

Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits?

Eric P. Palkovacs and David M. Post

*Department of Ecology and Evolutionary Biology, Yale University,
New Haven, Connecticut, USA*

ABSTRACT

Question: It is well established that predators can influence the structure and dynamics of prey communities and that changes in prey communities can drive predator evolution. Here we ask whether changes in prey communities, brought on by the effects of predators, can feed back to mould the evolution of predator foraging traits.

Study system: We sampled lakes in Connecticut (USA) containing either anadromous or landlocked (freshwater resident) alewife (*Alosa pseudoharengus*) populations in 2004 and 2005.

Methods: We examined alewife populations for differences in (1) seasonal effects on zooplankton communities, (2) feeding morphology, (3) prey size, and (4) prey selectivity.

Results: Landlocked alewives, which are year-round residents of lakes, permanently structure lake zooplankton communities, thereby creating a strong feedback on the evolution of their foraging traits. Anadromous alewives, which are seasonal residents of lakes, intermittently structure lake zooplankton communities, preventing a strong feedback on the evolution of their foraging traits. This difference in the strength of the eco-evolutionary feedback between predator and prey appears to have led to the divergence of foraging morphology and prey selectivity between alewife life-history forms.

Conclusions: Predator-induced changes to prey communities can feed back to drive the evolution of predator foraging traits under conditions where eco-evolutionary feedbacks are strong. Moreover, variation in the strength of eco-evolutionary feedbacks appears to shape patterns of ecological and evolutionary diversity in this predator–prey system.

Keywords: *Alosa pseudoharengus*, co-evolution, geographic mosaic, gill rakers, niche construction, size-selective predation, zooplankton.

INTRODUCTION

The past decade has seen a surge of interest in synthesizing ecological and evolutionary theories (Thompson, 1998; Bohannan and Lenski, 2000; Saccheri and Hanski, 2006; Urban and Skelly, 2006; Whitham *et al.*, 2006; Johnson and Stinchcombe, 2007). This interest stems, at least in part, from the increasing realization that the core processes in ecology and evolution are inextricably linked (Elser *et al.*, 2000; Odling-Smee *et al.*, 2003; Fussmann *et al.*, 2007; Kokko and López-Sepulcre, 2007). The business of living (eating and excreting) causes organisms to alter the biotic and abiotic conditions of their environment; meanwhile, the process of natural selection causes populations to adapt to their environment. When these processes occur on similar time-scales (Hairston *et al.*, 2005; Carroll *et al.*, 2007), they can create eco-evolutionary feedbacks that may influence both ecological and evolutionary processes.

Studying eco-evolutionary feedbacks as two-way interactions is critical for understanding interactions between ecology and evolution (Fussmann *et al.*, 2007; Kokko and López-Sepulcre, 2007). However, the reciprocal nature of these interactions also makes field studies in natural systems challenging. One method for studying eco-evolutionary interactions in natural ecosystems has been to measure ecological and evolutionary changes over time and infer how changes in ecology have influenced evolution and vice versa. This approach has been applied to time-series data on Darwin's finch (*Geospiza fortis*) beak evolution and seed dynamics. For this system, eco-evolutionary interactions have been inferred to be important determinants of both evolutionary and ecological dynamics – beak size responds evolutionarily to changes in seed availability and seed availability responds ecologically to the intensity of finch predation (Grant and Grant, 2006). This feedback is facilitated by rapid evolutionary changes in finch beak size (Hairston *et al.*, 2005).

For most natural ecosystems, however, long-term data on both traits and environments are not available. In such cases, an alternative approach is to compare the dynamics of systems with the potential for strong eco-evolutionary feedbacks to the dynamics of systems lacking the potential for feedbacks. For example, Yoshida *et al.* (2003) compared the predator–prey dynamics of evolving rotifer–algae systems (stocked with multiple algal clones) with the dynamics of non-evolving systems (stocked with a single clone). Here we take a similar approach by comparing systems where the eco-evolutionary feedbacks between fish predators and zooplankton prey are strong versus systems where the feedbacks are weak. We exploit natural variation in the strength of eco-evolutionary feedbacks created by differences in predator migratory behaviour.

Alewife (*Alosa pseudoharengus*) populations occur in two discrete life-history forms – a landlocked (freshwater resident) form and an anadromous form. Both landlocked and anadromous alewives are zooplankton predators. Landlocked alewives spend their entire lives in freshwater lakes (Graham, 1956), making interactions between landlocked populations and their zooplankton prey continuous (Post *et al.*, 2008). Anadromous alewives spawn in the spring, and juveniles spend several months in freshwater lakes before migrating to sea (Loesch, 1987), making interactions between anadromous populations and their freshwater zooplankton prey intermittent (Post *et al.*, 2008). As a keystone species in eastern North American lakes (Power *et al.*, 1996), alewives are the dominant force structuring zooplankton communities (Brooks and Dodson, 1965; Wells, 1970; Hutchinson, 1971; Warshaw, 1972; Vigerstad and Cobb, 1978; Gregory *et al.*, 1983; Harman and Albright, 2002; Post *et al.*, 2008). Lakes with landlocked alewives consistently harbour smaller-bodied zooplankton than lakes without alewives, and the introduction of alewife populations into lakes previously lacking alewives causes rapid

declines in zooplankton body size (Brooks and Dodson, 1965; Wells, 1970; Hutchinson, 1971; Warsaw, 1972; Harman and Albright, 2002).

Landlocked and anadromous alewife populations both have strong effects on zooplankton communities, but seasonal differences in predation drive different zooplankton dynamics (Post *et al.*, 2008). In lakes with resident landlocked populations, zooplankton communities are under constant predation pressure. Therefore, zooplankton size remains small but relatively constant over the course of the growing season (Post *et al.*, 2008). In lakes with migratory anadromous alewife populations, predation pressure fluctuates in response to the annual spawning cycle. Therefore, the zooplankton community transitions annually between large-bodied in the spring and small-bodied in the summer (Post *et al.*, 2008).

Differences in zooplankton dynamics have likely consequences for the strength of eco-evolutionary feedbacks. In landlocked lakes, where predation pressure is continuous, changes in zooplankton communities caused by one alewife generation are likely to carry over to drive strong natural selection on the traits of the next generation. Under this scenario, eco-evolutionary feedbacks are expected to be strong. In anadromous lakes, where predation pressure is intermittent and zooplankton communities rebound annually, changes in zooplankton driven by one alewife generation are less likely to carry over to influence natural selection on the traits of the next generation. Under this scenario, eco-evolutionary feedbacks are expected to be weak.

The annual recovery of large-bodied zooplankton in anadromous lakes represents a break in the ecological side of the eco-evolutionary feedback for anadromous alewives. But there is an evolutionary side to the feedback as well. Landlocked alewives experience natural selection in the lake environment only. In contrast, anadromous alewives experience selection during their time spent foraging in the marine environment. This alternative environment represents a break in the evolutionary side of the eco-evolutionary feedback. If strong selection causes anadromous alewife traits to track marine prey size, then traits cannot easily respond to changes in freshwater prey size (even if these changes do occur). Therefore, selection in the marine environment may further weaken the eco-evolutionary feedback by constraining the extent to which ecological changes in lakes can shape anadromous alewife evolution.

We tested the hypothesis that differences in the strength of the eco-evolutionary feedback between predator and prey have caused divergence between landlocked and anadromous alewife freshwater zooplankton communities and foraging traits. We examined landlocked and anadromous alewife populations for differences in (1) seasonal effects on zooplankton communities, (2) feeding morphology, (3) prey size, and (4) prey selectivity. If continuous predation by landlocked alewives creates zooplankton communities that are dominated by small-bodied zooplankton all year round, we predict that landlocked alewives will be adapted for foraging on small zooplankton. If intermittent predation by anadromous alewives creates zooplankton communities that are dominated by large-bodied zooplankton in the spring and/or if selection for foraging in the marine environment is strong, we predict that anadromous alewives will be adapted for foraging on large zooplankton. Specifically, we predict that landlocked alewives will display smaller gape width, smaller gill raker spacing, and select smaller prey items compared with anadromous alewives. By comparing systems with strong eco-evolutionary feedbacks to systems with weak feedbacks, we are able to consider the importance of eco-evolutionary interactions for generating ecological and evolutionary diversity in nature without relying on long-term data, which are not readily available for most natural ecosystems.

METHODS

Study lakes

We conducted this study at six lakes in coastal Connecticut (USA). All study lakes are less than 15 km from Long Island Sound, with elevations ranging from 5 to 55 m. The most distant of these lakes are 42.5 km apart (linear distance). Lakes serving as spawning and rearing habitat for anadromous alewives (hereafter 'anadromous lakes') included Bride Lake, Dodge Pond, and Gorton Pond. Lakes containing resident landlocked populations (hereafter 'landlocked lakes') included Quonnipaug Lake, Pattagansett Lake, and Rogers Lake. Genetic data suggest that the evolutionary transition from anadromy to freshwater residency occurred in the past 300–5000 years for these landlocked populations, making them independent eco-evolutionary replicates that have undergone rapid evolutionary changes in the recent past (Palkovacs *et al.*, 2008).

Alewives are iteroparous and mature in 2–3 years for landlocked populations and 3–4 years for anadromous populations (Graham, 1956). Once mature, anadromous alewives return annually to their natal lakes to spawn (Loesch, 1987), although population genetic analysis reveals significant gene flow between coastal Connecticut populations (Palkovacs *et al.*, 2008). In Connecticut, anadromous alewife spawning begins in March, and the out-migration of juveniles is complete by November (Kissil, 1974), giving anadromous populations annual freshwater residence times of about 8 months. Adults can spend up to 3 months in fresh water, but usually return to sea after a few days to weeks (Kissil, 1974). Therefore, the biomass of juveniles in lakes, and the predation pressure exerted by them, far exceeds that of adults throughout most of the growing season (E.P. Palkovacs and D.M. Post, unpublished data).

Abiotic conditions and non-alewife planktivores

We examined landlocked and anadromous lakes for differences in abiotic conditions and the relative abundances of non-alewife planktivores. Abiotic conditions for study lakes were taken from Frink and Norvell (1984), Jacobs and O'Donnell (2002), and Post *et al.* (2008). The abundances, in terms of catch-per-unit-effort (CPUE), of non-alewife planktivores were from electrofishing surveys performed from 2004 to 2007 by us and by the Connecticut Department of Environmental Protection. Variables were \log_{10} -transformed to conform to normality, and all parametric statistics were performed in SPSS 11.0. We set alpha at 0.05 for determining statistical significance, although we will refer to *P*-values < 0.10 as 'marginally significant' to highlight potentially important trends.

Zooplankton dynamics

We examined anadromous and landlocked lakes for differences in the seasonal dynamics of zooplankton communities. Mean zooplankton size and biomass for each of our study lakes were calculated from samples taken in 2004 (summer only) and in 2005 (spring and summer). We collected zooplankton samples monthly in each lake and estimated the spring means from data collected in March and April and the summer means from data collected from July to September. Within seasons, samples from the same lake were pooled. Years and seasons were treated as independent because, in bi-weekly zooplankton time-series data including both anadromous and landlocked alewife lakes, we found no significant autocorrelation in zooplankton length at lags longer than 4 weeks (Post *et al.*, 2008). Each lake

was sampled using a plankton net (diameter 30 cm, length 90 cm, mesh 80 μm). Two vertical tows were taken from the deepest basin of each lake, combined in a single jar, and preserved in 70% ethanol. Zooplankton were identified and enumerated under a dissecting microscope. Each sample was split using a plankton splitter until 200–400 crustaceans remained in the subsample. Cladocerans and copepods were identified and measured 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 rami. Using length data, zooplankton dry biomass was estimated from species-specific length–mass regressions according to Downing and Rigler (1984).

Zooplankton differences were examined for cladocerans and copepods separately, since these groups have been found to differ in their relative abilities to escape fish predation (Drenner *et al.*, 1978; Drenner and McComas, 1980). We tested for differences in mean cladoceran and mean copepod size and biomass between lake types (anadromous and landlocked) and between seasons (spring and summer) using analysis of variance (ANOVA). Zooplankton size and biomass were ln-transformed to conform to normality.

Alewife sampling

We collected alewives in 2004 and 2005 from June to September with a pelagic purse seine (depth 4.87 m, length 35.36 m, mesh 3.18 mm). Three to five purse seine sets per lake were performed on each sampling date to estimate alewife density, and 20–30 alewives per sampling date were preserved in 70% ethanol for diet examination and morphological analysis. In 2004, alewife sampling was done two to three times per lake in Bride Lake, Gorton Pond, Pattagansett Lake, and Rogers Lake. In 2005, alewife sampling was conducted five times per lake in Bride Lake, Dodge Pond, Gorton Pond, Pattagansett Lake, Quonnipaug Lake, and Rogers Lake (sampling dates provided in the Appendix). Alewife samples represent young of the year anadromous alewives and all age-class landlocked alewives. All fish sampling was conducted under Yale University Institutional Animal Care and Use Committee Protocol #2003-10734 and State of Connecticut Scientific Collector Permit #SC-04016.

Morphology: wild phenotypes

We examined the morphology of anadromous and landlocked alewife feeding structures to determine whether the two life-history forms have diverged evolutionarily in response to different zooplankton environments. Zooplankton predation is a multi-stage process involving prey detection, pursuit, capture, retention, and digestion (Lazzaro, 1987). Gape width is important for prey capture, where the opening of the mouth and the expansion of the buccal cavity creates a directed suction that draws in prey items (Wainwright *et al.*, 2007). Gill raker spacing is important for prey retention. In some species, the gill rakers act as a crossflow filter (Sanderson *et al.*, 2001), enabling the retention of particles smaller than the inter-raker distances (Langeland and Nøst, 1995; Sanderson *et al.*, 2001). While the specific biomechanics of planktivory differ among species (Sanderson *et al.*, 1991), many studies (reviewed in Lazzaro, 1987; Robinson and Wilson, 1994), including one performed on alewives (MacNeill and Brandt, 1990), have shown that smaller inter-raker spacings, typically associated with larger numbers of gill rakers, favour the capture of smaller prey.

We measured alewife total length to the nearest millimetre. We measured gape width and gill raker spacing from at least five individuals per 5-mm length class from each study lake whenever sample sizes permitted (samples taken at different times were pooled for analysis). Gape width for fish <30 mm total length was measured under a dissecting microscope with an ocular micrometer. Gape width for fish >30 mm total length was measured with electronic digital calipers. Sample sizes for gape width were 225 for anadromous alewives and 334 for landlocked alewives (population-level sample sizes: Bride Lake, $n = 75$; Dodge Pond, $n = 64$; Gorton Pond, $n = 86$; Pattagansett Lake, $n = 112$; Quonnipaug Lake, $n = 109$; Rogers Lake, $n = 113$).

For measurement of gill raker attributes, the first branchial arch on the left side was removed and examined under a dissecting microscope. The first arch was examined because this arch has the most highly developed gill rakers and performs most of the filtering in alewives (MacNeill and Brandt, 1990). Gill raker traits were measured only for fish >30 mm total length because of the difficulty involved in removing gill arches from the smallest fish (<30 mm) without damaging them. Gill raker spacing was not measured directly due to the tendency for gill rakers to become stuck together in preserved fish. Therefore, gill raker spacing was calculated as:

$$GRS = (L - N * W)/N \quad (1)$$

where *GRS* is the average distance between gill rakers, *L* is the sum of the lengths of the upper and lower gill arches, *N* is the total number of gill rakers, and *W* is the average of the widths of the first rakers on the upper and lower gill arches. Sample sizes for *GRS* were 164 for anadromous alewives and 247 for landlocked alewives (population-level sample sizes: Bride Lake, $n = 56$; Dodge Pond, $n = 49$; Gorton Pond, $n = 59$; Pattagansett Lake, $n = 76$; Quonnipaug Lake, $n = 90$; Rogers Lake, $n = 81$).

Morphology: common garden phenotypes

To determine whether morphological differences remain under common environmental conditions, we constructed common garden enclosures. Eight clear plastic, solid-walled circular enclosures (diameter 2 m, depth 6 m) were suspended in Rogers Lake. Each enclosure was filled with unfiltered lake water and allowed to sit for 3 weeks to enable the establishment of zooplankton communities. On 24 June, four enclosures were stocked with 15 anadromous alewives and four were stocked with 15 landlocked alewives. The choice to keep groups of alewives together in large field-enclosures was based on our observations that alewives do not feed normally or survive well if kept in small tanks or in isolation. Landlocked and anadromous alewives for stocking were captured from Rogers Lake and Gorton Pond, respectively, and placed directly in the enclosures. Fish were between 30 and 45 mm total length at stocking, and mean length at stocking did not differ between the groups. On 24 August, all fish were removed from the enclosures. For each specimen, total length, gape width, and gill raker spacing were measured as described above. Fish were between 40 and 65 mm in total length upon collection, indicating that substantial growth occurred within the common garden enclosures. It is important to note that because fish were collected from the wild, early life plasticity was carried over into the common garden.

Morphology: statistical analysis

We examined differences in gape width and gill raker spacing between anadromous and landlocked alewives. We examined fish from common garden enclosures and fish collected from the wild in separate analyses. Total length, gape width, and gill raker spacing were \log_{10} -transformed for analysis. Simple linear regression was used to examine population-level relationships between foraging traits and total length. For all populations, total length explained a large proportion of the variation in foraging traits (gape width: $R^2 = 0.88$ – 0.95 ; gill raker spacing: $R^2 = 0.84$ – 0.93). Therefore, analysis of covariance (ANCOVA) was used to examine trait differences between life-history forms, with total length included as a covariate. The life-history \times length interaction was used to determine whether slopes were significantly different. If slopes were different ($P < 0.05$), means were not tested because ANCOVA assumes homogeneity of regression slopes. If equality of slopes could not be rejected ($P > 0.05$), the interaction term was removed from the model and means were tested. For common garden fish, the slopes did not differ significantly. Therefore, mean differences were evaluated using ANCOVA.

For wild fish, the slopes did differ significantly, both between life-history forms and among populations within life-history forms. A steeper slope indicates a steeper ontogenetic trajectory – foraging traits increased more rapidly with body size in anadromous than in landlocked populations. Slope differences precluded an evaluation of mean differences using ANCOVA. Instead, we partitioned the data set into 10-mm size classes (e.g. size class 20 is comprised of fish with a total length of 20–29 mm) and tested for mean trait differences within each size class using ANOVA (with populations nested within life-history types). We compared foraging traits in alewives up to 80 mm in total length because we had small sample sizes for anadromous young of the year >80 mm total length (most had departed for the ocean).

Prey size

To ascertain whether morphological divergence between anadromous and landlocked alewives has led to dietary divergence, we examined alewife stomach contents. The stomach contents of each fish were removed and transferred into a counting tray. The methods used for counting and measuring zooplankton from diets were the same as those used for counting and measuring zooplankton from lake tows. Items that were fragmented or partially digested were identified to the lowest taxonomic level possible but not measured. Diets from 10 fish per sample were examined. Thus, a total of 100 diets (50 per life-history type) were examined from 2004, and a total of 300 diets (150 per life-history type) were examined from 2005.

Overall differences in prey size were assessed for diet samples collected from populations that were sampled in both 2004 and 2005 (Bride Lake, Gorton Pond, Pattagansett Lake, and Rogers Lake). Prey size data were \ln -transformed for analysis. Prey size differences were examined for cladocerans and copepods separately. Two-way ANOVA, with population nested within life-history type and year included as a random effect, was used to evaluate overall prey size differences. Because we found no significant autocorrelation in zooplankton size between years (Post *et al.*, 2008), the independent units of replication were the mean diet values for the four populations sampled in 2004 and 2005 ($n = 8$). Seasonal changes in prey size were evaluated from diet samples collected from all six populations

at 4-week intervals (five sampling dates per lake) from June to September in 2005. Because we did find evidence for significant autocorrelation in zooplankton size at 4-week lags (Post *et al.*, 2008), repeated-measures ANOVA, with population (nested within life-history type) as the independent unit of replication ($n = 6$), was used to test for mean prey size differences and for significant differences in changes in prey size over the course of a season (time \times life-history interaction).

Prey selectivity

A true measure of diet selectivity must quantify both prey availability and prey consumption, because differences in prey availability may have a strong influence on diet composition even if prey selectivity does not differ (Link and Keen, 1999). To calculate indices of prey selectivity, we sampled zooplankton concurrently with alewives in 2005. Prey selectivity for each alewife diet examined was calculated as:

$$L_i = r_i - p_i \quad (2)$$

where L_i is the measure of prey selectivity, r_i is the relative abundance of prey item i in the diet of a given fish, and p_i is the relative abundance of prey item i in the environment at the time the fish was sampled (Strauss, 1979). This index of prey selectivity takes on values from +1 to -1, with positive values indicating preference, values near 0 indicating random feeding, and negative values indicating avoidance. The aim of this analysis was to assess size selectivity. Therefore, prey selectivity L_i was calculated for large cladocerans (>0.5 mm) and large copepods (>1.0 mm).

In addition to calculating prey selectivity according to the relative abundances of prey items, we also examined size selectivity directly by developing an index representing the deviation of the average prey size in the diet from the average prey size in the environment. Thus, we calculated size selectivity for each alewife diet as follows:

$$S_i = d_i - e_i \quad (3)$$

where S_i is the measure of size selectivity, d_i is the average size of item i in the diet of a given fish, and e_i is the average size of item i in the environment at the time the fish was sampled. Values of S near 0 indicate either random feeding or selection for prey of average size. High values indicate positive size selection, or a strong preference for the largest prey items available, and low values indicate negative size selection. Because prey size is not a proportion, S_i (unlike L_i) is not bounded by +1 and -1. We calculated S_i for cladocerans and copepods (excluding nauplii).

We used a Monte Carlo simulation approach to assess whether large prey selectivity L_i or size selectivity S_i deviated significantly from 0 (random feeding). For each sample, X prey items were drawn randomly, with replacement, from the zooplankton tow data. X represents the average number of prey items found in the diets of the fish sampled from a given population on a given date (hereafter referred to as a 'lake-date'). This process generated a random diet (i.e. the simulated diet of a single fish). From this random diet, selectivity indices were calculated. This process was repeated 10,000 times, using 10,000 random diets, to create null distributions for each lake-date. From the null distributions, 95% and 99% confidence intervals were constructed. Selectivity was considered significantly positive (or negative) if the average empirical selectivity value fell above (or below) the 95% confidence bound. This resampling procedure was executed in Matlab 7.0.

RESULTS

Abiotic conditions and non-alewife planktivores

Landlocked and anadromous lakes did not differ in maximum depth ($F_{1,4} = 1.454$, $P = 0.294$; Table 1) or spring total phosphorus concentrations ($F_{1,4} = 0.173$, $P = 0.699$; Table 1). For the lakes examined here, landlocked lakes did tend to have a significantly larger surface area than anadromous lakes ($F_{1,4} = 16.884$, $P = 0.015$; Table 1), but we found no significant differences in a larger sample of lakes (Post *et al.*, 2008). Alewife populations in Connecticut lakes co-exist with a suite of other planktivorous fish species, including yellow perch (*Perca flavescens*), bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), redbreast sunfish (*Lepomis auritus*), black crappie (*Pomoxis nigromaculatus*), golden shiner (*Notemigonus crysoleucas*), and white perch (*Morone americana*). Data from electrofishing surveys reveals landlocked lakes to have significantly higher non-alewife planktivore catch-per-unit-effort than anadromous lakes ($F_{1,3} = 10.636$, $P = 0.047$; Table 1). Yellow perch was the most abundant planktivore in anadromous lakes, whereas the sunfishes (*Lepomis* spp.) were the most abundant planktivores in landlocked lakes. The abundance of yellow perch did not differ significantly between lake types ($F_{1,3} = 4.389$, $P = 0.127$; Table 1). The abundance of *Lepomis* spp. was significantly higher in landlocked lakes than in anadromous lakes ($F_{1,4} = 41.750$, $P = 0.003$; Table 1). Within *Lepomis*, bluegill were significantly more abundant than pumpkinseed in landlocked lakes ($F_{1,4} = 46.659$, $P = 0.002$), while pumpkinseed were marginally more abundant in anadromous lakes ($F_{1,4} = 4.669$, $P = 0.097$).

Table 1. Abiotic conditions, including surface area (SA), maximum depth (Depth), and spring total phosphorus concentrations (TP), and non-alewife planktivore abundance, in terms of mean catch-per-unit-effort from electrofishing surveys, for anadromous (A) and landlocked (L) alewife lakes

Lake	SA (m ²)	Depth (m)	TP (µg·l ⁻¹)	Non-alewife planktivore abundance (fish per hour)		
				<i>Perca</i>	<i>Lepomis</i>	Total
Bride Lake (A)*	18.2	10.7	15.45	–	270.0	–
Dodge Pond (A)	13.2	14.5	24.45	400.4	225.9	626.3
Gorton Pond (A)	21.5	2.3	19.80	316.7	304.6	32.3
Anadromous	17.6	9.2	19.90	358.6	266.8	629.3
Pattagansett Lake (L)	49.2	10.7	17.30	54.9	1138.6	1209.6
Quonnipaug Lake (L)	44.6	14.5	47.05	9.0	1052.3	1068.3
Rogers Lake (L)	106.0	20.0	14.85	136.5	655.3	820.15
Landlocked	66.6	15.1	26.40	66.8	948.7	1032.7

* Bride Lake is not included in routine fish sampling by the Connecticut Department of Environmental Protection (unlike our other study lakes). It was sampled by one of us (D.P.) for a related study that quantified *Lepomis* catch-per-unit-effort only.

Note: Mean values for each lake type are given in **bold**.

Zooplankton dynamics

As expected, landlocked and anadromous lakes differed in the seasonal dynamics of their zooplankton communities (Fig. 1). In the spring, landlocked lakes had smaller zooplankton than anadromous lakes. The difference was significant for cladocerans ($F_{1,4} = 11.317$, $P = 0.028$) and marginally significant for copepods ($F_{1,4} = 5.182$, $P = 0.085$). During summer, this trend reversed, and landlocked lakes had significantly larger zooplankton than anadromous lakes (cladocerans: $F_{1,9} = 19.461$, $P = 0.002$; copepods: $F_{1,9} = 5.463$, $P = 0.044$). This seasonal reversal occurred because the average size of zooplankton in anadromous lakes decreased significantly between spring and summer (cladocerans: $F_{1,6} = 28.485$, $P = 0.002$; copepods: $F_{1,6} = 12.092$, $P = 0.013$), whereas the average size of zooplankton in landlocked lakes did not change (cladocerans: $F_{1,7} = 0.499$, $P = 0.503$; copepods: $F_{1,7} = 0.094$, $P = 0.768$). Biomass trends followed closely those of zooplankton size, although most differences were not significant due to large lake-to-lake variation in zooplankton biomass. The exception was for summer copepod biomass, which was significantly higher in landlocked lakes than in anadromous lakes ($F_{1,9} = 19.135$, $P = 0.002$). These results are congruent with the results of Post *et al.* (2008), in which we surveyed seasonal zooplankton dynamics in a broader set of lakes containing anadromous or landlocked alewives.

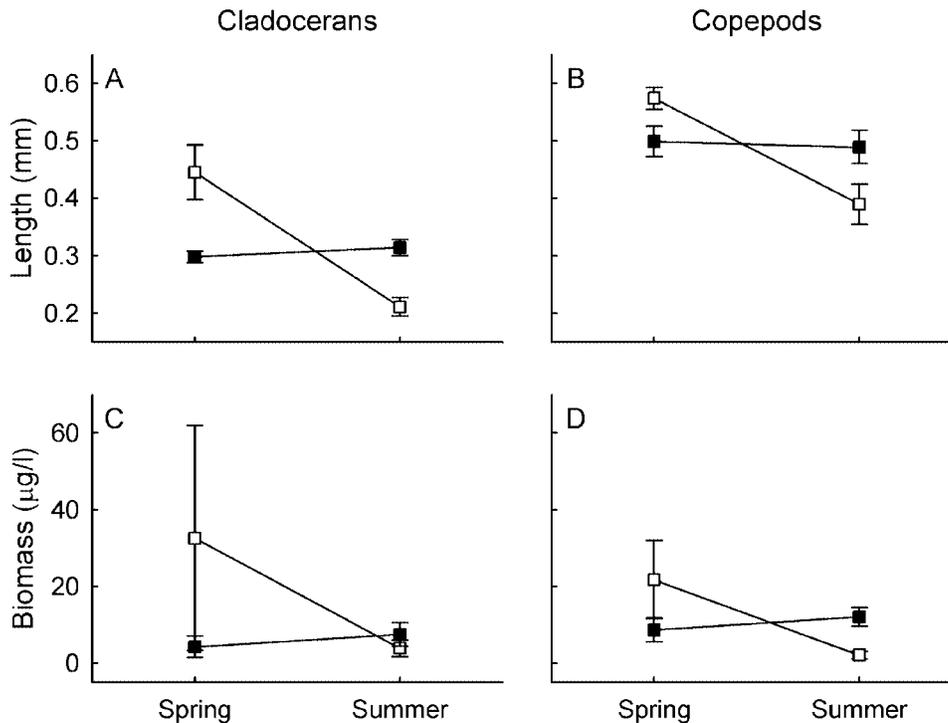


Fig. 1. Mean zooplankton size (A, B) and biomass (C, D) for cladocerans and copepods in anadromous lakes (open symbols) and landlocked lakes (closed symbols) in the spring and summer. Error bars represent standard errors calculated across lake by year means.

Morphology

For wild fish, \log_{10} trait– \log_{10} total length slopes differed significantly (violating the assumption of ANCOVA). For gape width and gill raker spacing, slopes were less steep for landlocked than for anadromous alewives. When foraging traits were compared using size-partitioned data, landlocked populations displayed a significantly smaller gape width at total lengths of 50–59 mm and at 70–79 mm (the 40–49 mm and the 60–69 mm size classes were marginally significant). Gill raker spacing for landlocked populations was significantly smaller at sizes > 50 mm total length (the 40–49 mm size class was marginally significant) (Table 2, Fig. 2).

When reared in common garden enclosures, \log_{10} trait– \log_{10} total length slopes did not differ significantly. Analysis of covariance revealed landlocked alewives to have a significantly smaller gape width ($F_{1,47} = 12.104$, $P = 0.001$) and gill raker spacing ($F_{1,47} = 35.007$, $P < 0.001$) than anadromous alewives (mean gape width: landlocked = 2.42 mm, anadromous = 2.53 mm; mean gill raker spacing: landlocked = 0.149 mm; anadromous = 0.164 mm). For common garden fish, mean total length did not differ between the life-history forms ($F_{1,48} = 0.043$, $P = 0.836$).

Table 2. Results of nested ANOVA for divergence in foraging traits between wild anadromous and wild landlocked alewife populations by size class (see text for details)

Size class	Gape width	Gill raker spacing
20 (20–29 mm)	$F_{1,4.039} = 0.693$, $P = 0.452$	N.A.
30 (30–39 mm)	$F_{1,4.079} = 1.893$, $P = 0.240$	$F_{1,4.019} = 1.623$, $P = 0.271$
40 (40–49 mm)	$F_{1,4.049} = 5.494$, $P = 0.078$	$F_{1,4.024} = 5.742$, $P = 0.074$
50 (50–59 mm)	$F_{1,4.079} = 12.151$, $P = \mathbf{0.024}$	$F_{1,4.013} = 18.547$, $P = \mathbf{0.012}$
60 (60–69 mm)	$F_{1,4.058} = 7.159$, $P = 0.055$	$F_{1,4.037} = 105.847$, $P < \mathbf{0.001}$
70 (70–79 mm)	$F_{1,4.111} = 9.618$, $P = \mathbf{0.035}$	$F_{1,4.083} = 15.668$, $P = \mathbf{0.016}$

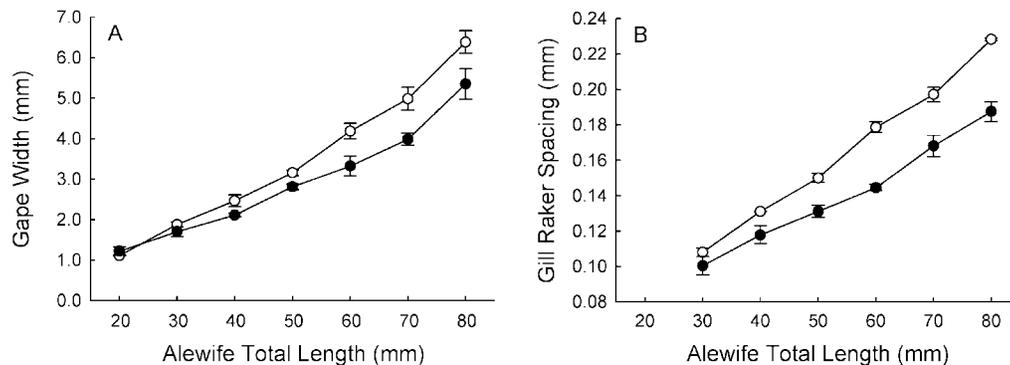


Fig. 2. Mean gape width (A) and gill raker spacing (B) for wild anadromous populations (open symbols) and wild landlocked populations (closed symbols) calculated for 10-mm size classes. Error bars represent standard errors calculated across population means.

Prey size

Generally, landlocked alewives consumed smaller prey than anadromous alewives. This difference was consistent across populations and more pronounced for copepods than for cladocerans. We found no effect of life-history type on cladoceran prey size ($F_{1,2} = 7.017$, $P = 0.118$) but a significant effect of life-history type on copepod prey size ($F_{1,2} = 127.56$, $P = 0.008$), with landlocked populations feeding on smaller copepods than anadromous populations. The effect of year was not significant for either cladoceran ($F_{1,3} = 0.633$, $P = 0.485$) or copepod prey size ($F_{1,3} = 1.716$, $P = 0.281$). Analysis of prey data collected over the course of 2005 using repeated-measures ANOVA indicated a marginally significant effect of life-history form on cladoceran prey size ($F_{1,4} = 4.921$, $P = 0.091$) and a significant effect of life-history form on copepod prey size ($F_{1,4} = 22.004$, $P = 0.009$), with landlocked alewives, again, favouring smaller prey (Fig. 3A, B). The time \times life-history interaction was not significant for cladoceran prey size ($F_{4,16} = 1.647$, $P = 0.211$), but was significant for copepod prey size ($F_{4,16} = 3.480$, $P = 0.032$). For anadromous populations, copepod prey size increases from spring to mid-summer and then declines during late summer; for landlocked populations, copepod prey size remains relatively constant from spring to mid-summer and then declines slightly during late summer (Fig. 3B).

Prey selectivity

Anadromous populations had both a greater proportion and a greater magnitude of positive size selectivity than did landlocked populations (Fig. 3C–F). Anadromous populations showed significant positive size selectivity on 70% of the lake-dates sampled, neutral size selectivity on 30% of the lake-dates sampled, and never displayed significant negative size selectivity. In contrast, landlocked populations showed significant positive (30%), neutral (38%), and significant negative (32%) size selectivity in roughly equal proportions. On sampling periods when both landlocked and anadromous populations were positively size-selective, the magnitude of positive selectivity was greater for anadromous populations (with one exception), suggesting that differences in prey size between landlocked and anadromous populations were driven by differences in prey selectivity, not differences in prey availability. Similar to the results for prey size, differences in size selectivity were greater for copepods than for cladocerans.

DISCUSSION

We tested the hypothesis that differences in the strength of eco-evolutionary feedbacks have caused ecological divergence between landlocked and anadromous alewife zooplankton communities and evolutionary divergence between landlocked and anadromous alewife feeding morphology and prey selectivity. Our results show that constant predation by landlocked alewives created zooplankton communities that were dominated by small-bodied zooplankton all year round. In contrast, intermittent predation by anadromous alewives created zooplankton communities that were dominated by large-bodied zooplankton in the spring and small-bodied zooplankton in the summer. Based on these ecological differences, we predicted that landlocked alewives would show morphological adaptations for foraging on smaller prey, consume smaller prey, and be less selective for large prey compared with anadromous alewives. Our results support these predictions.

In terms of ecological divergence, we found that landlocked and anadromous lakes

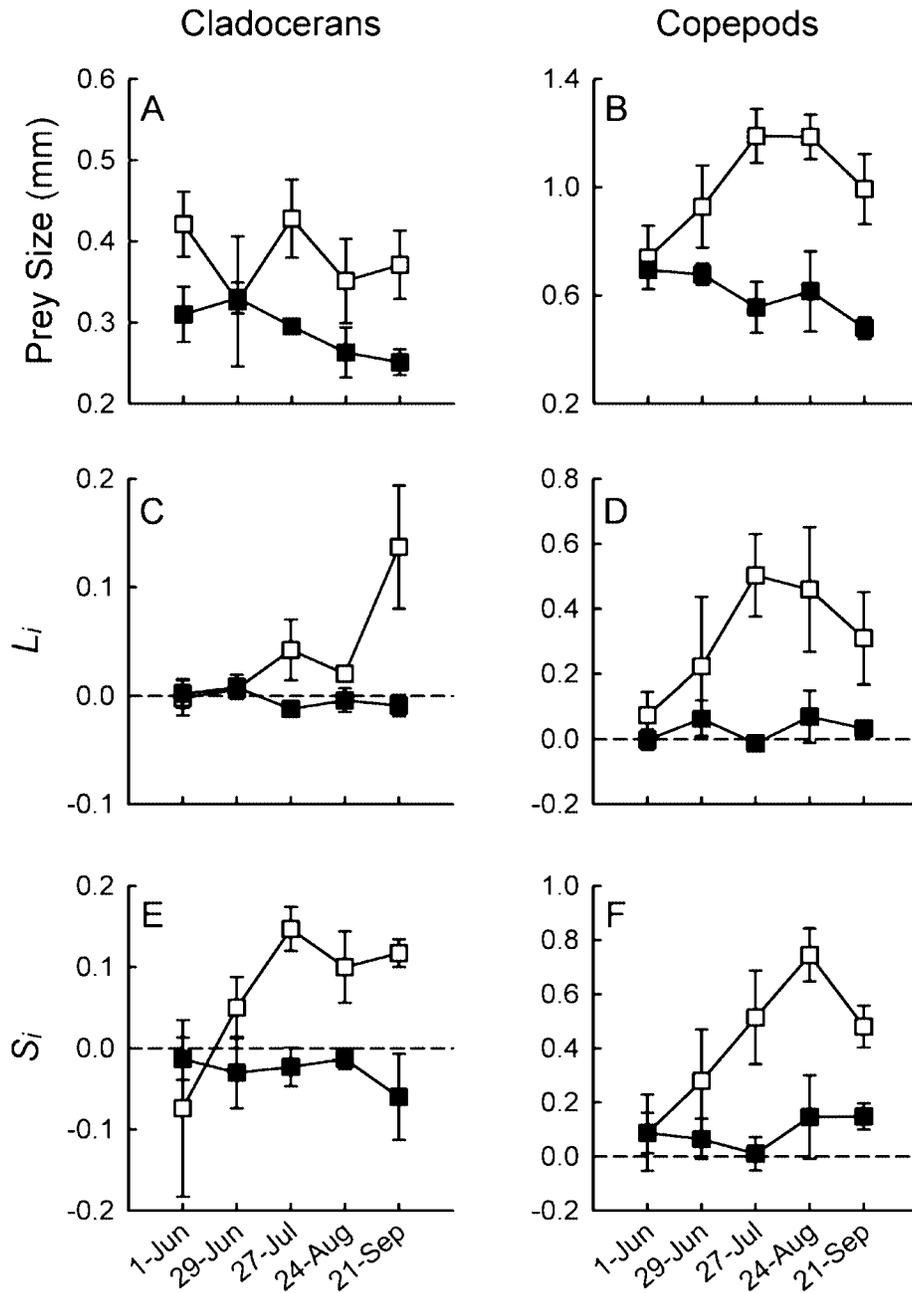


Fig. 3. Mean prey size (A, B), large prey selectivity L_i (C, D), and size selectivity S_i (E, F) for anadromous (open symbols) and landlocked (closed symbols) alewife populations feeding on cladoceran and copepod prey items. Error bars represent standard errors calculated across population means.

differed markedly in their zooplankton dynamics (Fig. 1). Anadromous lakes were characterized by a high biomass of large-bodied zooplankton in the spring and a low biomass of small-bodied zooplankton in the summer. In contrast, landlocked lakes were characterized by a relatively low biomass of small-bodied zooplankton in the spring and summer. These results are consistent with the long-recognized ability of alewife populations to act as the dominant force structuring zooplankton communities in the lakes they inhabit (Brooks and Dodson, 1965), and reinforce that the ecological effects of anadromous alewives on zooplankton communities are not equivalent to the effects of landlocked alewives (see also Post *et al.*, 2008).

In terms of evolutionary divergence, anadromous and landlocked alewife populations exhibited differences in feeding morphology, prey size, and prey selectivity. For wild populations, the two life-history forms differed significantly in the ontogenetic trajectories of their foraging traits, with landlocked populations showing less rapid increases in gape width and gill raker spacing with body size than anadromous populations. When foraging traits were compared using size-partitioned data, landlocked alewives were found to have significantly (or marginally significantly) smaller foraging trait values than anadromous alewives at total lengths >40 mm (Table 2, Fig. 2). For common garden fish, the two life-history forms differed significantly in the mean values of foraging traits. Again, landlocked alewives showed significantly smaller gape width and gill raker spacing than anadromous alewives. There is strong evidence from a diversity of fish species that gill raker traits are highly heritable (Hagen, 1973; Foote *et al.*, 1999; Bernatchez, 2004; Funk *et al.*, 2005). We cannot rule out the possibility that plasticity early in life drove the phenotypic differences observed in the common garden enclosures (see Meyer, 1987). However, the common garden experiment shows that when substantial growth occurs in the absence of environmental heterogeneity, phenotypic differences remain.

A narrower gape width and smaller gill raker spacing are adaptations for foraging on smaller prey (Drenner *et al.*, 1984; Mummert and Drenner, 1986; MacNeill and Brandt, 1990; Hjelm *et al.*, 2000; Hjelm and Johansson, 2003) and, indeed, landlocked populations consumed significantly smaller prey and were less selective for large prey than anadromous populations (Fig. 3), especially with respect to copepods, which are more difficult to capture than cladocerans (Drenner *et al.*, 1978; Drenner and McComas, 1980). Over the course of the growing season, anadromous alewives increased their preference for large copepod prey, whereas landlocked alewives did not (Fig 3). Therefore, as they grow, anadromous alewives are able to take advantage of the large, evasive copepods that were unavailable to them at smaller sizes. Anadromous alewives appear particularly well adapted to exploit large copepods, which are seasonally abundant in anadromous lakes; they continue to search for these prey items even after they have become depleted from the lake.

Taken together, our results suggest that a change in alewife migratory habit has strengthened the nature of eco-evolutionary feedbacks and led to ecological and evolutionary divergence between anadromous and landlocked alewife systems (Fig. 4). In landlocked lakes, intense predation permanently eliminates large prey items from the environment, placing landlocked populations under strong selection for foraging on small zooplankton. In contrast, anadromous alewives encounter large-bodied zooplankton each spring. When anadromous alewives eliminate these large prey from the freshwater environment, they emigrate to the marine environment where they again encounter and feed on large zooplankton, especially *Meganyctiphanes norvegica*, which are 20–40 mm in length (Stone and Daborn, 1987; Stone and Jessop, 1994). This switch from the freshwater to the marine environment,

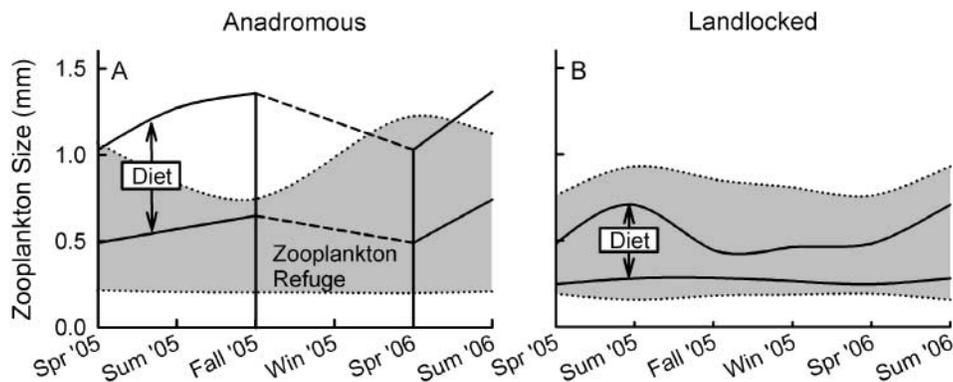


Fig. 4. Zooplankton dynamics and alewife prey size for Bride Lake, an anadromous lake (A), and Rogers Lake, a landlocked lake (B). The dotted lines and grey shading indicate the interval between the 10th and 90th percentiles for zooplankton size in the lakes. The non-shaded area between the solid lines represents the area between the 10th and 90th percentiles for prey size in alewife diets. Zooplankton size in anadromous lakes undergoes regular seasonal fluctuations due to the zooplankton refuge created by the fall alewife out-migration. Therefore, anadromous alewives experience large zooplankton each spring. In landlocked lakes, large zooplankton are unable to re-establish due to constant alewife predation pressure, creating a feedback that places landlocked populations under selection to consume smaller zooplankton prey.

coupled with the annual recovery of large-bodied zooplankton in anadromous lakes, appears to maintain natural selection on anadromous alewife foraging traits that facilitates the capture of large prey items. We do not know the relative contributions of selection in the freshwater versus the marine environment. The fact that anadromous alewives appear to select larger than optimal zooplankton prey (even with respect to the large prey environment in anadromous lakes in spring; see Fig. 4) suggests that marine selection may indeed be important.

Non-anadromous (planktivorous) populations of other species have also been found to differ from their anadromous ancestors in foraging traits, especially gill rakers. More numerous gill rakers, which are typically associated with smaller gill raker spacing and smaller prey, have been found in freshwater resident populations of sockeye salmon (*Oncorhynchus nerka*) (Wood and Foote, 1996; Foote *et al.*, 1999), rainbow smelt (*Osmerus mordax*, 'dwarf form') (Taylor and Bentzen, 1993), and threespine sticklebacks (*Gasterosteus aculeatus*, 'limnetic form') (McPhail, 1994). Anadromous–freshwater resident systems are widely accepted to be examples of parallel evolutionary divergence (e.g. Taylor *et al.*, 1996; Schluter *et al.*, 2004; Palkovacs *et al.*, 2008). But what about parallelism in the ecology of anadromous–freshwater resident systems? If the transition from anadromy to freshwater residency is commonly associated with predator-induced decreases in mean prey size followed by adaptation to small-prey conditions, then these systems may represent cases of parallel eco-evolutionary divergence.

Interestingly, anadromous alewives, which are adapted for foraging on large-bodied zooplankton, reduce zooplankton size below that in landlocked lakes during mid-summer (Fig. 1). This effect could result from (1) differences in alewife density, (2) differences in size or ontogenetic stage, or (3) differences in foraging traits and prey selectivity between anadromous and landlocked alewives. To evaluate these alternative hypotheses, Palkovacs (2007) conducted an experiment in which anadromous and landlocked alewives were

stocked into pelagic mesocosms at equal sizes and densities and the response of the zooplankton community was measured. The results of this experiment support the hypothesis that differences in foraging traits and prey selectivity drive mid-summer differences in zooplankton size. This is because anadromous alewives consistently select the largest zooplankton from the environment, constantly driving mean prey size down, even after large-bodied zooplankton (>0.5 mm) are eliminated. Landlocked alewives also feed selectively, but only as long as large-bodied zooplankton are common. After large-bodied zooplankton are reduced, landlocked alewives transition to non-selective feeding and, therefore, do not continue to have a strong directional effect on zooplankton size.

Our observations raise an additional question. If landlocked alewives forage non-selectively when faced with a small-bodied zooplankton community, what prevents the re-establishment of large-bodied zooplankton in landlocked lakes (see Fig. 4)? Two factors may be important. First, as mentioned above, landlocked alewife foraging behaviour is known to be flexible. Landlocked alewives can switch between non-selective filter feeding and selective particulate feeding (Janssen, 1976, 1978, 1980). This means that while landlocked alewives typically forage on zooplankton of average size, they can switch to targeting large-bodied zooplankton if they become common. The rapid elimination of large zooplankton from lakes invaded by landlocked alewives is evidence for this behavioural flexibility (Brooks and Dodson, 1965; Wells, 1970; Hutchinson, 1971; Warshaw, 1972; Harman and Albright, 2002). Second, the abundance of non-alewife planktivores is greater in landlocked lakes than in anadromous lakes (Table 1). It is likely that differences in planktivore abundance and species composition are caused by strong competition with alewives. Nonetheless, the greater abundance of size-selective, particulate feeding planktivores such as *Lepomis* spp. in landlocked lakes may help prevent the re-establishment of large-bodied zooplankton (see Lazzaro, 1987, and references therein). In anadromous lakes, where non-alewife planktivores are less abundant, large-bodied zooplankton re-establish readily when alewives depart for the ocean.

Divergence time estimates using molecular genetic data suggest that the transition from anadromy to freshwater residency in the alewife populations examined here occurred no longer than 5000 years ago and perhaps as recently as 300 years ago, pointing to a rapid rate of phenotypic evolution for landlocked alewife foraging traits (Palkovacs *et al.*, 2008). An extremely rapid rate of phenotypic evolution has also been found for Darwin's finch beak evolution [calculated by Hendry and Kinnison (1999) and Hairston *et al.* (2005) with data from Grant and Grant (1995) and Grant and Grant (2002), respectively]. This suggests not only that rapid evolution may promote strong eco-evolutionary feedbacks, but also that strong feedbacks may promote rapid evolution. This may be especially true for foraging traits, which both shape (ecologically) and are shaped by (evolutionarily) changes in prey resources.

CONCLUSIONS

Our results provide evidence that predators can shape their own foraging traits by causing changes in prey resources, but that this can only occur in systems where eco-evolutionary feedbacks are strong. If the strength of feedbacks differs from patch to patch (in this case lake to lake), then a spatial mosaic of eco-evolutionary interactions emerges, similar to that which has been proposed for co-evolutionary interactions (Thompson, 2005). Patches with strong feedbacks may diverge both ecologically and evolutionarily from patches with weak

feedbacks. Thus, spatial variation in the strength of eco-evolutionary interactions may be an important engine shaping patterns of ecological diversity (e.g. community structure) and evolutionary diversity (e.g. phenotypic variation) in nature.

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APPENDIX

Alewife densities, mean numbers of prey items per diet, and selectivity index values by lake and sampling date for anadromous (A) and landlocked (L) alewife populations sampled in 2005, with standard deviations in parentheses. Anadromous alewives were collected from Bride Lake (BL), Dodge Pond (DP), and Gorton Pond (GP). Landlocked alewives were collected from Pattagansett Lake (PL), Quonnipaug Lake (QL), and Rogers Lake (RL). Ten diets were examined for each sample

Pop.	Sample date ^a	Alewife density (fish/m ²)	Prey items/diet	Cladocerans			Copepods		
				Prey size (mm)	L_i	S_i	Prey size (mm)	L_i	S_i
BL (A)	2 June	3.67	8.6 (6.8)	0.501 (0.123)	0.2957**	-0.0354	0.943 (0.171)	0.2156*	0.275
BL	7 July	12.74	19.1 (18.4)	0.228#	0	0.0332	0.817 (0.181)	-0.0102	-0.0088
BL	27 July	0.34	159.5 (100.9)	0.433 (0.145)	0.0683**	0.1315**	1.178 (0.207)	0.4880**	0.2560**
BL	25 Aug	1.52	105.6 (37.9)	0.358 (0.092)	0.0296**	0.1037**	1.339 (0.086)	0.7573**	0.8724**
BL	20 Sep	1.11	67.0 (46.8)	0.335 (0.161)	0.0238**	0.0881**	1.173 (0.162)	0.5316**	0.4505**
DP (A)	2 June	5.95	5.8 (5.3)	0.377 (0.075)	-0.0175	-0.2798	0.740 (0.172)	-0.005	0.179
DP	7 July	3.64	161.2 (202.2)	0.265 (0.053)	0.0102	-0.0054	0.738 (0.142)	0.0316**	0.2144**
DP	27 July	2.83	68.2 (48.5)	0.342 (0.120)	0.0704**	0.1100**	1.023 (0.243)	0.2915**	0.4439**
DP	25 Aug	2.17	259.8 (321.4)	0.258 (0.035)	0.0163*	0.0217**	1.058 (0.264)	0.1003**	0.5546**
DP	20 Sep	0.62	614.2 (617.6)	0.322 (0.121)	0.2058**	0.1157**	0.741 (0.206)	0.0446**	0.3620**
GP (A)	7 June	3.78	45.0 (26.3)	0.386 (0.141)	-0.0185	0.0931**	0.536 (0.052)	0.0106	-0.189
GP	28 June	0.73	60.6 (29.0)	0.484 (0.057)	0.0089	0.1231	1.228 (0.149)	0.6481**	0.6354**
GP	28 July	0.27	77.75 (78.0)	0.508 (0.026)	-0.0134	0.2005**	1.366 (0.015)	0.7308**	0.8437**
GP	23 Aug	0.11	71.3 (43.0)	0.439 (0.064)	0.0154	0.1731**	1.161 (0.113)	0.5208**	0.8086**
GP	21 Sep	0.22	69.7 (32.5)	0.455 (0.083)	0.1818**	0.1482**	1.065 (0.125)	0.3529**	0.6277**

(continued)

APPENDIX—Continued

Pop.	Sample date ^a	Alewife density (fish/m ²)	Prey items/diet	Cladocerans			Copepods		
				Prey size (mm)	L_i	S_i	Prey size (mm)	L_i	S_i
PL (L)	1 June	0.04	824.0 (793.1)	0.374 (0.078)	0.0221**	0.0306**	0.745 (0.120)	0.0532**	0.1823**
PL	5 July	1.54	135.9 (100.8)	0.360 (0.044)	-0.0103	-0.0207	0.632 (0.111)	0.0136	-0.0198
PL	28 July	0.56	1400.4 (1555.4)	0.308 (0.020)	-0.0050**	0.0257**	0.601 (0.167)	-0.0144**	0.0438**
PL	23 Aug	1.60	146.7 (181.5)	0.209 (0.018)	0	-0.0361*	0.907 (0.361)	0.2270**	0.4506**
PL	21 Sep	0.62	273.0 (303.0)	0.219 (0.034)	0.002	-0.0054	0.528 (0.265)	0.0397**	0.2389**
QL (L)	7 June	0.06	862.1 (714.3)	0.300 (0.023)	-0.0215**	-0.0577**	0.647 (0.052)	-0.0550**	-0.0612**
QL	29 June	0.77	53.7 (58.6)	0.335 (0.108)	0.0275	-0.1099**	0.641 (0.064)	0.0033	-0.0017
QL	27 July	0.18	103.3 (98.1)	0.287 (0.024)	-0.0139	-0.0484**	0.694 (0.185)	0.0003	0.0970*
QL	24 Aug	0.32	68.3 (52.5)	0.315 (0.062)	0.0115	0.0088	0.507 (0.125)	0.0071	0.0301
QL	19 Sep	0.14	246.2 (235.2)	0.271 (0.038)	0	-0.0081	0.510 (0.271)	0.0653**	0.1458**
RL (L)	1 June	0.25	275.6 (164.8)	0.256 (0.012)	0.0072**	-0.0104	0.689 (0.076)	-0.0052	0.1394**
RL	1 July	0.06	184.5 (112.0)	0.294 (0.093)	0.0064	0.0412	0.756 (0.440)	0.1753**	0.2151**
RL	26 July	0.59	325.0 (141.2)	0.292 (0.040)	-0.0174*	-0.0452	0.373 (0.029)	-0.0260**	-0.1097**
RL	24 Aug	0.29	730.2 (669.4)	0.267 (0.020)	-0.0254**	-0.0118	0.431 (0.147)	-0.0269**	-0.0441**
RL	19 Sep	0.06	603.4 (430.3)	0.264 (0.016)	-0.0294**	-0.1657**	0.399 (0.056)	-0.0049**	0.0638**

^a Sample dates 2004: Bride Lake, 29 July, 23 August, 29 September; Gordon Pond, 24 June, 29 August; Pattiagsanett Lake, 6 July, 30 July; Rogers Lake, 29 June, 27 July, 31 August.

Only one diet from this sample contained cladocerans.

* Value falls outside of 95% confidence intervals.

** Value falls outside of 99% confidence intervals.