

# Evolution of body size and trophic position in migratory fishes: a phylogenetic comparative analysis of Clupeiformes (anchovies, herring, shad and allies)

DEVIN D. BLOOM<sup>1,2\*</sup>, MICHAEL D. BURNS<sup>3</sup> and TIFFANY A. SCHRIEVER<sup>1,2</sup>

<sup>1</sup>*Department of Biological Sciences, Western Michigan University, 1903 West Michigan Avenue, Kalamazoo, MI 49008-5410, USA*

<sup>2</sup>*Institute of the Environment and Sustainability, Western Michigan University, Kalamazoo, MI 49008-5419, USA*

<sup>3</sup>*Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA*

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Migration is a widespread phenomenon among animals and has a profound influence on the evolution of species traits. Diadromous fishes provide an extreme example of migration, moving between marine and freshwaters, often travelling thousands of kilometres for feeding and reproduction. Diadromy has been linked to changes in feeding ecology, body size and various life-history attributes. However, most studies have focused on intraspecific variation and associated mechanisms. In this study, we use phylogenetic comparative methods to analyse body size and trophic position across Clupeiformes (anchovies, herring, shad and allies), a large clade of fishes that includes both diadromous and non-diadromous species. We found that diadromous species are larger than non-diadromous species, but there is no difference in trophic position, and that these patterns are not attributable to common ancestry. Diadromous species show a decoupling of body size and trophic position, whereas non-diadromous clupeiforms have a positive relationship between body size and trophic position. Using a model-fitting approach, we detected a signal of strong selection driving diadromous fishes to different adaptive peaks from non-diadromous fishes for body size, but a single adaptive peak for trophic position. We suggest that diadromous fishes have evolved larger body size than obligate marine and freshwater species as an adaptation to maximize energy expenditure during long-distance migration.

ADDITIONAL KEYWORDS: anadromy – animal movement – catadromy – diadromy – life history – migration.

## INTRODUCTION

Migration is a widespread phenomenon in animals and can play an important role in shaping species ecology and evolution (Baker, 1978; Winker, 2000; Dingle, 2014). In fishes, > 250 species migrate between marine and freshwaters for feeding and reproduction, an extreme type of migration known as diadromy (McDowall, 1987, 1992). This complex behaviour can have a profound effect on species traits (Baker, 1978; Dingle, 2014). At the intraspecific level, diadromy has been linked to variation in survivorship (Gross, 1987), trophic ecology (Palkovacs *et al.*, 2008), reproductive investment (Kinnison *et al.*, 2001), mating strategy (Gross, 1991)

and gene flow (Hasselman *et al.*, 2013). However, the connection between intraspecific variation and macroevolutionary patterns remains elusive (Kinnison & Hendry, 2003). Phylogenetic comparisons of trait variation between migratory and non-migratory lineages can provide key insights into the evolution of diadromy (Kinnison & Hendry, 2003; Bowlin *et al.*, 2010; Shaw, 2016) and explain geographical patterns of phenotypic variation (Griffiths, 2011).

There are three modes of diadromy: anadromy, catadromy and amphidromy (McDowall, 1988). Anadromous fishes reproduce in freshwaters and migrate to the ocean to feed and grow, whereas catadromous fishes reproduce in the ocean and migrate to freshwaters to feed and grow. Amphidromous species migrate between marine and freshwaters as juveniles,

\*Corresponding author. E-mail: [devin.bloom@wmich.edu](mailto:devin.bloom@wmich.edu)

but the timing of migration is variable and not tightly linked to reproduction. The first two modes of diadromy are closely tied to trophic ecology (Gross *et al.*, 1988; Post & Palkovacs, 2009), and all modes of diadromy require individuals to move between migration end points, with migration distances varying from tens to thousands of kilometres (Baker, 1978; Feutry *et al.*, 2013; Righton *et al.*, 2016). The importance of trophic ecology and swimming efficiency in migratory fishes suggests that traits associated with feeding and locomotion might exhibit the strongest adaptive response following the evolution of diadromy.

Body size and tropic position are important and often ecologically linked traits in fishes, and often vary among different habitat types (Collar *et al.*, 2010; Des Roches *et al.*, 2016). Body size is a fundamental axis of animal ecology because it co-varies with various attributes of physiology, species interactions, life-history and biomechanical traits (Peters, 1986). Intraspecific studies of salmon and whitefish (Vangerwen-Toyne *et al.*, 2008), rainbow trout (Kendall *et al.*, 2015), brown trout (L'Abée-Lund, 1991), alewives (Post *et al.*, 2008) and stickleback (Snyder & Dingle, 1990; Snyder, 1991) often reveal a pattern of larger body size in diadromous than non-diadromous individuals. But few studies have compared body size among diadromous and non-diadromous lineages using a phylogenetic framework, and the ultimate mechanisms driving the apparent pattern of larger body size in migratory fishes remain unclear. One possible explanation is the link between body size and trophic position. Both theory and empirical data have suggested that the evolution of diadromy is associated with trophic ecology, and migration patterns are explained by species capitalizing on higher productivity in either marine or freshwater environments (Gross *et al.*, 1988; Post *et al.*, 2008; Johnson & Schindler, 2013). This suggests that the trophic niche of diadromous fishes may be under strong selection. Body size and trophic position typically scale positively in fishes (Romanuk *et al.*, 2010); therefore, if diadromous fishes experience selection towards a higher trophic niche they may also be under selection for larger body size. Alternatively, life-history theory suggests that larger body size optimizes trade-offs between the energetic demands of migration and other life-history characteristics (Gross, 1987). Roff (1991) argued that larger fishes maximize the trade-off between fecundity and migration distance because the energetic cost of swimming is inversely related to body size; larger fishes have higher swimming efficiency, thus diadromous fishes may be larger than non-diadromous fishes owing to the biomechanical advantages of larger body size for moving long distances, often swimming against strong currents and tides and overcoming obstacles. Larger fishes may also

have greater energy reserves than smaller fishes (Roff, 1988), suggesting multiple adaptive advantages for large body size in migratory fishes.

Phylogenetic comparative methods offer a powerful framework for exploring patterns of trait evolution, and evolutionary models can reveal the processes underlying trait variation across phylogenetic scales (O'Meara, 2012). There are two primary models used in comparative phylogenetics: Brownian motion (BM) and Orenstein–Uhlenbeck (OU). Brownian motion models describe a trait that has evolved under a stochastic process, such as drift. An OU model best fits a trait that has evolved under directional or stabilizing selection towards single or multiple evolutionary optima (Beaulieu *et al.*, 2012).

Clupeiformes (herring, sardines, anchovies and shad) are an excellent system for investigating the role of diadromy in shaping species traits. Comprising ~400 species, Clupeiformes include exclusively marine and freshwater species and > 30 diadromous species. Clupeiforms are one of the few major fish clades that includes both anadromous and catadromous species, and the proportion of diadromous species is 10 times higher than in any other major fish clade (McDowall, 2003). Clupeiformes display a wide diversity of body sizes, with species ranging from 2 cm (e.g. *Amazonsprattus scintilla*) to 100 cm (*Chirocentrus dorab*) maximal standard length (SL). Although generally characterized as filter-feeding planktivores, trophic position varies broadly among clupeiforms, with various species feeding on shrimp, fish, insects, zooplankton and phytoplankton (Whitehead *et al.*, 1988).

In this study, we examined macroevolutionary patterns of body size and trophic position among marine, freshwater and diadromous Clupeiformes. Specifically, we ask whether diadromous fishes have larger body sizes than non-diadromous fishes, whether body size is linked to trophic position, and we investigate the nature of the macroevolutionary processes that best explain variation in these traits. Our phylogenetic comparative investigation of diadromous and non-diadromous lineages offers critical insight into the role of migration in shaping phenotypic variation across clades.

## MATERIAL AND METHODS

### PHYLOGENY AND TRAIT DATA

We compiled data on maximal body size expressed as SL from FishBase (Froese & Pauly, 2017), Whitehead (1988) and Carpenter (2002). When different maximal lengths were given, we used the longest reported length for a given species. We obtained trophic position from FishBase, which is calculated by adding one to the mean trophic position, determined from the relative

abundance of all reported food items for a given species. Kline & Pauly (1998) demonstrated that this metric is correlated closely with trophic position estimates based on stable isotope ratios, and Romanuk *et al.* (2010) successfully used this metric to investigate trophic position across bony fishes. We generated two data sets for body size and trophic position; the first included all species of Clupeiformes, and the second was pruned to match the taxon sampling for the phylogeny from Bloom & Lovejoy (2014). We  $\log_{10}$  transformed body size and trophic position data for all statistical analyses. Our body size and trophic position data sets are available in the Supporting Information (Table S1).

For comparative analyses, we used a time-calibrated phylogeny of Clupeiformes from Bloom & Lovejoy (2014). This phylogeny was based on a multi-gene data set that included 152 of the ~400 species, representing 64 of the 84 currently recognized genera and all five families of clupeoids. Our taxon sampling covers all geographical regions where Clupeiformes are found, includes 18 of the ~30 diadromous species, and is the most comprehensive available for this group. The phylogeny covers the size spectrum observed in the Clupeiformes, including the largest (*Chirocentrus dorab*) and smallest (*Amazonsprattus scintilla*) species. Bloom & Lovejoy (2014) used ancestral character reconstruction to determine the number of origins of anadromy and catadromy in Clupeiformes. We updated the coding of five species from Bloom & Lovejoy (2014): *Pellonula leonensis*, *Pellonula vorax*, *Hilsa kelee*, *Ilisha megaloptera* and *Coila nasus*; here, we code these taxa as anadromous based on recent publications (Potter *et al.*, 2015; Chen *et al.*, 2017) and personal communications. We re-conduct the character mapping following the parameter settings used by Bloom & Lovejoy (2014). Each species was coded as either marine, freshwater, anadromous or catadromous. We used maximum likelihood ancestral character reconstruction implemented in Mesquite v. 3.04 (Maddison & Maddison, 2011). We used the R package phytools (Revell, 2012) to visualize body size and trophic position variation across the clupeiform phylogeny.

#### STATISTICAL ANALYSES

We used phylogenetic ANOVA (Garland *et al.*, 1992) and standard ANOVA to test for differences in body size among marine, freshwater and diadromous fishes. We combined anadromous and catadromous into a single 'diadromous' variable because only two species included in the phylogeny are catadromous. We conducted the phylogenetic ANOVA using the R package (R Core Team, 2013) *geiger* (Harmon *et al.*, 2008). For the phylogenetic ANOVA, we conducted 10 000 simulations under a Brownian motion model and implemented a Wilks *post hoc* test statistic. We

generated box plots to examine variation in body size and trophic position of marine, freshwater, anadromous and catadromous species. To test for a relationship between body size and trophic position, we used standard linear regression using the *vegan* package in R (Oksanen *et al.*, 2013) and phylogenetic generalized least squares regression (PGLS) using *geiger*. PGLS is a least squares regression model that accounts for the autocorrelation attributable to shared ancestry (Grafen, 1989; Martins & Hansen, 1997; Symonds & Blomberg, 2014). We evaluated linear model assumptions using the diagnostic plots for generalized linear models. The graphical check showed heteroscedasticity of residuals, which we confirmed statistically using the non-constant error variance test (*ncvTest*, R package *car*; Fox & Weisberg, 2011). The *ncvTest* resulted in a *P*-value < 0.05; therefore, we can infer that heteroscedasticity is present, thus confirming our graphical inference.  $\log_{10}$  transformation of body size did not remove heteroscedasticity. Consequently, we used weighted least squares regression to test for a relationship between body size and trophic position, because it can be used when the assumption of constant variance in the errors is violated.

To determine the trajectory of trait evolution, we visualized the evolution of log body size and log trophic position using the traitgram method (Ackerly, 2009; Revell, 2013) in the R package *phytools* (Revell, 2012). Traitgrams project a phylogeny into phenotypic space, with time on the *x*-axis and the phenotype on the *y*-axis (Revell, 2013). Traitgrams allow us to test whether diadromous lineages have evolved away from the ancestral trait space and, if so, whether the directionality was towards a common optimum.

We tested five evolutionary models in the R package OUwie (Beaulieu *et al.*, 2012; Beaulieu & O'Meara, 2015) to determine whether diadromous and non-diadromous fishes evolved towards different adaptive peaks in log body size and trophic position. The ancestral condition of diadromy and non-diadromy was reconstructed on 1000 trees from the posterior distribution of Bloom & Lovejoy (2014) using Bayesian stochastic character mapping (Huelsenbeck *et al.*, 2003) in *phytools*. To assess the best model for the transition matrix, we fitted a model with an equal rate of transition between diadromy and non-diadromy and a model with all rates different using the function *ace* in the R package *ape* (Paradis *et al.*, 2004). We then compared the fit of these two models through a likelihood ratio test and found that the model with equal rates was supported over the model with all rates different. We used the 'equal rates' (ER) model and estimated the prior distribution of the states at the root of the tree and used the Markov chain Monte Carlo option to set the parameters of the Q matrix. The evolutionary models were run on all 1000 trees to take into account

uncertainty in the life-history strategy of different lineages. The first two evolutionary models we tested were models of Brownian motion, which assumes no trait differences between diadromous and non-diadromous lineages, with trait variation accruing randomly as a proportion of time. The next model, a single OU, assumes that diadromous and non-diadromous lineages are evolving towards a shared trait optimum. The next sets of models were multi-peak OU models, with increasing parameter complexity. The simplest multiple-peak OU model was OUM, which assumes different trait optima ( $\theta$ ) for diadromous and non-diadromous lineages, but each lineage has the same pull towards the optimal trait value ( $\alpha$ ) and the same rate parameter ( $\sigma^2$ ). The OUMA model allows  $\alpha$  to vary between lineages, and OUMV allows lineages to differ in  $\sigma^2$  values.

Model fit was evaluated using the Akaike information criterion with a correction for small sample size (AICc) (Burnham & Anderson, 2002). The AICc values were calculated for each iteration and averaged across all iterations for each model. Mean AICc values were used to calculate AICc weights, and the model with the highest AICc weight was selected as the best model. Eigen decomposition of the Hessian matrix provides an indication of whether the model search returned the maximum likelihood estimate (Beaulieu *et al.*, 2012). If the eigenvalues are positive, then the results are considered reliable. To ensure that all maximum likelihood results were reliable, we removed any model run that returned a negative eigenvalue before evaluating the model fit. OUwie uses complex OU models that cannot always be detected reliably when the statistical power is low (Boettiger *et al.*, 2012), and low power can lead to complex OU models being favoured incorrectly over models of Brownian evolution (Ho & Ané, 2014; Cooper *et al.*, 2016). To determine whether we had significant power to detect the complex models accurately, we performed 1000 OUwie simulations for log trophic position and log body size using the function OUwie.sim. The simulated data sets were performed with the parameter estimates for the best-fit model of log trophic position and log body size in our empirical data set. The simulated data were then run through all five models in OUwie to determine whether the simulated model could be recovered accurately with our sample size.

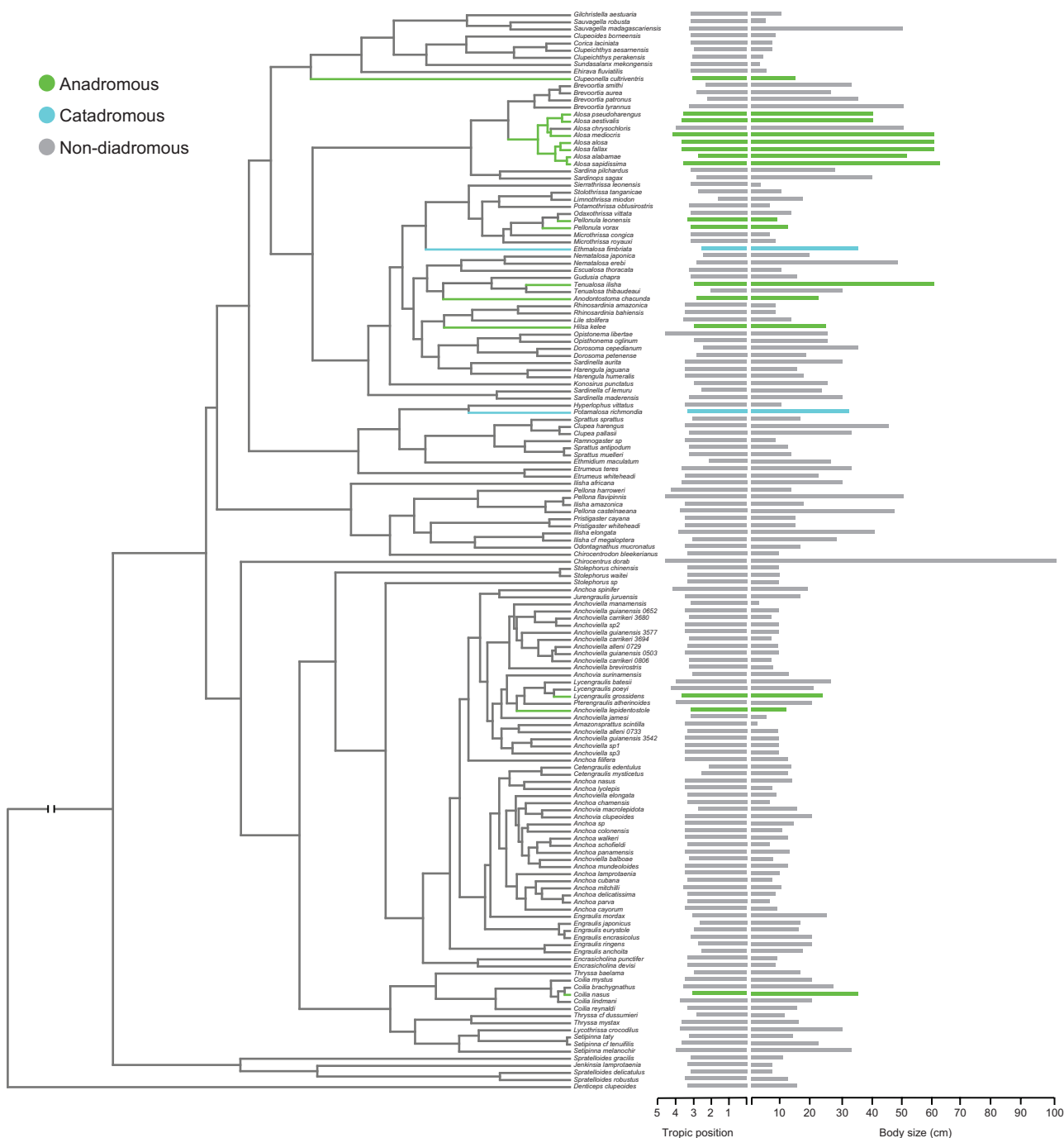
## RESULTS

Our ancestral character reconstruction showed that diadromy has evolved at least ten and as many as 12 times (Fig. 1). Diadromy is dispersed throughout the clupeiform phylogeny (Fig. 1), with two independent origins of catadromy and eight to ten origins of

anadromy. A qualitative comparison reveals that diadromous species are generally larger than their closest non-diadromous relative (Fig. 1). Trophic position is widely variable among diadromous and non-diadromous lineages, with no clear qualitative pattern emerging.

Both standard ( $F_{2,359} = 49.78, P \leq 0.001$ ) and phylogenetic ANOVA ( $F = 22.57, P = 0.008$ ) show that diadromous fishes have significantly larger body sizes than non-diadromous species (Fig. 2). *Post hoc* comparisons using Tukey's HSD test indicate that the mean body size of diadromous fishes is significantly larger than marine and freshwater lineages, and that freshwater and marine lineages are not different in body size. Standard ( $F_{2,359} = 2.269, P = 0.11$ ) and phylogenetic ANOVA ( $F = 0.004, P = 0.98$ ) indicate that there is no difference in trophic position between diadromous and non-diadromous clupeiforms (Fig. 2). With only two catadromous species, we were not able to test statistically for differences between catadromous and anadromous modes of diadromy, but visual inspection of box plots suggests that the pattern of larger body size in migratory lineages holds for both modes of diadromy (see Supporting Information, Fig. S1). Our standard regression of all clupeiforms shows a significant positive relationship between body size and trophic position ( $F_{1,360} = 15.47, R^2 = 0.041, P = 0.0001$ ; Fig. 3). The regression line tells us that for every additional millimetre in body length, trophic position is expected to increase by an average of 0.007 of a trophic level (trophic position [TP] =  $3.12 + 0.007_{\text{body size}}$ ). This relationship is upheld within marine ( $F_{1,245} = 4.244, R^2 = 0.017, P = 0.04$ , marine TP =  $3.02 + 0.197_{\text{body size}}$ ) and freshwater species ( $F_{1,88} = 7.262, R^2 = 0.076, P = 0.008$ , freshwater TP =  $2.92 + 0.288_{\text{body size}}$ ), but there is no relationship between body size and trophic position in diadromous species alone ( $P = 0.769$ ). Weighted least squares regression for all Clupeiformes reveals a significant relationship between body size and trophic position ( $F_{1,360} = 13.45, R^2 = 0.036, P = 0.0003$ ) and a non-significant relationship in diadromous species ( $F_{1,32} = 2.434, R^2 = 0.0707, P = 0.129$ ). Our PLGS analysis also shows a significant relationship between body size and trophic position across all Clupeiformes ( $P \leq 0.001$ ). Clupeiforms show minimal variance in trophic position at small sizes, with the distribution centred on a trophic level of three. There is a substantial increase in the variance of trophic position in larger body sizes, a pattern consistent across marine, freshwater and diadromous species.

Our traitgram (Fig. 4) shows that diadromous lineages generally have a larger body size than their closest non-diadromous relatives, and the inferred ancestral size. Diadromous lineages exhibit some of the largest body sizes that have evolved in Clupeiformes. Trophic position shows a much more variable pattern; in some

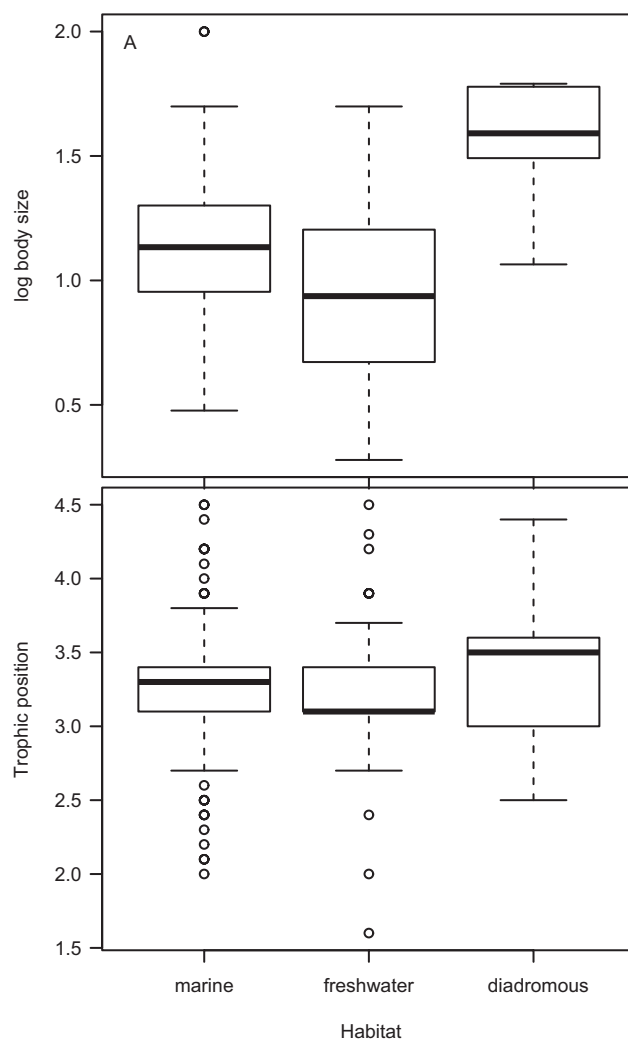


**Figure 1.** Phylogeny of Clupeiformes from Bloom & Lovejoy (2014), showing ancestral reconstructions of anadromous (green) and catadromous (light blue) lineages. The panel on the right of the phylogeny shows the trophic position and body size distribution for each species in the phylogeny. Diadromous species (and clades) are generally larger than non-diadromous relatives.

cases, diadromous species have higher trophic position, but other species show decreases compared with non-diadromous relatives. Some of the species that show a notable decrease in trophic position (e.g. *Alosa alabama*) have increased in body size, illustrating the

decoupling of trophic position and body size in diadromous lineages.

The OUwie analyses of log body size for diadromous vs. non-diadromous lineages indicate that the best-fit model is OUMV, a model supporting different  $\theta$  (optimal

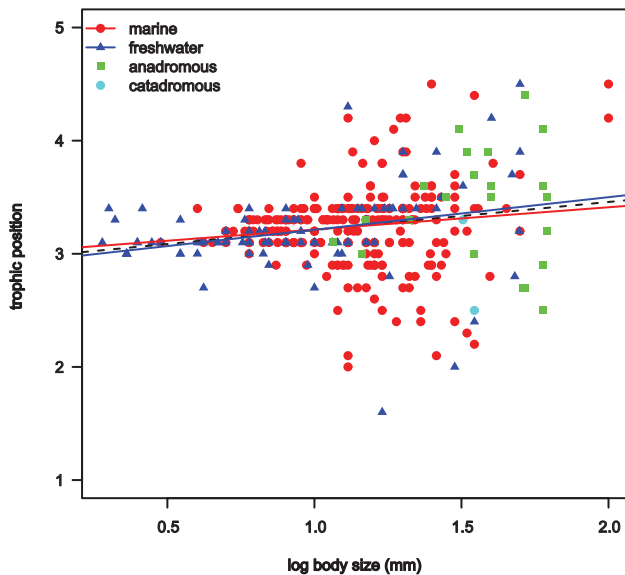


**Figure 2.** Box plots of marine, freshwater and diadromous species for log body size (A) and trophic position (B). There is no difference in trophic position between any of the groups shown. Diadromous (anadromous and catadromous) clupeiforms have significantly larger body size than non-diadromous species. There is no difference in body size between marine and freshwater species.

trait value), different  $\alpha$  (pull towards the optima) values between character states and different  $\sigma^2$  (rates) (Table 1). Diadromous lineages were estimated to have a larger  $\theta$  and  $\alpha$  than non-diadromous fishes for body size, which indicates strong selection towards a larger body size in diadromous fishes. The top three models that were selected included different adaptive peaks for body size between diadromous and non-diadromous lineages. The OUwie analysis on log trophic position inferred a single OU for all species, indicating that there is not strong selection for a different trophic position between diadromous and non-diadromous lineages.

The results of our simulations show that our data set has enough statistical power to separate clearly the different OU models from the models of Brownian motion (Supporting Information, Fig. S2). The suite

of different OU models consistently have much lower AICc scores than the two models of Brownian motion for both body size and trophic position (Supporting Information, Fig. S2). The body size simulations had difficulty separating the OUMA and OUMV models of evolution, with overlap between the AICc scores for the two models. However, the OUMV was recovered as the best model in the majority (70.3%) of the simulations, whereas OUMA was recovered as the best model in only 29.7% of simulations. The trophic position simulations had difficulty distinguishing between the different OU models, with substantial overlap in AICc scores for the OU, OUM and OUMV models. The single peak OU model was recovered as the best fitting model in only 46.5% of the simulations vs. 26.6% for OUM and 26.9% for OUMV.



**Figure 3.** Plot of log body size and trophic position for marine, freshwater, anadromous and catadromous Clupeiformes. Regression lines are shown for groups with significant relationships: all Clupeiformes (dashed line), marine (red line) and freshwater (blue line).

## DISCUSSION

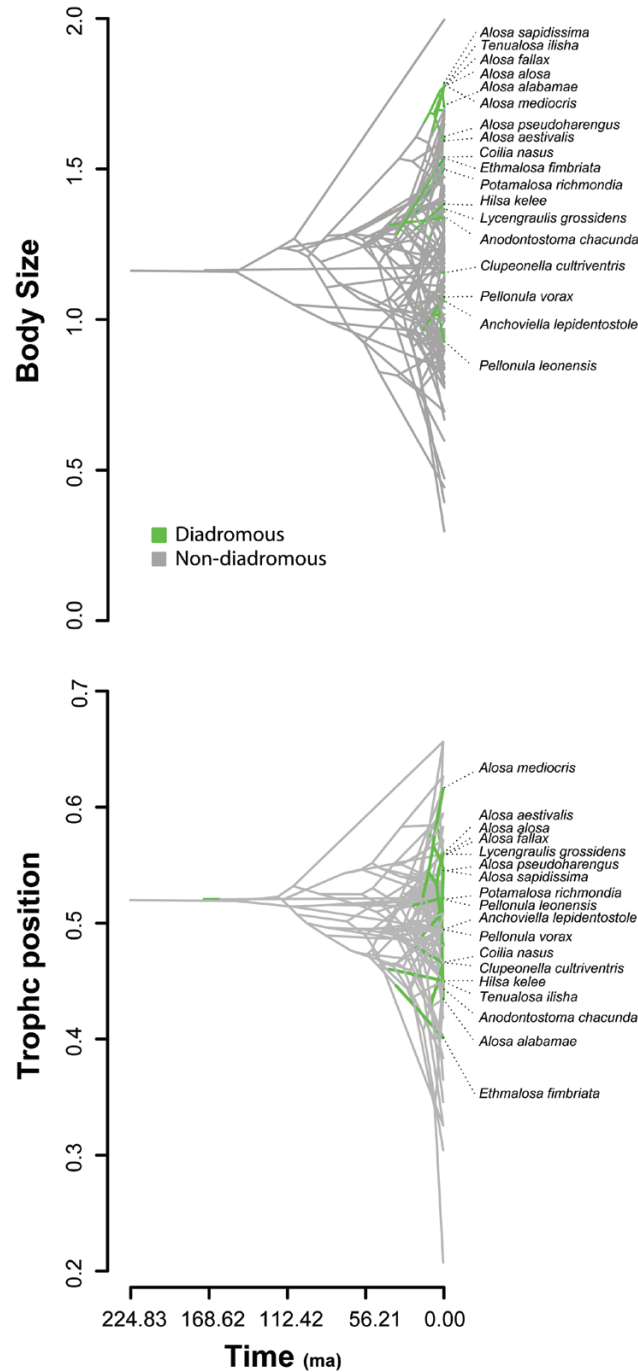
Diadromous fishes migrate between marine and freshwaters, often travelling thousands of kilometres (McDowall, 1988). As a result, diadromous fishes must have adaptations for both oceans and rivers and for movement between these environments (Hendry *et al.*, 2003). We find that there is no difference in body size between marine and freshwater clupeiforms, which suggests that differences between these environments do not explain the larger body size in diadromous fishes. Furthermore, there appears to be no difference in body size between anadromous and catadromous species, indicating that the pattern holds regardless of the respective reproductive and feeding environment. Comparisons between diadromous fishes and non-diadromous relatives show that diadromous fishes are larger than non-diadromous species and show an increase in size relative to their nearest non-diadromous common ancestor regardless of trophic position.

The decoupling of body size and trophic position in diadromous fishes differs considerably from the pattern observed across most fishes (Romanuk *et al.*, 2010; Ou *et al.*, 2017), including strictly marine and freshwater Clupeiformes (Fig. 3). Gross *et al.* (1988) posited that the driving force for the evolution of diadromy was to capitalize on foraging opportunity offered by higher productivity in either marine or freshwater environments. Our results suggest that the evolution of diadromy does not facilitate feeding at higher trophic levels; in fact, diadromous species feed across

a broad spectrum of trophic levels (Fig. 1). We cannot rule out the possibility that diadromous fishes benefit from increased productivity, but this does not result in feeding at a higher trophic level. However, there is little support for the phylogenetic model proposed by Gross's productivity hypothesis (Bloom & Lovejoy, 2014). Moreover, our OUwie analyses indicate a single adaptive peak for both diadromous and non-diadromous lineages, and we interpret the lack of selection on trophic position as evidence that productivity is not the primary factor driving the evolution of diadromy.

Theory suggests that larger body size in migratory fishes results in higher swimming efficiency, which reduces energetic requirements, allows for longer migrations and increases the ability to overcome barriers to migration, such as natural dams (Roff, 1991; Hendry *et al.*, 2003). In the present study, we present multiple lines of evidence supporting the hypothesis that larger body size confers increased swimming efficiency and speed that help to mitigate the costs of migration (Roff, 1991). Our OUwie model-fitting results indicate that the optimal body size for diadromous fish is three times larger (on a logarithmic scale) than the optimal size for non-diadromous fishes. We also find that diadromous fishes experienced strong selection for larger body size, whereas non-diadromous species did not experience selection for larger body size. Model selection involves some uncertainty (Cooper *et al.*, 2016); however, the top three models include multiple adaptive peaks, and our ANOVA and traitgram analyses suggest that diadromous fishes are larger in general and tend to show an increase in size relative to non-diadromous relatives. Taken together, these results support the hypothesis that diadromous fish reside on a different adaptive peak from non-diadromous fishes, with respect to body size. Roff (1991) speculated that if the cost of migration is higher for smaller fishes than larger fishes then migratory fishes would be constrained to larger size, whereas non-migratory species would be free to evolve either large or small body size. Our data show that Clupeiformes are generally consistent with this pattern.

Our results align with evidence from several other studies supporting the hypothesis that larger body size decreases the cost of migration. Bernatchez & Dodson (1987) compared the body mass and bioenergetics of 15 anadromous species and populations and found an exponential decrease in energetic cost per unit distance with increasing body mass. Several studies investigating intraspecific variation found that migration distance increases with body size (Schaffer & Elson, 1975; Glebe & Leggett, 1981; L'Abée-Lund, 1991; Jonsson & Jonsson, 2006), which may be the outcome of greater swimming efficiency and larger energy stores (Roff, 1988, 1991). Griffiths (2010) investigated body size patterns in fishes of North America and found that migratory species are larger than non-migratory species, indicating that



**Figure 4.** Traitgram projections of trophic position and body size for Clupeiformes using the phylogeny from Fig. 1. The vertical position represents the relative trophic position or body size, and the  $x$ -axis illustrates absolute time in millions of years. Diadromous taxa are green and non-diadromous taxa grey.

our results are broadly relevant to the interpretation of body size variation in bony fishes. We propose that comparative studies of other clades that include diadromous fishes will reveal that selection for larger body size explains the disparity in body size between diadromous and non-diadromous fishes across phylogenetic scales.

Larger body size in diadromous fishes may also be explained by selection on traits that co-vary with size, rather than selection on body size directly. Intraspecific studies have indicated that larger body size is attributable to factors such as mate preference (Hutchings & Myers, 1988; Kinnison *et al.*, 2001; Weir *et al.*, 2016),



**Table 1.** Comparison of model fits and trait optima ( $\theta$ ) for trophic position and body size between diadromous and non-diadromous species

	Model	Rank	AICc	$\Delta$ AICc	AICc weight	$\theta_{\text{non}}$	$\theta_{\text{dia}}$	$\alpha_{\text{non}}$	$\alpha_{\text{dia}}$	$\sigma^2_{\text{non}}$	$\sigma^2_{\text{dia}}$
Trophic position	<b>OU1</b>	<b>1</b>	<b>1384</b>	<b>0</b>	<b>0.82</b>	–	–	<b>0.081</b>	<b>0.081</b>	<b>0.00073</b>	<b>0.00073</b>
	OUM	2	1388	4	0.11	0.50	0.53	0.082	0.082	0.0007	0.0007
	OUMV	3	1389	5	0.07	0.50	0.54	0.072	0.072	0.0006	0.0008
	BMS	4	1460	76	0	–	–	–	–	0.0001	0.0002
	BM1	5	1475	91	0	–	–	–	–	0.0002	0.0007
	OUMA*	–	–	–	–	–	–	–	–	–	–
Body size	<b>OUMV</b>	<b>1</b>	<b>–5.28</b>	<b>0</b>	<b>0.45</b>	<b>1.17</b>	<b>2.16</b>	<b>0.022</b>	<b>0.022</b>	<b>0.004</b>	<b>0.002</b>
	OUMA	2	–5.00	0.28	0.39	1.18	2.18	0.041	0.086	0.004	0.004
	OUM	3	–2.30	2.98	0.10	1.18	2.29	0.021	0.021	0.004	0.004
	OU1	4	–1.16	4.12	0.06	–	–	0.020	0.020	0.003	0.003
	BM1	5	18.70	23.98	0	–	–	–	–	0.002	0.002
	BMS	6	19.27	24.55	0	–	–	–	–	0.002	0.001

Rows in bold represent the best-fit model based on lowest AICc score. Abbreviations: AICc, Akaike information criterion with a correction for small sample size; BM1, a single-rate Brownian motion model; BMS, a Brownian motion model with different rate parameters for each state on the tree; OU1, an Ornstein-Uhlenbeck model with a single optimum for all species; OUM, an Ornstein-Uhlenbeck model with different state means between diadromous and non-diadromous lineages and a single  $\alpha$  and  $\sigma^2$  acting on all lineages; OUMA, an Ornstein-Uhlenbeck models that assume different state means as well as different  $\alpha$  diadromous and non-diadromous lineages; OUMV, an Ornstein-Uhlenbeck models that assume different state means as well as different  $\sigma^2$  between diadromous and non-diadromous lineages;  $\theta_{\text{non}}$ , estimated trait optimum for non-diadromous species;  $\theta_{\text{dia}}$ , estimated trait optimum for diadromous species;  $\alpha_{\text{non}}$ , estimated pull towards the optimal trait value for non-diadromous species;  $\alpha_{\text{dia}}$ , estimated pull towards the optimal trait value for diadromous species;  $\sigma^2_{\text{non}}$ , estimated rate parameter for non-diadromous species;  $\sigma^2_{\text{dia}}$ , estimated rate parameter for diadromous species. \*OUMA model unable to converge.

egg size (Fleming, 1996; Closs *et al.*, 2013; Kendall *et al.*, 2015) and fecundity (Closs *et al.*, 2013; Gross, 1987). Unfortunately, these traits are not well known for most Clupeiformes. The best evidence in favour of larger body size conferring increased fitness is found in salmonids (Hendry *et al.*, 2003), but it is unclear whether this pattern is widespread across diadromous fishes, and exceptions abound. For example, in salmonids some species show a positive correlation between migration distance (which co-varies with size) and fecundity (Kinnison *et al.*, 2001), whereas others show the opposite pattern (Crossin *et al.*, 2004) or no relationship at all (Vangerwen-toyne *et al.*, 2008). Moreover, in some cases non-migratory fishes have larger eggs than migratory species (Closs *et al.*, 2013); therefore, larger size does not guarantee increased fitness. Larger body size may present additional advantages, such as reduced risk of predation or greater breadth of trophic niche, but these possibilities are largely unexplored. The most likely scenario is that the increased body size of diadromous fishes offers multifactorial advantages; for example, larger body size may increase swimming efficiency, which allows individuals to maximize fecundity while reducing the risk of predation. There is also likely to be geographical variation in the strength of selection on these traits; selection for energy efficiency may be particularly strong in the tropics because higher water temperatures require higher energy expenditure (Dingle, 2014). It may not be possible to determine the mechanisms underlying larger body size in diadromous

fishes solely using phylogenetic comparative methods because even the most sophisticated approaches will not identify the source of selective pressures. Testing these alternative hypotheses will require the integration of data on life-history and species traits, both across phylogenetic scales and using contemporary experimental approaches (Weber & Agrawal, 2012).

Explanations for larger size in diadromous fishes have typically focused on microevolutionary processes (Kinnison & Hendry, 2003), whereas the role of macroevolutionary processes in shaping phenotypic patterns has been largely overlooked. If the probability of speciation and extinction are linked to either migration or body size, this will at least partly explain body size variation across phylogenetic scales (Maurer *et al.*, 1992; Maddison *et al.*, 2007). There is some evidence that diversification rates are linked to rates of phenotypic evolution (e.g. Rabosky *et al.*, 2013), which suggests that macroevolutionary processes may play an important role in determining interspecific body size patterns. Alternatively, if lineage diversification is decoupled from phenotypic evolution (e.g. Harmon *et al.*, 2010), then microevolutionary processes writ large are likely to be the primary explanation for larger body size in anadromous species. Studies on contemporary extinction have shown that extinction risk increases in marine species, and both small- and large-bodied freshwater species have an increased risk of extinction (Olden *et al.*, 2007), probably owing to various life-history traits associated with body size (Winemiller, 2005). These contemporary

studies also indicate that there are potential conservation implications from our study, because extinction risk is correlated with body size, adding to the myriad of anthropogenic threats to migratory fishes (Limburg & Waldman, 2009). Determining the relative role of macroevolutionary and microevolutionary processes in structuring body size disparity between diadromous and non-diadromous fishes will be a crucial step for interpreting patterns of phenotypic diversity.

#### CONCLUSIONS

In this study, we used phylogenetic comparative methods and model fitting to infer the processes that have generated phenotypic patterns among diadromous and non-diadromous fishes. We found evidence to support the hypothesis that increased body size is an adaptation to mitigate the energetic expense of long-distance migration. The finding that selection has led to larger body size in diadromous fishes has broad implications, because diadromous fishes are renowned as keystone species (Limburg & Waldman, 2009; Carlson *et al.*, 2011; Tonra *et al.*, 2015) and have direct and indirect effects on ecosystem functions and other species in the community. For instance, Carlson *et al.* (2011) found that the body size of salmon could influence foraging behaviour in bears. Furthermore, the marine-derived nutrients from diadromous fishes may create a feedback loop that determines the fitness of their own offspring (Auer *et al.*, 2018). These results suggest that selection for larger-bodied diadromous fishes may drive evolution in the ecology of both diadromous fishes themselves and other organisms in the ecosystem. These relatively inconspicuous links between body size evolution in diadromous fishes and their interactions with other organisms and the ecosystem are a promising frontier for exploration (Post & Palkovacs, 2009; Weber *et al.*, 2017).

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### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** Body size and trophic position data.

**Figure S1.** Density plot of Akaike information criterion with a correction for small sample size (AICc) scores for the different evolutionary models from the 1000 simulated data sets under the best-fit model parameters for body size and trophic position. Dashed line represents the AICc score from the empirical test.