

# Eco-Evolutionary Feedbacks Drive Niche Differentiation in the Alewife

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**Abstract** Intraspecific niche variation can differentially impact community processes and can represent the initial stages of adaptive radiation. Here we test for intraspecific differences in niche use in a keystone species, the alewife (*Alosa pseudoharengus*). To test whether feedbacks between predator foraging traits and prey communities have led to differences in niche use, we compare the diet composition and trophic position of anadromous and landlocked alewife populations. These populations differ in phenotypic traits related to foraging (gill raker spacing, gape width, and prey selectivity). Trait differences appear to have resulted from eco-evolutionary feedbacks between alewives and their zooplankton prey, and suggest that these two life history forms are exploiting different niches. Direct diets show that anadromous alewives consume a greater biomass of predatory copepods than do landlocked alewives. Anadromous alewives also consume more ostracods—a littoral prey item—as the growing season progresses. These diet differences do not translate into a significant difference in trophic position, as estimated from

stable isotopes. However, stable-isotope estimates of diet source show that during early fall, anadromous alewives obtain significantly more of their dietary carbon from the littoral food web. This increased reliance on littoral prey is likely a result of a diet switch that occurs in response to the alewife-driven exhaustion of large-bodied prey items available in the pelagic zone, i.e., alewife niche construction. These findings show the existence of important intraspecific niche differences in the alewife and support the role of eco-evolutionary feedbacks in shaping these niche differences. The initiation of alewife divergence is the result of dam building by humans. Therefore, alewife niche differentiation can be considered to be an eco-evolutionary byproduct of human cultural niche construction.

**Keywords** *Alosa pseudoharengus* · Eco-evolutionary dynamics · Intraspecific variation · Niche construction · Predation

## Introduction

Striking cases of niche differentiation can evolve as populations adapt to available resources or habitat characteristics. Seminal examples from terrestrial systems include Darwin's finches in the Galapagos (Grant 1981; Grant and Grant 2002) and *Anolis* lizards in the Caribbean (Williams 1983; Losos et al. 1998). Fishes also provide classic examples, including sticklebacks (Schluter 1996), coregonids (Bernatchez et al. 1999), and cichlids (Meyer et al. 1990). In addition to responding evolutionarily to environmental changes, fishes may also drive community and ecosystem changes (Brooks and Dodson 1965; Carpenter et al. 1987). Both interspecific and intraspecific differences in niche use by fishes have been shown to affect prey-community composition and ecosystem

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processes (Post et al. 2008; Harmon et al. 2009; Palkovacs and Post 2009; Bassar et al. 2010) and can therefore be regarded as instances of niche construction (Odling-Smee et al. 1996, 2003). Intraspecific differences in niche use may also represent the initial stages of speciation (Dieckmann and Doebeli 1999; Schluter 2001; McKinnon et al. 2004; Albert and Schluter 2005). Thus, understanding the causes of intraspecific niche differences, and recognizing that organisms can initiate evolutionary episodes through niche construction, has the potential to deepen our understanding of the processes shaping community structure and adaptive diversification.

The classic view of niche differentiation is unidirectional, with organisms adapting to the suite of existing resources (e.g., Langerhans et al. 2006; Losos et al. 2006; Gavrillets and Losos 2009). However, a few recent studies have emphasized that changes in predator foraging traits can shape prey communities (Yoshida et al. 2003; Hairston et al. 2005; Post et al. 2008), which may then feed back to further influence predator foraging traits (Palkovacs and Post 2008, 2009; Post and Palkovacs 2009). Such feedbacks between predator foraging traits and prey communities are a potential driver of niche differentiation (Post and Palkovacs 2009).

Here we test whether differences in predator foraging traits and prey communities have led to intraspecific niche differences among alewife (*Alosa pseudoharengus*) populations. Two life history forms of alewives exist in northeastern North America. Anadromous alewives spawn in freshwater lakes, where the young-of-the-year (YOY) reside through the summer before leaving to complete their maturation in the ocean. Landlocked alewife populations, which independently evolved multiple times from anadromous populations, spend their entire lifecycle in freshwater lakes (Palkovacs et al. 2008). These divergent life histories have different effects on zooplankton communities, which appear to have influenced phenotypic divergence in alewife foraging traits (Post et al. 2008; Palkovacs and Post 2009).

The alewife is the archetypal size-selective predator (Brooks and Dodson 1965). Lakes with landlocked alewives contain zooplankton communities dominated year-round by small-bodied species, including *Bosmina longirostris* and *Tropocyclops extensus* (Brooks and Dodson 1965; Post et al. 2008). The annual seaward migration of anadromous alewives provides a temporal refuge for large-bodied zooplankton. Therefore, zooplankton communities in lakes with anadromous alewives cycle between an assemblage dominated by large-bodied species, including *Daphnia* spp., in the spring to one dominated by small-bodied species in the summer and fall. Small numbers of large cyclopoid copepods persist in anadromous lakes throughout the year (Post et al. 2008), perhaps because large cyclopoids are adept at avoiding predation by

planktivorous fishes (Drenner et al. 1978). *Daphnia* life history traits and phenotypic plasticity have evolved in response to differences in anadromous and landlocked alewife predation pressures (Walsh and Post 2011, 2012). The year-round residency of landlocked alewives has resulted in strong feedbacks between landlocked alewife foraging traits and zooplankton community composition, while the seasonal residency of anadromous alewives has resulted in weaker feedbacks between anadromous alewife foraging traits and zooplankton community composition (Palkovacs et al. 2008; Post and Palkovacs 2009).

Consistent with local adaptation to these distinct zooplankton communities and the differing strengths of the feedbacks between foraging traits and zooplankton communities, landlocked and anadromous alewives exhibit divergence in foraging traits. Landlocked alewives have smaller gill raker spacing and smaller gape width—adaptations for feeding on small-bodied prey (Palkovacs and Post 2008). Although evidence suggests that they are positively size-selective when introduced into a lake with abundant large-bodied zooplankton (Brooks and Dodson 1965), landlocked alewives are neutrally size-selective when feeding on the small-bodied zooplankton assemblages found in lakes where they are well established (Palkovacs and Post 2008). Anadromous alewives have larger gill raker spacing and larger gape width—adaptations for foraging on large-bodied prey—and are positively size-selective, consuming more predatory cyclopoids than landlocked alewives (Palkovacs and Post 2008).

Two distinct food webs exist within lakes, dominated by carbon derived from either the littoral (shallow-water) or pelagic (open-water) zones. Alewives are pelagic schooling fish, and previous research suggests that landlocked alewives feed almost exclusively in the pelagic zone (Mills et al. 1992, 1995; Pothoven and Vanderploeg 2004; Post et al. 2008). Much less is known about anadromous alewife diets, but previous dietary studies show that they consume pelagic zooplankton (Palkovacs and Post 2008; Post et al. 2008).

These differences in zooplankton community composition and foraging traits suggest that landlocked and anadromous alewives are exploiting different niches—niches that are constructed in large part by their own effects on prey communities. In this study, we combine direct diet data and stable-isotope data to test for niche differentiation between landlocked and anadromous alewives, focusing on differences in trophic position and diet source. The direct diet data give detailed snapshots of consumption, and the stable-isotope techniques provide an integrated measure of diet over a longer timeframe. Together, these two types of data allow us to investigate whether the alewife-induced changes in zooplankton communities—alewife niche construction—have in turn helped drive divergence in alewife niche use.

## Materials and Methods

### Study Site

We sampled six lakes in Connecticut: three with anadromous alewives, hereafter referred to as anadromous lakes (Bride Lake, Gorton Pond, and Dodge Pond) and three with landlocked alewives, hereafter referred to as landlocked lakes (Patagansett Lake, Rogers Lake, and Lake Quonipaug). Lakes serve as independent replicates for all analyses. Genetic data show that the landlocked alewife populations are independently evolved from downstream anadromous populations (Palkovacs et al. 2008). Therefore, these populations represent true replicates from an evolutionary standpoint. The lakes studied here are a subset of the lakes studied by Post and colleagues (2008) and the same lakes studied by Palkovacs and Post (2008). In this subset, landlocked lakes have larger surface area than anadromous lakes but do not differ in productivity or maximum depth (Palkovacs and Post 2008).

### Sample Collections

We collected YOY anadromous or landlocked alewives approximately every 4 weeks from early June through late September in each lake (five sampling dates per lake). Landlocked alewife (YOY) were too small to sample in early June, so we only have anadromous alewives from that time point. We collected all fish at night using a 4.87-m-deep by 35.36-m-long purse seine with 3.18-mm mesh. Fish were euthanized in MS-222 and preserved in 70 % ethanol (for direct diet analysis) or frozen (for stable-isotope analysis). We collected baseline organisms from five of the six study lakes (excluding Gorton Pond). From all five lakes we collected short-lived consumers, periphyton and zooplankton, every 1–4 weeks from early or late May through late August or September. Periphyton and zooplankton provided the baseline end members for the littoral and pelagic food webs, respectively. To sample periphyton, we collected rocks from two locations in the littoral zone of each lake. Using a toothbrush and water, we scraped the periphyton from the rocks and filtered it through 30- $\mu\text{m}$  mesh and onto pre-ashed Whatman GF-C filters. We pooled periphyton from several rocks at each location. We took vertical zooplankton hauls with an 80- $\mu\text{m}$  mesh plankton net from the deepest basin of each lake, from approximately 1 m below the hypolimnion. All baseline organisms were frozen prior to analysis.

### Trophic Position and Diet-Source Calculations from Isotope Data

We used stable-isotope ratios of carbon and nitrogen in alewives and baseline organisms to estimate diet source

(littoral versus pelagic) and trophic position. We use the standard notation of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . We used the two-end-member-mixing model (Post 2002) to estimate diet source and trophic position:

Trophic position =  $\lambda$

$$+ (\delta^{15}\text{N}_{\text{sc}} - [\delta^{15}\text{N}_{\text{base1}} \cdot \alpha + \delta^{15}\text{N}_{\text{base2}}(1 - \alpha)]) / \Delta n,$$

where  $\alpha$  is the proportion of carbon obtained from the base of food web 1

$$\alpha = (\delta^{13}\text{C}_{\text{sc}} - \delta^{13}\text{C}_{\text{base2}}) / (\delta^{13}\text{C}_{\text{base1}} - \delta^{13}\text{C}_{\text{base2}})$$

$\lambda$  is the trophic position of the baseline organisms,  $\delta^{15}\text{N}_{\text{sc}}$  and  $\delta^{13}\text{C}_{\text{sc}}$  are the stable-isotope ratios of the secondary consumer of interest, and  $\Delta n$  is the average fractionation of  $\delta^{15}\text{N}$  per trophic transfer = 3.4 ‰.

Our two end members were the bases of the pelagic and littoral food webs (base 1 and base 2, respectively). The  $\alpha$  was constrained to be between 0 and 1. To best match tissue turnover rates in baseline organisms and YOY alewives (Post 2002), we used short-term baselines to estimate trophic position and diet source for YOY alewives. The short-term baseline was designed to capture the rapid dilution and turnover of tissue in rapidly growing young organisms (Fry and Arnold 1982; Hesslein et al. 1993). Our short-term baseline consisted of zooplankton (pelagic) and periphyton (littoral) collected every 1–4 weeks. We added 3.4 ‰ to periphyton  $\delta^{15}\text{N}$  values to account for their lower trophic position compared to zooplankton, and we used a  $\lambda$  value of 2 in the mixing model. For each fish sampling date, we used mean zooplankton and periphyton isotopic values calculated from all samples collected from the start of sampling through the week of fish sample collection. We analyzed 10–15 alewives per lake per sample date.

### Stable-Isotope Processing and Analysis

The zooplankton baseline on each sampling date consisted of either pure herbivore samples (cladocerans; one sampling date) or bulk samples (cladoceran herbivores plus copepod omnivores) corrected for the average difference between  $\delta^{15}\text{N}$  of bulk and pure herbivore samples (mean difference = 0.264 ‰,  $n = 11$ , stdev = 0.191, with one outlier omitted) in samples from Bride Lake, Patagansett Lake, and Linsley Pond (a no-alewife lake studied by Post and colleagues (2008)). On one date in Bride Lake, we used a sample of pure *Mesocyclops* (a predatory cyclopoid copepod) corrected for the average difference between  $\delta^{15}\text{N}$  of *Mesocyclops* and pure herbivore samples (mean difference = 2.887 ‰,  $n = 6$ , standard deviation = 1.238) in samples from Dodge Pond and Linsley Pond. We did not correct  $\delta^{13}\text{C}$  values because  $\delta^{13}\text{C}$  of bulk samples and *Mesocyclops* did not differ significantly from  $\delta^{13}\text{C}$  of

corresponding pure herbivore samples (bulk samples, paired  $t$  test:  $t = -1.3238$ ,  $df = 11$ ,  $p = 0.2124$ ; *Mesocyclops* samples, paired  $t$  test:  $t = -0.5025$ ,  $df = 5$ ,  $p = 0.6367$ ).

All samples were dried and homogenized before being analyzed on a ThermoFinnigan Delta<sup>PLUS</sup> Advantage stable-isotope mass spectrometer (Thermo Scientific, Boca Raton, FL) coupled to a Costech ECS 4010 EA elemental analyzer (Costech Analytical Technologies, Valencia, CA). Each run included house standards to correct for variation among runs and drift within runs. Standard deviation of reference samples across all runs was 0.32 ‰ ( $\delta^{15}\text{N}$ ) and 0.14 ‰ ( $\delta^{13}\text{C}$ ) for the cocoa house standard (periphyton runs) and 0.07 ‰ ( $\delta^{15}\text{N}$ ) and 0.24 ‰ ( $\delta^{13}\text{C}$ ) for the trout house standard (animal runs).  $\delta^{13}\text{C}$  numbers for fish and zooplankton were lipid-corrected following Post et al. (2007). We did not lipid-correct samples that had C:N ratios less than 3.5 because these samples contain less than 5 % lipid and correction is unnecessary (Post et al. 2007). We did not lipid-correct periphyton values because of their typically low lipid content.

#### Direct-Diet Analysis

We examined stomach contents from 6 to 10 YOY alewives per lake per sampling date, for a total of 255 fish. The stomach contents of each fish were removed and split using a plankton splitter until they contained 200–400 crustaceans. We used a dissecting microscope to identify all prey items to genus or species, with the exception of ostracods, diaptomus copepods, copepod nauplii, and terrestrial insects, which were not further differentiated. We identified 14 prey taxa: *Bosmina*, *Cerodaphnia*, *Chaoborus* (larval and pupal stages), *Chydorus*, cyclopoid copepods, *Daphnia*, *Diaphanosoma*, *Diaptomus*, *Holopedium*, adult terrestrial insects, copepod nauplii, ostracods, and *Polyphemus*. We could not assign trophic position or diet source to the adult insects, so we excluded fish containing adult insects (six fish from a single date in Gorton Pond) from further analyses. We counted all diet items and measured a proportion of the intact cladocerans and cyclopoids using an ocular micrometer. Cladocerans were measured from the tip of the head to the base of the carapace, excluding tail spines. Copepods were measured from the anterior end of the cephalic segment to the terminus of the caudal ramus. Partially digested or fragmented items were identified to the lowest possible taxonomic level but were not measured. We calculated an average dietary composition for each lake and sampling date based on the diets of 6–10 fish (three fish for Gorton Pond in late July). We used length–weight regressions to estimate the biomass of crustacean zooplankton (Downing and Rigler 1984) and used measurements of the average biomass of *Chaoborus*

larvae and pupae in zooplankton samples collected concurrently with fish samples to estimate *Chaoborus* biomass. The average sizes of cladocerans and copepods in alewife diets were reported previously in Palkovacs and Post (2008). Here we include new data on *Chaoborus* from alewife diets and estimate the biomass of each prey type in each diet.

#### Statistical Analyses

To test whether anadromous alewives consumed more predatory zooplankton than did landlocked alewives, we focused specifically on the two major predatory prey items in the diets, large cyclopoids (primarily *Mesocyclops*) and *Chaoborus*. To test whether anadromous and landlocked alewives consumed different amounts of littoral prey, we focused on ostracods, a major littoral prey item in the diet. For each fish, we calculated the dietary proportion by biomass of large cyclopoids (greater than 1 mm), *Chaoborus*, and ostracods. We then calculated a mean dietary proportion for each lake and sampling date by averaging the proportions of 6–10 fish (three fish for Gorton Pond in late July). We used Welch's  $t$  test, which assumes unequal variance, to test for differences in mean proportions of each prey type in anadromous versus landlocked lakes on individual dates.

We tested for differences in two niche characteristics using isotope data: diet source (pelagic dietary fraction) and trophic position. Our isotope data include two replicates for anadromous populations (Dodge Pond and Bride Lake) and three replicates for landlocked populations (all three of our landlocked study lakes), with the exception of early June, when we have data from only anadromous lakes because landlocked alewife spawn later in the year and thus were too small to sample, and late June/early July, when we have isotope data from a single anadromous population (Dodge Pond) and two landlocked populations (Patagansett Lake and Lake Quonnipaug). We therefore tested for differences in niche characteristics from late July through September (three sampling dates), the dates for which we had at least two replicates for each life-history type. Within each population, we calculated a single value for each niche characteristic by averaging the values of all fish from that date. We used Welch's  $t$  test to test for differences in the mean trophic position or diet source in anadromous versus landlocked lakes in individual months.

We tested for differences in variation among anadromous and landlocked prey consumption or niche characteristics on each date using an  $F$ -test (for normally distributed samples) or a Levene's test (for non-normally distributed samples; only two samples). The  $t$ -tests were performed in R (version 2.6.2, R Foundation for Statistical Computing, Vienna, Austria).

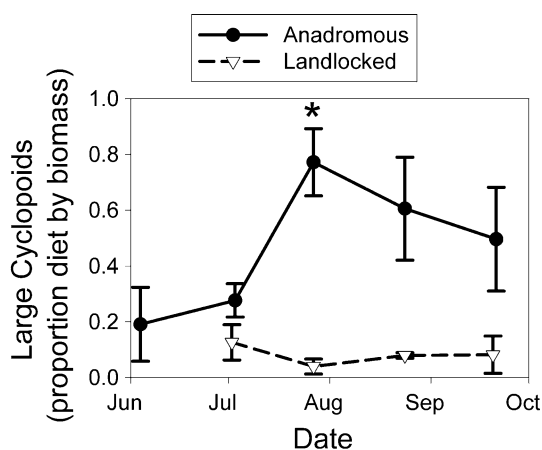
## Results

### Direct Diets

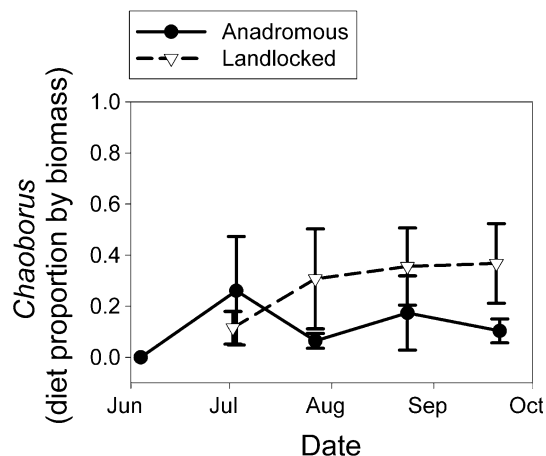
Direct diets give detailed snapshots of consumption on individual dates. We focused on consumption of the two primary predatory prey items found in diets, large cyclopoids and *Chaoborus*. In addition, we calculated the dietary proportions of ostracods, a littoral zooplankton species, in order to provide insight into littoral versus pelagic prey consumption.

Anadromous alewives consumed more large cyclopoids than did landlocked alewives (Fig. 1), with a significant difference in late July ( $t = 5.94$ ,  $df = 2.2$ ,  $p = 0.02$ ). Anadromous alewife consumption of large cyclopoids increased from relatively low levels in late June, peaked in late August, and declined into September. Mean consumption of large cyclopoids ranged from 0 to 98 % in individual anadromous lakes, with mean consumption above 20 % in individual lakes on most dates (12 out of 15 samples). In contrast, landlocked alewives consumed few, if any, large cyclopoids on almost all dates (Fig. 1). Mean consumption of large cyclopoids ranged from 0 to 21 % in individual landlocked lakes, with fish in only one lake consuming a mean of more than 20 % on a single date.

In general, landlocked alewives consumed more *Chaoborus* than did anadromous alewives, but differences were not significant (Fig. 2). Anadromous alewives in individual lakes consumed an average of 0–68 % *Chaoborus*, with no clear trend during the season. Landlocked alewives in individual lakes consumed an average of 0–67 % *Chaoborus*, and mean consumption across all landlocked lakes



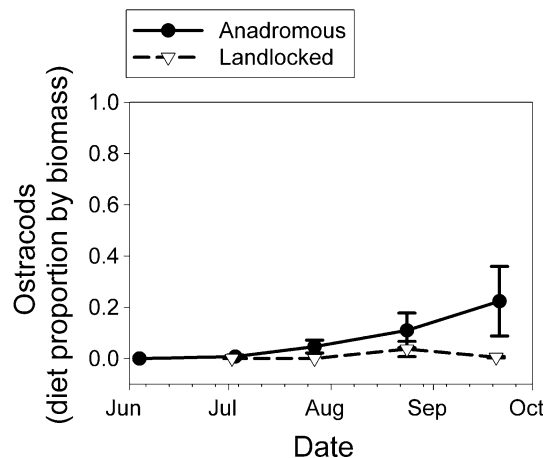
**Fig. 1** Dietary proportion (by biomass) of cyclopoids >1 mm from direct diet examination of anadromous (filled symbols, solid line) and landlocked (open symbols, dotted line) alewives collected from three anadromous lakes and three landlocked lakes. When replicate lakes were not sampled on the same day, sampling date represents midpoint of sampling period. Asterisk represents statistically significant difference



**Fig. 2** Dietary proportion (by biomass) of *Chaoborus* from direct diet examination of anadromous (filled symbols, solid line) and landlocked (open symbols, dotted line) alewives collected from three anadromous lakes and three landlocked lakes. When replicate lakes were not sampled on the same day, sampling date represents midpoint of sampling period

increased during the season, although fish from individual lakes did not exhibit an obvious temporal trend. Both life-history types exhibited high variability among lakes.

Ostracods made up a considerable proportion of anadromous alewife diets, particularly late in the season, whereas landlocked alewives rarely consumed ostracods (Fig. 3). However, these differences were not statistically significant. Mean ostracod consumption in individual anadromous lakes ranged from 0 to 48 %, with high variability. Mean ostracod consumption ranged from 0 to 10 % in landlocked lakes.



**Fig. 3** Dietary proportion (by biomass) of ostracods from direct diet examination of anadromous (filled symbols, solid line) and landlocked (open symbols, dotted line) alewives collected from three anadromous lakes and three landlocked lakes. When replicate lakes were not sampled on the same day, sampling date represents midpoint of sampling period

Comparisons of variances of anadromous and landlocked diet composition showed greater variability among anadromous lakes. Variance of anadromous alewife cyclopoid consumption was higher than that of landlocked alewives on most dates, with a significant difference in August ( $F_{2,2} = 345.45$ ,  $p < 0.01$ ). Variance of landlocked alewife *Chaoborus* consumption was higher than that of anadromous alewives on most dates, with a significant difference in late July ( $F_{2,2} = 0.02$ ,  $p = 0.04$ ). Anadromous alewife populations also exhibited a higher variance in ostracod consumption compared to landlocked alewives on most dates, with significant differences in early July (Levene's test, test stat = 10.54,  $p = 0.03$ ) and September ( $F_{2,2} = 2485.28$ ,  $df = 2,2$ ,  $p < 0.01$ ), and a marginally significant difference in late July (Levene's test, test stat = 5.25,  $p = 0.08$ ). The high variability among lakes likely decreases our ability to observe statistically significant differences among dietary proportions for all three prey items.

#### Diet Source and Trophic Position

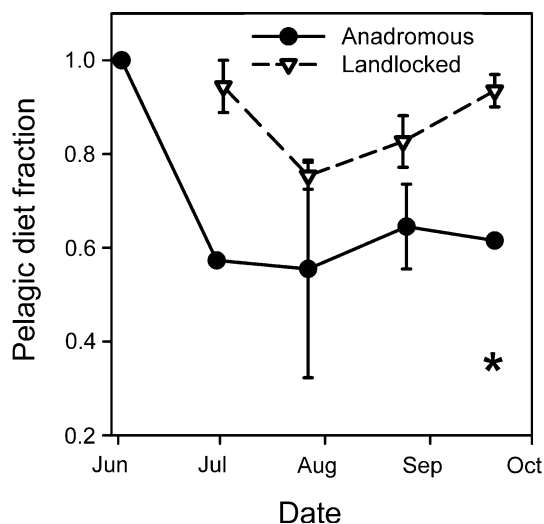
We used stable isotopes to provide integrated measures of trophic position and diet source, complementing the short-term estimates of consumption provided by direct diet analysis. Landlocked alewives obtained more carbon from pelagic sources than did anadromous alewives (Fig. 4), with a significant difference in September ( $t = -8.95$ ,  $df = 2.31$ ,  $p < 0.01$ ). Landlocked alewives obtained the majority of

their dietary carbon from pelagic sources on all dates, with mean pelagic diet fractions between 75 and 94 %. Anadromous alewives initially obtained 100 % of their dietary carbon from pelagic sources, but from late June through September they obtained only around 60 % of their dietary carbon from pelagic sources. Variation in landlocked alewife diet source was lower than that of anadromous alewives in late July and August, with a significant difference in late July ( $F_{1,2} = 43.12$ ,  $p = 0.045$ ). Variation in diet source was insignificantly higher in landlocked lakes compared to anadromous lakes in September.

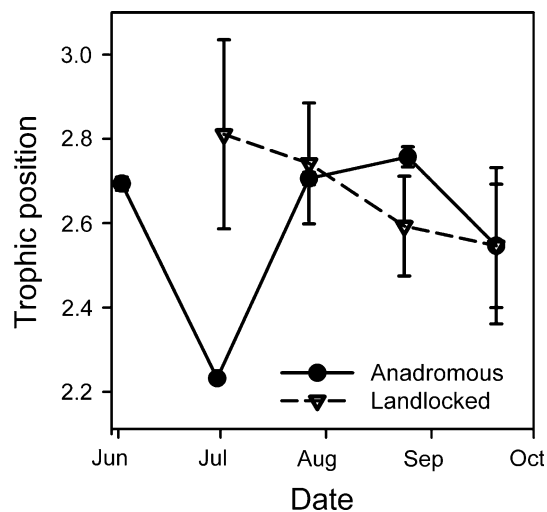
Landlocked and anadromous alewives did not differ in trophic position during the sampling period (all comparisons using Welch's  $t$ -tests were insignificant; Fig. 5).

#### Discussion: Eco-Evolutionary Feedbacks Result in Niche Differentiation

Previous research has clearly shown that anadromous and landlocked alewives structure their prey communities in different ways, thereby influencing prey availability (Brooks and Dodson 1965; Post et al. 2008; Palkovacs and Post 2009). Alewives also exhibit differences in gill raker spacing, gape width, and prey selectivity consistent with adaptation to these different prey communities (Palkovacs and Post 2008). These lines of evidence suggest an eco-evolutionary feedback between alewives and their zooplankton prey, in which differences in life history strategy affect prey availability, which in turn influences foraging



**Fig. 4** Pelagic diet fraction (mean  $\pm$  SE) of anadromous (filled symbols, solid line) and landlocked (open symbols, dotted line) alewives. Data from three landlocked lakes and two anadromous lakes are shown, with the exception of late June/early July (two landlocked lakes, one anadromous lake). When replicate lakes were not sampled on the same day, sampling date represents midpoint of sampling period. Asterisk represents statistically significant difference



**Fig. 5** Trophic position (mean  $\pm$  SE) of anadromous (filled symbols, solid line) and landlocked (open symbols, dotted line) alewives. Data from three landlocked lakes and two anadromous lakes are shown, with the exception of late June/early July (two landlocked lakes, one anadromous lake). When replicate lakes were not sampled on the same day, sampling date represents midpoint of sampling period. Asterisk represents statistically significant difference. The low anadromous data point for July represents a single lake sample

traits. In this framework, niche differences between anadromous and landlocked alewives both result from and perpetuate this feedback, with the strength of this feedback mediated by differences in the duration of residence (Palkovacs and Post 2008; Post and Palkovacs 2009; Post et al. 2008), providing an example of niche construction.

The direct-diet data presented here show that anadromous alewives consume a significantly greater dietary proportion of large cyclopoid copepods than do landlocked alewives (Fig. 1). A diet dominated by large cyclopoids is consistent with both their greater availability in anadromous as compared to landlocked lakes (Post et al. 2008) and the positive size selectivity exhibited by anadromous alewives (Palkovacs and Post 2008). Decreased consumption of large cyclopoids by landlocked alewives (Fig. 1) is consistent with both the lower abundance of large cyclopoids in landlocked lakes (Post et al. 2008) and the neutral prey-size selectivity of landlocked alewives (Palkovacs and Post 2008). However, the direct diets show that landlocked alewives compensate for the low availability of large predatory cyclopoids by consuming a considerable proportion of *Chaoborus* (Fig. 2). *Chaoborus* consumption by landlocked alewives explains why we fail to see differences in trophic position between anadromous and landlocked alewives (Fig. 5). Even though anadromous alewives consume more predatory zooplankton prey, landlocked alewives have access to another large-bodied, predatory prey species.

Stable-isotope data show that landlocked alewives rely predominantly on pelagic prey throughout the season (Fig. 4). This is consistent with their low consumption of ostracods (Fig. 3). Because of their year-round residence, landlocked alewives deplete large-bodied zooplankton (Post et al. 2008). However, their adaptations for foraging on small-bodied prey (Palkovacs and Post 2008) appear to allow them to continue to forage in the pelagic zone despite the low biomass of zooplankton and very low biomass of large-bodied zooplankton. This, in turn, may further strengthen selection pressure for smaller gape and gill raker spacing to feed even more efficiently on small-bodied pelagic zooplankton. Independently derived populations of landlocked alewives have converged on a similar strategy to adapt to year-round residence in freshwater lakes. In contrast, the isotope and diet data show that anadromous alewives increase their consumption of littoral prey as the season progresses (Figs. 4 and 5). The increased littoral component of anadromous alewife diets shown by the stable-isotope data is consistent with the higher late-season consumption of ostracods by anadromous alewives. Shifting to littoral prey may allow anadromous alewives to escape the selection pressures caused by the crash in large-bodied pelagic zooplankton.

This diet shift is consistent with other studies showing that fish switch to alternative prey or add novel dietary items when preferred prey are scarce or competition increases (Persson and Greenberg 1990; Svanback and Bolnick 2007; Araújo et al. 2008; Sternberg et al. 2008). Anadromous fish also leave the system through the summer and in the fall and feed on larger prey (krill and large copepods) in the marine environment (Stone and Jessop 1994). The increased reliance on freshwater littoral prey and adult marine diets may weaken the selection pressure for morphology adapted to feeding on small-bodied zooplankton (e.g., smaller gill raker spacing and gape width) in anadromous alewives. Thus, prey availability constrains the niches of anadromous and landlocked alewives, and phenotypic traits influence the ways in which alewives exploit these niches, leading to the observed niche difference.

Landlocked alewives from replicate lakes exhibit less variation in consumption of large cyclopoids and ostracods than do anadromous alewives (Figs. 1 and 3). Such a pattern suggests that independently evolved landlocked alewife populations have converged on a similar strategy for year-round residence in lakes, with morphology that allows them to feed continuously in the pelagic zone despite low zooplankton density and small zooplankton size. The strong feedback between alewives and their prey, which results from this year-round residency, has likely contributed to the similarity between landlocked alewife consumption strategies. In contrast, anadromous alewives will ultimately leave the system and face different selection pressures, which results in a weaker feedback between zooplankton prey density and predator foraging strategy. The greater diet variability among anadromous populations likely reflects both year-to-year and lake-to-lake variation in anadromous alewife densities (which influence the rate of depletion of large-bodied zooplankton) and the greater variety of foraging strategies employed by anadromous alewife once they deplete large-bodied zooplankton, including migrating from the lake, foraging on littoral prey, or continuing to forage on pelagic zooplankton.

We believe this variation in alewife density and foraging strategies explains the higher variation in large cyclopoids and ostracods in anadromous alewife diets. Landlocked alewives exhibit greater variability in consumption of *Chaoborus* compared to anadromous alewives. Because landlocked alewives feed non-selectively with respect to prey size (Palkovacs and Post 2008), and because *Chaoborus* may be more adept at escaping the niche constructing effects of alewife predation via their terrestrial adult life stage, the higher variation in landlocked consumption may reflect differences in *Chaoborus* abundance in landlocked lakes.

Intraspecific niche differentiation can be the first step in speciation (Dieckmann and Doebeli 1999; Schluter 2001; McKinnon et al. 2004; Albert and Schluter 2005). To date,

most studies on speciation and adaptive radiation have assumed that organisms adapt to an extrinsically structured environment (e.g., Losos et al. 1998, 2006; Langerhans et al. 2006). However, consumers often impact their environment by structuring their resource base (e.g., Brooks and Dodson 1965; Paine 1966; Kitchell et al. 1994; Wahlstrom et al. 2000; Jurgens and Matz 2002), and several studies provide evidence that predator–prey interactions feed back to affect predator foraging traits (Grant and Grant 2006; Palkovacs and Post 2008). We would expect that when species or populations have different effects on their prey communities, they will face different selection pressures as a result.

Here we present evidence for an intraspecific niche difference that appears to have emerged from differences in the feedbacks between two life history types of alewives and their respective prey communities. Our results are consistent with the existence of an eco-evolutionary feedback that drives intraspecific niche differentiation in alewives. Ultimately, such a feedback might result in speciation and adaptive radiations (Seehausen 2009). Intraspecific variation also affects ecological processes (Bassar et al. 2010; Whitlock et al. 2010), suggesting that eco-evolutionary feedbacks can influence community structure and function. Landlocked alewife populations likely diverged from anadromous populations following dam construction during European settlement (Palkovacs et al. 2008), making the phenotypic divergence between these two life-history types an eco-evolutionary byproduct of human cultural niche construction (Laland et al. 2001; Palkovacs et al. 2012). Broader consideration of eco-evolutionary feedbacks has the potential to affect our understanding of both adaptive evolution and the function of ecological communities and ecosystems, including potential anthropogenic impacts on these processes.

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