

Diadromy Drives Elevated Rates of Trait Evolution and Ecomorphological Convergence in Clupeiformes (Herring, Shad, and Anchovies)

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ABSTRACT: Migration can have a profound influence on rates and patterns of phenotypic evolution. Diadromy is the migration between marine and freshwater habitats for feeding and reproduction that can require individuals to travel tens to thousands of kilometers. The high energetic demands of diadromy are predicted to select for ecomorphological traits that maximize swimming and locomotor efficiency. Intraspecific studies have shown repeated instances of divergence among diadromous and nondiadromous populations in locomotor and foraging traits, which suggests that at a macroevolutionary scale diadromous lineages may experience convergent evolution onto one or multiple adaptive optima. We tested for differences in rates and patterns of phenotypic evolution among diadromous and nondiadromous lineages in Clupeiformes, a clade that has evolved diadromy more than 10 times. Our results show that diadromous clupeiforms show convergent evolution for some locomotor traits and faster rates of evolution, which we propose are adaptive responses to the locomotor demands of migration. We also find evidence that diadromous lineages show convergence into multiple regions of multivariate trait space and suggest that these respective trait spaces are associated with differences in migration and trophic ecology. However, not all locomotor traits and no trophic traits show evidence of convergence or elevated rates of evolution associated with diadromy. Our results show that long-distance migration influences the tempo and patterns of phenotypic evolution at macroevolutionary scales, but there is not a single diadromous syndrome.

Keywords: diadromy, migration, convergence, ecomorphology, evolutionary rates.

Introduction

Convergence is a widespread phenomenon that has sculpted phenotypic diversity patterns across the tree of life. The repeated and predictable appearance of common forms that confer increased fitness in similar environments (i.e., adaptive landscape) is one of the most powerful lines of evidence for deterministic evolution (Losos 2011). Studies demonstrating convergent evolution in similar habitats (Rundle et al. 2000; Collar et al. 2010; Mahler et al. 2014) and dietary regimes (Grant and Grant 1989; Rüber and Adams 2001; Davis and Betancur-R 2017) are common in evolutionary biology, largely because these are key ecological axes that exert strong selective pressures (Simpson 1953; Mayr 1963; Schluter 2000; Losos and Ricklefs 2009). However, other sources of ecological variation that abound across the tree of life, including the repeated evolution of different life history strategies, can alter the phenotypic adaptive landscape and drive convergent evolution (Stearns 1976, 1992; Palkovacs 2003; Bonett et al. 2018).

Migration is an extraordinary life history strategy that has independently evolved in almost every major vertebrate lineage (Dingle 2014) and confers adaptive benefits, such as increased fitness, higher survival rates in temporally variable environments, and the capacity to exploit a spectrum of heterogeneous resources (Winemiller and Rose 1992; Alerstam et al. 2003; Dingle 2014). These potential benefits are often counterbalanced by the energetic cost of long-distance migration, as migrants traverse tens to thousands of kilometers through different habitats while becoming progressively vulnerable to predation due to exhaustion and depletion of energy reserves (Dingle and Drake 2007; Bowlin et al. 2010; Shaw 2016). In response to the costs associated with

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migration, selection is predicted to drive ecomorphological adaptations that lessen the demands of migration (Roff 1991; Dingle 2006).

Ecological function has a strong link to morphological form (Koehl 1996), and traits associated with locomotion may experience strong selective pressures and elevated rates of evolution in migratory species. For example, relative to nonmigratory populations, migratory insects have evolved longer wings (Dockx 2007) and migratory birds have evolved more pointed wings with greater aspect ratios (Mönkkönen 1995; Vágási et al. 2016), indicating that an optimal wing morphology is a key adaptation for efficient migration in flying animals. Some migratory fish populations have more dorsal and anal fin rays and a relatively streamlined body shape compared with conspecific resident populations, which presumably are adaptations for increased swimming efficiency (Taylor and McPhail 1986; Humphries 1990; Crossin et al. 2004; Smith et al. 2020). Roff (1991) proposed that migratory populations should evolve a larger body size than nonmigratory populations because bioenergetic costs are inversely related to body mass. Intraspecific studies of fishes and insects support Roff's hypothesis (L'Abée-Lund 1991; Hendry et al. 2003; Thériault and Dodson 2003; Jonsson and Jonsson 2006), and a few interspecific studies showed that the pattern of a larger body size in migratory fishes is writ large across phylogenetic scales (Bloom et al. 2018; Burns and Bloom 2020). Together these studies suggest that migration may drive adaptive phenotypic evolution across the tree of life and convergence among migratory lineages (Roff 1988, 1991; Gleiss et al. 2011).

Approximately 400 of the 35,000 ray-finned fishes migrate between freshwater rivers and oceans, an extreme type of migration known as diadromy (McDowall 1997; Delgado and Ruzzante 2020). Myers (1949) and McDowall (1988) characterized three forms of diadromy: anadromy, catadromy, and amphidromy. Anadromous and catadromous fishes have mirror opposite migration patterns; anadromous fishes feed and grow in oceanic habitats and then migrate to freshwater rivers to spawn, while catadromous fishes grow and feed in freshwater systems and then migrate to oceanic habitats to spawn. Amphidromous fishes migrate between oceans and rivers, but the timing of migration is variable and not always tightly linked to reproduction. Diadromy has independently evolved in iconic fish clades, including lampreys, freshwater eels, sturgeons, salmonids, galaxiids, and shads (McDowall 2008; Delgado and Ruzzante 2020). Diadromous fishes hold paramount ecological importance because they transport massive amounts of energy among different ecosystems and function as keystone species (Willson and Halupka 1995; Limburg and Waldman 2009; Post and Walters 2009; Bowlin et al. 2010; Schindler et al. 2013; Auer et al. 2018; Samways et al. 2018), yet many species face

myriad conservation threats (Close et al. 2002; Post and Walters 2009).

Diadromous species are faced with a unique set of selective pressures because they traverse tens to thousands of miles between two contrasting habitats (rivers and oceans) that vary in abiotic conditions at different life stages (McDowall 2009). Habitat occupancy can influence macroevolutionary rates and patterns of diversification in fishes (Collar et al. 2011; Price et al. 2012; Bloom et al. 2013; Friedman et al. 2020; Larouche et al. 2020; Egan et al. 2021), and specifically transitions from marine to freshwater habitats can alter patterns of trait evolution (Betancur-R et al. 2012; Kolmann et al. 2020; Clarke 2021). Ocean and riverine habitats differ in abiotic factors such as structural complexity and water flow, which are known to exert contrasting selective pressures on swimming performance and locomotor traits (Langerhans et al. 2003; Langerhans and Reznick 2010; Crow et al. 2013). In the marine environment, diadromous species may experience selection for locomotor traits that enhance prolonged swimming performance (e.g., fusiform body shape) because they inhabit the pelagic zone, which is structurally simple and often has constant, unidirectional water flows (Blake 2004; Langerhans and Reznick 2010; Friedman et al. 2020). In contrast, diadromous species navigating riverine systems may be under selection for locomotor traits that enhance maneuverability (e.g., deep-bodied shape) because rivers are narrow, structurally complex, and contain reaches with turbulent, multidirectional water flows (Langerhans et al. 2003; Langerhans and Reznick 2010; Larouche et al. 2020). This suggests that migrating between two distinct habitats, oceans and rivers, may uniquely affect phenotypic evolution. Intraspecific studies investigating the effects of diadromy on locomotory morphology have found contrasting results; anadromous threespine sticklebacks (*Gasterosteus aculeatus*) have a more fusiform body shape (Taylor and McPhail 1986), and anadromous alewives (*Alosa pseudoharengus*) have evolved a deeper body than resident populations (Jones et al. 2013; Velotta et al. 2018; Smith et al. 2020). Furthermore, the evolution of diadromy has long been tied to trophic ecology (Gross et al. 1988; Johnson and Schindler 2013), and traits associated with feeding have been shown to diverge among diadromous and nondiadromous populations. Palkovacs and Post (2008) found that populations of landlocked (i.e., nondiadromous) alewives (*A. pseudoharengus*) descended from anadromous ancestors repeatedly evolved smaller mouth gapes and exhibit faster rates of trophic evolution. These authors proposed that the phenotypic divergence evolved in response to differences in prey size availability between oceans and rivers (Palkovacs and Post 2008). Potential differences in prey size, abundance, and species availability between freshwater and marine environments may cause the trophic morphology of diadromous species to evolve along

different evolutionary trajectories. Despite widespread interest in migration biology, ecomorphological adaptations for diadromy remain largely unstudied at macroevolutionary scales.

Clupeiformes (herrings, shads, anchovies, sardines, and their allies) contains approximately 415 species, of which about 30 are diadromous, a proportion about 10 times greater than any other fish order (Whitehead et al. 1988; McDowall 2003; Egan et al. 2022). This high diversity of diadromous species is the result of 10–12 independent origins of diadromy (McDowall 2003; Bloom et al. 2018) among the approximately 400 species, offering a tractable and statistically powerful system for comparative analyses. Clupeiformes are highly abundant in many aquatic ecosystems, have a near global distribution, and exhibit a wide range of ecological and morphological diversity (Whitehead et al. 1988; McDowall 2003; Egan et al. 2018, 2022). Previous studies have used Clupeiformes to study the evolution of diadromy and found that diadromous and nondiadromous populations show repeated and consistent phenotypic divergence among locomotor and foraging traits (Palkovacs et al. 2008; Smith et al. 2020). Bloom et al. (2018) showed that diadromous Clupeiformes rapidly evolved a larger body size than nondiadromous lineages, likely in response to strong directional selection. These previous studies spanning intra- and interspecific levels suggest that Clupeiformes provide an ideal phylogenetic framework for investigating macroevolutionary dynamics of trait evolution in diadromous fishes.

In this study, we explored whether the evolution of diadromy can influence rates and patterns of trait evolution across macroevolutionary scales. We used a molecular phylogeny, a suite of morphometric traits, and phylogenetic comparative analyses to answer three questions. First, did the evolution of diadromy drive phenotypic divergence among diadromous and nondiadromous lineages? Second, did diadromous lineages experience convergent evolution and evolve toward a single or multiple adaptive optima? And third, are there differences in rates of trait evolution among diadromous and nondiadromous lineages? Our study provides critical insight into how the evolution of diadromy can drive phenotypic evolution and influence rates of trait evolution across macroevolutionary scales.

Methods

Data Collection and Classification

We collected linear trait data from 392 museum specimens representing 151 (37%) of the approximately 415 described species of Clupeiformes (table S4; tables S1–S4 are available online). Our taxon sampling captured the majority of the morphological variation and biogeographical

distribution of the group. We included representatives of 9 of the 10 described families and 60 out of the 82 described genera, with missing species from the family Denticipitidae (one species), a family that does not contain diadromous species (Wang et al. 2022). Our dataset consisted of 17 ecomorphological traits collected from the left side of one to six adult specimens per species. Measurements were taken using digital calipers and recorded to the nearest 0.01 mm. The 17 traits (fig. 1) are commonly used in fish ecomorphology studies and included traits associated with diet, locomotion, and overall body shape (Watson and Balon 1984; Webb 1984; Winemiller 1991; Blake 2004; Wainwright et al. 2007; Langerhans and Reznick 2010; Fox and Bellwood 2013; Rojo et al. 2020). Traits associated with diet included head height, head length, gape vertical, gape horizontal, orbit diameter, snout length, and maxilla length. Traits associated with locomotion included body width, body depth, body position of maximum depth, caudal peduncle length, caudal peduncle width, pectoral fin length, dorsal fin base length, anal fin base length, and fineness ratio. Standard length was also measured, as body size has previously been demonstrated to covary with migration (Roff 1991; Bowlin et al. 2010; Bloom et al. 2018; Burns and Bloom 2020). We measured body position of maximum depth, a less common trait, because biomechanical theory proposes that a large anterior body depth reduces energy loss when a large amount of thrust is generated during prolonged swimming (Webb 1984; Blake 2004). Fineness ratio is used to describe the degree to which bodies are fusiform (Blake 2004; Ohlberger et al. 2006; Velotta et al. 2018) and was calculated by dividing standard length by body depth (Langerhans and Reznick 2010). A fusiform body shape maximizes body volume while simultaneously producing minimal drag; a fineness ratio of 4.5 is considered an optimal value for prolonged swimming performance (Langerhans and Reznick 2010). Fishes with fineness ratios lower than 4.5 have deep, robust body shapes that are associated with increased maneuverability in highly structured habitats. Taxa with fineness ratios above 4.5 have narrow and elongate body shapes optimized for maneuvering in waters with high velocities (Watson and Balon 1984; Medeiros and Ramos 2007; Langerhans and Reznick 2010). We averaged all trait values from multiple specimens per species (~2.59 specimens per species) to create one composite representative for each species (table S3). Averaged data were log transformed for downstream analyses except for fineness ratio, which we left as a raw ratio. Detailed descriptions of how each trait was measured can be found in table S4.

We size corrected all log-transformed linear traits using the *phyl.resid* function in the R package *phytools* (Revell 2009, 2012). This function uses a phylogenetic least squares regression, regresses each univariate trait against log standard

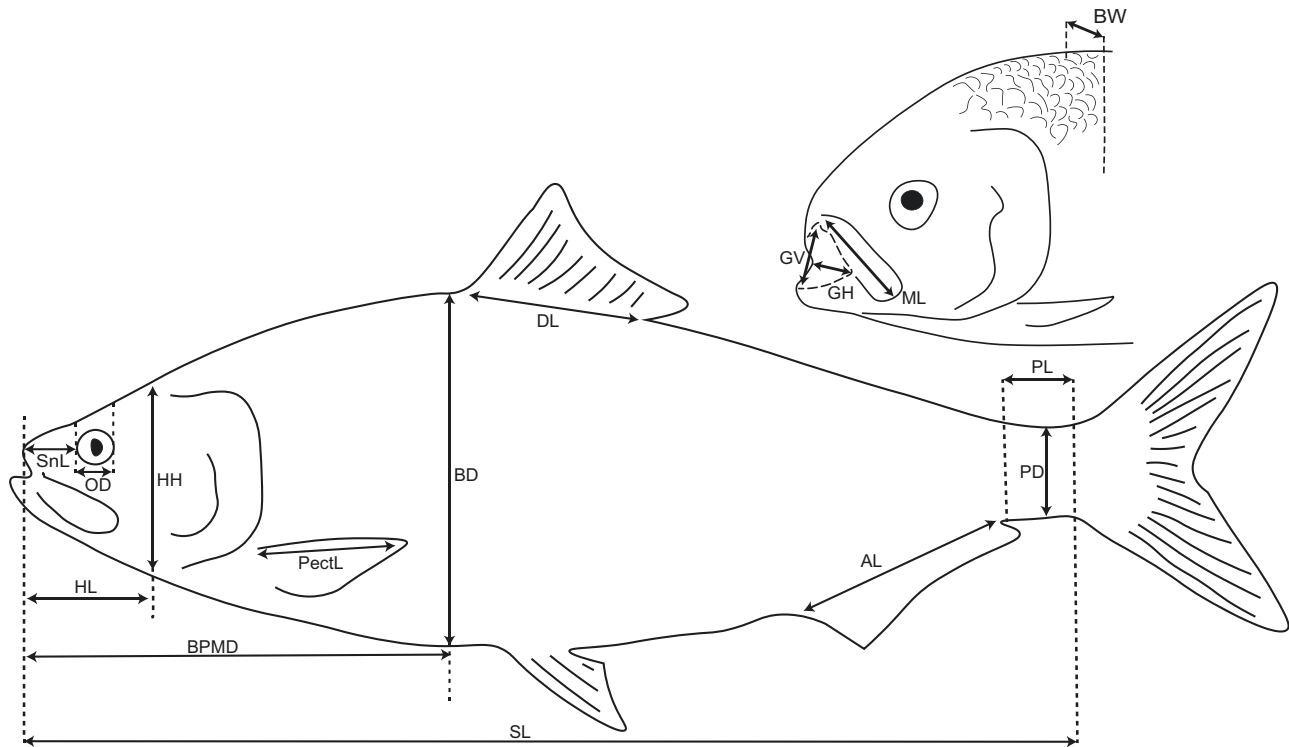


Figure 1: Illustration of 17 linear measurements: standard length (SL), head height (HL), head height (HH), orbit diameter (OD), pectoral fin length (PectL), body depth (BD), body position of maximum depth (BPMD), dorsal fin base length (DL), anal fin base length (AL), caudal peduncle length (PL), caudal peduncle depth (PD), body width (BW), gape vertical (GV), gape horizontal (GH), snout length (SnL), maxilla length (ML), and fineness ratio (FR). Detailed explanations of how each trait was measured can be found in table S4.

length, and recovers size-corrected residuals. However, the residuals themselves are not phylogenetically independent of one another (Revell 2009). Thus, we used the size-corrected residuals as species trait values in all downstream phylogenetic comparative methods.

Phylogeny and Ancestral State Reconstruction

For comparative methods, we used a previously published time-calibrated phylogeny of Clupeiformes (Egan et al. 2018). This phylogeny was constructed using four nuclear and two mitochondrial genes and is the most comprehensive phylogeny for this group to date, containing 67 of the 82 genera and about 47% of described clupeiform species (Egan et al. 2018). This phylogeny spans the majority of the morphological and ecological diversity within the clade, including marine, freshwater, and diadromous lineages and a variety of trophic guilds, such as zooplanktivores, crustaceans, and piscivores (Egan et al. 2018). We pruned the phylogeny to match our morphometric dataset using the *drop.tip* function in the R package *ape* (Paradis and Schliep 2019).

We created two datasets: (1) a dataset categorizing taxa as marine, freshwater, and diadromous (three-state dataset)

and (2) a dataset categorizing taxa as diadromous and non-diadromous (two-state dataset). Classifications of marine, freshwater, and diadromous species followed those of Bloom et al. (2018) with the following changes: *Pellonula leonensis* and *Pellonula vorax* were previously classified as diadromous, but there is no evidence these species enter marine habitats (Whitehead et al. 1988), and *Pellonula leonensis* has been recorded to spawn in freshwater habitats (Ezenwaji and Offiah 2003). We classified these two species as freshwater and nondiadromous in the present study. The two-state dataset included 17 diadromous taxa and 134 non-diadromous taxa, and the three-state dataset included 17 diadromous taxa, 98 marine taxa, and 36 freshwater taxa.

To trace the phylogenetic history of diadromy, we conducted ancestral state reconstruction using stochastic character mapping (Huelsenbeck et al. 2003; Bollback 2006) with the two-state dataset (diadromous and non-diadromous) and the *make.simmap* function in the R package *phytools* (Revell 2012). We fit two transition models, an equal-rates model that allows for equal transition rates between diadromous and nondiadromous character states, and an all-rates-different model that allows for different transition rates between the character states. We evaluated both transition models using the *ace* function in

the R package *ape* (Paradis and Schliep 2019). We used the *lr.test* function in the R package *extRemes* (Gilleland and Katz 2016) to conduct a likelihood ratio test and compare the two transitions models, which selected the equal-rates model as the best-fit model for our data. We simulated *make.simmap* 100 times using the equal-rates model to estimate the character states of the 100 trees in the posterior distribution to account for phylogenetic uncertainty.

Principal Component Analysis and Phylogenetic ANOVA-MANOVA

We performed a phylogenetic principal component analysis (pPCA), which computes PC axes while taking into account nonindependence due to shared ancestry; however, the PC scores may still be phylogenetically structured (Revell 2009). Using all 17 morphological traits, we computed the phylogenetic PC axes using the *phyl.pca* function in the R package *phytools* using the correlation matrix under a Brownian motion (BM) model (Revell 2009, 2012). We identified the number of significant PC axes using a broken-stick model and plotted PC axes to visualize whether diadromous lineages converged into similar regions of multivariate morphological space.

We used a phylogenetic ANOVA to test for differences among all 17 univariate trait values between diadromous and nondiadromous lineages using the two-state dataset. We used the *plotTree.wBars* function in the R package *phytools* (Revell 2012), which plots the phylogeny with trait values at the tips to visualize the pairwise comparisons of univariate traits that were reported to be significantly different between diadromous and nondiadromous taxa. To explore potential adaptive differences in phenotypic traits associated with function, we created three multivariate subsets, a subset including all traits associated with locomotion (locomotive subset), a subset including all traits associated with diet (diet subset), and a multivariate dataset including all 17 traits (all-traits dataset). We performed a phylogenetic MANOVA on all three multivariate datasets. We used the *procD.pgls* function in the R package *geomorph* (Collyer and Adams 2018; Adams et al. 2021; Baken et al. 2021; Collyer and Adams 2021) to run the phylogenetic ANOVA and phylogenetic MANOVA for 10,000 iterations across the pruned phylogeny. This function uses a phylogenetic least squares regression under a BM model of evolution to quantify differences in morphological variance between two or more groups. We chose to use the *procD.pgls* function in the R package *geomorph* because it uses a randomized residual permutation process to test for statistical significance, which has greater statistical power than nonpermutation methods (Adams and Collyer 2018).

Rates of Phenotypic Evolution

We tested for differences in rates of evolution using the three-state dataset, which comprises marine, freshwater, and diadromous taxa, to determine whether migrating between two habitats accelerated rates of trait evolution. We used the *compare.evol.rates* function in the R package *geomorph* (Collyer and Adams 2018; Adams et al. 2021; Baken et al. 2021; Collyer and Adams 2021) to estimate the rates of evolution across the branches of the phylogeny under a BM model. The analysis uses a Euclidean distance approach to estimate evolutionary rates among two or more predefined groups of species and generates a rate ratio describing differences in evolutionary rates among groups of interest. When three or more groups of species are defined, the rate ratio is comprised the group with the fastest rate to the group with the slowest rate, and this ratio is then used as a test statistic to determine significance (Adams 2014). Simulation is then used to infer whether the results deviate from a null hypothesis (Adams 2014). We estimated rates of phenotypic evolution across all univariate traits and the three multivariate datasets using the simulations method iterated 1,000 times across the pruned phylogeny.

Tests of Convergence in Morphospace

Convergence is often defined as the repeated evolution of similar phenotypes among distantly related lineages in response to shared selective pressures, a definition we follow herein (Meachen-Samuels 2012; Grossnickle et al. 2020). We tested for the presence of convergence in morphospace using *C* metrics in the R package *convevol* (Stayton 2015). This method uses a variety of ways to calculate whether the group of taxa hypothesized to be convergent are more similar to one another than their most recent common ancestor using phenotypic distances portrayed by a *phylomorphospace*. The group of taxa hypothesized to show convergence will now be referred to as the focal group. The C_1 metric is calculated by dividing the phenotypic distance between the phylogenetic tips in the focal group by the maximum distance between ancestral nodes of the focal group; this ratio is then subtracted by 1. The C_1 metric represents the proportion of phenotypic distance that has been closed due to convergence between the focal group and its most recent common ancestor (MRCA). The C_2 metric measures the magnitude of convergent evolution by subtracting the phenotypic distance between the phylogenetic tips in the focal group from the maximum phenotypic distance between the ancestral nodes in the focal group. C_3 and C_4 are scaled metrics of C_2 . C_3 is calculated by dividing C_2 by the sum of the branch lengths in the focal group,

and C_4 is calculated by dividing C_2 by the sum of the branch lengths in the whole clade. All resulting metrics range from 0 to 1, and larger values signify greater convergence. We calculated C_1 – C_4 values using a focal group consisting of all 17 diadromous taxa.

Visual inspection of the morphospace generated from our PCA suggested that most diadromous lineages clus-

tered into three regions of morphospace along PC1–PC2 (fig. 2). Therefore, we conducted three additional convervol analyses to statistically test whether diadromous lineages converged on multiple regions of morphospace using three focal groups corresponding to these three regions of morphospace. These three focal groups of diadromous taxa included (1) *Ethmalosa fimbriata*, *Tenualosa ilisha*, and *Hilsa*

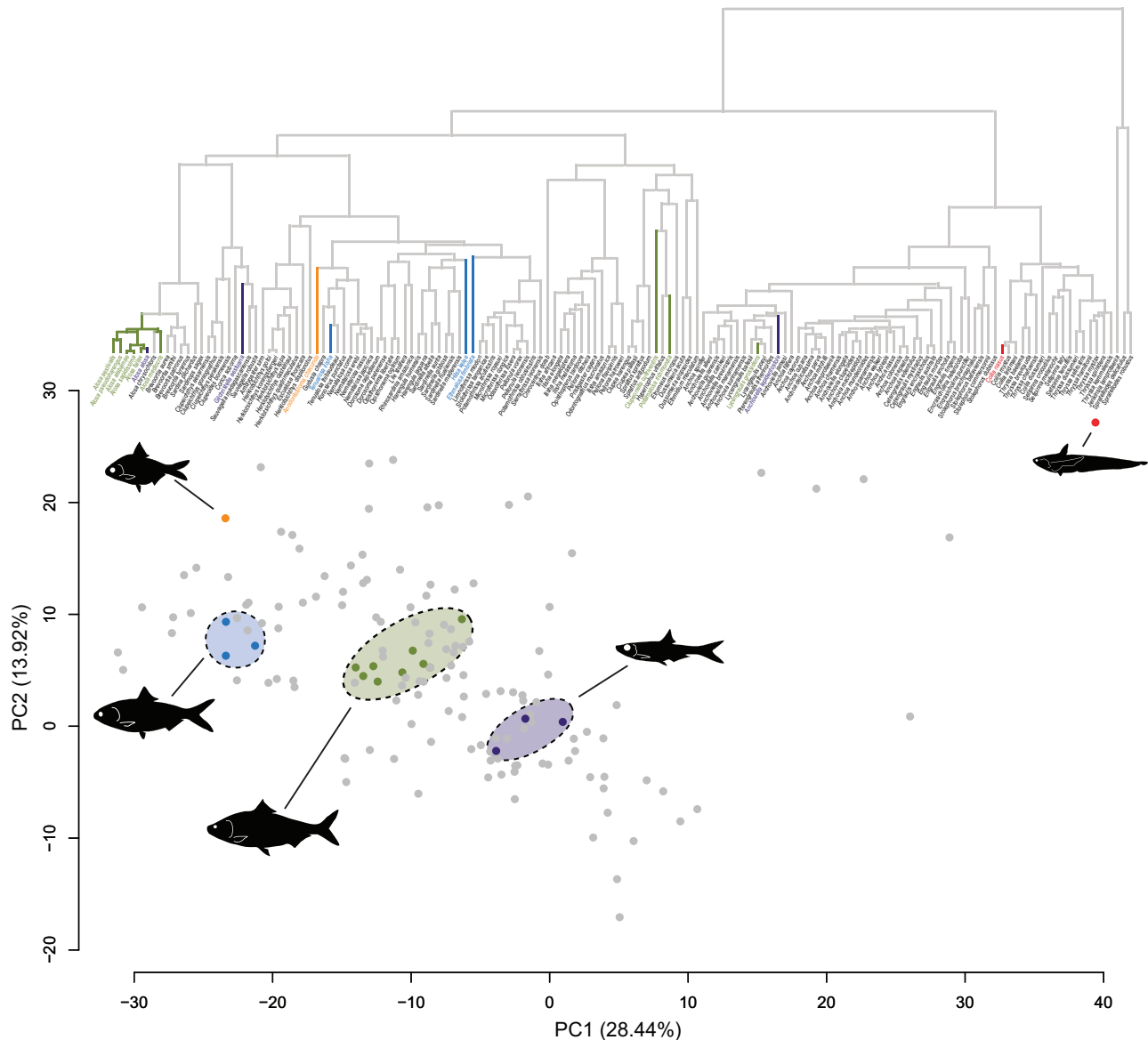


Figure 2: Clupeiformes phylogeny and phylogenetic principal component analysis results using PC1–PC2. Colors on the phylogeny match the colors of the corresponding diadromous lineages in trait space. All nondiadromous lineages are gray. Dashed and shaded-in ellipses represent the three regions of trait space that distantly related diadromous lineages converge into. The ellipses (listed from left to right) contain the following diadromous taxa: blue region—*Ethmalosa fimbriata*, *Tenualosa ilisha*, and *Hilsa kelee*; green region—*Alosa aestivalis*, *Alosa pseudoharengus*, *Alosa alabamiae*, *Alosa sapidissima*, *Alosa fallax*, *Alosa mediocris*, *Clupeonella cultriventris*, *Potamalosa richmondia*, and *Lycengraulis grossidens*; purple region—*Anchoviella lepidentostole*, *Gilchristella aestuaria*, and *Alosa alosa*. Diadromous lineage *Coilia nasus* is red, and diadromous taxa *Anodontostoma chacunda* is orange. The silhouettes, which illustrate the phenotype characteristic of each adaptive peak, represent diadromous species (listed from top left to right): *Anodontostoma chacunda*, *Hilsa kelee*, *Alosa sapidissima*, *Gilchristella aestuaria*, and *Coilia nasus*.

kelee; (2) *Alosa aestivalis*, *Alosa pseudoharengus*, *Alosa alabamiae*, *Alosa sapidissima*, *Alosa fallax*, *Alosa mediocris*, *Clupeonella cultriventris*, *Potamalosa richmondia*, and *Lycengraulis grossidens*; and (3) *Anchoviella lepidentostole*, *Gilchristella aestuaria*, and *Alosa alosa*. All C_1 – C_4 values were calculated using the `convrat` function (Stayton 2015). We used the `convratsig` function to test for significance of C_1 – C_4 values across 500 simulations in the R package `convevol` (Stayton 2015).

We quantified the strength of convergence in morphospace using the Wheatsheaf index. Unlike the C metrics, the Wheatsheaf index analysis requires the investigator to verify that convergence is present within the focal group using a prior analysis (i.e., `convevol`). Once convergence among the focal group is detected, the Wheatsheaf index is then used to quantify the strength of convergence by dividing the mean of the phenotypic pairwise comparisons between all species in the phylogeny by the mean of the phenotypic pairwise comparisons between the taxa in the focal group, all while penalizing the species trait values for phylogenetic relatedness (Arbuckle et al. 2014). The more clustered the focal group is and the more isolated the focal group is from the nonfocal group, the stronger the convergence. The Wheatsheaf index was then evaluated for significance by generating a P value using a bootstrapping approach explained in Arbuckle et al. (2014). The P value does not represent the presence of convergence because the Wheatsheaf index is calculated under the assumption that convergence has previously been detected in the focal group by a prior analysis. Instead, the P value tests whether convergence among the focal group is significantly stronger than what would be expected when compared with a random distribution of species trait values across a given phylogeny (Arbuckle et al. 2014). We calculated the Wheatsheaf index four times, once for each of the focal groups used in the `convevol` analysis. The larger the Wheatsheaf index values, the greater the strength of convergence. We used the `windex` and `test.windex` functions from the R package `windex` to calculate the Wheatsheaf index and assess the significance of this metric (Arbuckle and Minter 2015). The Wheatsheaf index and C_1 – C_4 metrics were calculated using our morphological dataset of 15 size-corrected traits, log standard length, and fineness ratio.

Macroevolutionary Model Fitting of Univariate Traits

We used a model-fitting framework to test whether diadromous and nondiadromous lineages are evolving toward two separate adaptive peaks in univariate trait space using the R package `OUwie` (Beaulieu et al. 2012; Beaulieu and O'Meara 2015). Given the abundance of ecomorphological traits used in this study and the rigorous computational

demands of `OUwie`, we restricted this analysis to the univariate traits that showed significantly different rates of evolution between diadromous and nondiadromous lineages under a BM framework (see “Rates of Phenotypic Evolution”). Univariate traits that showed significantly different rates of evolution between diadromous and nondiadromous lineages and used in `OUwie` analyses were standard length, head height, fineness ratio, caudal peduncle length, caudal peduncle length, and body depth.

We fit seven evolutionary models to 100 SIMMAP reconstructions that were produced from ancestral state reconstruction across all 100 trees to account for phylogenetic uncertainty. We tested two BM models, which assume that morphological variance accumulates randomly and proportionally to time. The BM1 model assumes that diadromous and nondiadromous lineages are evolving at the same stochastic rate of evolution (σ), and the BMS model assumes that two life histories are accumulating morphological variance at different evolutionary rates. We tested five Ornstein-Uhlenbeck (OU) models, which included two additional parameters: trait optima (θ) and the strength of selection (α ; measures pull toward the trait optima). The simplest OU model is a single-peak model (OU1), which assumes that diadromous and nondiadromous lineages share the same trait optima and evolutionary rate. We fit four multipeak OU models. The simplest was the OUM model, which assumes that diadromous and nondiadromous lineages are evolving toward different trait optima under the same evolutionary rate and strength of selection. The OUMV model assumes that diadromous and nondiadromous lineages are evolving at different rates of evolution toward separate trait optima, whereas the OUMA model tests for differences in the strength of selection and trait optima but assumes that the two life histories are evolving under the same evolutionary rate. Last, the OUMVA model assumes that diadromous and nondiadromous lineages differ in the rate of evolution, trait optima, and strength of selection. If our hypothesis is correct and diadromy is a strong selective force that drives convergent evolution due to the large energetic demands associated with this life history, then we would predict that one of the multipeak OU models (OUM, OUMA, OUMV, OUMVA) would be recovered as the best-fit model, rather than the single-peak OU model.

We identified the best-fit model using the Akaike information criterion for small samples (AICc). We averaged all AICc values for each model per trait and used the `aicw` function in the R package `gieger` (Harmon et al. 2008) to calculate the AICc weights (AICw) and the Δ AICc to measure the strength of support for each model. We recovered the best-fit model as the model with the lowest AICc score and greatest AICw. Prior to recovering the best-fit model, we removed all model fits that returned negative

eigenvalues, which suggests that the model did not accurately converge on reliable parameters (Beaulieu et al. 2012). Positive eigenvalues are considered reliable and were retained for assessing model fit.

Because of the limited number of independent origins of diadromy within the phylogeny and the capability of OUwie to favor overly complex models, we used OUwie.sim to evaluate whether we had significant power to accurately distinguish the simpler BM models from the complex OU models (Boettiger et al. 2012; Ho and Ané 2014). We simulated 1,000 datasets for each of the seven models per trait using the recovered model parameters from the empirical analyses. These simulated datasets were then run through all seven models in OUwie to determine whether the simulated model could be recovered.

Non-A Priori Tests of Convergence

We tested whether diadromous lineages evolved toward a single or multiple adaptive peaks without a predefined life history classification using the R package l1ou (Khabbazian et al. 2016). This analysis locates and evaluates the position and magnitude of phenotypic shifts along the branches of the phylogeny using LASSO (least absolute shrinkage and selection operator method; Tibshirani 1996; Tibshirani and Taylor 2011). The estimated phenotypic shifts were evaluated using both AICc and the phylogenetically aware Bayesian information criterion (pBIC). Using simulations, Khabbazian et al. (2016) found that AICc model selection criterion identified many true adaptive shifts but suffered from model overfitting and detected many false-positive shifts as well, whereas pBIC is more conservative and found fewer true adaptive shifts but did not detect false positives. The estimated shifts were then evaluated under an OU model using both AICc and pBIC model selection criteria (Khabbazian et al. 2016). Given the abundance of ecomorphological traits included in this study, we restricted our l1ou analysis to univariate traits that showed significant differences in the rate of evolution between diadromous and nondiadromous lineages: standard length, head height, body depth, fineness ratio, caudal peduncle length, and caudal peduncle depth.

Results

Ancestral State Reconstruction

Our ancestral state reconstruction showed that the root state of Clupeiformes is nondiadromous, and across all 100 simulations it detected, on average, 13.59 transitions between diadromy and nondiadromy. On average, transitions from a nondiadromous to a diadromous life history occurred 11.73 times and transitions from diadromous to nondiadromous life history occurred 1.86 times, indicat-

ing that reversals to a nondiadromous life history are relatively rare.

Phylogenetic Principal Component Analysis

Our broken-stick analysis of the pPCA reported four significant PC axes, which cumulatively represented 60.55% of the morphological variance in Clupeiformes. PC1 represented 28.44% of the morphological variation, and traits that loaded heavily included head height, caudal peduncle depth, and dorsal fin base length (fig. 2; table 1). Taxa with a deep head, deep caudal peduncle, and a long dorsal fin base length loaded heavily on the negative end of PC1, and species with a narrow head, narrow caudal peduncle depth, and short dorsal fin base length occupied the positive end of PC1. PC2 captured 13.92% of the morphological disparity and was predominantly driven by fineness ratio (fig. 2). The fineness ratio of diadromous taxon ranged from 2.17–6.36, with an average of 3.80. The fineness ratio of nondiadromous taxon ranged from 1.76–7.22, with an average of 4.15. Additionally, body depth and peduncle length loaded heavily on PC2 (table 1). Species with a deep body depth, short caudal peduncle length, and a large fineness ratio (>4.5) occupied the positive end of PC2, and species with an elongated caudal peduncle and a streamlined body shape occupied the negative end of PC2.

Table 1: Loadings of the phylogenetic principal component analysis (PCA)

Ecomorphological trait	PC1	PC2	PC3	PC4
Log standard length	-.016	.051	-.007	.040
Head length	-.094	-.117	-.221	-.538
Head height	-.371	.134	-.020	.144
Gape vertical	-.224	-.284	.353	.167
Gape horizontal	-.229	-.245	.311	.016
Orbit diameter	-.265	-.267	-.048	-.330
Snout length	-.184	-.347	.294	.012
Maxilla length	-.196	-.126	.116	-.274
Body depth	-.349	.378	-.028	.062
Body width	-.257	-.149	-.247	-.132
Body position of				
maximum depth	-.233	-.090	.229	.291
Caudal peduncle depth	-.303	.196	-.227	.142
Caudal peduncle length	-.162	-.322	-.301	.439
Pectoral fin length	-.212	.116	.179	-.373
Dorsal fin base length	-.289	-.046	-.334	-.047
Anal fin base length	-.044	.370	.475	-.101
Fineness ratio	.342	-.386	.031	-.062
% variance explained	28.44	13.92	10.68	7.51

Note: Shown are loadings of the first four PC axes. The PCA was analyzed using 16 linear traits and the fineness ratio.

We used the pPCA to visually explore whether diadromous lineages occupy similar regions of multivariate trait space. Figure 2 suggests that distantly related diadromous lineages clustered into three distinct regions of trait space comprising unique trait combinations with the exception of diadromous lineages, *Coilia nasus* and *Anodontostoma chacunda*. One region of morphospace loaded heavily on the negative end of PC1 and the positive end of PC2, and it included the diadromous species *Ethmalosa fimbriata*, *Tenualosa ilisha*, and *Hilsa kelee*, which have deep heads, deep robust body shapes, and deep caudal peduncles. The second region of morphospace is shared among the diadromous species *Anchoviella lepidostole*, *Gilchristella aestuaria*, and *Alosa alosa*, which have elongate bodies and long caudal peduncles. The third region of morphospace is the most speciose and included all members of *Alosa* (except diadromous *Alosa alosa* and nondiadromous *Alosa chrysochloris*), *Potamalosa richmondia*, *Lycengraulis grossidens*, and *Clupeonella cultriventris*. This region of morphospace contains taxa that have fusiform bodies, which are hypothesized to be favored for long-distance migration. Despite being sister taxa, diadromous species *Alosa fallax* and *Alosa alosa* occupy different regions of morphospace along PC2, which was predominately influenced by the fineness ratio. *Alosa alosa* has a fineness ratio of 4.85, whereas all other *Alosa* species have a fineness ratio between 3.20 and 3.76. Diadromous taxa *Coilia nasus* and *Anodontostoma chacunda* occupy unique regions along PC1 and PC2. The rat-tail anchovies (genus: *Coilia*) have all evolved very elongated bodies and anal fins, and *Anodontostoma chacunda* has evolved a very deep body compared with most diadromous Clupeiformes.

Gape vertical, gape horizontal, and anal fin base length dominated PC3, which represented 10.68% of the morphological variation (fig. S1; figs. S1–S15 are available online). Species with large gapes and a long anal fin base length occupied the positive end of PC3, and species with smaller gapes and shorter anal fin base lengths were on the negative side of PC3. PC4 described 7.51% of the variation and was predominately driven by head length.

Phylogenetic ANOVA and Phylogenetic MANOVA

Our phylogenetic ANOVA results showed that diadromous and nondiadromous lineages significantly differed in two traits: caudal peduncle length ($F = 5.09$, $df = 150$, $P = .029$) and head height ($F = 3.98$, $df = 150$, $P = .05$; table 2). Our bar plots showed that most diadromous lineages had a larger head height and shorter caudal peduncle length than their nondiadromous sister taxa (figs. S2, S3). Our phylogenetic MANOVA showed no significant differences between diadromous and nondiadromous lineages

Table 2: Results from our phylogenetic ANOVA (univariate traits) and phylogenetic MANOVA (locomotion subset, diet subset, and all-traits datasets)

Ecomorphological trait	<i>F</i>	<i>Z</i>	<i>R</i> ²	<i>P</i>
Log standard length	1.08	.64	.00718	.27
Head length	.49	.08	.00329	.48
Head height*	3.98	1.59	.02599	.05
Gape vertical	.32	-.15	.00215	.57
Gape horizontal	.77	.38	.00516	.36
Orbit diameter	1.56	.89	.01036	.11
Snout length	1.73	.94	.01149	.18
Maxilla length	.03	-1.05	.00022	.84
Body depth	.09	-.73	.00062	.76
Body width	.27	-.22	.00183	.59
Body position of				
maximum depth	2.34	1.16	.015	.13
Caudal peduncle depth	.02	-1.31	.00011	.90
Caudal peduncle length*	5.10	1.82	.033	.03
Pectoral fin length	1.43	.79	.00951	.22
Dorsal fin base length	.29	-.15	.00196	.57
Anal fin base length	.10	-.72	.00065	.75
Fineness ratio	.27	-.24	.00178	.6
Locomotion subset	.38	-.15	.00254	.56
Diet subset	.94	.23	.00629	.40
All traits	.48	-.21	.0032	.57

Note: An asterisk indicates traits that were found to significantly differ between diadromous and nondiadromous lineages ($P < .05$).

using the locomotive subset, diet subset, and the all-traits dataset (table 2). Our morphospace shows that *Coilia nasus*, a diadromous lineage, has an extremely elongate body and lies well outside the morphospace of other Clupeiformes. To explore whether *Coilia nasus* drove the results of the phylogenetic ANOVA, we removed the entire genus from our dataset and reran the analysis. After the removal of the genus *Coilia*, caudal peduncle length ($F = 1.332$, $df = 146$, $P = .709$) and head height ($F = 0.44$, $df = 146$, $P = .50$) were no longer significantly different between diadromous and nondiadromous species (table S1). However, we note that our bar plots showed that most of the diadromous lineages had a shorter caudal peduncle length and larger head height than their nondiadromous sister taxa, a pattern that was also found between *Coilia nasus* and its nondiadromous sister taxon *Coilia mystus*. Additionally, the removal of *Coilia nasus* reduced the spread of diadromous taxa along the phylogeny. Adams and Collyer (2018) found that strong group aggregation can reduce statistical power in comparative methods, which may lead to incorrect biological interpretation. Although *Coilia* is morphologically divergent from most other diadromous and nondiadromous Clupeiformes, our comparisons include nondiadromous species of *Coilia*. Thus, we chose to discuss the results of the phylogenetic ANOVA that

includes the genus *Coilia*, but the major conclusions of this study do not rely on this analysis alone.

Rates of Evolution

We used the three-state dataset that includes diadromous, marine, and freshwater classifications to analyze rates of trait evolution of each univariate trait and the three multivariate datasets: the locomotor subset, the diet subset, and the all-traits dataset. Using the all-traits dataset, we found that diadromous lineages are evolving three times faster than freshwater lineages and two times faster than marine lineages ($Z = 6.56$, $P = .001$; fig. 3). Our analysis recovered six univariate traits that are evolving significantly faster

in diadromous lineages than marine and freshwater lineages: standard length ($Z = 4.3$, $P = .001$), head height ($Z = 2.41$, $P = .01$), body depth ($Z = 1.68$, $P = .045$), caudal peduncle depth ($Z = 2.37$, $P = .01$), caudal peduncle length ($Z = 2.59$, $P = .008$), and fineness ratio ($Z = 2.21$, $P = .014$; fig. 3). We found that the standard length of diadromous fishes is evolving six times faster than freshwater taxa and 10 times faster than marine taxa ($Z = 4.3$, $P = .001$). All univariate traits that displayed significantly faster rates of evolution in diadromous lineages have been associated with fish locomotion by previous studies, with the exception of head height. Diadromous lineages show significantly faster rates of locomotor evolution than marine and freshwater taxa ($Z = 5.75$, $P = .001$)

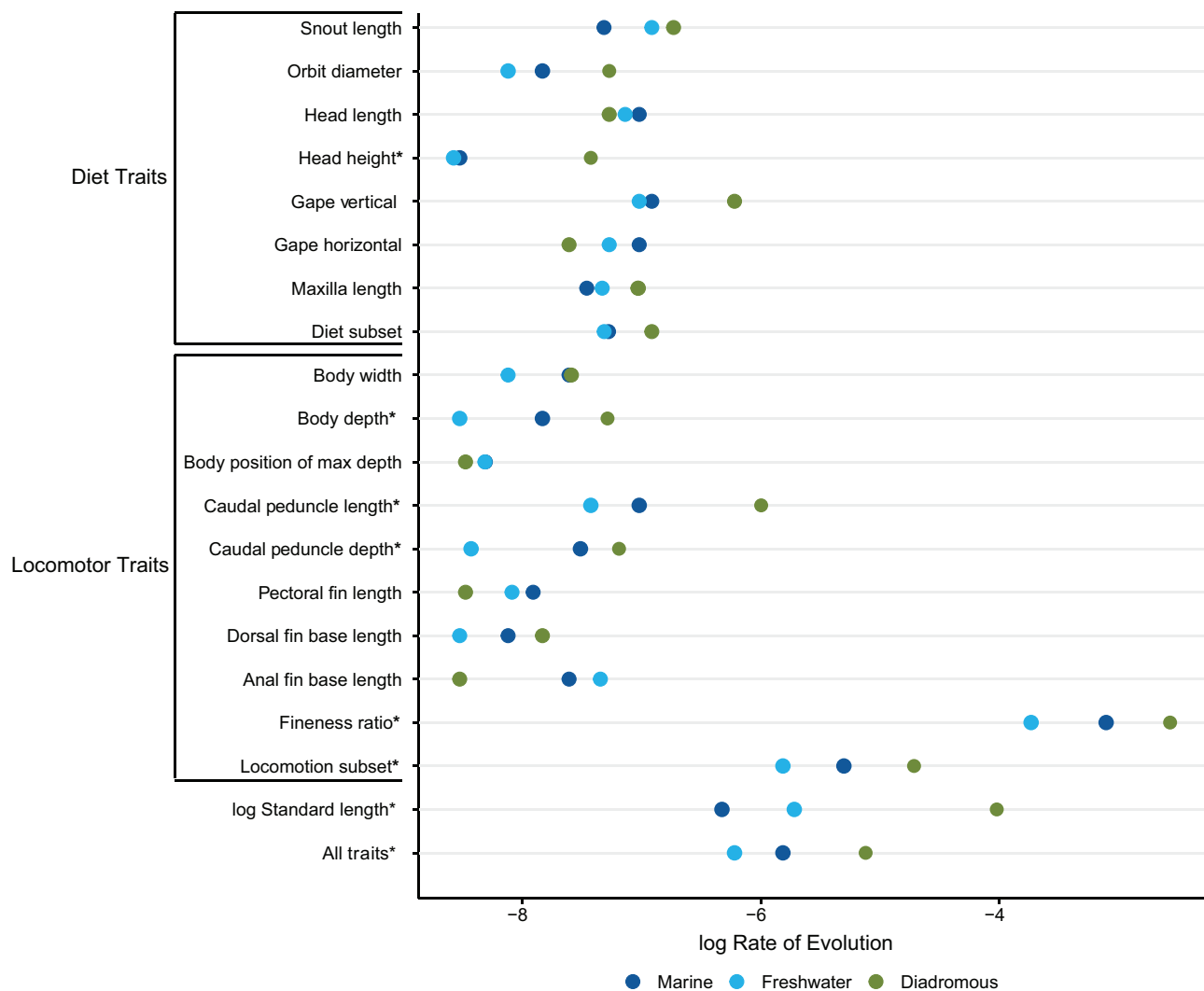


Figure 3: Log-transformed rates from our geomorph compare.evo.rates analysis (raw rates can be found in table S2). Rates of trait evolution were calculated for log standard length, fineness ratio, 15 size-corrected univariate traits, and three multivariate datasets. Traits that differed significantly in the rate of evolution between the three-character states ($P < .05$) have an asterisk.

but did not show faster rates of evolution in the diet subset ($Z = 1.45$, $P = .07$; fig. 3). The locomotor morphology of diadromous lineages is evolving roughly two times faster than marine taxa and three times faster than freshwater taxa. Head height was the only diet-associated trait that exhibited significantly faster rates of evolution in diadromous taxa than in marine and freshwater taxa.

Presence and Strength of Convergence in Trait Space

Our convervol results showed that all diadromous species significantly converged in morphospace (table 3). The C_1 value recovered was 0.268, indicating that evolution has closed 26.80% of the phenotypic distance between diadromous taxa and their MRCA. However, we also found stronger evidence for morphological convergence in three different regions of morphospace, indicating that diadromous taxa are being pulled toward three different estimated phenotypic optima (fig. 2; table 3). Distantly related diadromous lineages that converged into similar regions of morphospace show that evolution has closed 59.30% ($P < .001$), 41.60% ($P < .001$), and 60.50% ($P < .001$) of the phenotypic distance between the groups of diadromous taxa and their MRCA (table 3). We acknowledge the bias of post hoc analysis of taxa in similar regions of trait space. However, the diadromous taxa in the three hypothesized adaptive peaks are phylogenetically and geographically distinct and may have converged in similar regions of trait space due to shared selective pressures associated with different migration distances. Furthermore, we feel that an iterative approach to phylogenetic comparative methods that allows for exploring data is warranted (Pennell and Harmon 2013).

Our Wheatsheaf index shows that diadromous taxa show stronger convergence into three regions of trait space rather than just one (table 3). All w values were larger for each of the three clusters of diadromous taxa in our morphospace than for the focal group that included all 17 diadromous taxa. However, only the focal group that

included *Potamalosa richmondia*, *Lycengraulis grossidens*, *Clupeonella cultriventris*, and all diadromous *Alosa* species (except *Alosa alosa*) showed significantly strong convergence ($P < .05$).

Univariate Trait Convergence on Adaptive Optima

We ran OUwie on six univariate traits that showed significant differences in the rate of evolution among diadromous and nondiadromous lineages (see “Rates of Evolution”). Our OUwie results recovered the OUMA model as the best-supported model for five of the six univariate traits: standard length, head height, body depth, caudal peduncle length, and caudal peduncle depth (fig. 4; table S3). However, since the AICc values for OUMA, OUMV, and OUMVA were within 2 AICc of each other, we considered these models to be equally supported. Thus, our results show that diadromous and nondiadromous lineages are evolving toward different adaptive optima (θ ; fig. 4) in these five traits, but we cannot reliably distinguish whether diadromous lineages are being pulled toward these optima faster than nondiadromous taxa (σ), with a greater strength of selection (α), or under both processes simultaneously. No other models were closely supported, and all BM models were 20 or more AICc values away from the more complex OU models (table S3). However, the recovered θ parameter estimates for caudal peduncle length were unreliable and did not converge; thus, we excluded this result from the discussion.

The OUwie analysis recovered the simplest OU model (OU1) as the favored model for the fineness ratio, a model that supports that diadromous and nondiadromous lineages are evolving toward the same phenotypic optima at the same stochastic rate of variance (table S3). Fineness ratio was a metric we used to quantify body shape, which implies that evolving a diadromous life history does not drive selection for an optimal body shape. Although the OU1 model was the most supported, the AICc values for the remaining four OU models were within 2 values

Table 3: Results from our convervol (C_{1-4}) and Wheatsheaf index (w) analyses

Convergent taxa (focal group)	C_1	C_2	C_3	C_4	w
All diadromous taxa	.268*	.434*	.123	.003	1.12
<i>Ethmalosa fimbriata</i> , <i>Tenuulosa ilisha</i> , and <i>Hilsa kelee</i>	.593*	.528*	.277*	.004	2.24
<i>Alosa aestivalis</i> , <i>Alosa pseudoharengus</i> , <i>Alosa alabamiae</i> , <i>Alosa sapidissima</i> , <i>Alosa fallax</i> , <i>Alosa mediocris</i> , <i>Clupeonella cultriventris</i> , <i>Potamalosa</i> <i>richmondia</i> , and <i>Lycengraulis grossidens</i>	.416*	.536*	.174*	.004	1.27*
<i>Anchoviella lepidentostole</i> , <i>Gilchristella aestuaria</i> , and <i>Alosa alosa</i>	.605*	1.19*	.279*	.01*	1.67

Note: Convergence scores (C_{1-4}) and the Wheatsheaf index (w) were calculated for all diadromous taxa using the morphological dataset comprising log standard length, 15 size-corrected traits, and the fineness ratio. Convergence scores and the Wheatsheaf index were also calculated for three additional focal groups comprising diadromous taxa that showed convergence in three regions of trait space (fig. 2). C scores measure the presence of convergence in trait space, and the Wheatsheaf index measures the strength of convergence. C scores with an asterisk indicate significant convergence in morphospace, and Wheatsheaf index results with an asterisk indicate significantly strong convergence in morphospace ($P < .05$).

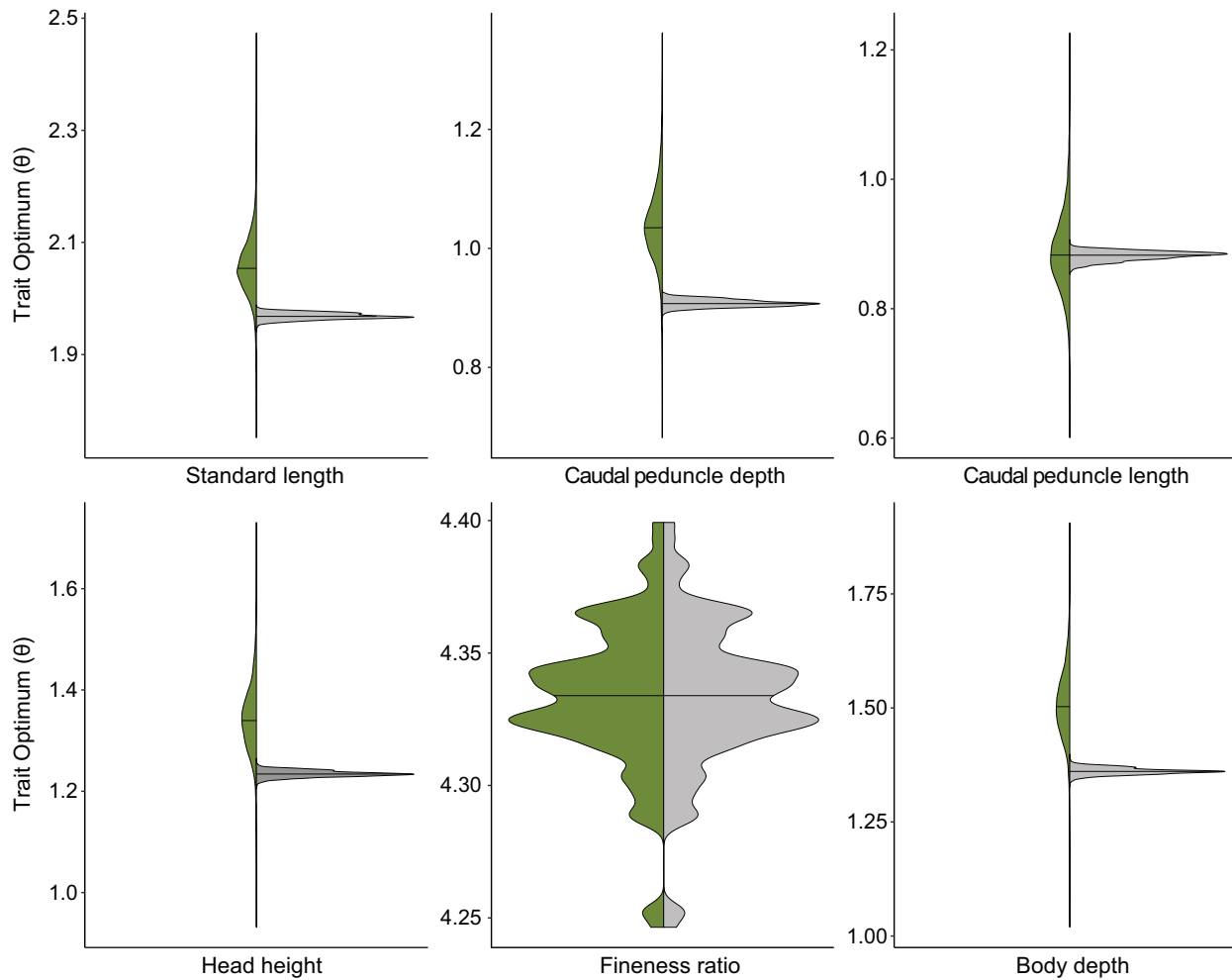


Figure 4: Recovered distribution of θ parameter estimates for diadromous (green) and nondiadromous (gray) lineages from the OUwie analysis. We ran OUwie across 100 SIMMAP reconstructions for each of the 100 phylogenetic trees in the posterior distribution. The x-axis represents the univariate trait, and the y-axis represents the distribution of phenotypic optima (θ) recovered under the best-supporting model for that trait. The favored model for standard length, caudal peduncle depth, caudal peduncle length, head height, and body depth was OUMA, a model that supported different θ and different strength of selection (α) between diadromous and nondiadromous lineages. The favored model for fineness ratio was OU1, a model that supported a the same θ and the same rate of variance (σ) between diadromous and nondiadromous lineages. Larger θ values represent larger trait values, and smaller θ values represent smaller trait values. Black horizontal lines in the distributions represent the median values.

of one another, which suggests that all OU models were equally supported. However, the OU1 model was selected as the favored model 86% of the time, whereas the remaining OU models received support 6% or less of the time.

Our simulation results showed that we have enough statistical power to distinguish between the simple BM models and the complex OU models for each of the six univariate traits, demonstrating that our empirical analyses were not subject to model overfitting (figs. S4–S9). The BM1 and BMS models were recovered as the best-fit models more than 65% of the time during their respective simulations, but the BM1 and BMS models were found to be equally

supported for each univariate trait. Our multipeak OU simulations did not always recover their respective model as the best fit and instead found equal support for the OUMA, OUMV and OUMVA models. This discrepancy could be because most of the univariate traits in our empirical analyses found equal support for multiple complex OU models and is driving our simulations to recover similar results. This implies that we have enough power to demonstrate that diadromous and nondiadromous lineages are evolving toward different adaptive peaks (θ) for all traits besides caudal peduncle length and the fineness ratio, but we cannot reliably distinguish different α and σ parameter estimates

for any of the six univariate traits that favored a multipeak model.

Our I1ou analysis on the six univariate traits recovered numerous adaptive shifts and converged on multiple different adaptive optima. Because of the high number of shifts present across the phylogeny for each univariate trait, these results will not be explained in detail but can be visualized in the supplemental PDF (figs. S10–S14). Using the AICc model selection criterion, our analysis recovered 14 or more adaptive shifts among each univariate trait, which converged on a range of seven to nine adaptive optima. These adaptive shifts occurred across the phylogeny; some shifts occurred very early in the lineage's history, other shifts occurred in more recent clades (e.g., *Coilia*), and some adaptive shifts were specific to a single taxon. Many distantly related diadromous lineages experienced shifts in mean trait values and converged on the same phenotypic optima. However, these adaptive optima also included many nondiadromous lineages, which suggest that the recovered adaptive shifts are not due to the evolution of a diadromous life history. In addition, univariate traits, including peduncle length, the fineness ratio, body depth, and head height, show strong phylogenetic signal, and shifts that occurred early in the lineages history were maintained at the family level.

Our results using the pBIC model selection criterion were more conservative and on average detected two adaptive shifts within each univariate trait and converged onto an average of two phenotypic optima. Body depth and fineness ratio experienced no adaptive shifts using pBIC model selection. The detected adaptive shifts did not occur on or include diadromous lineages apart from diadromous taxa, *Coilia nasus*, which showed a reduction in caudal peduncle length relative to its nondiadromous sister taxon (fig. S11). We suspect that the absence of adaptive shifts recovered in relation to a diadromous life history is due to the lack of power to detect deviations in mean trait values between the numerous singleton diadromous lineages and their nondiadromous sister taxa.

Discussion

Diadromy is an extreme type of migration that often involves traversing vast distances and requires high energetic demands (Myers 1949; McDowall 2008). As a result, diadromous fishes may experience selection for morphological adaptations that optimize swimming efficiency. Our study shows that evolving a diadromous life history drives ecomorphological convergence of locomotor traits and faster rates of trait evolution than marine and freshwater lineages. However, not all functional traits showed predictable responses. Traits associated with foraging showed no adaptive response to a diadromous life history,

and the body shapes of diadromous lineages are highly variable. We also found evidence that diadromous lineages show convergence into multiple regions of trait space, which may be explained by differences in migration distance and other aspects of their ecology. Our study demonstrates that migration between rivers and oceans can influence the pattern and tempo of locomotor evolution, but there is not a single diadromous syndrome.

Ecomorphological Convergence of Locomotor Traits in Diadromous Lineages

We found that diadromous lineages show convergence in multivariate trait space (table 3) and on some, but not all, univariate locomotor traits (fig. 4). The locomotor performance of fishes is a primary axis of morphological (Dornburg et al. 2011; Astudillo-Clavijo et al. 2015; Nations et al. 2020; Friedman et al. 2021) and physiological (Lee et al. 2003; Dalziel et al. 2012; Eliason and Farrell 2016; Norin and Clark 2016) trait evolution because fishes rely on locomotor performance to forage, reproduce, escape predation, and migrate (Garland et al. 2017). Our OUwie analyses estimated similar adaptive optima (θ) in diadromous lineages of four locomotor traits, and these four traits also loaded heavily on PC1–PC2 (table 1). Compared with nondiadromous lineages, diadromous lineages have evolved larger body sizes and deeper bodies, heads, and caudal peduncles (fig. 4). Theoretical and empirical studies have shown that a larger body size, a slim caudal peduncle, and small anterior body allocation decreases locomotive costs by providing greater energy storage and generating larger water displacements while producing minimal drag during prolonged swimming (Webb 1984; Blake 2004; Langerhans and Reznick 2010).

While our body size results corroborate previous studies (Bloom et al. 2018; Burns and Bloom 2020) and are consistent with biomechanical theory for prolonged swimming performances (i.e., migration; Roff 1991), the deeper caudal peduncle depth and head height of diadromous versus nondiadromous lineages do not. These latter traits are typically associated with unsteady swimming modes (fast-start and burst-and-coast swimming), a type of locomotion not often associated with long-distance migrators (Langerhans and Reznick 2010). However, diadromous fishes may use burst swimming to surpass fast-flowing rapids and fallen structures and to access holding positions at river mouths to acclimate to decreases in salinity levels (Dodson et al. 1972; Groot et al. 1975; Brett 1995; Bernatchez and Dodson 1987; Drucker and Lauder 2003). Furthermore, the phenotypic traits examined may evolve in concert with the physiological demands of migration. For instance, metabolic rates scale positively with body size (Norin and Clark 2016), and fishes that inhabit hypoxic conditions have

repeatedly evolved larger heads and larger gills to increase oxygen uptake (Tobler et al. 2011). Thus, while head size is not typically associated with locomotion, diadromy may select for a larger head size to allow for increased oxygen uptake.

Some of the phenotypic patterns we discussed above are consistent with trait patterns detected in intraspecific studies. Anadromous populations of alewives (*Alosa pseudoharengus*; Palkovacs et al. 2008; Jones et al. 2013; Smith et al. 2020), threespine sticklebacks (*Gasterosteus aculeatus*; Taylor and McPhail 1986; Dalziel et al. 2012; Østbye et al. 2016), *Galaxias maculatus* (Rojo et al. 2020), and chum salmon (*Oncorhynchus keta*; Beacham 1984) generally have larger body sizes, deeper heads, and deeper body depths than conspecific populations. Moreover, anadromous populations have repeatedly been shown to have greater swimming performances (fatigue less quickly and have greater metabolic rates) than resident populations, which is likely in response to relaxed selection on the locomotor performance of resident populations (Taylor and McPhail 1986; Dalziel et al. 2012; Velotta et al. 2018). Diadromous fishes that undergo more strenuous migrations (longer migrations, higher elevation changes, faster water flows) have greater swimming performance and show higher metabolic rates than populations that make less vigorous migrations (Lee et al. 2003; Dalziel et al. 2012). The consistency of these phenotypic patterns recovered at intraspecific and macroevolutionary scales suggests that selection may be acting on locomotory traits in diadromous fishes.

Incomplete Convergence of Diadromous Lineages in Multivariate Trait Space

While our model-fitting and evolutionary rate results suggest that some univariate locomotor traits in diadromous lineages exhibit convergence toward a single adaptive peak, our multivariate pattern-based convergence metrics (convevol and Wheatsheaf index) suggest a narrative of incomplete convergence among diadromous lineages in trait space. Using an iterative exploratory approach, we find evidence that distantly related diadromous lineages show morphological convergence into multiple regions of trait space (fig. 2; table 3). We propose that the different regions of trait space occupied by diadromous lineages may be explained by differences in migration ecology. For example, although all diadromous lineages move between rivers and oceans, diadromous species exhibit high variability in migration distance, habitat associations, and trophic ecology. This variability increases the spread of diadromous lineages across trait space, resulting in multiple respective regions of trait space shared by diadromous taxa that have independently evolved similar migration strategies. Below

we discuss how these differences in migration and trophic ecology may influence trait evolution and result in incomplete convergence among diadromous lineages in multivariate trait space.

Migration distance has been linked to patterns of phenotypic evolution in populations of migratory birds (Fiedler 2005) and fishes (Schaffer and Elson 1975; Hess et al. 2014). Diadromous Clupeiformes have migration distances ranging from a few to more than 1,000 km. Figure 2 shows that distantly related diadromous taxa *Lycengraulis grossidens*, *Clupeonella cultriventris*, *Potamalosa richmondia*, and several *Alosa* spp. cluster in trait space, and our pattern-based convergence metrics detected strong convergent evolution among these lineages (table 3). Each of these lineages have evolved a similar fusiform body shape (fig. 2, green region), and *Alosa* spp. have some of the largest body sizes in clupeiforms (Bloom et al. 2018), both traits known to decrease locomotor costs (Webb 1984; Langerhans and Reznick 2010). The evolution of highly energetically efficient body shapes in these lineages may be due to the extreme distances these convergent species migrate. These lineages complete the longest migrations of all diadromous clupeiforms and exceed migration distances of more than 1,000 km into freshwater rivers (Bernatchez and Dodson 1987; Aprahamian et al. 2003; Limburg et al. 2003; Mai and Vieira 2013). *Lycengraulis grossidens* is an exception; it completes short to moderate migrations and includes populations that are exclusively marine (Mai et al. 2014). However, this species occupies highly dynamic and tidal habitats with flows similar to high-gradient rivers and is a predator that feeds on evasive prey, such as small fishes and crustaceans (Whitehead et al. 1988; Mai and Vieira 2013; D. D. Bloom, personal observation), which may also select for locomotor traits that enable prolonged swimming performance.

Our convevol analysis detected convergence among the distantly related and geographically dispersed anadromous species *Anchoviella lepidentostole* (Engraulidae; Neotropics), *Gilchristella aestuaria* (Ehiravinae; South Africa), and *Alosa alosa* (Alosinae; Mediterranean/North Atlantic; table 3; fig. 2, purple region). These species migrate relatively short distances, traveling roughly 20 km from estuarine habitats to the lower reaches of freshwater rivers (Whitehead et al. 1988; Whitfield and Harrison 1996; Mendonça and Sobrinho 2013). Our morphospace shows that these species cluster together in a region of trait space separate from other diadromous taxa and differ in traits including a narrow body shape (high fineness ratio), a long caudal peduncle, and a short head height, which are hypothesized to be optimal for maneuvering in waters with high velocities (Watson and Balon 1984; Medeiros and Ramos 2007). However, our Wheatsheaf index indicates that the convergence detected among these lineages are weak

(table 3). We hypothesize that species that undergo short migrations may experience only weak selection on locomotor traits, which may result in weak signatures of convergence. Moreover, body size varies considerably among these three species, ranging from less than 10 cm (*Gilchristella aestuaria*) to greater than 80 cm (*Alosa alosa*); because body size inversely scales with energetic efficiency (Roff 1991) and is strongly associated with migration (Bloom et al. 2018; Burns and Bloom 2020), there may be trade-offs between locomotor traits and body size, resulting in incomplete convergence in trait space. Finally, it is worth noting that these three taxa are separated by 85 million years of evolution (Egan et al. 2018), a rather notable evolutionary distance for convergence to occur.

Despite different modes of diadromy, catadromous *Ethmalosa fimbriata* and anadromous *Tenualosa ilisha* and *Hilsa kelee* cluster into a third region of multivariate trait space (fig. 2, blue region). Our convervol analyses detected convergence among these diadromous taxa, and our pPCA suggests that these lineages share deep bodies, deep heads, and short caudal peduncles (table 3). Nonetheless, our Wheatsheaf analysis indicated that the observed convergence is weak (table 3). These species all display intermediate migration distances of roughly 50–200 km (Charles-Dominique and Albaret 2003; Arai et al. 2019) and show more similarity in body shape to the diadromous taxa that migrate long distances than those that migrate short distances (fig. 2). However, *Hilsa kelee* has been reported to migrate much farther on occasion (Bhaumik and Sharma 2012; Bhaumik 2013; Hossain et al. 2019), a source of variation that may increase intraspecific variation and dampen the strength of convergence with distantly related taxa. While the deep heads and bodies of these three species may enhance maneuverability in highly structured environments (Friedman et al. 2020; Larouche et al. 2020), the strength of convergence among these taxa may also be dampened by abiotic differences in feeding habitats (mode of diadromy) and trophic ecology. In the marine environment, anadromous *Tenualosa ilisha* and *Hilsa kelee* remain near shore and primarily feed in coastal areas (Arai et al. 2019), whereas the catadromous *Ethmalosa fimbriata* feeds in lower reaches of freshwater rivers that undergo seasonal flooding, which results in turbulent flows throughout the year (Charles-Dominique and Albaret 2003). While all three species are considered microphagous, there are differences in the trophic ecology of these species that may impose selection on locomotor traits, limiting convergence. The diet of *Tenualosa ilisha* primarily comprises phytoplankton (De and Datta 1990; Dutta et al. 2014), *Ethmalosa fimbriata* consumes similar quantities of phytoplankton and zooplankton (Fagade and Olaniyan 1972; Blay and Eyeson 1982; Ajah et al. 2012), and *Hilsa kelee* has a diet that contains zooplankton, small crustaceans, and phytoplankton (Blaber

1979; Mwijage et al. 2017; Soe et al. 2021). Given the differences in mode of diadromy and trophic ecology, detecting convergence among these three taxa, albeit weak, suggests that migration can act as a strong selective force in fishes.

Diadromous lineages do not show convergent evolution in the fineness ratio, a metric we used to quantify body shape (fig. 4). Body shape has postulated links to migration because fishes that undergo long-distance migration are hypothesized to evolve a fusiform body shape (Webb 1984; Langerhans and Reznick 2010). However, our OUwie and l1ou analyses failed to detect adaptive shifts in the fineness ratio among diadromous taxa, and our pPCA shows that body shapes are highly variable among diadromous lineages. The three regions of trait space occupied by distantly related diadromous taxa appear to exhibit a body shape continuum. For example, one end of this continuum is represented by diadromous taxa with a deep body shape (low fineness ratio), and the other end is represented by the few diadromous taxa that display a slender body shape (high fineness ratio). Additionally, two diadromous clupeiforms, *Coilia nasus* and *Anodontostoma chacunda*, occupy unique regions of morphospace compared with all other diadromous taxa and thus extends this body shape continuum to even greater extremes. *Coilia* is the only clupeiform lineage to have evolved a highly elongated and tapered eel-like body and apparent anguilliform swimming mode (D. D. Bloom and L. M. DeHaan, personal observation). Diadromous taxa with an anguilliform swimming mode are not rare; other examples include anadromous lamprey and catadromous anguillid eels, the latter of which migrate up to 6,000 km (Van Ginneken et al. 2005; Quintella et al. 2009; Pfaff et al. 2016). Additionally, *Anodontostoma chacunda* has a large body depth-to-standard length ratio, which is unique among diadromous lineages in this study. This species is classified as diadromous because it has been observed in both coastal oceanic habitats and lower river reaches (Beumer 1978; Hanif et al. 2019). However, it is uncertain whether and how far this species migrates into freshwater systems to spawn, raising the possibility that the poorly known ecology of this species has resulted in it being erroneously classified as diadromous. The extreme deep body morphotype may be due to the detritivorous diet of this species (Beumer 1978). Detritivory has been linked to the evolution of deep bodies in fishes (Burns 2021).

Morphological Rates of Evolution

We found that diadromous lineages have faster rates of locomotor trait evolution than nondiadromous lineages in two separate analyses (fig. 3; table S3). Our analyses showed almost no difference in rates of diet trait evolution, which supports previous findings that the interplay between

trophic niche and diadromy is not a primary target for selection (Bloom et al. 2018). Natural selection is predicted to act strongly on traits that are most relevant to the organism's ecological role, and these traits should show faster rates of trait evolution (Futuyma and Moreno 1988). For example, mammals with specialized locomotor modes (i.e., arboreal and amphibious) show faster rates of locomotor evolution than mammals utilizing a variety of substrates (Nations et al. 2020). Our results show that univariate traits functionally relevant to swimming performance, including body size, fineness ratio, caudal peduncle depth, caudal peduncle length, body depth, and head height, all showed significantly faster rates of trait evolution in diadromous lineages than marine and freshwater taxa (Webb 1984; Blake 2004; Langerhans and Reznick 2010). We also found that the locomotor trait subset had significantly faster rates of evolution in diadromous lineages than nondiadromous lineages. Our results are consistent with previous studies that found that migratory fishes rapidly evolved a larger body size than non-migratory fishes (fig. 3; Bloom et al. 2018; Burns and Bloom 2020), a trait with established links to swimming efficiency (Roff 1991). Previous studies and our results indicate that locomotor traits frequently exhibit an adaptive response (i.e., faster rates of evolution) in migratory fishes than traits associated with other aspects of the ecological niche, such as diet (Jones et al. 2013; Bloom et al. 2018; Velotta et al. 2018; Smith et al. 2020). Therefore, diadromy may play a dominant role in shaping patterns of phenotypic diversity within clades containing diadromous lineages, such as clupeiforms.

Conclusions

Linking convergent morphologies to shifts in habitat and diet are hallmark examples of adaptation and a staple inquiry in evolutionary biology. Studies of life history evolution often focus on convergent patterns in classic life history traits (e.g., egg size, age at maturity). Few studies have integrated these concepts and demonstrated that shifts in life history strategies can drive changes in phenotypic evolution (Bonett et al. 2018), thus missing a critical ecological axis of variation (Winemiller et al. 2015). We provide evidence that the evolution of migration can drive convergent evolution in a diverse clade of bony fishes. Our results provide a compelling case that traits associated with locomotion are under selection, resulting in convergent evolution in diadromous lineages, a phenomenon that spans biological scales from genes (e.g., Willoughby et al. 2018) to phenotypes (our study) and from populations (e.g., Palkovacs et al. 2008; Smith et al. 2020) to clades (our study). We also found examples of traits that vary widely among diadromous clupeiforms, highlighting the role of contingency in phenotypic evolution. Our study addresses a ma-

jor gap in the understanding of migration biology and highlights the role of life history evolution in shaping widespread patterns of phenotypic diversity (Bowlin et al. 2010).

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Statement of Authorship

Conceptual study design: D.D.B.; funding acquisition: D.D.B., L.M.D.; data collection: D.D.B., L.M.D., J.P.E.; data analysis: L.M.D.; coding: L.M.D., M.D.B.; writing—original draft: L.M.D., D.D.B.; writing—review and editing: D.D.B., L.M.D., J.P.E., M.D.B.

Data and Code Availability

All data, scripts, and tree files used in this study are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.5hqbzkhbp>; DeHaan 2023).

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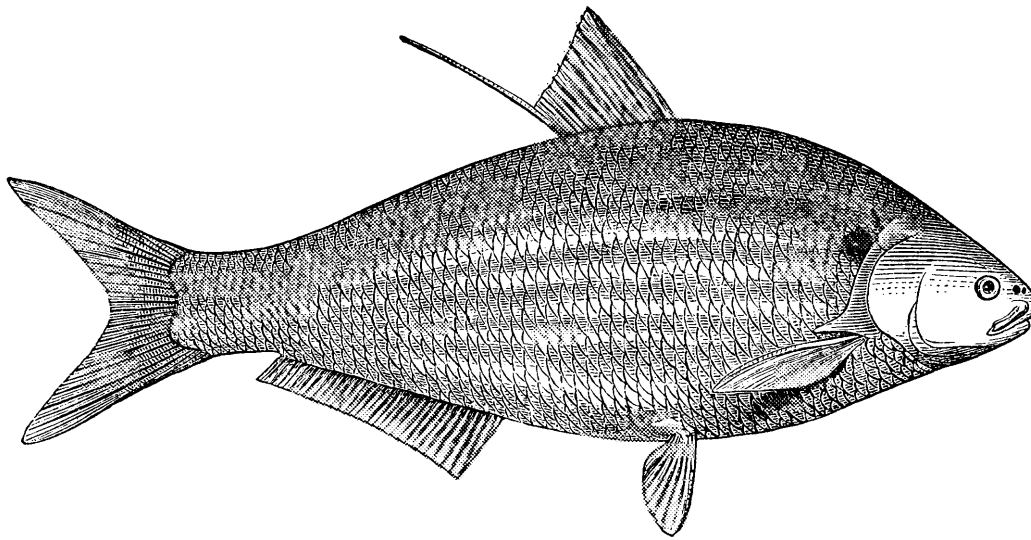
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“We know of one or two creeks that are annually visited by a few of these herring, and have occasionally seen *several bushels* hauled from the deep holes in the creeks they had entered. They appear in the Delaware early in March, before the other representatives of the Clupeidae do, and as they are not ever taken in very great numbers, as are the other herring in the river, we judge that the immense quantities occasionally taken in creeks, is to be explained in the suggestion that those that come in the spring do not return. We have seen them in mid-winter frozen to death, apparently, and have reason to believe that they bury themselves in the mud when they take up their winter quarters in creeks and ponds.” Figured: “Gizzard Shad, *Dorosoma Cepedianum*.” From “Notes on Fresh-Water Fishes of New Jersey” by Charles C. Abbott (*The American Naturalist*, 1870, 4:99–117).