locomotion.

A notable departure from patterns observed in locomotor traits was found for lower jaw length, which was most diverse and evolved fastest at shallow depths (Figure 5; Table S10). Small-mouthed species were common in the shallow ocean but conspicuously absent in the deep sea (Figure 3a, bottom of plot). This pattern of increased jaw size with ocean depth is often presented anecdotally or in particular taxonomic groups (e.g., Ebeling & Cailliet, 1974) and is consistent with dominance of an opportunistic feeding strategy in the deep sea, befitting rare encounters with sparsely distributed prey. The greater diversity of jaw sizes in the shallow depth zone included both large mouthed species, possibly as an adaptation to overcome gape-limitation while feeding (Mihalitsis & Bellwood, 2017), as well as species with shorter jaws that feed on attached benthic prey, including many deep-bodied manoeuvrable species common in reef habitats (Larouche et al., 2020).

Body plan evolution along environmental gradients

Biologically relevant environmental variation often exists along gradients, representing dimensions along which selection may vary continuously (Conover et al., 2009). Environmental gradients, therefore, play an important role in morphological evolution, impacting the nature and pattern of trait variation in organisms (Conover & Schultz, 1995; Goldberg & Lande, 2006; Juarez et al., 2019; Mullen & Hoekstra, 2008). In this study, we used discrete depth categories to reconstruct character histories and provide context for examining morphological consequences of transitions between broad depth zones. Reconstructions suggested that the incredible diversity contained within spiny-rayed fishes has ancestral origins in deep-sea environments (Figure S1), but that these fishes spent most of their evolutionary history diversifying in shallow seas (Figure 1a; Figure S1). These deep origins are corroborated by multiple phylogenetic estimates (Betancur-R

et al., 2017; Davis et al., 2016; Hughes et al., 2018), showing lantern fishes (Myctophiformes) as sister to Acanthomorpha, followed by primarily deep-sea lineages like lizardfishes (Aulopiformes), jellynose fishes, (Ateleopodiformes), and dragonfishes (Stomiiformes). Early transitions out of deep ocean regions into shallower depths appear to have promoted the evolution of strong sustained swimming abilities and enhanced manoeuvrability. Numerous independent recolonizations of the deeper sea came with a reduction in activity levels, each time adding to the proliferation of weakly swimming forms present in that region, from the extremely elongate to the downright globular. We note that future reconstructions incorporating fossils or other historical data may help to improve or revise our understanding of the evolutionary history of ocean depth occupation.

CONCLUSIONS

From the sea surface to abyssal plains, the ocean depth gradient (including environmental, physiological, and ecological factors that vary along it) has served as an important organizing force for global patterns of both mode and tempo of teleost body plan evolution. Still, it represents only a subset of the dimensions across which selection has acted and alone cannot possibly explain the astounding morphological diversity contained in this group. Further work is needed to compare and integrate the impacts of ocean depth with other known factors influencing body shape diversity, like habitat structure and trophic strategy. Given that different suites of traits appear to be favoured at different depths, investigations on the role of evolutionary integration of body plans is also warranted. With these and other studies, a more comprehensive picture of the overarching themes structuring morphological diversity and evolution of fishes will emerge.

CONFLICT OF INTEREST
The authors have no conflicts to declare.

AUTHORSHIP
CMM and PCW designed the study. All authors (excluding CMM) collected data. CMM and STF analysed morphological data. CMM wrote the manuscript. All authors contributed substantially to the preparation of the manuscript.

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Data for this study have been archived in the Dryad data repository (https://doi.org/10.25338/B8K048).

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Additional supporting information may be found online in the Supporting Information section.