Contemporary trait change in a classic ecological experiment: rapid decrease in alewife gill-raker spacing following introduction to an inland lake

ERIC P. PALKOVACS*, ELIZABETH G. MANDEVILLE[†] AND DAVID M. POST[‡]

Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, U.S.A.

[†]*Program in Ecology and Department of Botany, University of Wyoming, Laramie, WY, U.S.A.*

[‡]*Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, U.S.A.*

SUMMARY

1. Ecological experiments showing large effects are predicted to drive contemporary trait changes resulting from evolution and phenotypic plasticity. However, few classic ecological experiments conducted in the wild have been investigated for evidence of contemporary trait change.

2. We examined a classic experiment in trophic ecology, the introduction of alewife (*Alosa pseudoharengus*) to Crystal Lake, Connecticut, U.S.A. (Brooks & Dodson, 1965), for the presence of contemporary trait change.

3. Alewife were introduced to Crystal Lake, an inland lake isolated from the coastal ocean, from an anadromous (migratory sea-run) source population. We utilised museum specimens collected soon after introduction and modern samples to measure changes in gill-raker morphology for the Crystal Lake alewife population since its introduction. We compared the gill-rakers of the Crystal Lake population to those of other nearby anadromous and landlocked (freshwater resident) alewife populations.

4. At introduction, the Crystal Lake population showed gill-raker spacing (GRS) similar to that of anadromous populations. Following introduction, we found evidence for a rapid decrease in GRS, an important trait for size-selective prey capture in fishes. This decrease occurred alongside a dramatic decline in zooplankton size, shown by Brooks and Dodson (1965) to be caused by the onset of alewife predation. After 45 years of isolation in freshwater, the Crystal Lake population showed GRS typical of landlocked populations.

5. Brooks and Dodson's study is a classic example of the strong effects predators can have on prey communities. Our study shows that such community effects of predators may feed back to shape predator trophic morphology. The rate of trait change observed for the Crystal Lake alewife population is comparable to rates observed from evolutionary experiments conducted explicitly to examine trait changes over contemporary time scales.

6. We conclude that strong ecological effects of introduced populations may be important drivers of contemporary trait change. We propose that classic ecological experiments represent underutilised resources for examining interactions between contemporary trait change and ecological effects in the wild.

Keywords: eco-evolutionary feedbacks, invasion, niche construction, predation, rapid evolution

Introduction

Classic experiments performed in nature have paved the way for new paradigms in ecology. For the study of trophic dynamics, such studies include the removal of the sea star *Pisaster* from rocky intertidal communities (Paine, 1966) and the experimental introduction of a planktivorous fish, the alewife (*Alosa pseudoharengus*), to a temperate coastal lake (Brooks & Dodson, 1965). These experiments helped to establish the important

Correspondence: Eric P. Palkovacs, Long Marine Laboratory, University of California-Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, U.S.A. E-mail: epalkova@ucsc.edu

role of predators in shaping prey communities and ecosystem dynamics, now a fundamental principle in ecology and conservation biology (Estes *et al.*, 2011). Predator introductions and removals are associated with rapid rates of evolution (Hendry, Farrugia & Kinnison, 2008). But what are the consequences, if any, of such classical ecological manipulations for rates of trait change?

We examined a classic predator introduction, the introduction of alewives to Crystal Lake, Connecticut (U.S.A.) in 1955 (Brooks & Dodson, 1965), for evidence of contemporary trait change. Brooks and Dodson sampled the zooplankton community of Crystal Lake before (1942) and after (1964) the introduction of alewives to the lake. Crystal Lake, an inland lake isolated from the ocean, was stocked from an anadromous (migratory searun) source population, which became landlocked in this geographical setting. Brooks and Dodson's results showed that the zooplankton community of Crystal Lake rapidly shifted from dominance by large-bodied zooplankton species to dominance by small-bodied species. Size-selective predation by introduced alewives caused this shift. Brooks and Dodson's study was fundamental in establishing the importance of predators for shaping prey communities (Peet, 1991), paving the way for the study of trophic cascades in ponds and lakes (Hurlbert, Zedler & Fairbank, 1972; Carpenter *et al.*, 1987). But what was the effect of the alewife-driven zooplankton community size shift for alewife foraging traits?

To investigate this question, we compared gill-raker morphology (an important trait for size-selective prey capture) from ten alewife populations known from previous studies (Palkovacs *et al.*, 2008; Post *et al.*, 2008) to display either an anadromous or landlocked (freshwater resident) life history. Among these, we examined alewife specimens from Crystal Lake collected soon after introduction (1960) and more recently (2005). We hypothesised that changes in the size structure of the zooplankton community, caused by alewife predation, drive feedbacks that shape alewife foraging traits. This process may underlie phenotypic divergence between anadromous and landlocked populations (Palkovacs & Post, 2008). Therefore, we predicted that gill-raker morphology of the Crystal Lake population has changed between 1960 and 2005 from an anadromous phenotype equipped for large-bodied prey capture to a landlocked phenotype better suited for small-bodied prey capture. We compared the rate of trait change for this alewife introduction to rates from classic evolutionary experiments conducted in the wild.

Methods

We examined variation in gill-raker morphology for ten alewife populations in coastal Connecticut, U.S.A. (Table 1). Three populations display an anadromous life history: Bride Lake (BL), Dodge Pond (DP) and Gorton Pond (GP). Seven populations display a landlocked life history: Pattagansett Lake (PL), Rogers Lake (RL), Saltonstall Lake (SL), Long Pond (LP), Amos Lake (AL), Quonnipaug Lake (QL) and Crystal Lake. The ecology and evolutionary history of the alewife populations in these lakes have been described previously (Palkovacs *et al.*, 2008; Post *et al.*, 2008). With the exception of Crystal Lake, the examined landlocked populations became isolated in fresh water between 300 and 5000 years ago, possibly as a result of human dam construction (Palkovacs *et al.*, 2008). In contrast, the Crystal Lake population was introduced from an anadromous source (probably the Connecticut River) around 1955. Brooks and Dodson erroneously considered the species introduced to Crystal Lake to be blueback herring (*Alosa aestivalis*), but current sampling and historical surveys going back to 1955 indicate that it was alewife (Connecticut Department of Energy and Environmental Protection, unpublished data). Alewife is the landlocked *Alosa* species present in other Connecticut lakes (Jacobs & O'Donnell, 2002).

Table 1 Biological characteristics of alewife populations sampled, including sample sizes (*n*), mean total length (TL), mean size-standardised gill-raker spacing (GRS) and population groupings based on Cluster Analysis. Standard deviations are given in parentheses

Population	Type	n	TL mm (SD)	GRS mm (SD)	Group
Bride Lake (BL)	Anadromous	56	54.14 (14.62)	0.192 (0.015)	1
Dodge Pond (DP)	Anadromous	49	54.59 (15.41)	0.197 (0.018)	1
Gorton Pond (GP)	Anadromous	58	57.36 (15.97)	0.191 (0.016)	1
Crystal Lake 1960	Introduced	27	84.85 (9.54)	0.182 (0.015)	1
Crystal Lake 2005	Introduced	26	89.15 (9.52)	0.163 (0.009)	2
Amos Lake (AL)	Landlocked	20	94.55 (17.13)	0.153 (0.008)	2
Long Pond (LP)	Landlocked	16	56.00 (8.99)	0.161 (0.009)	2
Pattagansett Lake (PL)	Landlocked	76	71.22 (29.56)	0.166 (0.014)	2
Quonnipaug Lake (QL)	Landlocked	90	86.30 (42.11)	0.162 (0.015)	2
Rogers Lake (RL)	Landlocked	80	62.16 (21.76)	0.172 (0.017)	2
Saltonstall Lake (SL)	Landlocked	25	87.56 (16.54)	0.158 (0.009)	2

We obtained specimens from all study lakes between 2004 and 2008 using purse seine, gill net or electrofishing boat. We obtained museum specimens collected from Crystal Lake in 1960. Sampling was performed from June through August; therefore, anadromous specimens represent young-of-the-year fish collected before their marine migration, and landlocked fish (including those introduced to Crystal Lake) represent a mixture of age classes. For modern samples, fish were frozen immediately following capture and stored at −20 °C. Museum specimens were fixed in formalin and stored in 70% ethanol. While both freezing and formalin fixation can cause shrinkage in small fish, such effects have been found to be negligible for fish >5 mm in length (Hjorleifsson & Kleinmacphee, 1992), which includes all specimens examined in this study (Table 1).

We measured average gill-raker spacing (GRS) and total length (TL) for each specimen according to previously published methods (Palkovacs & Post, 2008). Due to body size heterogeneity among populations, GRS was standardised to the mean overall body size in the dataset. We log_{10}-transformed TL and GRS and performed least-squares linear regression for each population independently. We used the slope of each regression as the allometric scaling constant b and calculated the standardised trait value for each specimen according to:

$$GRS_t = GRS_o(TL_t/TL_o)^b$$

where GRS_t = standardised trait value, GRS_o = observed trait value (untransformed), TL_t = target body length and TL_o = observed body length.

Size-standardised trait values were ln-transformed. ANOVA with *post hoc* Tukey's HSD tests was used to examine differences among populations. Crystal Lake 1960 and 2005 were considered to be independent for statistical purposes. Mean size-standardised trait values were calculated for each population, and Cluster Analysis was used to detect groupings among populations using the *K*-means Clustering Method with the number of clusters set *a priori* at *k* = 2 (representing the two forms: anadromous and landlocked). ANOVA and Cluster Analysis were implemented using PASW Statistics 18.0 (IBM Corporation, Somers, NY, U.S.A.).

The rate of trait change for Crystal Lake GRS was calculated in *haldanes* as:

$$h = ((x_2/s_p) - (x_1/s_p))/g$$

where h = rate of trait change, x = mean trait value at times 1 and 2, s_p = pooled standard deviation and g = generations.

Generation time was set at 1.5 years, as estimated previously for landlocked alewives (Palkovacs *et al.*, 2008). Because rates of trait change scale with time interval, *haldanes* numerator was plotted against number of generations to compare among rates (Kinnison & Hendry, 2001). For comparison, we included all rates from a recently published database (Hendry *et al.*, 2008) that involved experimental introductions in the wild. The resulting data included evolutionary rates for classic experimental introductions of Trinidadian guppies (*Poecilia reticulata*) and *Anolis* lizards (*Anolis sagrei*) (Endler, 1980; Reznick & Bryga, 1987; Reznick, Bryga & Endler, 1990; Magurran *et al.*, 1992, 1995; Losos, Warheit & Schoener, 1997; Reznick *et al.*, 1997).

Results

The introduced Crystal Lake alewife population showed a clear decrease in GRS between 1960 and 2005 (Table 1, Fig. 1). We found significant differences in GRS among populations (ANOVA: $F_{10, 512}$ = 43.783, $P < 0.001$) and a significant change in the Crystal Lake population between 1960 and 2005 (Tukey's HSD: $P = 0.001$). Cluster Analysis grouped Crystal Lake 1960 specimens with anadromous populations and 2005 specimens with landlocked populations (Table 1, Fig. 1), indicating that the formerly anadromous population changed to display landlocked trophic morphology over the 45-year time period examined. The resulting rate of trait change (0.0502 *h*) was in the top 36%
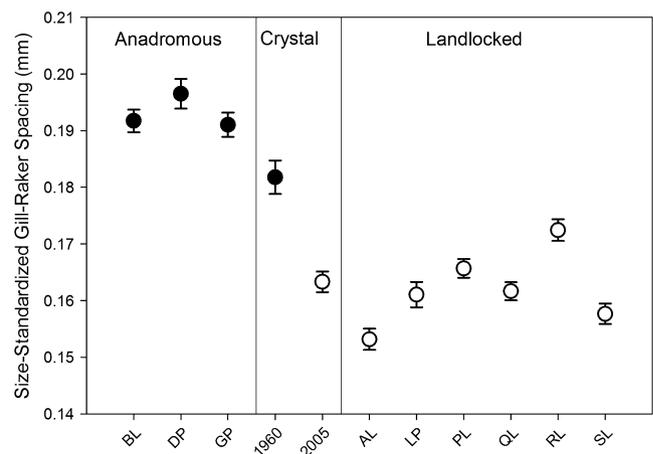

Fig. 1 Size-standardised gill-raker spacing (mean ± SE) for coastal Connecticut alewife populations displaying either an anadromous (migratory sea-run) or landlocked (freshwater resident) life history. The Crystal Lake population was introduced from an anadromous source in 1955 and rapidly changed to display gill-raker morphology typical of other landlocked populations, which have been isolated in fresh water for hundreds of years. Filled and open symbols represent populations grouped by Cluster Analysis.

of rates measured from introduction experiments, being faster than the mean rate observed from the experimental introduction of *Anolis* lizards (0.0385 *h*) but slower than that observed for guppies (0.1250 *h*). The magnitude of trait change (*haldanes* numerator) was in the top 12% of those observed (Fig. 2).

Discussion

Ecological experiments that produce large effects are likely to drive trait change via natural selection and phenotypic plasticity, yet few such experiments have been examined for the presence of contemporary trait change (Strauss *et al.*, 2008). Our examination of the classic introduction of alewives to Crystal Lake showed that the population, introduced from an anadromous source, rapidly changed to display gill-raker morphology typical of a landlocked population. Anadromous alewives display a suite of morphological and behavioural traits that facilitate large-bodied prey capture (Palkovacs & Post, 2008) and, as a result, cause seasonal declines in zooplankton body size (Post *et al.*, 2008; Palkovacs & Post, 2009). However, the annual juvenile out-migration provides a seasonal prey refuge, allowing large-bodied zooplankton species to re-establish. When an anadromous population becomes landlocked, as it did in Crystal Lake, large-bodied zooplankton species are extirpated, resulting in a zooplankton community dominated by small-bodied species (Brooks & Dodson, 1965; Post *et al.*, 2008). This change in the zooplankton community appears to feed back to drive changes in alewife foraging traits.
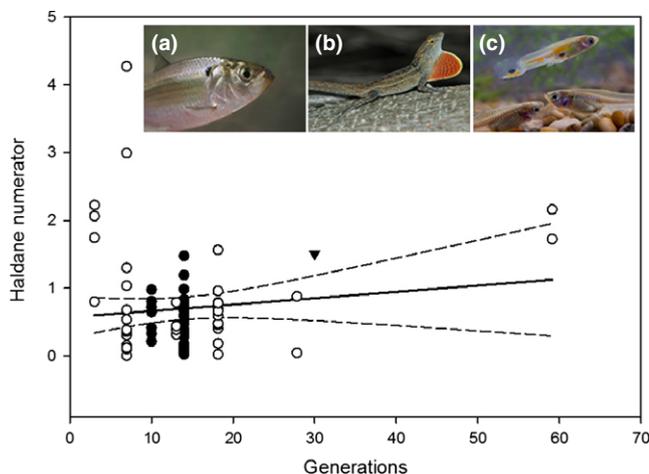

Fig. 2 The rate of trait change for Crystal Lake alewives (a, triangle) is comparable to classic cases of experimental introduction and contemporary trait change involving *Anolis* lizards (b, filled circles) and Trinidadian guppies (c, open circles). Least squares regression (with 95% confidence intervals) is shown.

Previous evidence has suggested that alewife trophic morphology could shift from an anadromous phenotype to a landlocked phenotype over a time period of hundreds of years (Palkovacs *et al.*, 2008). Here, we show that this process can occur much faster. Over the 45 years of this study, the Crystal Lake population attained gill-raker morphology typical of populations that have been landlocked for hundreds of years. Indeed, GRS may have already declined in the interval between the 1955 introduction and our sampling in 1960. Thus, strong ecological effects of predators on prey communities may be an important agent of trait change in the context of species introductions.

Several evolutionary experiments have been conducted for the explicit purpose of examining the process of trait changes over contemporary time scales (Irschick & Reznick, 2009). Such experiments have involved the introduction of guppies to Trinidadian streams (Endler, 1980; Reznick & Bryga, 1987; Reznick *et al.*, 1990, 1997; Magurran *et al.*, 1992, 1995) and *Anolis* lizards to Bahamian islands (Losos *et al.*, 1997). Our results show that the introduction of alewives to Crystal Lake resulted in a rate of trait change comparable to those observed in these prior introduction experiments. Interestingly, guppies and *Anolis* lizards, well-known systems for studying contemporary evolution, also show recent evidence for ecological consequences of contemporary trait changes (Palkovacs *et al.*, 2009; Bassar *et al.*, 2010, 2012; Palkovacs, Wasserman & Kinnison, 2011; Schoener, 2011). Thus, interactions between trait change and ecological effects may be widespread in nature. Our results suggest that ecological experiments represent underutilised resources for studying interactions between contemporary trait change and ecological effects as they unfold in the wild.

Acknowledgments

References

Bassar R.D., Ferriere R., Lopez-Sepulcre A., Marshall M.C., Travis J., Pringle C.M. *et al.* (2012) Direct and indirect

ecosystem effects of evolutionary adaptation in the Trinidadian guppy (*Poecilia reticulata*). *American Naturalist*, **180**, 167–185.

Bassar R.D., Marshall M.C., López-Sepulcre A., Zandonà E., Auer S., Travis J. *et al.* (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences USA*, **107**, 3616–3621.

Brooks J.L. & Dodson S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.

Carpenter S.R., Kitchell J.F., Hodgson J.R., Cochran P.A., Elser J.J., Elser M.M. *et al.* (1987) Regulation of lake primary productivity by food web structure. *Ecology*, **68**, 1863–1876.

Endler J.A. (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, **34**, 76–91.

Estes J.A., Terborgh J., Brashares J.S., Power M.E., Berger J., Bond W.J. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Hendry A.P., Farrugia T.J. & Kinnison M.T. (2008) Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, **17**, 20–29.

Hjorleifsson E. & Kleinmacphee G. (1992) Estimation of live standard length of winter flounder *Pleuronectes americanus* larvae from formalin-preserved, ethanol-preserved, and frozen specimens. *Marine Ecology Progress Series*, **82**, 13–19.

Hurlbert S.H., Zedler J. & Fairbank D. (1972) Ecosystem alteration by mosqitofish (*Gambusia affinis*) predation. *Science*, **175**, 639–641.

Irschick D.J. & Reznick D.N.. 2009. Field experiments, introductions, and experimental evolution: a review and practical guide. In: *Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments* (Eds T. Garland & M.R. Rose), pp. 173–193. University of California Press, Berkeley, CA.

Jacobs R.P. & O'Donnell E.B. (2002) *A Fisheries Guide to Lakes and Ponds of Connecticut Including the Connecticut River and Its Coves*. Connecticut Department of Environmental Protection, Hartford, CT.

Kinnison M.T. & Hendry A.P. (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica*, **112**, 145–164.

Losos J.B., Warheit K.I. & Schoener T.W. (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, **387**, 70–73.

Magurran A.E., Seghers B.H., Carvalho G.R. & Shaw P.W. (1992) Behavioral consequences of an artificial introduction of guppies (*Poecilia reticulta*) in N-Trinidad - evidence for the evolution of antipredator behavior in the wild. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **248**, 117–122.

Magurran A.E., Seghers B.H., Shaw P.W. & Carvalho G.R. (1995) The behavioral diversity and evolution of guppy, *Poecilia reticulata*, populations in Trinidad. *Advances in the Study of Behavior*, **24**, 155–202.

Paine R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.

Palkovacs E.P., Dion K.B., Post D.M. & Caccone A. (2008) Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. *Molecular Ecology*, **17**, 582–597.

Palkovacs E.P., Marshall M.C., Lamphere B.A., Lynch B.R., Weese D.J., Fraser D.F. *et al.* (2009) Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **364**, 1617–1628.

Palkovacs E.P. & Post D.M. (2008) Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evolutionary Ecology Research*, **10**, 699–720.

Palkovacs E.P. & Post D.M. (2009) Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology*, **90**, 300–305.

Palkovacs E.P., Wasserman B.A. & Kinnison M.T. (2011) Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. *PLoS One*, **6**, e18879.

Peet R.K. (1991) Lessons from nature: case studies in natural systems. In: *Foundations of Ecology: Classic Papers with Commentaries*. (Eds Real L.A. & Brown J.H.), pp. 605–615. University of Chicago Press, Chicago, IL.

Post D.M., Palkovacs E.P., Schielke E.G. & Dodson S.I. (2008) Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology*, **89**, 2019–2032.

Reznick D.A., Bryga H. & Endler J.A. (1990) Experimentally induced life-history evolution in a natural population. *Nature*, **346**, 357–359.

Reznick D.N. & Bryga H. (1987) Life-history evolution in guppies (*Poecilia reticulata*): 1. phenotypic and genetic changes in an introduction experiment. *Evolution*, **41**, 1370–1385.

Reznick D.N., Shaw F.H., Rodd F.H. & Shaw R.G. (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, **275**, 1934–1937.

Schoener T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science*, **331**, 426–429.

Strauss S.Y., Lau J.A., Schoener T.W. & Tiffin P. (2008) Evolution in ecological field experiments: implications for effect size. *Ecology Letters*, **11**, 199–207.