

Indirect trophic interactions with an invasive species affect phenotypic divergence in a top consumer

P. E. Hirsch · P. Eklöv · R. Svanbäck

Received: 13 June 2012 / Accepted: 5 February 2013 / Published online: 6 March 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract While phenotypic responses to direct species interactions are well studied, we know little about the consequences of indirect interactions for phenotypic divergence. In this study we used lakes with and without the zebra mussel to investigate effects of indirect trophic interactions on phenotypic divergence between littoral and pelagic perch. We found a greater phenotypic divergence between littoral and pelagic individuals in lakes with zebra mussels and propose a mussel-mediated increase in pelagic and benthic resource availability as a major factor underlying this divergence. Lakes with zebra mussels contained higher densities of large plankton taxa and large invertebrates. We suggest that this augmented resource availability improved perch foraging opportunities in both the littoral and pelagic zones. Perch in both habitats could hence express a more specialized foraging morphology, leading to an increased divergence of perch forms in lakes with zebra mussels. As perch do not prey on mussels

directly, we conclude that the increased divergence results from indirect interactions with the mussels. Our results hence suggest that species at lower food web levels can indirectly affect phenotypic divergence in species at the top of the food chain.

Keywords Indirect effects · Morphological response · Food web · Phenotypic plasticity · Disruptive selection

Introduction

Phenotypic divergence within populations often precedes genetic divergence and is an important process in adaptive radiation (Schluter 2000). Phenotypic divergence within a population can result from trade-offs in adaptive traits between different environments. Direct interactions with a competitor or a predator are important drivers of phenotypic divergence (Nosil and Crespi 2006) and phenotypic responses to direct competition or predation are classically viewed to initiate the divergence between subsets of individuals within populations (Darwin 1859). Indirect species interactions however, have only recently received attention as drivers of phenotypic or evolutionary changes (Abrams 2000). The ubiquity of indirect interactions between predator and prey or competitors is undisputed (Schmitz et al. 2004) but empirical evidence for phenotypic changes triggered by such indirect interactions, especially from natural systems, is still rare [but see e.g. Walsh and Reznick (2008)]. Recently, Eklöv and Svanbäck (2006) experimentally showed that top predator presence can have indirect effects on the phenotypic divergence of prey at lower trophic levels. Indirect non-lethal interactions with predators caused prey to shift habitats, which in turn changed the prey's resource use and morphology (Eklöv

Communicated by Scott Peacor.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-013-2611-1) contains supplementary material, which is available to authorized users.

P. E. Hirsch · P. Eklöv · R. Svanbäck
Department of Ecology and Genetics/Limnology,
Evolutionary Biology Centre, Uppsala University,
Norbyvägen 18 D, 75236 Uppsala, SE, Sweden
e-mail: peter.eklov@ebc.uu.se

R. Svanbäck
e-mail: richard.svanback@ebc.uu.se

P. E. Hirsch (✉)
Man–Society–Environment, University of Basel,
Vesalgasse 1, CH-4051 Basel, Switzerland
e-mail: philipp.hirsch@unibas.ch

and Svanbäck 2006). However, whether indirect interactions across more than one trophic level affect phenotypic divergence remains, to the best of our knowledge, unstudied.

The question then becomes if indirect interactions can propagate through the food web to trigger phenotypic responses in species further distant in the food chain than in the adjacent trophic level. Generally, studies assessing the evolutionary potential of indirect trophic interactions are complicated by the fact that every species is embedded in a complex web of direct and indirect species interactions. This makes it difficult to examine how a specific indirect consumer-resource interaction may lead to phenotypic divergence (Werner and Peacor 2003). Species invasions can be considered “natural experiments” sensu Stockwell et al. (2003). An invasive species constitutes a new interaction component “added” to a system and may thus allow the study of indirect interactions affecting divergence by comparison of invaded and pristine ecosystems.

Introductions of species have mostly been demonstrated as having direct demographic effects, i.e. causing changes in the occurrence or number of native species (e.g. Ward and Ricciardi 2007). Many ecosystems feature a great diversity of phenotypes within populations that can be affected indirectly by alteration of the ecosystems. For example, major changes in lakes’ nutrient levels have recently been invoked in triggering dramatic changes in the divergence among forms of whitefish: eutrophication has led to flattened selection gradients and caused the collapse of clearly separated forms of whitefish into a phenotypically unimodal hybrid swarm (Vonlanthen et al. 2012). Our study addresses this topic by asking if changes in the ecosystem triggered by an invasive species can indirectly affect the biodiversity within a native top consumer.

Recent research on biodiversity within populations, especially on trophic polymorphisms in fish, has argued for the evolutionary significance of intra-population divergence in traits related to foraging (Komiya et al. 2011; Smith and Skúlason 1996). Ecological theory predicts that if an environment features distinct rewards, e.g. food sources, then phenotypes closely matching a specific reward may attain higher fitness than intermediate phenotypes (Schluter 2000; Thibert-Plante and Hendry 2011). Selection against intermediate phenotypes and in favour of specialized phenotypes can then drive a phenotypic and ultimately genetic divergence (Hendry et al. 2009; Rueffler et al. 2006). Thus, phenotypes with different types of trophic specialization within a single population constitute an important source of variation upon which natural selection can act to drive heritable changes (Pfennig et al. 2010). Natural selection is essentially blind towards the genotype (West-Eberhard 2003). Hence phenotypic plasticity in trophic traits can play a key role in generating the intra-

population diversity that constitutes the raw material for natural selection to act upon.

In the present study, we quantify phenotypic divergence in a trait related to foraging across several comparable populations of a top consumer. We then connect the differences in divergence to ecological background data on how an invasive species on a lower trophic level indirectly affects the top consumer populations. This allows us to study whether the invasive species indirectly triggers phenotypic changes in native consumers at higher trophic levels.

As a model system we use Swedish lakes where invasive zebra mussels (*Dreissena polymorpha*) have been established. The zebra mussels’ effects on the lakes’ lower trophic levels might indirectly affect divergence in native perch populations (*Perca fluviatilis*). The zebra mussel is an efficient filter feeder that has notable consequences for both pelagic and benthic resources (Higgins and Vander Zanden 2010). Its selective filtering activity influences the size structure of the plankton community. The mussels’ incurrent siphons limit the size of ingestible particles, allowing the mussels to filter out small zooplankton and phytoplankton (MacIsaac et al. 1995). If phosphorus concentrations are high enough to sustain compensatory phytoplankton growth (as in meso-eutrophic lakes) then phytoplankton can compensate for mussel ingestion, stabilize at lower population densities and continue to serve as food for zooplankton (Hessen 2008; Urabe et al. 1997). Larger zooplankton taxa that escape mussel ingestion are superior to smaller-sized taxa and may be favoured by the ability to exploit lower levels of phytoplankton biomass. This mechanism likely underlies the shift towards larger zooplankton taxa in some zebra mussel-invaded lakes (Davenport et al. 2000; Idrisi et al. 2001).

Pelagic zooplanktivorous fish selectively feed on large zooplankton species (Brooks and Dodson 1965) and hence might benefit from a mussel-mediated increase in zooplankton size. Littoral fish forage selectively on large epifaunal invertebrates (Diehl 1992) and hence might benefit from a mussel-mediated increase in epifaunal invertebrate density. The mussels’ egestion of pelagic nutrients and their shells provide a surplus of food and structure for epifaunal (i.e. living on the substrate) invertebrates which increase in density where zebra mussels occur (Ward and Ricciardi 2007).

We examined the indirect response of perch to the zebra mussels’ changes in ecological context by comparing perch populations from meso- to eutrophic south-eastern Swedish lakes with and without zebra mussels. Perch are the most abundant top consumers in most northern European lakes but do not prey on zebra mussels. Perch show phenotypic differences in morphology related to habitat (Svanbäck and Eklöv 2002; Svanbäck and Eklöv 2003) whereby perch in

the littoral zone express a deeper-bodied phenotype allowing for higher manoeuvrability, which maximizes intake of benthic food (Svanbäck and Eklöv 2003). In contrast, perch in the pelagic zone have a more streamlined phenotype, which minimizes drag forces while cruise-swimming, maximizing foraging efficiency on plankton (Svanbäck and Eklöv 2003). Common garden experiments demonstrated that this phenotypic divergence chiefly results from a plastic response to feeding on habitat-specific resources (Svanbäck and Eklöv 2006).

Given the responsiveness of perch phenotypes to littoral and pelagic resources and the zebra mussel's demonstrable effects on a lake's lower trophic levels we hypothesize that plastic responses of perch phenotypes to indirect interactions with the zebra mussel affect intra-population divergence in perch. We predict that if the availability of benthic resources and of large zooplankton increases simultaneously (i.e. phosphorus levels suffice to sustain a high growth rate of phytoplankton as a food source for zooplankton), perch should experience a surplus of resources in both habitats, leading to increased consumption of habitat-specific resources. We would thus expect a greater morphological divergence between littoral and pelagic forms.

Materials and methods

Study lakes

We sampled perch from three lakes with and five without zebra mussels. We chose lakes that were similar in trophic state and fish community composition. We studied a large range of parameters that could potentially confound the zebra mussels' effect on perch such as the relative availability of littoral versus pelagic habitat, mean and maximum lake depth, concentration of phosphorus (i.e. the trophic state of the lakes), and human influences (e.g. shoreline constructions, commercial, and recreational fisheries). After analysing a large range of parameters (see Electronic supplementary material for details), we did not find that lakes with mussels differed from lakes without mussels in any of the parameters. Further support for the role zebra mussels play in the lakes comes from the fact that a positive correlation between nutrients (total phosphorus) and primary producers [phytoplankton density measured as chlorophyll (chl) *a* concentration] (Dillon and Rigler 1974) was absent in lakes with zebra mussels (see "Results"). The decoupling of nutrient concentration and phytoplankton density strongly suggests that the zebra mussels' filtering activity changes the ecological context in invaded lakes. A detailed description of all the information we gathered on the lakes is given in the Electronic supplementary materials.

Field sampling

We used standard-type multi-mesh Nordic gillnets to sample fish in the littoral and pelagic habitats of each lake. Sampling took place between the end of July and the beginning of August to ensure that all fish were active and not in their spawning season. Littoral nets (1.5 m deep and 30 m long) were set at 2 m depth just outside of the vegetation in the littoral zone. Pelagic nets (6 m deep and 27.5 m long) were set at approximately 200 m from the littoral nets towards the deepest part of the lake. All nets were set in the afternoon and retrieved 16–18 h later. The littoral catch from the gill nets was low in two of the lakes (Strandsjön and Fälaren), therefore for diet and growth estimates we also used drop nets to increase the sample size of fish in the littoral zone. For perch morphology as well as for fish biomass (catch per unit effort) we only compared fish caught with the same sampling technique, thus we only used fish from the multi-mesh Nordic gillnets in the littoral and pelagic zones for this. Fish were measured and weighed immediately after capture and subsequently frozen for later analysis. In total, 1,172 perch were caught and analysed for diet, growth, length and age as described below.

Analysis of phenotypic divergence

We analysed the morphology of all perch caught in the pelagic and littoral zones of each lake. After thawing, each individual was photographed with its fins spread and fixed to the surface of a styrofoam or glass ball bed. All fish were frozen and thawed for comparable time and under the same conditions. We therefore assumed potential morphological differences between populations to remain unaffected by the freezing and thawing treatment. We then digitized 20 landmarks on the left side of each specimen following Olsson et al. (2006) using the software Ds-digit (Slice 1994). To quantify morphological variation in body shape among individuals, we performed multivariate geometric shape analysis. We analysed the relative position of digitized landmarks and hence overall variation in body shape using thin-plate spline relative warp (TPSRW) (Rohlf 1993). TPSRW was used to calculate the uniform and partial warp scores that denote the differences in shape among the individuals. Shape differences were scaled to the centroid (a landmark-derived mean size) to account for size differences that could potentially affect morphology.

As an initial screening test for differences in morphology we constructed a multivariate analysis of covariance (MANCOVA) model with body shape (all uniform and partial warps) as a response variable, form of perch (littoral or pelagic) and lake as categorical predictors and centroid size as a continuous covariate. To better express the degree

of phenotypic divergence between habitats we analysed both uniform and partial warp scores with a multivariate discriminant function analysis (DFA) based on the classification of individuals according to their littoral or pelagic origin. A subsequent canonical function analysis that maximally discriminates between the pelagic and littoral individuals combined all partial warps and uniform scores for each individual into one numerical value [morphological index (MI)]. The MI thus gave us an individual measure of each specimen's morphology relative to the phenotypic spectrum of its conspecifics ranging from the most extreme littoral to the most extreme pelagic phenotype in each lake.

To measure phenotypic divergence, we then calculated the distance in the means of all the MIs between littoral and pelagic individuals for each lake (i.e. the degree of morphological divergence between littoral and pelagic). To statistically test for differences in the magnitude of divergence between littoral and pelagic forms among lakes with and without zebra mussels we used the assignment success of the DFAs in each lake as a measure of how divergent fish are between the littoral and pelagic habitats of lakes. The assignment success is the percentage of individuals that, based on their morphology, could be correctly classified by the DFA into the littoral and pelagic habitats. MIs obtained from these lake-wise analyses were exclusively used for visualization of the divergence in each lake and to confirm that differences in means can serve to describe phenotypic divergence. The number of fish caught in the littoral and pelagic varied among lakes. Therefore, to obtain a visualization of divergence independent of the number of littoral or pelagic fish we applied an iteration approach. We randomly re-sampled 20 individuals' MIs from both the pelagic and the littoral using the Monte Carlo function in the PopTools add-on for Excel and calculated the divergence between the means of the 20 littoral and pelagic individuals' MIs. Iterating that procedure 100 times resulted in a median of divergence for each lake that we used for visualization.

In addition to the lake-wise DFAs assignment success we used two approaches to provide measures of divergence that are more directly comparable between lakes. First, we calculated the mean Mahalanobis' distances between the littoral and pelagic individuals to the habitats' centroids (the "mean point" of all individuals in each habitat) in each lake and second we performed a complementary single DFA that comprised all lakes. Mahalanobis' distances are comparable to Euclidean distances yet more applicable to morphometric data because they provide a measure of distance in a multivariate space of correlated variables, i.e. the uniform and partial warps scores matrix. They allow for a direct comparison between lakes because the direction of variation among groups (littoral and

pelagic) is rescaled so that variation across all groups becomes isotropic and hence comparable [see Klingenberg and Monteiro (2005) for more details on this method].

Total length of perch did not significantly differ between lakes with and without zebra mussels or between habitats but varied across lakes. In contrast to the separate DFAs that only compared fish within one lake we found that the DFA comprising all lakes integrated over a much larger number of individuals with differing lengths. Therefore, to account for the differing sizes among the lakes within one analysis, we corrected the MI for the size of each individual by regressing centroid size, the most applicable size descriptor in geometric morphometrics, with the MI from the DFA comprising all lakes. We then calculated the divergence as the difference between the means of residuals from all individuals in each habitat and each lake.

Dietary data, age, and growth analyses

The stomach contents were identified to the lowest taxonomic level possible and the length of the first ten (or all if less than ten) individuals of each taxon was measured. Digestion of dietary items only allowed classification into the following groups: benthic invertebrates, cladocerans, copepods and other zooplankton, and fish.

Age, yearly growth and von Bertalanffy growth parameters were indirectly inferred from the opercula bones of the fish. By counting the number of winter bands, the age of the fish can be determined. By relating the distance between two winter rings to the length of the fish the growth can be back-calculated [for further details on this standard method see Bagenal and Tesch (1978)]. We back-calculated the growth of perch (as length increase in millimetres) in their 1 year of life from the opercula bones, because juvenile growth is important for an adult perch individual's condition. As a commonly applied measure for comparison of the different perch populations' overall growth, we used the growth performance index ϕ after Pauly (1981). This measure, based on von Bertalanffy's theory of growth, has proven to be particularly appropriate for comparing several separated fish populations (Froese and Binohlan 2003; Holker and Thiel 1998). We derived the Bertalanffy's growth parameters, body growth coefficient (k ; which measures the rate of approach to the asymptotic size of the fish) and asymptotic size (L_∞) from Ford-Walford plots. The Ford-Walford plots are linear regressions of size at age $L_{(t+1)}$ against size at age L_t , with t being years. The slope and the intercept of the linear regression line allow calculation of k [$=-\ln(\text{slope})$] and of L_∞ [$=(1-\text{intercept}) k^{-1}$]. Based on a separate plot for each population, we calculated the populations' growth performances as $\phi = \log k + 2\log L_\infty$ after Holker and Thiel (1998).

Higher values of the index indicate that a population's individuals grow faster.

Zooplankton sampling and data analysis

A zooplankton net (200- μm mesh, diameter 25 cm) was lowered to the bottom, opened, and retrieved vertically at a speed of approximately 0.5 m s^{-1} thus catching zooplankton throughout the water column. We are confident that repeating this procedure three times in both the littoral and pelagic zones constitutes a robust representation of the local zooplankton community relevant for perch. To further account for temporal variation of the zooplankton community we repeated our zooplankton sampling on three occasions in the littoral and pelagic zones at the end of June, middle of August and beginning of September. This corresponds to the major part of the growth season of perch in our lakes. Zooplankton samples were preserved and stained with Lugol's solution until further analysis. Zooplankton were then identified to the lowest possible taxonomic level and the body lengths of 15 individuals (or all individuals if <15) of each taxon from each sample were measured. Lengths were then transformed to biomass by using our own length-to-weight regressions. Fish prey selectively on large zooplankton (Brooks and Dodson 1965). Therefore, based on previous studies on perch length-selectivity of zooplankton food (Persson et al. 1996; Raess and Maly 1986) and our own length measurements we classified zooplankton into two groups: large cladocerans (preferred perch food) and small cladocerans, cyclopoid copepods, and calanoid copepods (not preferred). The large cladocerans group comprised taxa with an average length $>0.46 \text{ mm}$ (*Daphnia*, *Polyphemus*, *Bosmina*, *Diaphanosoma*, *Acroperus*, *Eurycerus*, *Sida* and *Leptodora*), while the small cladoceran group consisted of taxa with an average length $<0.46 \text{ mm}$ (*Ceriodaphnia*, *Scapholeberis* and all Chydorida species).

Benthic invertebrate sampling and data

Benthic invertebrates were sampled with a core sampler or an Ekman grab sampler with a diameter of 10 cm and $15.5 \times 16 \text{ cm}$ base dimensions, respectively. To account for spatial heterogeneity of benthic invertebrates, we took four samples in the littoral and in the deeper benthic zones, respectively (at approximately 3–10 m depth) close to where the nets were set in each lake. Benthic invertebrates are relatively immobile and we therefore assume our sampling scheme to give a reliable estimate of the benthic resources of perch during the growing season. Samples were preserved in 70 % ethanol and stained with rose bengal. We then separated all invertebrates from the sediment, identified them to the lowest taxonomic level

possible and measured individual body lengths to determine biomass using our own length-to-weight regressions. Previous research on benthic resource acquisition in perch has shown that epifaunal and infaunal taxa differ in availability to perch as food. While infaunal taxa are a less accessible food for perch, epifaunal taxa are more vulnerable to perch predation (Diehl 1992; Persson et al. 1996). Accordingly, we classified the invertebrates into infaunal (only chironomids in our lakes) and epifaunal (Isopoda, Amphipoda, Hirudinea spp., Hydracarina spp., *Chaoborus* larvae, Trichoptera larvae, Coleoptera spp., Ephemeroptera spp., and Ceratopogonidae). The isopod *Asellus aquaticus* was the most dominant species in the epifaunal group and comprised 44 % of the group's total biomass. As perch typically do not consume mussels or snails (Diehl 1992), we excluded them from all analyses.

Determination of chl *a* concentration and Secchi depth

Chl *a* concentration was measured in the middle of June and in the middle of September. Between 0.5 and 2 L of water was filtered with a glass fibre filter (MGC; pore size = $1 \mu\text{m}$) and the protocol ISO (1992) for the spectrophotometric determination of chl *a* concentration was followed. Secchi depth is a standard measure of water clarity and is determined by lowering a Secchi disk (a white circular plate attached to a line) and then recording the depth at which it is no longer visible from the surface.

Statistical analyses

Statistical analyses were conducted with Statistica version 11, with the exception of using PRIMER version 6 for the analyses of similarity (ANOSIM) and PAST version 2.03 for the analyses of similarity percentage (SIMPER). The low replicate number and the unbalanced design (only three lakes with zebra mussels) precluded nested ANOVA models for resources, perch diet, growth and size because all three necessary levels (mussel presence, lake, and habitat) could not be incorporated without violating important assumptions of the models. Therefore, where possible we applied non-parametric ANOSIM models (see below) or used *t*-tests with a whole lake's population mean to compare between lakes with and without zebra mussels. To account for differences in variances within lakes we computed *t*-tests assuming unequal variances. The *df* were computed using the Satterthwaite method which accounts for both unequal sample sizes and differences in variances between the groups tested, hence the decimal *df*-values.

To examine differences in benthic invertebrate and zooplankton communities and in perch dietary composition we conducted analyses of similarities (ANOSIM). ANOSIM is a standard non-parametric significance test for

differences in community composition between two or more groups. ANOSIMs compare differences in communities among lakes to differences in communities between the a priori defined groups with and without zebra mussels. In our study, we tested for differences in composition of zooplankton and benthic invertebrate communities and fish diet between lakes with and without zebra mussels. For this we used the density data of the zooplankton (mg L^{-1}) and benthic invertebrates (mg m^{-2}) and the density of different dietary items (as weight percentage of total stomach contents). In the case of zooplankton communities we applied a nested design. The three sampling occasions of one summer were nested into either lakes with or without zebra mussels. In the case of dietary data and benthic invertebrates, we used one mean value per lake as the replicate unit.

After each ANOSIM we computed a SIMPER analysis that gave insight into which taxa contributed most to the dissimilarity between lakes with and without zebra mussels. Based on the results of the SIMPER analysis, we tested whether the taxa identified as responsible for the dissimilarity showed significant differences in density between lakes with and without zebra mussels. Using *t*-tests as described above we tested for differences in density of different zooplankton groups, infaunal or epifaunal benthic invertebrates, and different dietary items. Since we conducted several comparisons per lake and group of dietary item (zooplankton or benthic invertebrate), we corrected the *P*-value of our *t*-tests using the false discovery rate (FDR). We used the free software tool Qvalue (Storey 2002) as implemented in R to calculate the *q*-values. We applied the default settings of the program and set the threshold for *q*-values at 0.05. The output *q*-values were used as indicators of statistical significance. For clarity we only present differences in the density of various zooplankton, benthic invertebrate, and dietary groups that were significant at the corrected *P*-level (i.e. *q*-value). For tests of our study not conducted with subsets of resources or dietary groups, we accepted a *P*-value <0.05 as statistically significant and a *P*-value <0.1 as marginally significant but ecologically relevant. Dietary data were square root transformed, and we applied an ln transformation to chl *a*, growth in 1 year, Secchi depths, and growth performance data which contained outliers (values deviating more than 50 % from the mean).

Results

Effect of zebra mussels on phenotypic divergence

We found a strong significant interaction between lake and form of perch (littoral or pelagic) (MANCOVA; interaction

form \times lake: Wilks' $\lambda = 0.60$, $F = 2.37$, $df = 7$, df effect = 252, $P < 0.001$; see Table S1 for full results of the MANCOVA model). This suggests that the magnitude of divergence might differ between lakes with and without zebra mussels. This was first confirmed by a higher assignment success of the DFAs in lakes with zebra mussels: the morphology of perch in lakes with zebra mussels allowed for a correct classification into either habitat in 97 % of all cases whereas in lakes without zebra mussels only 87 % of perch were correctly assigned ($t = 4.94$, $df = 5.58$, $P = 0.003$; mean across lakes with zebra mussels \pm SD = 97 % \pm 1.5, mean across lakes without zebra mussels \pm SD = 87 % \pm 1.7; Table S2). Visualizations of the divergence based on the lake-wise DFAs clearly depict a higher phenotypic divergence if calculated as the differences in means of MIs derived from the lake-wise DFA (Fig. 1). The combined single DFA including fish in all lakes confirmed the pattern of a higher divergence in lakes with zebra mussels. Perch from lakes with zebra mussels showed a marginally higher divergence between the littoral and pelagic habitats than perch from lakes without zebra mussels ($t = 2.51$, $df = 4.82$, $P = 0.055$; mean \pm SD_{with} = 1.22 \pm 0.5, mean \pm SD_{without} = 0.58 \pm 0.25; Fig. S1). Finally, the Mahalanobis' distances also revealed that phenotypic divergence between habitats was higher in lakes with zebra mussels ($t = 4.46$, $df = 3.3$, $P = 0.028$; mean \pm SD_{with} = 42.74 \pm 1.7, mean \pm SD_{without} = 38.39 \pm 1.1; Fig. 2).

The morphological diversity did not differ between lakes with and without zebra mussels, meaning that all lakes contained both littoral and pelagic forms. We provide morphology visualizations based on the landmarks for each lake and a boxplot containing all the individuals' MIs from the overall DFA comprising all lakes in the electronic supplementary material (Figs. S1, S2).

Effect of zebra mussels on primary production and water clarity

Indirect measures of phytoplankton density (chl *a* concentration) suggested a lower phytoplankton density in lakes with zebra mussels, as chl *a* concentration was marginally lower in lakes with zebra mussels than in lakes without zebra mussels (*t*-test, $t = -1.95$, $df = 4.28$, $P = 0.057$, mean \pm SD_{with} = 5.70 \pm 0.8 $\mu\text{g L}^{-1}$, mean \pm SD_{without} = 27.04 \pm 31.10 $\mu\text{g L}^{-1}$). Water clarity, measured as Secchi depth, was marginally higher in lakes with zebra mussels than in lakes without zebra mussels (*t*-test, $t = 2.25$, $df = 4.45$, $P = 0.054$, mean \pm SD_{with} = 4.53 \pm 1.67 m, mean \pm SD_{without} = 2.04 \pm 0.96 m). The ostensible decoupling of the typically positive correlation between phosphorus (Dillon and Rigler 1974) and phytoplankton density in lakes with zebra mussels further

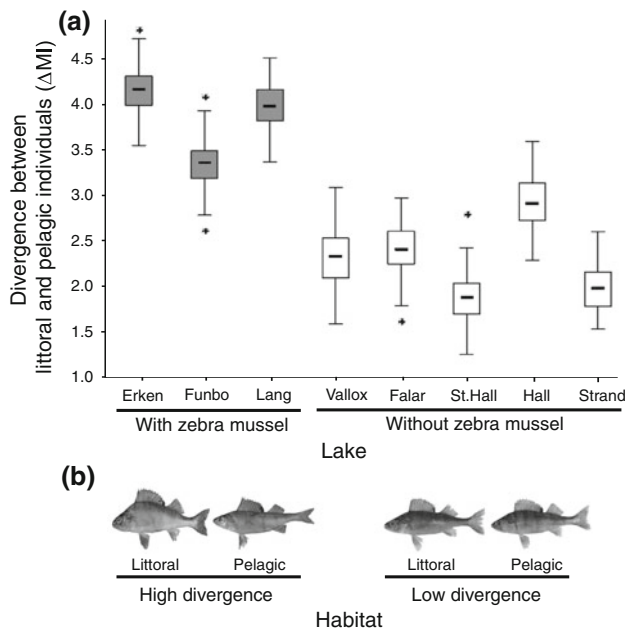


Fig. 1 Morphological divergence between littoral and pelagic perch (*Perca fluviatilis*) from eight lakes near Uppsala, Sweden **a** with and without zebra mussels (*Dreissena polymorpha*). Divergence is expressed as the iterated difference in means of morphological indices (ΔMIs) from lake-wise discriminant function analyses (see “Materials and methods” for details). Lake abbreviations and sample sizes n (littoral)/ n (pelagic): Erken 46/201, Funbosjön (Funbo) 48/71, Långsjön (Lang) 44/112, Valloxen (Vallox) 66/75, Fälaren (Falar) 54/43, StoraHällsjön (St. Hall) 51/97, Hällsjön (Hall) 65/31, Strand-sjön (Strand) 127/51. Boxes represent 25–75 % quartiles with medians as thick horizontal line in centre, non-outlier range is shown by vertical lines, outliers are indicated by asterisks. **b** Photographs of fish with extreme and intermediate habitat-specific morphology caught in the littoral and pelagic zone of one of the study lakes (for illustrative purposes only). See Figs. S1 and S2 for additional data

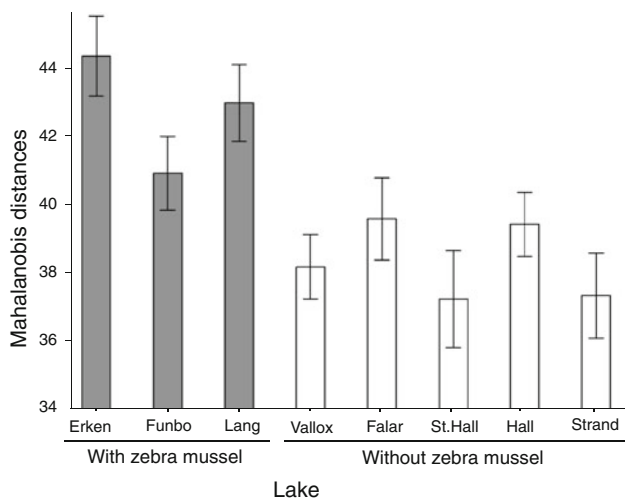


Fig. 2 Mahalanobis’ distances between littoral and pelagic perch and the littoral and pelagic group centroid i.e. the “mean point” of each habitat’s individuals in lakes with and without zebra mussels. Values represent mean squared distances $\pm SE$. Lake name abbreviations as described in Fig. 1

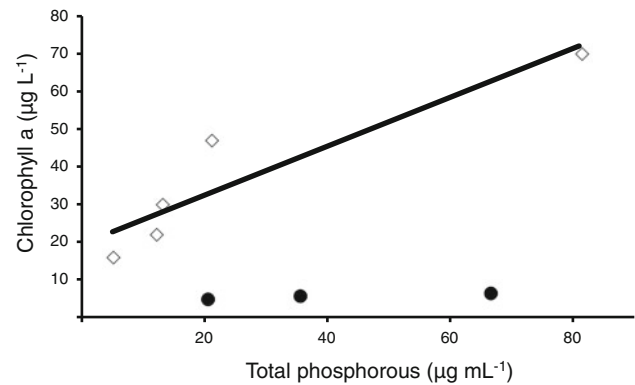


Fig. 3 Ostensible decoupling of the relationship between the major phytoplankton-limiting nutrient phosphorus and the phytoplankton density as indicated by the concentration of chlorophyll a (*chl a*) in lakes with zebra mussels (filled circles) and lakes without zebra mussels (open diamonds). The solid line represents a linear fit for the relationship in lakes without mussels

demonstrates the effect of zebra mussels on lake resources (lakes without zebra mussels $r = 0.92$, $P = 0.024$; lakes with and without zebra mussels combined $r = 0.38$, $P = 0.349$; Fig. 3).

Effect of zebra mussels on pelagic resources for perch

Zooplankton communities were marginally dissimilar between lakes with and without zebra mussels (ANOSIM, Bray-Curtis $R = 0.42$, $P = 0.070$). SIMPER analysis revealed that large cladoceran zooplankton contributed most to this dissimilarity (30.9 % contribution to dissimilarity), followed by calanoid copepods (27.3 %), cyclopoid copepods (25.9 %), and small cladocerans (15.6 %). Closer inspection of zooplankton groups revealed that lakes with zebra mussels showed a higher biomass of large cladocerans compared to lakes without zebra mussels (t -test, $t = 4.02$, $df = 5.97$, $P < 0.01$, mean $\pm SD_{with} = 128.15 \pm 51.19 mg L^{-1}$, mean $\pm SD_{without} = 26.73 \pm 26.86 mg L^{-1}$; Fig. 4a). As a consequence, the average body length of zooplankton was significantly longer in lakes with zebra mussels than in lakes without zebra mussels (t -test, $t = 3.02$, $df = 3.54$, $P = 0.045$; mean $\pm SD_{with} = 0.68 \pm 0.07 mm$, mean $\pm SD_{without} = 0.53 \pm 0.05 mm$; Fig. 4b). All other comparisons were insignificant (see Table S4 for data).

Effect of zebra mussels on benthic resources for perch

The benthic invertebrate community differed between lakes with and without zebra mussels (ANOSIM, Bray-Curtis $R = 0.55$, $P = 0.018$). SIMPER analysis showed that epifaunal taxa contributed most to this dissimilarity (57.2 %, contribution of infaunal taxa: 42.7 %). In fact,

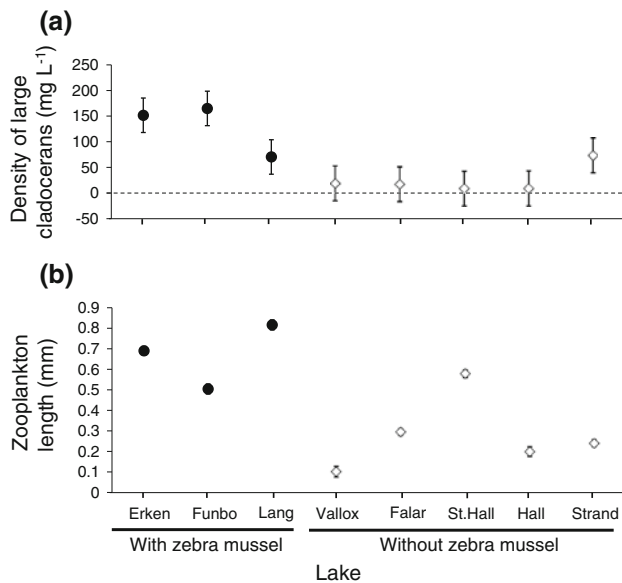


Fig. 4 Pelagic resources in lakes with (filled circles) and without (open diamonds) zebra mussels. **a** Density of large (body length >0.46 mm) cladocerans and **b** individual body length of zooplankton (mean \pm SE) in each lake. Lake name abbreviations as described in Fig. 1. For data separated by littoral and pelagic habitat see Table S4

lakes with zebra mussels contained a significantly higher density of epifaunal taxa than lakes without zebra mussels (t -test, $t = 4.58$, $df = 5.92$, $P < 0.01$, mean \pm SD_{with} = 6.66 ± 2.69 mg m⁻², mean \pm SD_{without} = 1.04 ± 0.71 mg m⁻²; Fig. 5a). As a consequence, the overall individual biomass of benthic invertebrates was significantly higher in lakes with zebra mussels compared to lakes without zebra mussels (t -test, $t = 3.17$, $df = 4.83$, $P = 0.025$, mean \pm SD_{with} = 0.67 ± 0.15 mg, mean \pm SD_{without} = 0.28 ± 0.17 mg; Fig. 5b). All other comparisons were insignificant (see Table S4 for data).

Effect of zebra mussels on perch dietary composition

Littoral perch consumed more benthic invertebrates whereas pelagic perch consumed more zooplankton (see Table S4 for data). Perch dietary composition differed between lakes with and without zebra mussels (ANOSIM, Bray-Curtis $R = 0.48$, $P = 0.036$). SIMPER analysis revealed that cladocerans contributed most to this dissimilarity (43.2 %) followed by copepods (24.2 %), fish (19.6 %), infaunal (12.6 %) and epifaunal (0.1 %) benthic invertebrates. On closer inspection we found that perch in lakes with zebra mussels consumed a significantly higher proportion of cladocerans than perch in lakes without zebra mussels (t -test, $t = 7.05$, $df = 5.29$, $P < 0.001$, mean \pm SD_{with} = 57.99 ± 6.32 %, mean \pm SD_{without} = 21.8 ± 0.06 %; Fig. 6). All other comparisons were insignificant (see Table S4 for data).

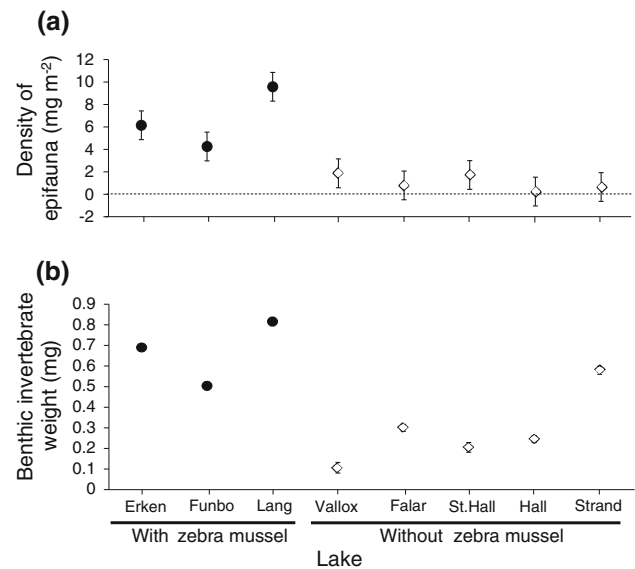


Fig. 5 Benthic resources in lakes with (filled circles) and without (open diamonds) zebra mussels. **a** Density of epifaunal benthic invertebrates (mean \pm SE) and **b** individual body weight of benthic invertebrates (mean \pm SE). Epifaunal taxa include all taxa living on the substrate as opposed to infaunal taxa dug into the sediment. Lake name abbreviations as described in Fig. 1. For data separated by littoral and pelagic habitat see Table S4

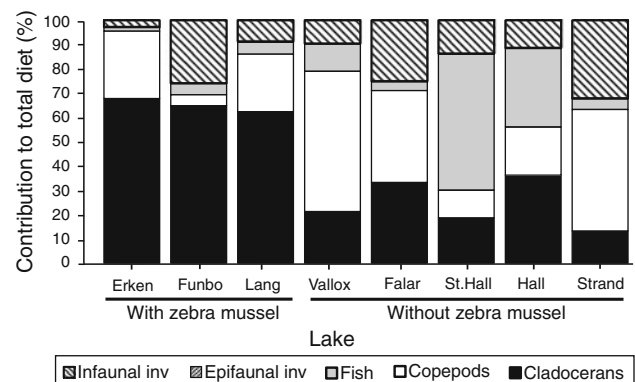


Fig. 6 Contribution of different dietary items to total stomach contents in perch populations from lakes with and without zebra mussels (shown as mean percent of total diet). Lake name abbreviations as described in Fig. 1. For data separated by littoral and pelagic habitat see Table S4

Perch growth, size and age

Perch populations in lakes with zebra mussels showed marginally higher growth performance than populations from lakes without zebra mussels (t -test, $t = 4.45$, $df = 3.02$, $P = 0.071$, mean \pm SD_{with} = 4.99 ± 0.08 , mean \pm SD_{without} = 4.51 ± 0.43). Perch grew on average 12 mm more in their 1 year of life in lakes with zebra mussels (74.68 mm \pm 15.58 SD) than in lakes without

zebra mussels ($62.44 \text{ mm} \pm 7.80 \text{ SD}$); however, this difference was not significant (t -Test, $t = 1.26$, $df = 2.61$, $P = 0.302$). Littoral and pelagic perch forms did not show any difference in growth, length or age (see Table S4 for data). Mean, modal and median age did not differ between perch from lakes with and without zebra mussels and also average length of perch from lakes with and without zebra mussels was not significantly different (see Table S4 for data).

Discussion

The results of this study are consistent with our predictions that zebra mussels affect resource availability and phenotypic divergence in perch populations. Perch in lakes with zebra mussels showed greater divergence into pelagic and littoral forms. Our results suggest that zebra mussels mediated this increased phenotypic divergence in perch via changes in the availability of pelagic and benthic resources. Earlier experimental studies on both zebra mussels and perch autecology allow us to establish the mechanistic link between zebra mussel presence and the phenotypic divergence of perch. After outlining how zebra mussels have changed resources for perch, we will consider two main possibilities regarding how these resource changes might have increased perch divergence. First, increases in littoral and pelagic resources allow for stronger plastic responses that better suit pelagic and littoral individuals for their different environments. Second, changes in water clarity and resource abundance might increase disruptive selection acting on morphology—although direct evidence is lacking.

Resource changes caused by mussels

We found differences in pelagic resources for perch in the form of a higher biomass of cladoceran plankton and larger zooplankton in lakes with zebra mussels. This is in line with previous studies that documented a shift to larger-sized zooplankton following a zebra mussel invasion (Idrisi et al. 2001). Zebra mussels not only effectively feed on phytoplankton, lowering the chl a content in the lakes, they also ingest smaller zooplankton. Small zooplankton include copepod nauplii larvae which typically do not exceed $100 \mu\text{m}$ in length. These are readily ingested by zebra mussels that consume particles between 1 and $150 \mu\text{m}$ (Horgan and Mills 1999). Consequently, smaller taxa and taxa with small larvae stages suffer most from mussel predation (Higgins and Vander Zanden 2010; Lehane and Davenport 2006). Large cladocerans, in contrast, release larger living offspring into the water column. The size of parthenogenetic daphnid neonates ranges from $800 \mu\text{m}$ to

larger than 1 mm in e.g. *Daphnia pulex* and *Daphnia magna* (Arbaciauskas 2004) making them less likely to be ingested by zebra mussels. As adults all species of cladocerans in our system are large enough to circumvent mussel predation (Davenport et al. 2000; Horgan and Mills 1999; Horgan and Mills 1997). Cladocerans are also better in coping with lower abundances of phytoplankton in lakes with zebra mussels. Daphnids have a high body phosphorus content and can thrive on lowered food abundance if food quality is sufficient (Hessen 2008; Urabe et al. 1997). This is also related to the length-efficiency hypothesis. Smaller zooplankton taxa have higher energy demands and a lower starvation tolerance than larger taxa leading to larger zooplankton species in general being better competitors than smaller ones by more efficiently feeding on lower phytoplankton densities (Brooks and Dodson 1965; Hessen 2008).

Larger zooplankton length means lower handling costs and higher energy gain for planktivorous perch (Persson 1986), and because of their greater conspicuousness, fish selectively forage on large zooplankton (e.g. daphnids; Brooks and Dodson 1965). Additionally, zooplankton may be more visible in lakes with zebra mussels, due to higher water clarity (greater Secchi depth). Perch are visual feeders. Clearer water therefore leads to a higher detection rate and improved foraging on zooplankton (Ljunggren and Sandström 2007). A higher detection rate combined with increased prey density allows for higher swimming speed in pelagic fish (Park et al. 2007). The slender body morphology of pelagic perch minimizes drag forces during fast swimming when feeding on zooplankton (Pettersson and Hedenström 2000). Clearer water and a higher zooplankton density in lakes with zebra mussels might lead to the expression of more pronounced pelagic (i.e. more slender-bodied) phenotypes. The more slender-bodied pelagic individuals in lakes with zebra mussels would lead to an increase in the overall difference in body shapes between littoral and pelagic forms. Regrettably, because the stomach contents were partly digested we could not achieve the same level of taxonomic resolution for dietary items as for resources. Our finding of increased consumption of cladoceran plankton of perch in lakes with zebra mussels, however, supports our claim that perch utilize the improved foraging opportunities, at least in the pelagic zone.

Benthic resources for perch are characteristically favoured by zebra mussel invasions, and we detected a higher density of large epifaunal taxa and a significantly higher individual biomass of benthic invertebrates in lakes with zebra mussels. This supports the findings of Ward and Ricciardi (2007) that the invasion of zebra mussels preceded a boost in the density of large epifaunal taxa (mainly scrapers, grazers, and predators). The increase in epifaunal scrapers and grazers likely results from the provision of

suitable feeding grounds in the form of shells and mussel-deposited material (Stewart and Haynes 1994). The increase in epifaunal predators follows the surplus of invertebrate prey in mussel beds (Ward and Ricciardi 2007). Scrapers, grazers (e.g. *Asellus aquaticus*), and predatory invertebrates are generally larger and easier to detect than infaunal taxa and hence are preferred benthic food resources for perch (Diehl 1992; Rask and Hiisivuori 1985). We expected littoral-feeding perch to gain more energy from the larger epifaunal prey (cf. Borgmann 1982). High energy gain from large invertebrates also led to increased growth of yellow perch (*Perca flavescens*) in an enclosure study with zebra mussels (Thayer et al. 1997). Yet, contradictory to our predictions our stomach content analyses did not confirm that epifaunal invertebrates were consumed in a larger proportion by perch in lakes with zebra mussels. The reason why we did not see a higher proportion of epifaunal invertebrates in the more specialized littoral perch diet might be the short-term picture of dietary choice that stomach contents provide. Future research of long-term dietary use could help to elucidate the role epifaunal invertebrates play for littoral perch dietary choice and morphological specialization.

Why resource changes increase divergence

Both experimental and field studies have shown that perch with a higher growth rate develop a more pronounced habitat-specific morphology and diverge more between habitats (Olsson et al. 2006, 2007). Individuals with a higher growth rate seem to have a surplus of energy they can use for modulation of their body morphology (Olsson et al. 2007). A higher growth rate of perch in lakes with zebra mussels (as indicated by the marginally higher growth performance) could allow perch in both habitats to adjust their morphology to optimize feeding. Theory predicts that if conditions are favourable, i.e. less stressful, then the costs of plasticity are lower (e.g. van Buskirk and Steiner 2009). More abundant resources in lakes with zebra mussels might reduce the costs of plasticity making a plastic response to the environment more likely which then leads to increased morphological divergence.

Besides allowing a greater plastic response of perch to the different resources, zebra mussels' effects on the lakes' resources could alter the selection regime to become more disruptive and increase phenotypic divergence by favouring specialized and disfavoring intermediate phenotypes (Schluter 2000). In perch this would require that the fitness of intermediate forms relative to specialized forms be lower in lakes with zebra mussels than in lakes without zebra mussels. Such disruptive selection could then, in turn, either select for increased genetic divergence or increased phenotypic plasticity (Rueffler et al. 2006).

Interestingly, this is the opposite to what is predicted by adaptive speciation theory (e.g. Schluter 2000, Thibert-Plante and Hendry 2011), as well as by empirical work (Bolnick 2004; Svanbäck and Persson 2009). That is, most studies predict that increasing resources (as seen here in lakes with zebra mussels) should reduce disruptive selection. The question then becomes whether disruptive selection can be more pronounced in lakes with zebra mussels, given the higher resource densities. A recent study using stable isotopes showed that littoral and pelagic perch in lakes with higher water clarity increased divergence in dietary use (Bartels et al. 2012). As zebra mussels increase water clarity, this could also be the case in our lakes. The increase in dietary divergence between littoral and pelagic perch might then lead to a stronger connection between diet and phenotype that might affect the selective regime. However, whether increasing dietary divergence with increasing water clarity in lakes with zebra mussel will affect the selective regime needs to be investigated in future studies.

One important question from an evolutionary point of view is whether the differences in divergence we found in perch reflect genetic changes or result from phenotypic plasticity. Previous research on this topic revealed that most morphological differences between the habitats are due to phenotypic plasticity (Svanbäck and Eklöv 2006). Recent studies have shown that the ability to express plasticity can differ between populations and that plasticity itself can evolve. For example, Lind and Johansson (2007) found that the degree of phenotypic plasticity differed with ecological context for populations of common frogs (*Rana temporaria*). Whether the differences in divergence in our study lakes reflect differences in plasticity between the populations or result from genetic changes caused in response to the disruptive selection regime remains to be studied.

Besides the effect of zebra mussels, inter- and intra-population density effects such as competition with roach (*Rutilus rutilus*) or conspecifics can play a role in determining perch growth, length, and morphology (Persson 1986; Svanbäck and Persson 2004). For example, recent studies have shown that intra-specific competition can promote disruptive selection and thus population divergence (Bolnick 2004; Svanbäck and Persson 2009). However, we found no significant differences in density of intra-specific (perch) or inter-specific (roach) competitors for perch between lakes with and without zebra mussels (see Electronic supplementary material for details).

Conclusions

It has long been acknowledged that the magnitude of intra-population divergence can vary widely between different populations. For example, Siwertsson et al. (2010) found

that whitefish in Fennoscandinavia can show different degrees of intra-specific divergence ranging from lakes that feature one phenotypically unimodal population to lakes that hold as many as three forms that are phenotypically clearly separated along the pelagic-benthic resource axis. Changes in the ecological context (e.g. differences in resource distribution) are frequently implicated in generating such differences (Landry and Bernatchez 2010; Smith et al. 1997). Yet, the availability of resources is seldom measured (Schluter 2000; but see Martin and Pfennig 2010; De León et al. 2011). Our study bridges the gap between divergence in consumers and the availability of their resources by providing detailed background data on the whole food chain from primary producers (phytoplankton) to the resources for top consumers (perch).

It is commonly accepted that indirect interactions may be relevant for both ecological and evolutionary processes. Yet, there are still few studies demonstrating that indirect trophic interactions propagate through the food web to change the phenotypes of interaction partners in non-adjacent trophic levels. Our study adds to the much-needed literature supporting the notion that indirect interactions can have phenotypic and thus eventually also evolutionary implications.

Acknowledgments We thank M. Amcoff, A. Kellerman, R. Naddafi, A. Rice, S. South and Andrew Hendry and one anonymous reviewer for helpful comments on the manuscript; K. Bergström, H. Enderskog, R. Fransson, E. Geibrink, J. Malmberg, M. Puffer, and U. Westerlund for help in the field and in the lab; and P. Bartels, H. Peter, P. Innocenti, C. Michel, and B. Rogell for statistical advice. This study was financed by grants from the Swedish Research council for Environment, Agricultural Sciences and Spatial Planning (FORMAS) to P. E.; the Swedish Research Council (VR) to P. E. and R. S.; and the Malméns stiftelse to P. E. H.

Conflict of interest The authors declare that they have no conflict of interest.

References

- Abrams PA (2000) Character shifts of prey species that share predators. *Am Nat* 156:45–61
- Arbaciauskas K (2004) Life-history characteristics and fitness in descendants of parthenogenetic and ex-ephippion females of *Daphnia magna*. *Hydrobiologia* 526:211–218
- Bagenal TB, Tesch FW (1978) Age and growth. In: Bagenal T (ed) *Methods for assessment of fish production in fresh waters*. IBP handbook no. 3. Blackwell, Oxford, pp 101–136
- Bartels P, Hirsch PE, Svanbäck R, Eklöv P (2012) Water transparency drives intra-population divergence in Eurasian Perch (*Perca fluviatilis*). *PLoS One* 7(8):e43641
- Bolnick DI (2004) Does intraspecific competition generate disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* 58:608–618
- Borgmann U (1982) Particle-size-conversion efficiency and total animal production in pelagic ecosystems. *Can J Fish Aquat Sci* 39:668–674
- Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. *Science* 150:28–35
- Darwin C (1859) *On the origin of species*. Murray, London
- Davenport J, Rowan J, Smith JW, Packer M (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. *Mar Ecol Prog Ser* 198:131–137
- De León LF, Raeymaekers JAM, Bermingham E, Podos J, Herrel A, Hendry AP (2011) Exploring possible human influences on the evolution of Darwin's finches. *Evolution* 65:2258–2272
- Diehl S (1992) Fish predation and benthic community structure—the role of omnivory and habitat complexity. *Ecology* 73:1646–1661
- Dillon PJ, Rigler FH (1974) Test of a simple nutrient budget model predicting phosphorus concentration in lake water. *J Fish Res Bd Can* 31:1771–1778
- Eklöv P, Svanbäck R (2006) Predation risk influences adaptive morphological variation in fish populations. *Am Nat* 167:440–452
- Froese R, Binohlan C (2003) Simple methods to obtain preliminary growth estimates for fishes. *J Appl Ichthyol* 19:376–379
- Hendry AP, Huber SK, De León LF, Herrel A, Podos J (2009) Disruptive selection in a bimodal population of Darwin's finches. *Proc Biol Sci* 276:753–759
- Hessen DO (2008) Efficiency, energy and stoichiometry in pelagic food webs; reciprocal roles of food quantity and food quality. *Freshwater Rev* 1:43–57
- Higgins SN, Vander Zanden MJ (2010) What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecol Monogr* 80:179–196
- Holker F, Thiel R (1998) Biology of ruffe (*Gymnocephalus cernuus* (L.))—a review of selected aspects from European literature. *J Great Lakes Res* 24:186–204
- Horgan MJ, Mills EL (1997) Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. *Can J Fish Aquat Sci* 54:249–255
- Horgan M, Mills E (1999) Zebra mussel filter feeding and food-limited production of *Daphnia*: recent changes in lower trophic level dynamics of Oneida. *Hydrobiologia* 411:79–88
- Idrisi N, Mills EL, Rudstam LG, Stewart DJ (2001) Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. *Can J Fish Aquat Sci* 58:1430–1441
- ISO (1992) ISO 10260 Water quality—measurement of biochemical parameters—spectrometric determination of the chlorophyll-a concentration. International Organisation for Standardization, Geneva
- Klingenberg CP, Monteiro LR (2005) Distances and directions in multidimensional shape spaces: implications for morphometric applications. *System Biol* 54:678–688
- Komiya T, Fujita S, et al. (2011) A novel resource polymorphism in fish, driven by differential bottom environments: an example from an ancient lake in Japan. *PLoS One* 6:e17430
- Landry L, Bernatchez L (2010) Role of epibenthic resource opportunities in the parallel evolution of lake whitefish species pairs (*Coregonus* sp.). *J Evol Biol* 23:2602–2613
- Lehane C, Davenport J (2006) A 15-month study of zooplankton ingestion by farmed mussels (*Mytilus edulis*) in Bantry Bay, Southwest Ireland. *Estuar Coast Shelf Sci* 67:645–652
- Lind MI, Johansson F (2007) The degree of adaptive phenotypic plasticity is correlated with the spatial environmental heterogeneity experienced by island populations of *Rana temporaria*. *J Evol Biol* 20:1288–1297
- Ljunggren L, Sandström A (2007) Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. *J Fish Biol* 70:1319–1334
- MacIsaac HJ, Lonner CJ, Leach JH (1995) Suppression of microzooplankton by zebra mussels: importance of mussel size. *Freshwater Biol* 34:379–387

- Martin RA, Pfennig DW (2010) Field and experimental evidence that competition and ecological opportunity promote resource polymorphism. *Biol J Linn Soc* 100:73–88
- Nosil P, Crespi BJ (2006) Experimental evidence that predation promotes divergence in adaptive radiation. *Nature* 103:9090–9095
- Olsson J, Svanbäck R, Eklöv P (2006) Growth rate constrain morphological divergence when driven by competition. *Oikos* 115:15–22
- Olsson J, Svanbäck R, Eklöv P (2007) Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. *Oecologia* 152:48–56
- Park BK, Lee YS, Park SS (2007) Calculation of search volume on cruise-searching planktivorous fish in foraging model. *J Environ Biol* 28:537–543
- Pauly D (1981) The relationship between gill surface area and the growth performance in fish—a generalization of von Bertalanffy's theory of growth. *Meeresforschung Rep Mar Res* 28:251–282
- Persson L (1986) Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology* 67:355–364
- Persson L, Andersson J, Wahlström E, Eklöv P (1996) Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* 77:900–911
- Pettersson LB, Hedenström A (2000) Energetics, cost reduction and functional consequences of fish morphology. *Proc Biol Sci* 267:759–764
- Pfennig DW, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP (2010) Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol Evol* 25(8):459–467
- Raess F, Maly E (1986) The short-term effects of perch predation on a zooplankton prey community. *Hydrobiology* 140:155–160
- Rask M, Hiisivuori C (1985) The predation on *Asellus aquaticus* (L.) by perch, *Perca fluviatilis* (L.), in a small forest lake. *Hydrobiology* 121:27–33
- Rohlf FJ (1993) TPSRW: thin-plate spline relative warp analysis. Department of Ecology and Evolution, State University of New York, NY
- Rueffler C, Van Dooren TJM, Leimar O, Abrams PA (2006) Disruptive selection and then what? *Trends Ecol Evol* 21:238–245
- Schluter D (2000) The ecology of adaptive radiation. Oxford University Press, Oxford
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett* 7:153–163
- Siwertsson A, Knudsen R, Kahilainen KK, Praebel K, Primicerio R, Amundsen P-A (2010) Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. *Evol Ecol Res* 12:929–947
- Slice DE (1994) DS-DIGIT: basic digitizing software. Department of Ecology and Evolution, State University of New York, NY
- Smith TB, Skúlason S (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Ann Rev Ecol Syst* 27:111–133
- Smith TB, Wayne RK, Girman DJ, Bruford MW (1997) A role for ecotones in generating rainforest biodiversity. *Science* 276:1855–1857
- Stewart TW, Haynes JM (1994) Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. *J Great Lakes Res* 20:479–493
- Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends Ecol Evol* 18:94–101
- Storey JD (2002) A direct approach to false discovery rates. *J R Stat Soc B* 64:479–498
- Svanbäck R, Eklöv P (2002) Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia* 131:61–70
- Svanbäck R, Eklöv P (2003) Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos* 102:273–284
- Svanbäck R, Eklöv P (2006) Genetic variation and phenotypic plasticity: causes of morphological and dietary variation in Eurasian perch. *Evol Ecol Res* 8:37–49
- Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J Anim Ecol* 73:973–982
- Svanbäck R, Persson L (2009) Population density fluctuations change the selection gradient in Eurasian perch. *Am Nat* 173:507–516
- Thayer SA, Haas RC, Hunter RD, Kushler RH (1997) Zebra mussel (*Dreissena polymorpha*) effects on sediment, other zoobenthos, and the diet and growth of adult yellow perch (*Perca flavescens*) in pond enclosures. *Can J Fish Aquat Sci* 54:1903–1915
- Thibert-Plante X, Hendry AP (2011) Factors influencing progress toward sympatric speciation. *J Evol Biol* 24:2186–2196
- Urabe J, Clasen J, Sterner RW (1997) Phosphorus limitation of *Daphnia* growth: is it real? *Limnol Oceanogr* 42:1436–1443
- Van Buskirk J, Steiner UK (2009) The fitness costs of developmental canalization and plasticity. *J Evol Biol* 22:852–860
- Vonlanthen P, Bittner D, Hudson AG, Young KA, Mueller R, Lundsgaard-Hansen B, Roy D, Piazza Di, Largiader CR, Seehausen O (2012) Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature* 482:357–362
- Walsh MR, Reznick DN (2008) Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. *Proc Natl Acad Sci USA* 105:594–599
- Ward JM, Ricciardi A (2007) Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. *Divers Distrib* 13:155–165
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100
- West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, New York