

## Recent parallel divergence in body shape and diet source of alewife life history forms

Andrew W. Jones · Eric P. Palkovacs · David M. Post

Received: 13 July 2012 / Accepted: 23 April 2013 / Published online: 24 May 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** Recent work suggests that juvenile alewives (*Alosa pseudoharengus*) share similar phenotypes among independently derived landlocked (freshwater resident) populations. Based on this observation, it is possible that the alewife life history forms represent a case of parallel adaptive divergence. To further evaluate this hypothesis, we describe patterns of body shape divergence between anadromous and landlocked alewife life history forms using geometric morphometrics. Our results suggest that body shape differs significantly between juveniles of the alewife forms: anadromous fish were more robust, with larger heads and deeper caudal peduncles, while landlocked fish from three independently isolated populations were more fusiform with thinner caudal peduncles and smaller heads. These differences matched population level dietary patterns, which suggest that anadromous fish consumed more littoral resources than landlocked fish. Finding consistent differences across populations of the same form supports the notion that landlocked alewives have diverged from their anadromous ancestors in a parallel manner, in response to pressures associated with being isolated in freshwater lakes. Comparing alewife phenotypes to expectations from the literature suggests that neither migration distance of the population, nor the relative availability of habitats in each lake, are likely drivers of the pattern we report. Instead, the pattern is consistent with the hypothesis that divergence between alewife forms results from the distinct effects of each form on its zooplankton prey.

---

A. W. Jones (✉) · D. M. Post  
Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect St.,  
New Haven, CT 06511, USA  
e-mail: andrew.jones@yale.edu

D. M. Post  
e-mail: david.post@yale.edu

E. P. Palkovacs  
Department of Ecology and Evolutionary Biology, University of California-Santa Cruz,  
100 Shaffer Rd, Santa Cruz, CA 95060, USA  
e-mail: epalkova@ucsc.edu

**Keywords** Adaptive divergence · Body shape · Geometric morphometrics · *Alosa pseudoharengus* · Diet · Stable isotopes · Eco-evolutionary dynamics

## Introduction

Adaptive divergence is common in fishes (Schluter 1996; Bell and Andrews 1997). Many fish species have diverged in response to the availability of benthic or pelagic resources, including threespine stickleback (*Gasterosteus aculeatus*), whitefish (*Coregonus* spp.), and arctic char (*Salvelinus alpinus*) (McPhail 1984; Lu and Bernatchez 1999; Walker and Bell 2000; Jonsson and Jonsson 2001). Some species, such as the Pacific salmonids (*Oncorhynchus* spp.) and New Zealand eleotrids (*Gobiomorphus* spp.), have diverged into distinct migratory and non-migratory forms (Wood and Foote 1996; Narum et al. 2004; Michel et al. 2008), while other species like guppies (*Poecilia reticulata*) and mosquito fish (*Gambusia affinis*) have diverged in response to distinct predation regimes (Reznick and Endler 1982; Langerhans et al. 2007). Comparative and experimental work on this topic has provided insight into the pattern and process of adaptive diversification in fishes and other vertebrates (Schluter 2000).

The alewife (*Alosa pseudoharengus*), a clupeid native to the Atlantic Coast of North America, is an emerging example of adaptive divergence (Palkovacs and Post 2008; Schielke et al. 2011). This species exhibits two life history forms: an ancestral anadromous form and a derived landlocked form (Palkovacs et al. 2008). Over the past 300–5,000 years, independent populations have become landlocked by anthropogenic or natural damming of lake outlets, and are now genetically differentiated from their anadromous ancestors (Palkovacs et al. 2008). Juveniles of both forms have strong but distinct effects on their lake environments (Brooks and Dodson 1965; Post et al. 2008; Palkovacs and Post 2009), and display consistent differences in foraging traits, including gill raker spacing and gape width (Palkovacs and Post 2008; Schielke et al. 2011). Their trophic morphology has diverged in a manner that indicates inter-population variation in prey selectivity. Palkovacs and Post (2008) hypothesized that these differences were driven by the distinct ecological effects of each form, however many other forces could be working in concert to shape the morphology of each form.

To identify ecological forces potentially driving this emerging pattern of parallel divergence, we explored differences between the alewife forms in body shape. We chose to study body shape in anadromous and landlocked alewife for three reasons: first, populations exhibiting divergent trophic morphology often exhibit divergent body shape as well (Smith and Skúlason 1996; Robinson and Parsons 2002). Second, patterns of body shape divergence have been well studied in fishes (Domenici and Kapoor 2010), and ecological drivers of body shape divergence are relatively well understood (reviewed in Langerhans 2010). Thus, comparing the body shapes of anadromous and landlocked alewives may provide valuable information about potential ecological drivers of their divergence. Finally, describing body shape in independently derived landlocked populations provides a further test of the idea that these populations are diverging in parallel from their anadromous ancestors.

Migratory behavior, habitat availability and resource availability are all potentially important drivers of phenotypic divergence among alewife populations. Migratory differences between populations commonly drive divergence in body shape in fishes. Typically, populations that migrate longer distances display a more streamlined fusiform body

shape that makes for more efficient sustained swimming, whereas populations that migrate shorter distances display a less streamlined form (Taylor and Foote 1991; Fraser and Bernatchez 2005; Varian and Nichols 2010; but see Aguirre 2009 for an exception to this general rule). Migration is a particularly likely driver of divergence in alewife populations because the anadromous form undergoes a substantial migration, while the landlocked form does not migrate.

Habitat availability differs consistently between landlocked and anadromous lakes, and could play a role in driving the divergence of alewife forms. Typically, contrasting patterns of lacustrine habitat availability (and correlated differences in resource availability) leads to predictable patterns of body shape divergence among populations (Walker 1997; Robinson and Parsons 2002; Svanback and Eklov 2004; Riopel et al. 2008; Aguirre 2009). For example, populations in lakes with relatively more littoral habitat generally display deeper bodies, larger heads, and deeper and shorter caudal regions (Lavin and McPhail 1986; Robinson and Wilson 1994; Walker 1997; Wilson 1998). This robust body form provides improved acceleration and maneuverability, both of which help fish forage in structurally complex environments (Walker 1997; Langerhans 2010). In contrast, populations in lakes with relatively more pelagic habitat show a more fusiform body shape characterized by shallower bodies, smaller heads, and a slender caudal region. These more streamlined features enhance steady swimming ability and make for more efficient use of open habitats.

While resource availability is often correlated with habitat availability, it is possible for resources to become decoupled from habitat availability as a result of predation and resource depletion (Ward et al. 2006). For example when a predator population depletes a preferred prey it shapes both the prey community (e.g., Brooks and Dodson 1965; Sih et al. 1985) and the resources available to the predator population. This decoupling of resources from habitat availability could lead to a number of patterns of divergence, the most likely of which being that fish exhibit body shapes that correspond to the resources that are available (not the habitats). Based on the reported differences in diet selectivity (Palkovacs and Post 2008), and the effects of alewife on their prey resources (Post et al. 2008; Palkovacs and Post 2009), if this is the primary driver of divergence of alewife body shape we would expect that landlocked populations would exhibit a more fusiform shape while anadromous populations would be more robust.

To test for differences in body shape among anadromous and landlocked alewives, we collected individuals from three anadromous and three landlocked populations. We analyzed body shape in these replicate populations using standard geometric morphometric approaches. We compared our results to expectations based on the large literature on body shape as well as previous work related to alewife (Table 1). To add an additional line of evidence, we also explored the lacustrine diet source use of each form using carbon stable isotope data.

## Methods

### Field sampling

This study included six lakes, five in Connecticut and one in Massachusetts, USA. All Connecticut study lakes are less than 15 km from Long Island Sound, and the most distant of these lakes are 42.5 km apart (linear distance). Upper Mill Pond, in Massachusetts, is less than 2 km from Cape Cod Bay and approximately 200 km from the furthest

**Table 1** Expected patterns of divergence between alewife life history forms resulting from each ecological driver

Feature	Population	Ecological driver		
		Migratory behavior	Habitat availability (linked to resources)	Resource availability (resulting from predation)
Body shape	Anadromous	F	F	R
	Landlocked	R	R	F
Diet source	Anadromous	–	P > L	P < L
	Landlocked	–	P < L	P > L

Body shape expectations correspond to a mean shape that is more fusiform (F) and more robust (R). Diet source relates to the mean diet source of the population being comprised of more littoral (L) or pelagic (P) carbon

Connecticut Lake. The three anadromous lakes, lakes serving as spawning and juvenile rearing habitat for anadromous alewives, included Bride Lake, Dodge Pond, and Upper Mill Pond. The three landlocked lakes, which contain resident landlocked populations, included Quonnipaug Lake, Pattagansett Lake, and Rogers Lake. Individual lakes do not vary greatly in productivity or other environmental parameters aside from habitat availability (Table 2; Post et al. 2008). From July to October 2009, approximately 30–65 young-of-the-year (YOY) alewives per lake were collected with a small mesh research purse seine, euthanized, immediately placed on ice, and then stored at  $-20^{\circ}\text{C}$  until further analyses could be performed. We focused on YOY for this study because it is the age at which alewife life history forms are most comparable in size and the only age at which anadromous alewife forage in lakes (like many anadromous fishes, anadromous alewife adults do not feed on spawning runs; Dadswell et al. 1987). This study was conducted under our approved Yale University Institutional Animal Care and Use Committee Protocol #2009-10734. Fish sampling was conducted under State of Connecticut collection permit #SC-04016, and Commonwealth of Massachusetts collection permit #183.09SCF.

### Morphometric analysis

To compare morphologies between life history forms, we utilized both traditional measurements and geometric morphometrics. Traditional measurements included standard length, which was taken for each individual using digital calipers, and wet weight, which was measured using a digital scale. Gill raker spacing and gape width are known to differ between these forms (Palkovacs and Post 2008, 2009) and thus were not included in the analysis. Prior to analysis, data were  $\log_{10}$ -transformed to meet the assumptions of normality and homogeneity of variance. We tested for differences between mean standard lengths of the forms with linear mixed models using restricted maximum likelihood estimation. For each dependent variable, lake type was treated as a fixed effect while population was nested in lake type as a random effect. To test for differences in mean weights, we used a similar analysis but included standard length as a covariate. These analyses and other statistical tests were run as linear mixed models in SAS (SAS v. 9.2, SAS Institute, Cary, NC, USA). To effectively treat populations as the unit of replication, we used the between-within subject method to approximate the degrees of freedom in all tests of fixed effects. For this, the random effect of population nested within lake type was used as the

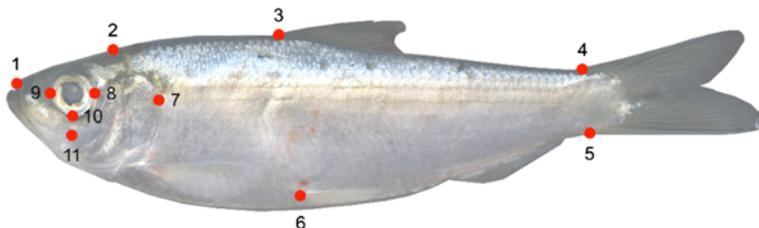
**Table 2** Descriptions of anadromous (A) and landlocked (L) lakes included in this study

	Latitude	Longitude	Area (ha)	Max depth (m)	Mean secchi depth (m)	Proportion pelagic habitat
Bride Lake (A)	41.33	72.24	29	11	2.5	0.73
Dodge Pond (A)	41.33	72.20	14	16	3.2	0.60
Upper Mill Pond (A)	41.73	70.12	102	9	2.3	0.58
Anadromous mean (SD)	41.46 (0.20)	71.52 (1.06)	48.33 (44.35)	12.00 (3.51)	2.67 (0.45)	0.64 (0.08)
Pattagansett Lake (L)	41.37	72.23	49	10	2.9	0.44
Quonnipaug Lake (L)	41.39	72.69	45	15	2.6	0.50
Rogers Lake (L)	41.36	72.23	106	20	2.7	0.50
Landlocked mean (SD)	41.37 (0.02)	72.38 (0.23)	66.67 (30.92)	15.00 (2.89)	2.73 (0.07)	0.48 (0.01)

The proportions of pelagic and littoral habitats were calculated as in Walker (1997). Differences in habitat availability were significant (Mann–Whitney  $U$  test;  $Z = -1.77$ ,  $p < 0.05$ ). Secchi depth mean values were calculated from measurements taken between June and September 2009. Mean values for each lake type are accompanied by standard deviations in parentheses

subject.  $F$  values are reported for fixed effects (lake type), and Wald  $Z$  values from a likelihood ratio test are reported for random effects (population).

To describe the lateral body shape of the fish, we employed landmark-based geometric morphometrics (Bookstein 1997; Adams et al. 2004). Prior to dissection, specimens were fully thawed, straightened with acupuncture pins, and the left side of each specimen was photographed using a 10 megapixel Canon Powershot A720. To minimize the potential for error, samples were processed in a random order, making it highly unlikely that preservation or variable positioning would account for any consistent differences found. To quantify body shape, we used 11 landmarks chosen based on previous work on clupeids (e.g., Silva 2003; Fig. 1). All landmarks were placed using tpsDig2 v2.16 (Rohlf 2010). Only individuals not damaged in collection with clearly visible landmarks were used for the analysis ( $n = 95$  landlocked,  $n = 192$  anadromous). The Procrustes fit function in MorphoJ v1.02e (Klingenberg 2011) was used to generate a consensus shape and remove variation due to scaling, rotation, and translation (Rohlf and Slice 1990; Adams et al. 2004; Zelditch 2004).



**Fig. 1** Location of landmarks used for analysis: 1 anterior tip of the maxilla, 2 posterior end of the supraoccipital, 3 anterior insertion of the dorsal fin, 4 dorsal insertion of the caudal fin, 5 ventral insertion of the caudal fin, 6 anterior insertion of the pelvic fin, 7 posterior insertion of the operculum, 8 posterior extent of the orbit, 9 anterior extent of the orbit, 10 ventral extent of the orbit, and 11 posterior extent of the maxilla

Rapidly growing juvenile fish undergo profound changes in shape and size; therefore, we determined the patterns of allometric change in each life history form. This is especially true given that patterns of allometry in other traits, such as gill raker spacing and gape width, are known to vary between anadromous and landlocked populations (Palkovacs et al. 2008). To test for differences in shape allometry between life history forms, we first conducted a preliminary principal components analysis (PCA) on the covariance matrix in MorphoJ. The first three principal components (PCs) summarized 75 % (36, 27, and 12 %, respectively) of the variation, and further PCs summarized less than 6 % of the variation. To test for an effect of shape on size, we then regressed the first three PCs on standard length (Sidlauskas et al. 2011). Standard length was significant for all three PCs ( $p < 0.001$ ), indicating that there was a strong effect of size on shape. However, the interaction term of each model was not significant ( $p > 0.05$ ), indicating that the slopes of the allometric relationship between shape and size does not differ between alewife life history forms (Zelditch 2004). Because of this strong and consistent allometric signal, we sought to distinguish size-dependent variation from size-independent variation in shape so that the size-independent variation among life history forms could be compared. To do this, we regressed the Procrustes coordinates on standard length using the pooled within sub-group regression in MorphoJ (Harrod et al. 2010; Sidlauskas et al. 2011). The residuals of this regression were subsequently used for further analysis.

To distinguish the axes of size-independent variation, we performed a second PCA on the covariance matrix of the residuals. Additionally, to describe the axis of variation that best distinguished the two life history forms, we performed a discriminant function analysis (DFA). The statistical differences in PCA and DFA scores were assessed using linear mixed models. Similar to other analyses, lake type was treated as a fixed effect, while population was nested within lake type and was treated as a random effect.

The convex hull occupied by the data points of each population was used as a measure of disparity. We chose this measure because it describes the total morphospace occupied by each population (Drake and Klingenberg 2010). Principal component axes 1 and 2 were used for this analysis because they contained most of the variation in the sample. A *t*-test comparing the sizes of the convex hulls was used to test for differences in disparity between life history forms. We also used the visualization of the convex hull to help illustrate regions of morphospace occupied by each population. For all analyses, shape variations in the DFA and PCA were visualized in the form of thin-plate splines. Scalable vector graphic files of the thin-plate splines were used to illustrate differences in body shape and were adjusted (color change, etc.) in Inkscape (v. 0.47).

### Stable isotope analysis

To assess the diets of individuals used for our study, we analyzed the ratios of stable carbon isotopes in epaxial muscle tissue from individuals used in the morphometric analysis (landlocked  $n = 93$ , anadromous  $n = 193$ ). This value was compared to stable isotope ratios of primary consumers of pelagic and littoral resources from each lake to determine the proportion of their diet that is derived from each source (Post 2002). To estimate the diet of an individual alewife we used the equation:

$$\alpha = (\delta^{13}\text{C}_{\text{ale}} - \delta^{13}\text{C}_{\text{lit}}) / (\delta^{13}\text{C}_{\text{pel}} - \delta^{13}\text{C}_{\text{lit}})$$

where  $\alpha$  equals the proportion of pelagic carbon in the diet of an individual,  $\delta^{13}\text{C}_{\text{lit}}$  and  $\delta^{13}\text{C}_{\text{pel}}$  are the baseline values from a given lake, and  $\delta^{13}\text{C}_{\text{ale}}$  is the value for a given individual. For this study, muscle tissue from 3 to 5 unioid mussels and 3 to 5 planorbid snails were used as pelagic and littoral baselines, respectively for each lake. Isotopic baselines and fish were collected concurrently. Muscle tissue samples from fish and baseline organisms were dried at 45 °C for >48 h, then ground to a homogenous powder using a mortar and pestle. One milligram of tissue from each sample was weighed into individual tin cups and analyzed on a ThermoFinnigan Delta<sup>PLUS</sup> Advantage stable isotope mass spectrometer (Thermo Scientific, Boca Raton, FL) coupled with a Costech ECS 4010 EA elemental analyzer (Costech Analytical Technologies, Valencia, CA). Each run included a house standard (trout muscle tissue) every 2–8 samples to correct for drift and amplitude effects through each run. Overall the lipid concentration in the tissues was low (C:N mean = 2.93, % lipid mean = 0.67), and a comparison of C:N values did not indicate significant variation among life history forms. Baseline samples were equally lipid depleted, thus mathematical lipid correction was deemed unnecessary and was not performed (Post et al. 2007). To test for differences between life history types, we again used a linear mixed model, with size as a covariate and population nested in lake type as a random effect.

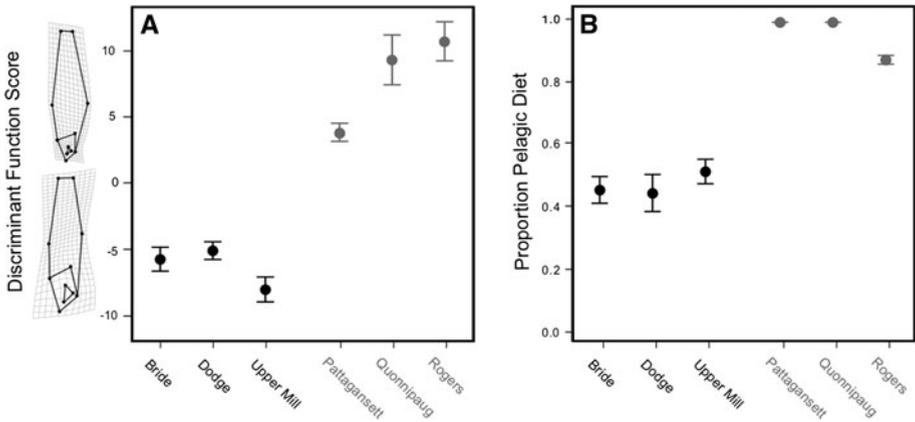
## Results

Landlocked and anadromous YOY alewives ranged in size (23–99 mm), but neither  $\log_{10}$ -transformed mean length ( $F_{1,4} = 0.34$ ,  $p = 0.59$ ) nor  $\log_{10}$ -transformed wet weight ( $F_{1,4} = 1.55$ ,  $p = 0.28$ ) differed significantly between life history forms.

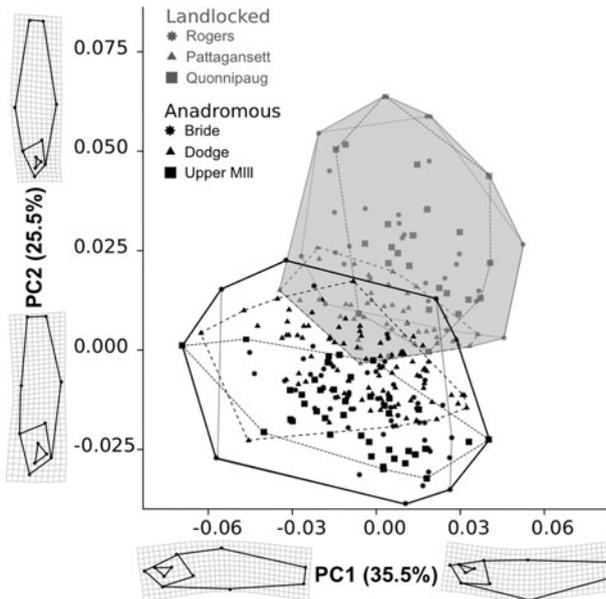
The discriminant function analysis showed highly significant differences between the mean shapes of the two life history forms (*Life History*:  $F_{1,4} = 38.85$ ,  $p = 0.003$ ; *Population*:  $Z = 1.21$ ,  $p = 0.92$ ). The axis that best differentiated the populations included differences in head size and caudal region shape. Landlocked fish consistently had smaller heads and more slender caudal regions, while anadromous fish had larger heads and deeper and shorter caudal regions (Fig. 2a).

In the principal component analysis, the first two components described 62 % of the variation (36.5 and 25.5 %, respectively), whereas components three and beyond described less than 10 % of the variation. Therefore, we focused on PC1 and PC2 for our analysis. PC1, which described the orientation of the mouth and general bend of the body, was significantly different between the landlocked and anadromous populations, but was not significant among populations (*Life History*:  $F_{1,4} = 22.82$ ,  $p = 0.009$ ; *Population*:  $Z = 0.27$ ,  $p = 0.39$ ). Landlocked fish generally had more positive PC1 values, corresponding to a more super-terminal mouth orientation. Anadromous fish showed the opposite pattern, with a more terminal to sub-terminal mouth orientation (Fig. 3). Bending in fish specimens, similar to what is seen in PC1, has been reported in other fish specializing on littoral or pelagic prey.

PC2 described three morphological features: (1) head size, (2) caudal peduncle shape, and (3) general body shape, which ranged from fusiform to robust. We observed significant differences along PC2 between the life history forms, but not among populations within forms (*Life History*:  $F_{1,4} = 20.04$ ,  $p = 0.01$ ; *Population*:  $Z < 1.35$ ,  $p = 0.09$ ). This axis clearly distinguished the two groups, with little overlap between them (Fig. 3). Landlocked alewives displayed a streamlined, fusiform body with reduced head size and a longer and



**Fig. 2** Patterns of morphological and dietary divergence between life history forms. Landlocked populations are represented with *gray circles* and anadromous populations are represented with *black circles*. *Error bars* represent 95 % confidence intervals. **a** The mean discriminant function analysis (DFA) score for body shape for each population. **b** The proportion pelagic diet based on carbon stable isotope analysis for each population



**Fig. 3** Size-corrected morphospace occupied by each life history form. *Black symbols* represent anadromous individuals and *gray symbols* represent landlocked individuals. Each population is represented by a *different symbol* with *thin lines* delineating the convex hull for each population. Thin-plate spline transformation grids show the extreme cases along each principal component axis

more slender caudal region. In contrast, anadromous alewives were more robust with larger heads and a deeper and shorter caudal region.

We found relatively similar amounts of morphological variation in each life history form (Fig. 3). The mean morphospace occupied by a population as measured by its convex hull was not significantly different between the two life history forms ( $t_4 = 0.5126$ ,  $p = 0.31$ ). For PC1, landlocked populations occupy a subset of the anadromous morphospace. However, for PC2 landlocked populations occupy a large region of morphospace not occupied by their anadromous ancestors. This novel region corresponds to the most extreme values for smaller heads and more fusiform bodies (PC2).

Mean population diets were distinctly different between alewife forms (Fig. 2b). Anadromous alewives obtained slightly less than half of their diet from pelagic sources ( $0.47 \pm 0.02$ , mean  $\pm$  SE), whereas landlocked alewives obtained nearly all of their diet from pelagic sources ( $0.98 \pm 0.01$ ). The slopes of the relationships between  $\log_{10}$  standard length and proportion pelagic diet were significantly different for each life history form (*Life History* \* *Log<sub>10</sub> SL*:  $F_{1,272} = 180.39$ ,  $p < 0.001$ ). The slope of the relationship between length and proportion pelagic diet was effectively flat for landlocked populations, whereas the proportion pelagic diet decreased with increasing size for anadromous fish. Again, populations within the same life history form did not differ significantly (*Population*:  $Z = 1.10$ ,  $p = 0.13$ ).

## Discussion

Our analysis revealed clear differences in body shape and diet between alewife life history forms, with consistent differences across replicate populations. Landlocked populations exhibited smaller heads and longer, more slender caudal regions than anadromous populations. Though maximum body depth was not dramatically different between the forms, landlocked populations exhibited a more fusiform shape than anadromous populations due to their smaller heads and slimmer caudal peduncles (Figs. 2a, 3). Each form occupied a similar total area of morphospace, but the regions occupied by each form were clearly distinct (Fig. 3). This result suggests that landlocked populations have diverged from ancestral anadromous populations, such that they occupy a large region of novel morphospace. This type of divergence into novel regions of morphospace is often associated with the colonization of new habitats or niches (e.g., Price et al. 2011). We also found significant differences in the diets of the two life history forms. Anadromous fish consumed approximately equal proportions of littoral and pelagic prey, whereas landlocked fish consumed almost exclusively pelagic prey (Fig. 2b). In addition, anadromous alewives appear to make an ontogenetic transition from pelagic to littoral prey, whereas landlocked alewives retain their pelagic niche through their ontogeny. Subtle differences in development among populations can lead to phenotypic differentiation (McPhee et al. 2012), and may contribute to the patterns we report here.

Many selective ecological forces could potentially be driving the phenotypic divergence of alewife life history forms; however, we can use our results to assess the likelihood of a few potential ecological drivers. While habitat availability and migratory behavior are two of the most commonly reported drivers of differences in body shape between recently diverged fish populations (Bell and Andrews 1997), it is unlikely that the landlocked alewife populations have diverged from their anadromous ancestors as a result of either of these selective forces. First, the diets of both alewife forms oppose what we would expect based on habitat availability in the lakes (Table 1): anadromous populations, which inhabit

lakes with relatively more pelagic habitat, consistently consume more littoral resources, and landlocked populations, which inhabit lakes with more littoral habitat, consistently consume almost entirely pelagic resources (Fig. 2b). Second, the body shape of the derived landlocked populations does not match general expectations of how body shape should change in response to habitat availability or migratory behavior. Specifically, we would expect landlocked alewives to exhibit a more robust shape than their anadromous ancestors (Robinson and Wilson 1994; Bell and Andrews 1997; Riopel et al. 2008; Langerhans 2010), but instead we find the opposite pattern.

Based on information from other studies, a few additional common drivers seem unlikely as well. Previous results indicate that abiotic factors including total lake area, maximum depth, and total phosphorus do not covary with alewife life history form, and thus are unlikely to have produced the pattern we have observed (Post et al. 2008). Predation and competition from other fish species are also potential drivers, but seem unlikely, in part because landlocked and anadromous alewife lakes do not vary systematically in fish species composition (Jacobs and O'Donnell 2002). Additionally, slight differences among lake types in the abundance and distribution of alewife competitors (Palkovacs and Post 2008) and predators (J.G. Howeth, J. Brodersen and D.M. Post, unpublished data) oppose what we would expect if these factors were driving alewife divergence. Thus, while predation and competition have been shown to affect the body shape of a number of fish species (Domenici et al. 2008; Langerhans 2010), given what we know about the alewife system they are likely not the primary drivers of morphological divergence.

Resource abundance is often assumed to covary with habitat availability in lakes, and the abundance of a habitat is often used as a proxy for resources when studying patterns of adaptation (Bell and Andrews 1997; Aguirre 2009). Predation can be decouple resources from habitat availability however, and because of this, it is not surprising that resource consumption in both alewife forms directly conflicts with habitat availability. Additionally, incorporating what we know about the specific effects of each alewife form on their pelagic zooplankton communities (e.g., Post et al. 2008), makes the pattern of resource utilization we report seem quite reasonable. Post et al. (2008) showed that it is the continuous presence and predation (on zooplankton) by landlocked alewives maintains a stable small-bodied prey community, while the periodic presence of anadromous alewives creates a cyclical dynamic in prey abundance (large-bodied zooplankton are initially abundant in spring but juvenile alewife predation drives them to low levels by summer). Given these differences in zooplankton resources among replicate lakes, and additional experimental evidence linking alewife form to zooplankton community composition (Palkovacs and Post 2009), it seems likely that these biotically driven differences in resource abundance have shaped patterns we observed in alewife diet. Furthermore, it seems probable that these effects could have fed back to shape alewife morphology (an eco-evolutionary feedback; Palkovacs and Post 2008; Post and Palkovacs 2009).

The patterns of body shape we report here are consistent with the idea that the strong but distinct ecological effects of each alewife form on their resources have played a role in shaping the morphological divergence between forms. The more robust body shape of anadromous populations, featuring a larger head and larger caudal region (Figs. 2b, 3), is likely related to their use of littoral habitats. This more robust morphology could also be favored in the estuarine or marine habitats of adult anadromous alewives. After emigrating from the lakes, anadromous alewives forage primarily on large-bodied invertebrates in these habitats (Stone and Daborn 1987; Stone and Jessop 1994). The morphologies observed in landlocked populations also closely match our expectations related to alewife

structured resource availability. Given the prey environment that landlocked alewives create (a stable environment of small-bodied zooplankton), it makes sense that this selects for traits that facilitate the capture of small-bodied pelagic zooplankton (Fig. 2a). A slimmer caudal peduncle region and smaller head (Figs. 2b, 3) serve this purpose well, as a more fusiform body shape increases steady swimming efficiency, thus improving their performance as pelagic filter feeders (Weihs 1989; Langerhans 2010).

The data we present here suggest that habitat availability and differences in migratory behavior are unlikely to be the primary drivers of divergence in body shape and diet of anadromous and landlocked alewives. Instead, the close correspondence between alewife form and resource availability (following the structuring of the prey community by each life history form of the alewife predator; Post et al. 2008), indicates that these populations may be diverging in response to their own ecological effects. While experimentally assessing both the functional consequences of these differences in body shape, as well as the heritability of these differences, remain key areas for future research, this work provides a clear path for future eco-morphological work in the alewife system. Developing our understanding of the process promoting divergence between alewife forms is especially vital because, as a likely example of an eco-evolutionary feedback (Post and Palkovacs 2009; Schoener 2011), they provide an opportunity to learn more about the mechanisms driving these processes. This mechanism may be especially important in fishes, because many species modify the conditions of their environment (e.g., Power et al. 1996), and exhibit rapid evolutionary responses to modified environmental conditions (Bell and Andrews 1997; Hendry et al. 2000). Thus, eco-evolutionary dynamics may be more common than they are currently considered, and should receive examination as mechanisms promoting adaptive diversification.

**Acknowledgments** We thank R. Beinart, J. Brodersen, T. Hanley, J. Howeth, M. Sorenson, J. Vellota, M. Walsh, J. Weis, and D. West for their assistance in the field and lab, and G. Olack and D. Collosi for their assistance with stable isotope analysis. Comments by anonymous reviewers, T. Hanley and M. Walsh helped significantly improve this manuscript. This research was supported by NSF DEB No. 0717265 to D. M. Post, and an NSF GRF to A. W. Jones.

## References

- Adams DC, Rohlf FJ, Slice DE (2004) Geometric morphometrics: ten years of progress following the 'revolution'. *Italian J Zool* 71(1):5–16. doi:10.1080/11250000409356545
- Aguirre WE (2009) Microgeographical diversification of threespine stickleback: body shape-habitat correlations in a small, ecologically diverse Alaskan drainage. *Biol J Linn Soc* 98(1):139–151. doi:10.1111/j.1095-8312.2009.01267.x
- Bell MA, Andrews CA (1997) Evolutionary consequences of colonization of fresh water by primitively anadromous fishes. In: Streit B, Städler T, Lively CM (eds) *Evolutionary ecology of freshwater animals: concepts and case studies*. Birkhäuser, Basel, pp 323–363
- Bookstein FL (1997) *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, Cambridge
- Brooks JL, Dodson SI (1965) Predation body size and composition of plankton. *Science* 150:28–35. doi:10.1126/science.150.3692.28
- Dadswell MJ, Klauda RJ, Moffitt CM, Saunders RL (1987) Common strategies of anadromous and catadromous fishes. American Fisheries Society, Bethesda
- Domenici P, Kapoor BG (2010) *Fish locomotion: an eco-ethological perspective*. Science Publishers, Enfield
- Domenici P, Turesson H, Brodersen J, Brönmark C (2008) Predator-induced morphology enhances escape locomotion in crucian carp. *Proc R Soc Lond B* 275:195–201

- Drake AG, Klingenberg CP (2010) Large-scale diversification of skull shape in domestic dogs: disparity and modularity. *Am Nat* 175:289–301. doi:[10.1086/650372](https://doi.org/10.1086/650372)
- Fraser DJ, Bernatchez L (2005) Adaptive migratory divergence among sympatric brook charr populations. *Evolution* 59:611–624. doi:[10.1554/04-346](https://doi.org/10.1554/04-346)
- Harrod C, Mallela J, Kahilainen KK (2010) Phenotype-environment correlations in a putative whitefish adaptive radiation. *J Anim Ecol* 79:1057–1068. doi:[10.1111/J.1365-2656.2010.01702.X](https://doi.org/10.1111/J.1365-2656.2010.01702.X)
- Hendry AP, Wenburg JK, Bentzen P, Volk EC, Quinn TP (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516–518. doi:[10.1126/science.290.5491.516](https://doi.org/10.1126/science.290.5491.516)
- Jacobs RP, O'Donnell EB (2002) A fisheries guide to lakes and ponds of Connecticut, including the Connecticut River and its coves. Connecticut Department of Environmental Protection, Hartford
- Jonsson B, Jonsson N (2001) Polymorphism and speciation in Arctic charr. *J Fish Biol* 58:605–638. doi:[10.1006/Jfbi.2000.1515](https://doi.org/10.1006/Jfbi.2000.1515)
- Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. *Mol Ecol Resour* 11:353–357. doi:[10.1111/j.1755-0998.2010.02924.x](https://doi.org/10.1111/j.1755-0998.2010.02924.x)
- Langerhans RB (2010) Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. In: Domenici P, Kapoor BG (eds) *Fish locomotion: an etho-ecological perspective*. Science Publishers, Enfield, pp 200–208
- Langerhans RB, Gifford ME, Joseph EO (2007) Ecological speciation in *Gambusia* fishes. *Evolution* 61:2056–2074. doi:[10.1111/j.1558-5646.2007.00171.x](https://doi.org/10.1111/j.1558-5646.2007.00171.x)
- Lavin PA, McPhail JD (1986) Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Can J Fish Aquat Sci* 43:2455–2463. doi:[10.1139/f86-305](https://doi.org/10.1139/f86-305)
- Lu GQ, Bernatchez L (1999) Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. *Evolution* 53:1491–1505. doi:[10.2307/2640895](https://doi.org/10.2307/2640895)
- McPhail JD (1984) Ecology and evolution of sympatric sticklebacks (*Gasterosteus*)—morphological and genetic-evidence for a species pair in Enos Lake, British-Columbia. *Can J Zool* 62:1402–1408
- McPhee MV, Noakes DL, Allendorf FW (2012) Developmental rate: a unifying mechanism for sympatric divergence in postglacial fishes? *Curr Zool* 58:21–34
- Michel C, Hicks BJ, Stoltzing KN, Clarke AC, Stevens MI, Tana R, Meyer A, van den Heuvel MR (2008) Distinct migratory and non-migratory ecotypes of an endemic New Zealand eleotrid (*Gobiomorphus cotidianus*)—implications for incipient speciation in island freshwater fish species. *BMC Evol Biol* 8:49. doi:[10.1186/1471-2148-8-49](https://doi.org/10.1186/1471-2148-8-49)
- Narum SR, Contor C, Talbot A, Powell MS (2004) Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, USA. *J Fish Biol* 65:471–488. doi:[10.1111/j.0022-1112.2004.00461.x](https://doi.org/10.1111/j.0022-1112.2004.00461.x)
- Palkovacs EP, Post DM (2008) Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evol Ecol Res* 10:699–720
- Palkovacs EP, Post DM (2009) Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology* 90:300–305. doi:[10.1890/08-1673.1](https://doi.org/10.1890/08-1673.1)
- Palkovacs EP, Dion KB, Post DM, Caccone A (2008) Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. *Mol Ecol* 17:582–597. doi:[10.1111/j.1365-294X.2007.03593.x](https://doi.org/10.1111/j.1365-294X.2007.03593.x)
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718. doi:[10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- Post DM, Palkovacs EP (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos T R Soc B* 364:1629–1640. doi:[10.1098/rstb.2009.0012](https://doi.org/10.1098/rstb.2009.0012)
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189. doi:[10.1007/s00442-006-0630-x](https://doi.org/10.1007/s00442-006-0630-x)
- Post DM, Palkovacs EP, Schielke EG, Dodson SI (2008) Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* 89:2019–2032. doi:[10.1890/07-1216.1](https://doi.org/10.1890/07-1216.1)
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *Bioscience* 46:609–620

- Price SA, Holzman R, Near TJ, Wainwright PC (2011) Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol Lett* 14:462–469. doi:[10.1111/j.1461-0248.2011.01607.x](https://doi.org/10.1111/j.1461-0248.2011.01607.x)
- Reznick D, Endler JA (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 36(1):160–177
- Riopel C, Robinson BW, Parsons KJ (2008) Analyzing nested variation in the body form of Lepomid sunfishes. *Environ Biol Fish* 82:409–420. doi:[10.1007/s10641-007-9303-9](https://doi.org/10.1007/s10641-007-9303-9)
- Robinson BW, Parsons KJ (2002) Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Can J Fish Aquat Sci* 59(11):1819–1833. doi:[10.1139/F02-144](https://doi.org/10.1139/F02-144)
- Robinson BW, Wilson DS (1994) Character release and displacement in fishes—a neglected literature. *Am Nat* 144:596–627. doi:[10.1086/285696](https://doi.org/10.1086/285696)
- Rohlf J (2010) TPSDig2. 2.16, Department of Ecology and Evolutionary Biology, SUNY, Stony Brook
- Rohlf FJ, Slice D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst Zool* 39(1):40–59. doi:[10.2307/2992207](https://doi.org/10.2307/2992207)
- Schielke EG, Palkovacs EP, Post DM (2011) Eco-evolutionary feedbacks drive niche differences in alewives. *Biol Theory* 6:211–219. doi:[10.1007/s13752-012-0031-9](https://doi.org/10.1007/s13752-012-0031-9)
- Schluter D (1996) Ecological speciation in postglacial fishes. *Philos T R Soc B* 351:807–814. doi:[10.1098/rstb.1996.0075](https://doi.org/10.1098/rstb.1996.0075)
- Schluter D (2000) The ecology of adaptive radiation. Oxford series in ecology and evolution. Oxford University Press, Oxford
- Schoener TW (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331:426–429. doi:[10.1126/science.1193954](https://doi.org/10.1126/science.1193954)
- Sidlauskas BL, Mol JH, Vari RP (2011) Dealing with allometry in linear and geometric morphometrics: a taxonomic case study in the *Leporinus cylindriformis* group (Characiformes: Anostomidae) with description of a new species from Suriname. *Zool J Linn Soc Lond* 162:103–130. doi:[10.1111/J.1096-3642.2010.00677.X](https://doi.org/10.1111/J.1096-3642.2010.00677.X)
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Annu Rev Ecol Syst* 16:269–311
- Silva A (2003) Morphometric variation among sardine (*Sardina pilchardus*) populations from the north-eastern Atlantic and the western Mediterranean. *ICES J Mar Sci* 60:1352–1360. doi:[10.1016/S1054-3139\(03\)00141-3](https://doi.org/10.1016/S1054-3139(03)00141-3)
- Smith TB, Skúlason S (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu Rev Ecol Syst* 27:111–133. doi:[10.1146/Annurev.Ecolsys.27.1.111](https://doi.org/10.1146/Annurev.Ecolsys.27.1.111)
- Stone HH, Daborn GR (1987) Diet of alewives, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid, macrotidal estuary. *Environ Biol Fish* 19:55–67. doi:[10.1007/BF00002737](https://doi.org/10.1007/BF00002737)
- Stone HH, Jessop BM (1994) Feeding habits of anadromous alewives, *Alosa pseudoharengus*, off the Atlantic coast of Nova Scotia. *Fish B NOAA* 92:157–170
- Svanback R, Eklov P (2004) Morphology in perch affects habitat specific feeding efficiency. *Funct Ecol* 18:503–510. doi:[10.1111/j.0269-8463.2004.00858.x](https://doi.org/10.1111/j.0269-8463.2004.00858.x)
- Taylor EB, Foote CJ (1991) Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *J Fish Biol* 38:407–419. doi:[10.1111/j.1095-8649.1991.tb03130.x](https://doi.org/10.1111/j.1095-8649.1991.tb03130.x)
- Varian A, Nichols KM (2010) Heritability of morphology in brook trout with variable life histories. *PLoS ONE* 5(9):e12950. doi:[10.1371/journal.pone.0012950](https://doi.org/10.1371/journal.pone.0012950)
- Walker JA (1997) Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. *Biol J Linn Soc* 61:3–50. doi:[10.1111/j.1095-8312.1997.tb01777.x](https://doi.org/10.1111/j.1095-8312.1997.tb01777.x)
- Walker JA, Bell MA (2000) Net evolutionary trajectories of body shape evolution within a microgeographic radiation of threespine sticklebacks (*Gasterosteus aculeatus*). *J Zool* 252:293–302
- Ward AJW, Webster MM, Hart PJB (2006) Intraspecific food competition in fishes. *Fish Fish* 7:231–261. doi:[10.1111/j.1467-2979.2006.00224.x](https://doi.org/10.1111/j.1467-2979.2006.00224.x)
- Weihls D (1989) Design features and mechanics of axial locomotion in fish. *Am Zool* 29:151–160
- Wilson DS (1998) Adaptive individual differences within single populations. *Philos T R Soc B* 353:199–205. doi:[10.1098/rstb.1998.0202](https://doi.org/10.1098/rstb.1998.0202)
- Wood CC, Foote CJ (1996) Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* 50:1265–1279. doi:[10.2307/2410667](https://doi.org/10.2307/2410667)
- Zelditch M (2004) Geometric morphometrics for biologists: a primer. Elsevier Academic Press, Amsterdam