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Original Article

Distinct evolutionary signatures underlie body shape diversity across deep sea habitats

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Abstract

The deep sea is known for challenging abiotic and biotic conditions; yet, deep-sea fishes have been shown to have higher phenotypic diversity than shallow relatives. An open question is whether different habitats within the deep sea differentially contribute to this surprising phenotypic diversity. Here, we explore the joint effects of two major environmental dimensions, the benthic-pelagic axis and ocean depth, on body shape diversification in marine teleost fishes. We found that increasing ocean depth shifted axes of phenotypic evolution and promoted diversification for benthic, demersal, and pelagic fishes alike. However, body shape diversity and rates of body shape evolution did not scale consistently across habitats. For benthic fishes, rate increased more strongly than diversity with increasing ocean depth, while the reverse was true for pelagic fishes. Analyses of habitat transitions suggested that independent invasions may help explain the diversity of deep-pelagic fishes without invoking high evolutionary rates. Relaxed selection may also explain this diversity, as suggested by the wide range of deep-pelagic forms observed along an evolutionary axis of body elongation. Overall, our results reveal a mosaic of pathways through which body plan diversity accumulated across a vertebrate radiation, underscoring the importance of considering finer-scale habitat variation in broad-scale studies.

Keywords: ecomorphology, macroevolution, deep sea, fish, pelagic

Introduction

The deep ocean is characterized by high pressure, little-to-no solar light, food limitation, cold temperatures, and massive expanses of space (Marshall, 1979; Priede, 2017; Ramirez-Llodra et al., 2010; Sutton, 2013). Yet, these extreme conditions and the challenges they present have not prevented the evolutionary diversification of deep-sea organisms over the past two hundred million years (Baucon et al., 2023; McClain & Hardy, 2010; Miller et al., 2022). Deep-sea fishes are surprisingly diverse (Günther, 1887; Priede, 2017), comprising up to 30% of marine teleost species (Cohen, 1970; Miller et al., 2022) and containing higher phenotypic diversity than shallow-water relatives (Heiple et al., 2023; Maile et al., 2020; Martinez et al., 2021; Miller et al., 2025).

While all marine environments deeper than 200 m are considered "deep sea," in reality this vast region includes a variety of habitats with different ecological conditions and selection pressures (Andresen et al., 2025; Drazen & Sutton, 2017; Eduardo et al., 2024; Levin & Dayton, 2009; Marshall, 1979; Paulus, 2021; Priede, 2017; Ramirez-Llodra et al., 2010; Rowden et al., 2010; Sutton, 2013; Woodworth et al., 2025). Like shallower waters, deep-sea habitats can be categorized by the degree of association with bottom substrate, with these habitats differing in abiotic and biotic conditions. For example and generally speaking, benthic environments (located on or near the substrate) are more structurally complex and productive than pelagic environments (within the water column). This generality seemingly applies to freshwater, coastal marine, and deep-sea environments alike (Angel & Boxshall, 1990; Burress & Hart, 2024; Drazen & Sutton, 2017; Friedman et al., 2016, 2022; Gratwicke & Speight, 2005; Sutton et al., 2010).

An open question is how the selection pressures unique to different habitats affect evolution and diversification in the deep sea. Changes in adaptive morphology along the benthic-to-pelagic axis are well documented in analogous shallow-water settings. Shallow-water fishes that depend on resources near the substrate tend to evolve laterally compressed bodies to aid in maneuverability, while fishes living higher in the water column evolve fusiform shapes that reduce drag for high-speed swimming (Burress & Hart, 2024; Friedman et al., 2016, 2022; Hamner, 1995; Larouche et al., 2020; Mihalitsis & Wainwright, 2024; Rincon-Sandoval et al., 2020; Sternes et al., 2024; Walker, 1997). The strength and directionality of selection on body shape may determine the tendency of lineages to adhere to (or deviate from) these rules. For instance, a widely cited example of evolutionary convergence is the fusiform body plan that arose inde-

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pendently in distantly related pelagic vertebrates, including tunas, jacks, sharks, dolphins, and ichthyosaurs (Hamner, 1995; Helfman et al., 2009; Marshall, 1971). Here, convergence is the outcome of strong directional selection, which is expected to have an overall limiting effect on phenotypic variation (Hamner, 1995). In contrast, benthic fishes have evolved greater phenotypic diversity than either pelagic or demersal species (i.e., those living near the substrate but not in direct contact with it) (Friedman et al., 2020; Larouche et al., 2020), suggesting that there are many body plans that are successful on the benthos. Among shallow-water habitats, coral reefs are thought to provide a wealth of ecological opportunities that promote diversification of benthic and demersal fishes in particular, owing to their high structural complexity (Burress & Wainwright, 2019; Corn et al., 2022; Evans et al., 2023; Larouche et al., 2020; Price et al., 2011).

To what extent do these ecomorphological patterns established for shallow-water fishes apply to the deep sea? There is evidence to suggest that the paradigm described above may unravel with increasing ocean depth. For example, demersal deep-sea fishes such as grenadiers, snailfishes, and halosaurs tend to have elongated body shapes, in contrast with their laterally compressed demersal counterparts in coastal waters (e.g., snappers, surgeonfishes, wrasses, and butterflyfishes) (Satterfield et al., 2023). Marshall (1971, 1979) originally proposed that these fishes (which he termed "benthopelagic") converged on an elongate, tapered body plan adapted for energy-efficient undulatory swimming, allowing individuals to travel long distances in search of sparse, patchily distributed resources (Armstrong et al., 1992; Milligan et al., 2020; Priede et al., 1990). The ubiquity of a posteriorly tapered body among deep-sea demersal fishes has been quantitatively substantiated since Marshall's prediction (Farré et al., 2016; Miller et al., 2022; Neat & Campbell, 2013).

Unlike roving deep-sea demersal ("benthopelagic") fishes, deep-sea pelagic fishes such as anglerfishes are typically sit-and-wait predators, with the notable exception of vertically migrating taxa (Andresen et al., 2025; Drazen & Sutton, 2017; Luck & Pietsch, 2008; Marshall, 1971; Priede et al., 1990; Stewart et al., 2024). It has recently been proposed that relaxed selection on locomotory abilities may explain the phenotypic diversification of deep-sea fishes (Martinez et al., 2021). This relaxation of selection pressure could help explain the presence of in situ evolutionary radiations in the bathypelagic zone (Heiple et al., 2023; Maile et al., 2025; Miller et al., 2025), despite the absence of similar radiations in pelagic habitats above 200 m (Gaither et al., 2016). Increasing ocean depth seems to provide opportunities for ecological and morphological divergence of pelagic organisms in the otherwise featureless water column (Burress & Hart, 2024; Buser et al., 2024; Friedman et al., 2019).

Taken together, these observations suggest that water column use (the benthic-pelagic axis) and ocean depth interact to drive phenotypic evolution in different ways. The deep sea is now widely recognized to contain substantial habitat heterogeneity (Levin et al., 2010; Paulus, 2021; Ramirez-Llodra et al., 2010), but the implications of this heterogeneity for diversification of marine fishes remain underexplored in the macroevolutionary literature. Here, we examine the contrasting effects of these two primary environmental dimensions of marine ecosystems on ecomorphological diversification. While previous work has investigated the role of these biologically important axes separately (Friedman et al., 2020; Martinez et al., 2021), this study integrates across the two axes to build a more comprehensive picture of the evolutionary processes that have generated body plan diversity across marine fishes. Our goals were twofold. First, we sought to determine whether similar phenotypes are preferred in benthic, demersal, and pelagic habitats regardless of ocean depth, or alternatively, whether deep-sea fishes look similar despite their position along the benthic-pelagic axis. Second, we asked whether the high diversity of deep-sea fishes found by previous research (Martinez et al., 2021) is distributed unevenly across benthic, demersal, or pelagic categories within the deep sea.

Methods

Data acquisition

We used the largest body shape dataset (Price et al., 2019, 2022) and time-calibrated phylogeny available for teleost fishes (Rabosky et al., 2018) to maximize evolutionary replication for comparative analyses. The FishShapes dataset (Price et al., 2022) contains eight linear body shape variables. Following Price et al. (2019), phenotypic data were size-adjusted using log-shape ratios, where each morphological trait was divided by the geometric mean of standard length, maximum body depth, and maximum fish width and finally log-transformed.

We coded habitat after Friedman et al. (2020) for water column use and Martinez et al. (2021) for maximum ocean depth. This was important for consistency of interpretation relative to these previous studies. Habitat categorizations from these studies were based on primary literature and/or documented observations as well as public databases (Table S1). Following these studies, water column use categories (hereafter "WCU") were defined for adult fishes as benthic (spend the majority of their time in direct contact with the bottom substrate), demersal (some interaction with substrate but rarely making direct contact with their entire body), and pelagic (live in the water column and rarely or never come into contact with substrate). Maximum depth categories were shallow (0–200 m), intermediate (200–1,000 m), and deep (>1,000 m). Note that the traditionally applied cut-off for the deep sea is below 200 m, so both "intermediate" and "deep" categories apply to fishes that occupy the deep sea. These depth categories are based on light attenuation from surface waters. The 200-m-cutoff reflects the maximum depth at which photosynthesis no longer occurs due to inadequate sunlight, which often coincides with the transition of the continental shelf into the continental slope (Priede, 2017). At depths below 1,000 m no trace of sunlight penetrates, and the only light sources are bioluminescent organisms (Priede, 2017). These cut-offs overlap with turnover in species communities. For example, nonmigratory pelagic organisms are dominant >1,000 m (Marshall, 1971).

The assignment of species to WCU categories is notoriously affected by limited observation, observer error, and the reality that these categories are flexible in nature (Rincon-Sandoval et al., 2020). Yet, discretized categories are a requirement for most phylogenetic comparative methods. We used two approaches to assess how these factors may influence our results. First, we compared WCU assignments from

Miller et al. (2022) to those from Friedman et al. (2020). These studies each conducted extensive (but independent) literature reviews to assign species to discretized categories (Table S1). Specifically, WCU was collectively based on 28 and 53 literature sources, respectively, in these two studies. Second, we repeated all analyses using a simpler scheme merging benthic and demersal states (with the merged state simply called "demersal" herein), since these can be difficult to distinguish in nature and are often combined in the deep-sea fish literature (Myers et al., 2021; Neat & Campbell, 2013; Priede, 2017). This approach reduces the potential for error arising from miscategorization, with the trade-off of losing resolution to detect true ecomorphological differences across habitat states.

We combined water column use and depth for a total of nine habitat categories (e.g., shallow-pelagic, deep-benthic, etc.) (hereafter "nine-state scheme") or six categories using the simpler WCU scheme (hereafter "six-state scheme"). After pruning the data to species that overlapped in the phylogeny, phenotypic, and habitat datasets, 2,882 marine species across 47 orders and 249 families remained for analysis. Taxonomic sampling across habitat categories is reported in Table S2.

Comparing axes of phenotypic variation

We visualized primary dimensions of diversity within the dataset using a principal component analysis (PCA) with a correlation matrix (scale = TRUE) performed with the "gm.prcomp" function in geomorph v.4.0.6 (Baken et al., 2021). To determine if there are similar axes of morphological diversification across habitats (for example, the tendency for body shape variation to be associated with elongation in some habitats but not others), we followed the procedure outlined in Friedman et al. (2022). We first performed a PCA of species in each habitat separately. We then extracted the first component axis (PC1) from each PCA and computed pairwise angles between PC1s across habitats (Adams & Collyer, 2009). Briefly, angles are calculated as the inner product between two vectors standardized by their Euclidean distances. As PC1 is the linear combination of traits that maximize variation across the dataset, it is commonly interpreted as the primary axis of multivariate diversity. Thus, the angle between these vectors represents a comparison of the primary dimension of diversity, with values varying from 0° (equivalent) to 90° (wholly uncorrelated). To ensure that these pairwise angles significantly differed from the null expectation, following Friedman et al. (2022), we simulated an eight-trait dataset (analogous to the eight body shape variables) under Brownian motion using the "mvSIM" function in the mvMORPH R package (Clavel et al., 2015) and similarly calculated pairwise angles between habitats. We iterated this procedure 1,000 times and assessed significance using a one-tailed test statistic.

Comparing average body shapes by habitat

We tested for differences in average body shapes across habitats using a phylogenetic MANOVA, inputting the eight size-adjusted body shape variables. This test was implemented using the "procD.pgls" function in geomorph with 10,000 simulations to assess significance, followed by a post hoc test using the "pairwise" function from the R package "RRPP" v.1.3.1 (Collyer & Adams, 2018).

Estimating phenotypic diversity of habitats

Using size-adjusted trait data, we estimated phenotypic variance by measuring the morphological disparity contained by each habitat using the "morphol.disparity" function in geomorph, with pairwise significance based on 10,000 iterations. In addition to the variance, we estimated the range of multivariate phenotypes found in each habitat by generating hypervolumes for each habitat based on the first six PC axes, which accounted for ~98% of total body shape variation, using the R package "hypervolumes" v.3.1.3 (Blonder et al., 2014, 2018). Whereas disparity is equivalent to multivariate variance, hypervolumes capture the range of the multivariate space for n-dimensional data. We also performed pairwise comparisons of the overlap of any two hypervolumes to assess differences in morphospace occupation across habitats. We statistically compared the size and overlap of hypervolumes by permuting habitat assignments across species and reestimating the hypervolume for each habitat, for 1,000 permutation trials (Corn et al., 2022). The observed value was considered significant if it fell outside the 95% quantile range of the permuted values. We performed pairwise overlap comparisons and permutation analyses using the six-state scheme only due to computational demands.

Explaining differences in phenotypic diversity across habitats

We compared rates of multivariate shape evolution using size-adjusted trait data among the nine habitats under a Brownian motion model using the "compare.evol.rates" function in geomorph, with significance based on 10,000 simulations. We give the caveat that traits may not be evolving characteristically of a Brownian motion model. Given that we are using a multivariate dataset and considering many states simultaneously (up to nine habitats), we chose this approach for calculating rates for its simplicity, ease of interpretation, and computational efficiency. Pairwise significance of rate differences across habitats was extracted from the output using a custom R script. To assess how depth-biased taxonomic sampling could modify evolutionary rates, we also performed a set of subsampling tests. To characterize how oversampling of shallow-water species could affect rate results, we randomly removed 50% of shallow-water species from the body shape dataset and phylogeny, then reestimated evolutionary rates, repeated over 1,000 trials. Likewise, to characterize how undersampling of deep-sea species could bias our results, we randomly removed 50% of species in the deepest category in a separate set of 1,000 trials.

Phenotypic diversity found within a habitat may be explained by multiple independent colonizations of the habitat, independent of evolutionary rates (Moen et al., 2013). To infer the frequency of historical transitions among habitats, we first used the "fit.mK" and "anova" functions in phytools to compare the fit of seven transition models: (1) all transition rates being equal, (2) symmetric forward-and-backward transition rates, (3) all transition rates being allowed to vary, (4) transitions to the deep-pelagic state being irreversible, (5) transitions to the deep-demersal state being

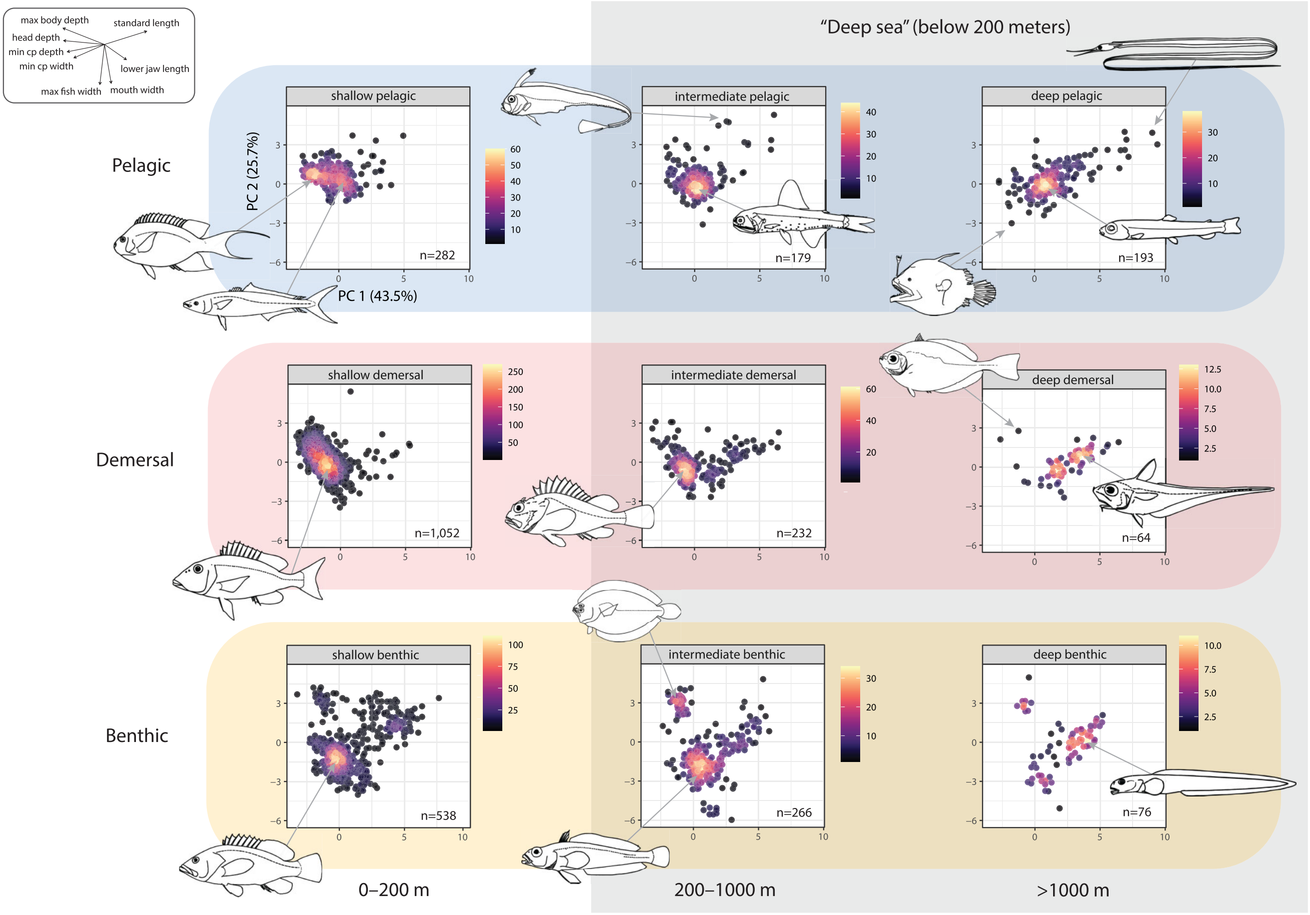

Figure 1. Body-shape morphospace of marine teleost fishes, with each habitat shown in a separate panel and trait loadings designated in the upper left. Points are colored by the density of species in morphospace. Illustrations were extracted from FAO fish identification guides. For simpler, six-state scheme, see Figure S1.

irreversible, (6) transitions to the deep-benthic state being irreversible, and (7) transitions to any of the deepest states (>1,000 m) being irreversible. Under the best-fitting model, we then generated 100 simulations of ancestral states using the "make.simmap" function in phytools v.2.1–1 (Revell, 2024) with Q="empirical" (using the most likely inferred rate matrix for simulations) and pi="estimated" (the stationary distribution on the root state is estimated and used as a prior). The "make.simmap" function outputs the average count of each transition type across the 100 simulations. To convert these counts into transition rates (Miller, 2021), we divided the number of each transition type by the total evolutionary time spent in each source habitat (proportion of branch lengths) as calculated by the SIMMAP function (Tables S3 and S4).

Results

Axes of phenotypic diversity by habitat

Across marine teleosts, the first two PC axes accounted for 65.2% of body shape variation. Consistent with previous studies using this same dataset, PC1 (43.5%) was most strongly associated with relative body elongation, while PC2 (25.7%) was associated with dorsoventral depression versus lateral compression of the body (Figure 1). Based on a visual inspection, it is apparent that the region of highest density of body shapes in morphospace consistently shifted with increasing ocean depth within all WCU categories, from relatively deep-bodied forms in shallow waters toward elongated shapes in deeper waters (Figure 1). This was apparent using both the nine- and six-state schemes (i.e., merging demersal and benthic, Figure S1).

Of the 2,880 species shared between the Friedman et al. (2020) and Miller et al. (2022) habitat datasets, 15.0% of species differed in WCU assignment between studies (Table S1). These differences reflect uncertainty in the lifestyle of individual species and flexibility in habitat use. Nonetheless, the shapes of the morphospaces formed by benthic, demersal, and pelagic species were similar under the two coding schemes (Figure S2). This suggests that at the broad phylogenetic scales examined in this study, consistent evolutionary patterns associated with WCU will emerge despite these sources of noise.

Within the deep sea, similar dimensions of body shape variation were found across WCU categories, as revealed by comparisons of angles between primary axes extracted from habitat-specific PCAs. Using the nine-state scheme, PC1 angles were smaller than expected by chance ($p < 0.05$) in 17 of 36 pairwise comparisons (Figure 2; Figure S3 and Table S5). Angles were smaller than expected among deep-benthic, deep-demersal, and deep-pelagic categories. This

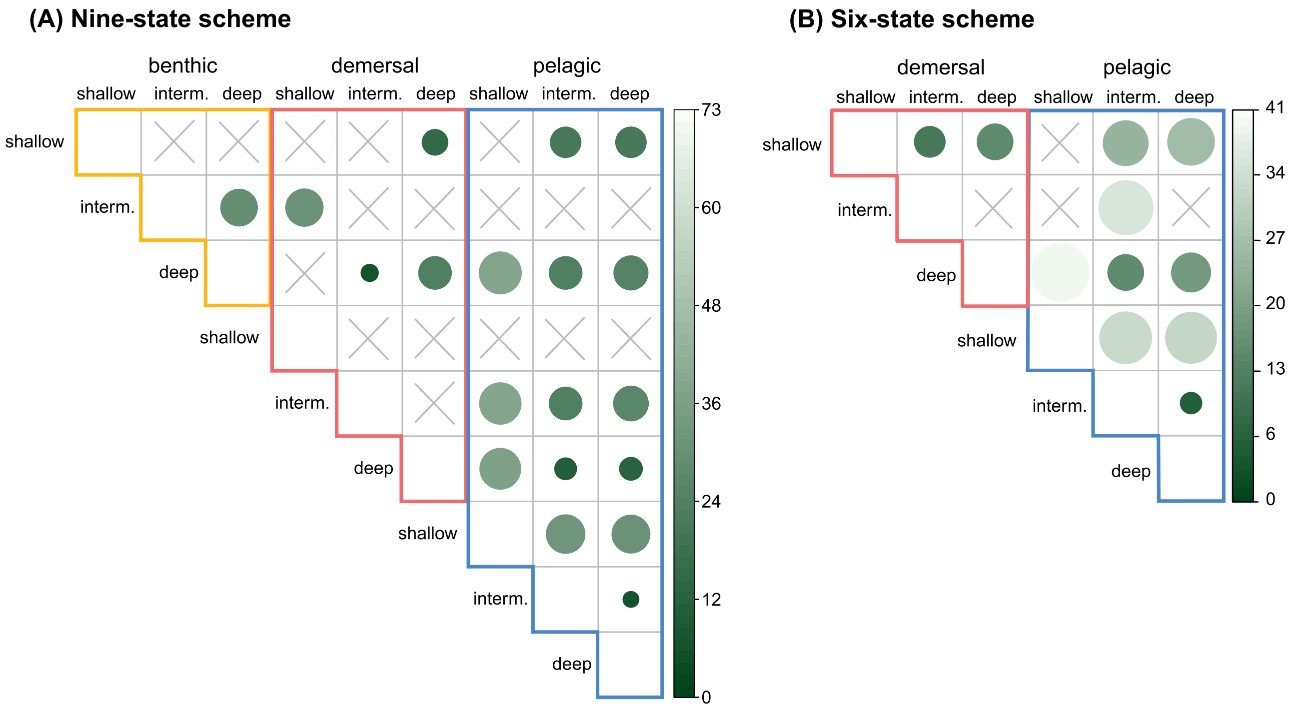

Figure 2. Comparing similarity in the primary axes of morphospace variation between habitats. Angles between PC1 of each habitat, using (A) nine-state scheme and (B) six-state scheme (benthic and demersal states merged). Smaller angles (indicated by smaller circles) indicate greater similarity between habitats. Nonstatistically significant comparisons are represented by an "X." See Figures S3 and S4 and Tables S5 and S6 for results of simulated angle comparisons and pairwise angles, respectively.

suggests that diversity evolves along similar trajectories in deep-sea fishes, such as selection for elongation, independent of the benthic-pelagic axis (Figure 1). Among other categories, angles were also more similar than expected between the shallow-benthic and the intermediate-pelagic, deep-demersal, and deep-pelagic categories, as well as between shallow-pelagic and all three deep-water categories (Figure 2, Table S5). This suggests that elongation is also an important axis of variation for shallow-benthic and shallow-pelagic fishes. Shallow-demersal fishes were unique for the relatively low contribution of caudal peduncle depth and width diversity to variation across PC1 (Figure 1). As such, this habitat had few significant pairwise comparisons in the size of PC1 angles (only similar to intermediate benthic) highlighting its unique trajectory of diversification (Figure 2). In contrast, the habitat with the most similarity to others was deep pelagic with six of eight comparisons significant (all but shallow demersal and intermediate benthic).

With the simpler six-state scheme (merged benthic and demersal categories into a single "demersal" group), PC1 angles were smaller than expected by chance in 11 of 15 pairwise comparisons (Figure S4 and Table S6). The different evolutionary trajectories between shallow pelagic and shallow demersal fishes were still apparent from this simpler scheme (angles not significantly smaller than expected by chance). As with the nine-state scheme, all deep-sea categories had angles smaller than expected by chance amongst each other (with the exception of intermediate versus deep demersal). A caveat is that the distinct evolutionary trajectory of shallow demersal (relative to shallow benthic) fishes was obscured in the six-state scheme due to the merging of these categories.

Differences in average shapes

A phylogenetic MANOVA comparing average body shape by habitat was significant for both nine- and six-state schemes (Table S7). However, explanatory power was low ($R^2 = 0.01$ for each test). None of the post hoc pairwise comparisons were significant (Table S8); therefore, we could not identify differences in average shape between any two habitats using this approach. Together, this indicates that average shape differences among habitats are subtle compared to the shape variation within each habitat.

Explaining the diversity of deep-sea fishes

Increasing ocean depth promoted phenotypic diversification in general. Within all WCU categories individually, fishes from intermediate and/or deep waters had significantly higher phenotypic disparity (Tables S9 and S10) and significantly faster evolutionary rates (Tables S11 and S12) than shallow-water counterparts. Deep-sea benthic and demersal lineages had the highest evolutionary rates across all marine fishes (Figure 3). This trend was persistent under simulated scenarios assuming oversampling of shallow-water fishes or undersampling of deep-sea fishes (Figure S5).

The size of hypervolumes (based on the six-habitat WCU scheme) formed by shallow pelagic, shallow demersal, and intermediate pelagic fishes was smaller than expected from 1,000 permutations of habitat state (Figure S6). All pairwise comparisons of habitat hypervolumes revealed significant differences in morphospace occupation for one or both habitats relative to permutations (Table S13 and Figure S7). The most extreme differences observed were deep demersal vs. shallow pelagic (88% and 57% of hypervolume unique, re-

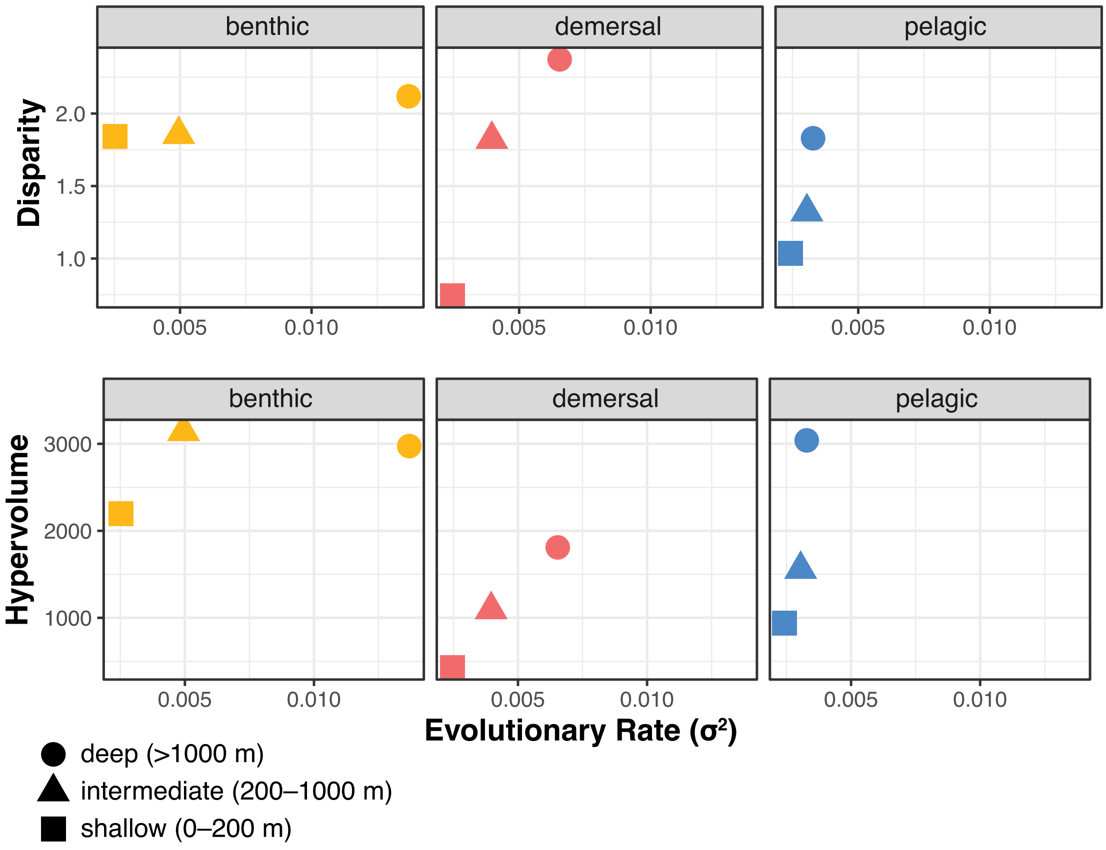

Figure 3. Scaling of phenotypic diversity with evolutionary rate by habitat. Body shape diversity was measured by disparity (top) or hypervolume size (bottom), respectively. See Tables S9 and S11 for pairwise significance of disparity and rates, respectively. For comparable results under the six-state scheme, see Figure S8 and Tables S10 and S12.

spectively), deep pelagic vs. shallow pelagic (84% and 42% unique, respectively), and deep pelagic versus shallow demersal (78% and 51%, respectively). These comparisons emphasize how different the range of deep-sea body shapes is compared to shallow-water fishes. Among deep-sea fishes, deep pelagic and deep demersal fishes were equally different from each other (54% of hypervolume unique for both categories).

The manner by which phenotypic diversity scaled with evolutionary rate in deep-sea fishes was dependent on WCU category (Figure 3). For benthic fishes, evolutionary rate increased with ocean depth by a larger factor than did phenotypic diversity (regardless if diversity was measured by disparity or hypervolume). The reverse was true for pelagic fishes: phenotypic diversity increased with depth more sharply than rate. Demersal fishes were intermediate between these two scenarios with similar relative increases in diversity and rate with ocean depth (Figure 3), as was the merged demersal category when using the six-state scheme (Figure S8). Together, these results suggest that while deep-sea fish body plans are generally diverse, the trajectories by which this diversity was generated differed within subhabitats of the deep sea.

Within deep-sea fishes, the range of phenotypes (measured by hypervolume size) was smaller for deep-demersal fishes than for deep-benthic or deep-pelagic fishes (Figure 3). However, phenotypic variance (i.e., the dispersion of body shapes, measured by disparity) was highest for deep-demersal fishes. Extremely compressed and depressed body plans (e.g., flatfishes and monkfishes, respectively) contributed to the large hypervolume of deep-benthic fishes (Figure 1), whereas these morphotypes were rare or absent in deep pelagic or demersal habitats. Unlike deep-benthic fishes, the large hypervolume of deep-pelagic fishes primarily reflects body shape variation along an axis related to body elongation, an axis of diversification found among all deep-sea habitats (Figure 1).

The best-fitting habitat transition model allowed all rates to vary, emphasizing that transitions into the deep sea are not irreversible (Table S14). The frequency of habitat transitions associated with depth was contingent on WCU state (Figure 4). This pattern manifested in two ways. First, within the benthic and demersal states transitions from deep-to-shallow were more common than shallow-to-deep; this pattern was not seen in the pelagic state. This indicates that depth transitions take place frequently along the continental shelf and slope. Second, transitions in WCU state within the deep sea occurred predominately in the benthic-to-pelagic direction. Routes to becoming deep pelagic were varied and included moving from shallow to deep within the pelagic state, as well as moving from benthic to pelagic within the deep sea. However, the deep-benthic category was primarily colonized from shallower benthic habitats (i.e., moving down along the seafloor). Transitions from deep-pelagic to deep-demersal habitats were not observed, and transitions from deep-demersal to deep-benthic were rare. These transition-rate patterns were consistent when using the six-state scheme (Figure S9).

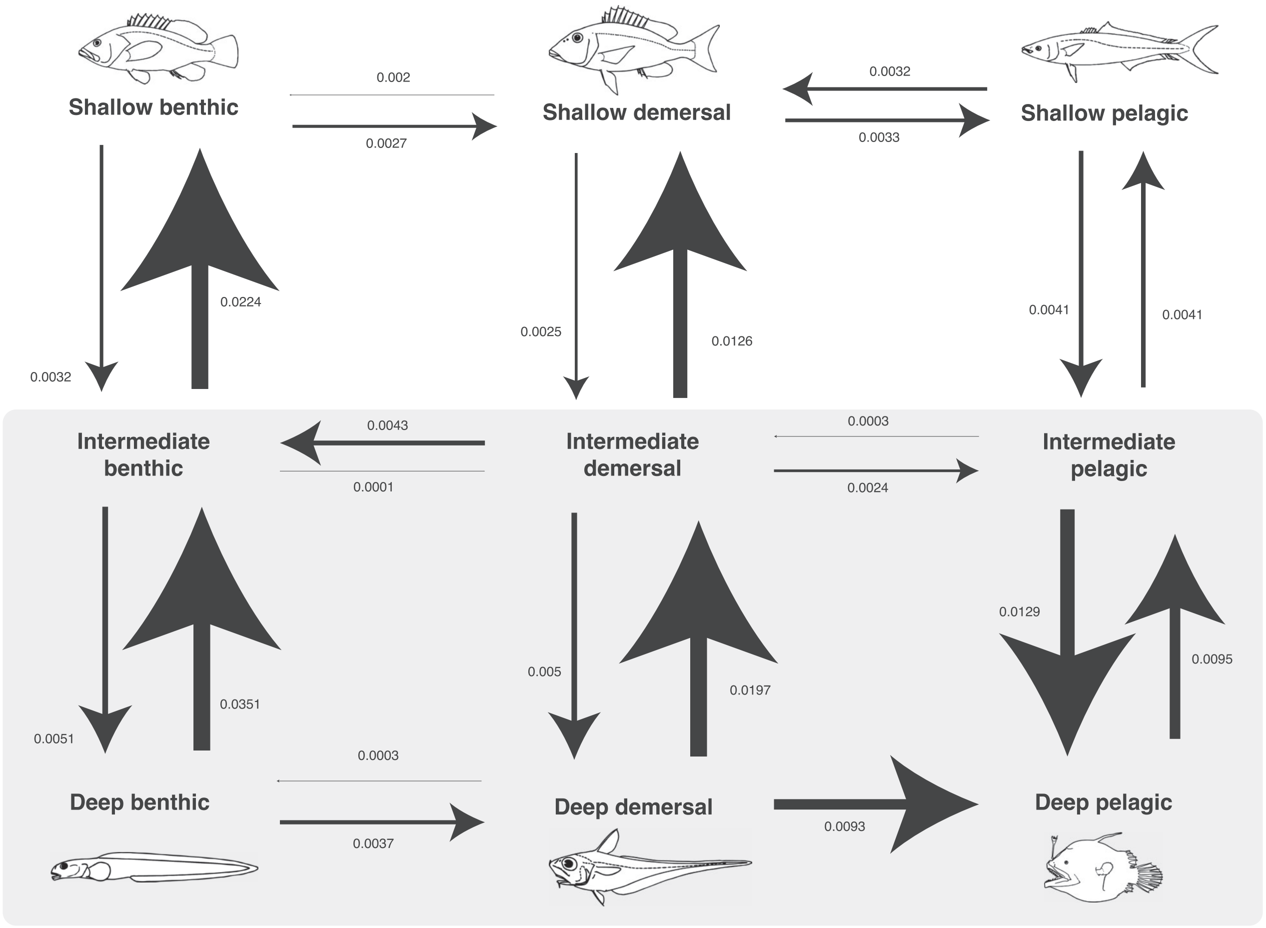

Figure 4. Transition rates among habitats inferred using SIMMAP under an all-rates-different model (Table S14). The width of arrows is proportional to the magnitude of rates. Gray box surrounds "deep sea" habitats (>200 m). See Table S3 for conversion of the count of events into a rate. Dual transitions (e.g., simultaneous change in WCU and depth, or transitions that "skip" depth zones) are not plotted for visual clarity and can be seen in Table S3. For comparable results under the six-state scheme, see Table S4 and Figure S9.

Discussion

Habitats differ in selection pressures, which should influence the characteristics of organisms found within them. Marine organisms segregate by both ocean depth and the degree of interaction with the substrate, such that the two environmental dimensions leave distinct evolutionary signatures. Here, we show that phenotypic diversity, and the evolutionary processes behind it, vary across marine teleost fishes according to the interaction between ocean depth and water column use. Our results help resolve the following open questions that remained after individual investigations of ocean depth (Martinez et al., 2021) and the benthic-pelagic axis (Friedman et al., 2020) on phenotypic diversity patterns in marine fishes. First, do benthic, demersal, and pelagic fishes evolve similar shapes in shallow and deep waters? Likewise, is the selection pressure imparted by the deep sea strong enough to overwhelm water-column-specific (i.e., benthic versus pelagic) adaptations? Lastly, how have deep-sea habitats with different selection pressures individually contributed to the overall diversity and diversification of deep-sea fishes? We discuss each of these questions below.

The general ecomorphological "rules" established for shallow-water fishes are that pelagic species evolve fusiform bodies, which reduce drag, while demersal fishes evolve laterally compressed, deep bodies, which improve maneuverability (Burress & Hart, 2024; Friedman et al., 2016; Hamner, 1995; Larouche et al., 2020; Mihalitsis & Wainwright, 2024; Rincon-Sandoval et al., 2020; Walker, 1997). Benthic fishes, which spend most of their lives in direct contact with substrate, evolve diverse body shapes, from elongate to extremely dorsoventrally depressed, owing to the many ways fishes may interact with substrate (Friedman et al., 2020). To what extent do deep-sea fishes break these rules?

In general, we found that deep-sea fishes evolve similar shapes and diversify along similar axes of diversity regardless of WCU (Figures 1 and 2; Figures S1, S3, and S7; Table S13). Arguably, the strongest deviation from the typical rules for shallow waters was seen within the demersal (or "benthopelagic") category. Laterally compressed bodies were common among shallow-water demersal fishes, while elongate shapes were preferred among deep-sea demersal fishes (Figure 1). Marshall's (1971) prediction of the importance of the tapered body plan in this habitat is therefore supported by our results and others (Farré et al., 2016; Martinez et al., 2021; Miller et al., 2022; Neat & Campbell, 2013). While demersal fishes in shallow nearshore habitats have access to abundant resources in close proximity, many deep-sea demersal fishes must constantly travel in search of food (Armstrong et al., 1992; Priede et al., 1990, 1991;

Woodworth et al., 2025). Scavenging, and even necrophagivory (feeding on animals attracted to carrion), is a common foraging strategy in the food-limited deep-sea environment, necessitating long excursions in search of carrion sources (Drazen & Sutton, 2017; Jamieson et al., 2009; Lampitt et al., 1983). For example, rattail species from the genus *Coryphaenoides* (family Macrouridae) move continuously in search of food, and may even journey thousands of kilometers across ocean basins in seasonal migratory patterns (Milligan et al., 2020). It is believed that the posteriorly tapered body plan common in deep demersal habitats allows for undulatory locomotion, which is the most efficient mode for steady swimming over long distances (Armstrong et al., 1992; Borazjani & Sotiropoulos, 2009; Farré et al., 2016; Neat & Campbell, 2013; Woodworth et al., 2025). More universally, the colder temperatures, higher water viscosity, and limited light availability of the deep sea encourage slower swimming speeds while searching for food (Borazjani & Sotiropoulos, 2009; Childress, 1995; Drazen & Seibel, 2007). More recent discoveries have captured video footage of elongate deep-sea species across four different families utilizing backward undulatory swimming, which is particularly advantageous in dark environments to retread the same path while investigating the benthos for food (D'Août & Aerts, 1999; Priede & Jamieson, 2025). Although the preferred shapes differ with depth (lateral compression in shallow versus elongation in deep waters), a similar theme shared by all demersal fishes regardless of depth is strong selection pressure on locomotion that ultimately limits the range of observed shapes (Martinez et al., 2021).

Challenges shared by all deep-sea habitats include food limitation, little-to-no sunlight, cold temperatures, and high pressures. Our results showed that elongation is consistently an important axis of body shape variation in fishes across the subhabitats of the deep sea (Figures 1 and 2; Figures S1, S3, and S4). The importance of elongation with ocean depth was previously suggested by Neat and Campbell (2013), but their study only investigated demersal fishes, so it was previously unclear if elongation was also relevant for deep-pelagic fishes. The adaptive significance of elongation has been less frequently discussed in the literature for pelagic and benthic deep-sea fishes than for their demersal counterparts, for which elongation is believed important for steady swimming above the benthos, as described above. Except for daily vertical migrators, deep-pelagic and benthic fishes are generally inactive sit-and-wait predators (Gates et al., 2012; Luck & Pietsch, 2008; Stewart et al., 2024). Elongation may be under selection for other reasons, such as aiding in communication and sensation by providing greater surface area for bioluminescent photophores or detecting vibrations (Davis et al., 2016; Neat & Campbell, 2013). For example, the presence of specialized caudal light organs can influence body shape evolution in lanternfishes (Myctophidae), indicating the strong selective pressures imposed by bioluminescence in the deep (Martin et al., 2022). Elongate body shapes may also minimize the silhouette of pelagic fishes, such as lancetfishes (Alepisauridae) and barracudinas (Paralepididae), which hunt while oriented vertically in the water column (Maile et al., 2020). Elongation may also have nonadaptive explanations such as phylogenetic inertia: residual ancestral traits that persist over macroevolutionary timescales due to lack of selection for another shape (Blomberg & Garland, 2002). Indeed, a pattern visible across the fish Tree of Life is that elongated body shapes evolved prior to deep-sea colonization (Miller et al., 2022), although this does not preclude increasing elongation due to directional selection.

The high taxonomic and phenotypic diversity of deep-sea fishes has been well established by previous studies (Günther, 1887; Heiple et al., 2023; Maile et al., 2020, 2025; Martinez et al., 2021; Miller et al., 2025). Our results are consistent with findings that phenotypic diversity and evolutionary rates are higher in deep-sea compared to shallow-water fishes (Martinez et al., 2021), but we further show that the pattern is recapitulated within each water column habitat separately (Figure 3; Figures S6 and S8). Importantly, this demonstrates that previous results were not driven by any single habitat or taxonomic group and that elevated diversification is a recurring feature of all deep-sea habitats. Still, we found that the relative magnitude of changes in disparity, hypervolume, and evolutionary rate across shallow, intermediate, and deep categories differed with water column use (Figure 3; Figure S8). Evolutionary rate increased most strongly with increasing ocean depth for benthic fishes, while hypervolume (range of phenotypes) increased more strongly with depth for pelagic fishes. In sum, these results show that the high phenotypic diversity of deep-sea fishes was generated in different ways within subhabitats defined by water column use.

A straightforward positive relationship is expected between rates of phenotypic evolution and resulting phenotypic diversity (Goswami & Clavel, 2025), but empirical studies do not always recover this relationship (Buser et al., 2024). When attempting to explain patterns of phenotypic diversity among habitat types, it is important to recognize that diversity can actually be generated by two processes: multiple independent colonizations of the habitat and in situ diversification of those lineages after colonization (Friedman et al., 2020; Moen et al., 2013). In other words, colonization of a habitat by lineages with variable body plans can explain high diversity of that habitat without invoking evolutionary rates. We found that deep-pelagic habitats were colonized by deep-demersal and shallow-pelagic lineages at similar frequencies (Figure 4; Figure S9). Therefore, there are more potential phenotypic "starting points" for fishes entering the deep pelagic, helping explain why phenotypic diversity of this habitat is high when evolutionary rates are not (Figure 3; Figure S8). In contrast, deep-benthic and deep-demersal habitats tend to be colonized by other benthic and demersal lineages. It has been shown previously that lineages colonizing the deep sea tend to already have small caudal peduncles characteristic of the tapered-tail body plan (Miller et al., 2022). This ecological filtering further limits the phenotypic starting points of deep-demersal fishes. Therefore, we suggest that phenotypic diversity of deep-sea benthic and demersal fishes may be generated by diversification following deep-sea colonization more so than by independent colonization of lineages with variable body plans. Consistent with our findings, previous studies also suggested that dispersal up and down the continental slope and rise is a key mechanism by which taxonomic and phenotypic diversity of deep-benthic and demersal fishes is generated (Friedman & Muñoz, 2023; Ingram, 2011).

Relaxed selection on locomotion has been proposed as an explanation for the higher diversity of deep-sea fishes compared to shallow relatives (Martinez et al., 2021). However, our more nuanced habitat-based approach reveals a more complex story. Locomotion should actually be under strong selection in deep-demersal fishes for the reasons described above (Marshall, 1971, 1979; Neat & Campbell, 2013). This seems to be supported by the concentration of elongate, tapered bodies in the morphospace of deep-demersal fishes (Figure 1). The relaxed selection hypothesis seems more applicable to deep-pelagic fishes, especially nonmigratory bathypelagic lineages (Eduardo et al., 2024). These fishes spend their entire life suspended in the water column, and many use lures to draw prey to close range rather than actively hunt (Drazen & Sutton, 2017; Luck & Pietsch, 2008; Stewart et al., 2024). Therefore, deep-pelagic fishes do not have the same emphasis on undulatory locomotion as deep-demersal fishes (Priede & Jamieson, 2025), nor the need to navigate across a substrate like deep-benthic fishes (Lundsten et al., 2012). While the primary axis of morphological diversity is shared across all subhabitats of the deep sea (Figures 1 and 2), deep-pelagic fishes show greater phenotypic range along this axis, which is associated with variation in elongation of the body. The most extreme shapes on both ends of this axis seen across all marine fishes are found in the deep-pelagic category, represented by globose ceratioid anglerfishes on one end and snipe eels on the other (Figure 1), with many shapes in between. Clearly many body plans are successful in the deep-sea water column, as reflected by the high phenotypic diversity of fishes observed for this habitat (Figures 1 and 3; Figures S1 and S8).

The application of phylogenetic comparative methods to studying deep-sea diversity is a relatively recent effort (Denton, 2018; Gerringer et al., 2021; Heiple et al., 2023; Kenaley et al., 2014; Martinez et al., 2021; Miller et al., 2022) that has picked up speed with the construction of phylogenies and phenotypic datasets spanning the entire teleost Tree of Life (Price et al., 2019; Rabosky et al., 2018). We recognize that these approaches are sensitive to sampling biases (Davis et al., 2013; Louca et al., 2022), and that the deep sea in particular suffers from undersampling (Webb et al., 2010). Still, it is encouraging that the rank order of evolutionary rate differences among habitats persisted when we subsampled shallow- and deep-sea taxa (Figure S6). A previous study did not find evidence for biased taxonomic sampling with depth in the same phylogeny of teleosts used here (Miller et al., 2022). Shallow-marine fishes from tropical areas are also undersampled and underdescribed (Brandl et al., 2018), such that sampling biases could "even out" when comparing shallow and deep-sea fishes, especially at broad phylogenetic scales. While new species will be continuously described from the deep sea, we assume that higher taxa (genera and families) are adequately sampled to capture the phylogenetic and morphological diversity at the taxonomic scales relevant to this study. This study and others (Martinez et al., 2021; Miller et al., 2022) gain statistical power from the phylogenetic replication of deep-sea colonization apparent at the scale of all teleost fishes, at the cost of information about any single clade of deep-sea fishes (Beaulieu & O'Meara, 2018). This conflict is apparent from our observation that 15% of species differed in water column use coding between independent literature reviews (Table S1), yet the resulting body-shape morphospaces were similar (Figure S2). Studies of individual clades will still be essential for linking ecology, selection, and macroevolution, but depend on more extensive taxonomic sampling. For example, a new phylogeny with expanded taxonomic sampling of anglerfishes was used to show that body elongation evolved repeatedly even within a single deep-pelagic lineage (Miller et al., 2025). Our knowledge of the ecology and distribution of deep-sea fishes is expanding, calling into question the traditional discretized categories of depth used here (Eduardo et al., 2024; Sutton, 2013). Macroevolutionary patterns should be reevaluated in light of this shifting picture of deep-sea ecology, pending ecological data for a critical mass of species across the phylogeny. Finally, deep-sea habitats can be further subdivided: for example, deep-benthic environments include the abyssal plain, hydrothermal vents, and hadal trenches that may impart unique selection pressures on morphology (Gerringer, 2019; Jamieson et al., 2021). This will be an exciting avenue for future investigation, but depends on improved genetic sampling to gain the necessary phylogenetic replication of the colonization of these habitats (Uyeda et al., 2018).

In conclusion, ocean depth and the benthic-pelagic habitat axis interacted to generate body plan diversity across marine teleost fishes. The high diversity of deep-sea fishes was generated by a mosaic of evolutionary mechanisms across subhabitats, with different contributions of ancestral body shape and postcolonization diversification associated with water column use. These results support a growing body of literature showing the deep sea is not homogeneous with regard to phenotypic diversification, and the habitats contained within this massive ecosystem should be considered separately in future evolutionary studies.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Input data and R scripts are deposited in a Dryad repository (doi: 10.5061/dryad.z612jm6r1).

Author contributions

E.C.S., S.T.F., and C.M.M. conceived the project, designed and performed the analyses, interpreted results, and wrote and edited the manuscript.

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Conflict of interest

The authors declare no conflict of interest.

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