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Habitat structure, feeding mode and morphological reversibility: factors influencing phenotypic plasticity in perch

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ABSTRACT

Questions: Do both habitat structure and feeding mode contribute to morphological divergence within fish populations? To what extent may an induced morphology be reversed?

Organism: Young-of-the-year Eurasian perch (*Perca fluviatilis* L.).

Methods: An aquarium experiment with a 2×2 factorial design (two levels of habitat structure and two levels of feeding mode). The habitat structure and feeding mode were reversed for perch in two habitat treatments midway through the experiment.

Results: Both habitat structure and feeding mode contributed to morphological divergence (40.7% and 4.9% of the total variation respectively), which suggests that both habitat complexity and prey type diversity influence morphological adaptations in this fish species. Perch morphology is highly plastic and can be reversed in as short a time as 4 weeks.

Keywords: feeding mode, geometric morphometrics, habitat structure, morphological reversibility, phenotypic plasticity, trophic polymorphism.

INTRODUCTION

Phenotypic plasticity, the ability of a single genotype to produce more than one alternative form of morphology in response to environmental conditions (West-Eberhard, 1989), has been demonstrated to occur in all major groups of organisms (reviewed in Via *et al.*, 1995; Agrawal, 2001; West-Eberhard, 2002). Plasticity has been hypothesized to act as an important strategy for organisms to cope with environmental variations (Stearns, 1989; Scheiner, 1993), and a plastic response to a changing environment might be adaptive in that individuals displaying such a response have higher fitness than those that do not (Price *et al.*, 2003). Furthermore, phenotypic plasticity is likely to play an important role as a diversifying factor in evolution (West-Eberhard, 1989; Agrawal, 2001), and recent theoretical work suggests that moderate levels of adaptive plasticity may facilitate genetic evolution (Price *et al.*, 2003).

Intraspecific morphological divergence related to resource and habitat use has been demonstrated in several species across a wide range of animal taxa and is generally referred

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to as a trophic polymorphism (reviewed in Robinson and Wilson, 1994; Skulason and Smith, 1995; Smith and Skulason, 1996; Bolnick *et al.*, 2003). In general, the genetic basis behind the divergence is poorly understood (Smith and Skulason, 1996), but in fish phenotypic plasticity seems important for the morphological divergence observed (Lindsey, 1981; Meyer, 1987; Wimberger, 1992; Day *et al.*, 1994; Robinson and Wilson, 1995, 1996; Mittelbach *et al.*, 1999). To date, most alternative morphological forms found within the same species appear to be conditional and non-reversible, but it is also possible that the morphological forms could be reversible (Meyer, 1987; Proulx and Magnan, 2004). Despite the evidence for reversible plasticity, very little is known about the degree of morphological plasticity among taxa displaying trophic polymorphisms (but see Proulx and Magnan, 2004). We believe that this deserves more attention, since the span of the reaction norm of a plastic trait could provide insight into the relative influence of heritable versus environmentally induced control of the trait (Proulx and Magnan, 2004). Furthermore, the degree of morphological plasticity could also have profound influences on evolutionary and ecological outcomes. The degree of plasticity in a species could, for example, influence the ability to track environmental changes and thus regulate the potential for character divergence. Furthermore, competitive interactions between species might be altered if one of the competitors has a highly plastic morphology that enables it to efficiently utilize a wider range of resources than would otherwise be possible.

The fish fauna of northern hemisphere post-glacial lakes displays an intraspecific morphological divergence tightly coupled to the spatially variable environment found within the lakes (Robinson and Wilson, 1994; Skulason and Smith, 1995; Smith and Skulason, 1996). The lakes in which these polymorphisms are found usually consist of two distinct habitats with a discrete resource distribution: a vegetated shallow littoral zone and a deeper non-structured pelagic zone (Schluter and McPhail, 1993; Robinson and Wilson, 1994). The littoral zone is usually inhabited by a littoral benthivorous phenotype with a blunt snout, a longer upper jaw and a more deep-bodied morphology, whereas a planktivorous phenotype with a more pointed snout, equally sized jaws, usually longer and more numerous gill rakers, and a more slender body form is found in the pelagic zone (Malmquist *et al.*, 1992; Schluter and McPhail, 1992, 1993; Robinson *et al.*, 1993; Robinson and Wilson, 1994; Snorrason *et al.*, 1994; Svanbäck and Eklöv, 2002, 2003). A few studies have demonstrated a fitness trade-off in optimal morphology between the two habitats (Ehlinger, 1990; Schluter, 1993; Robinson *et al.*, 1996; Robinson, 2000; Svanbäck and Eklöv, 2003, 2004), indicating that the different habitat-specific morphologies seem to be adaptive. Two obvious environmental differences that can give rise to divergent selection pressures between the littoral and pelagic habitats are the physical structure of the habitat as well as the habitat-specific feeding mode. The littoral habitat has a structure that generally consists of vegetation, whereas the pelagic habitat is non-structured and open. Fish in the littoral habitat pick littoral prey attached to the vegetation or the bottom substrate, whereas pelagic fish feed on widely dispersed planktonic prey in the open water column. Some studies of fish have addressed the effect of diet-induced morphological divergence, and demonstrated that different diets and/or feeding modes required by these different diets can trigger a morphological response (see, for example, Robinson and Wilson, 1995; Day and McPhail, 1996; Meyer, 1990; Mittelbach *et al.*, 1999; Hegrenes, 2001; Andersson, 2003; Proulx and Magnan, 2004). To our knowledge, however, no study has examined whether different habitat structures could trigger a morphological divergence. How organisms respond to multiple environmental variables acting in concert has also received little attention.

The aims of this experiment were two-fold. First, we examined whether both the habitat-specific structure and feeding mode could trigger a morphological response. More specifically, we looked at how much of the morphological variation was attributable to these two environmental variables. Second, we looked at whether an induced morphology could be reversed. Since it has previously been shown that individual growth rate might have a large influence on morphological plasticity (J. Olsson, R. Svanbäck and P. Eklöv, unpublished manuscript), we also quantified individual growth for all treatments. Perch is a suitable organism for studying these questions, since it has been found to display a habitat-dependent divergence in morphology that is mainly attributed to phenotypic plasticity (Svanbäck and Eklöv, 2002, 2003; R. Svanbäck and P. Eklöv, unpublished manuscript). Furthermore, perch usually go through two ontogenetic niche shifts during their life (Persson, 1988) where each niche favours a distinct morphology (Svanbäck and Eklöv, 2003, 2004), and we therefore expected that perch might display a reversible plastic morphology as a response to the trade-offs in optimal morphology experienced over the ontogeny.

MATERIALS AND METHODS

Experimental set-up

Young-of-the-year perch were caught by electrofishing the littoral zone of Lake Siggeforasjön (latitude: 66°51′77″N, longitude: 15°75′56″E), and brought to the laboratory on the day of capture. To acclimate the fish to laboratory conditions, they were put in an aerated 1000-litre holding tank for at least 8 days before the start of the experiment. During this period, the fish were fed once a day with a mixture of frozen chironomides (*Chironomus* sp.) and frozen brine shrimps (*Artemia salina*). The experiment was carried out in 90-litre aquaria between July and August 2002, and lasted for 59 days. The aquaria were all visually isolated from each other, had a 2.5 cm layer of fine sand on the bottom, and were connected to a flow-through system (flow approximately $0.5\ \mathrm{l \cdot min^{-1}}$ per aquarium) with regular tap water. The photoperiod was 10 hours light/14 hours dark, and the temperature ranged between 16 and 18°C during the experiment.

To determine whether different habitat structures and feeding modes could trigger a morphological divergence, a 2×2 factorial design (replicated four times) was applied by using two levels of habitat structure (structure, open) and two different feeding treatments (littoral feeding mode, pelagic feeding mode). Aquaria with fish in a structured habitat had artificial vegetation made of green polypropylene strings attached to a plastic net (mesh size 25 mm, $300\ \mathrm{strings \cdot m^{-2}}$) that was buried in the sand. Aquaria with fish in an open habitat lacked artificial vegetation. Fish with littoral feeding mode were fed frozen chironomides stuffed into 5×5 cm patches of plastic doormat (Astroturf®) distributed on the bottom of the aquaria. By this procedure the fish had to pick the attached chironomides from the bottom (personal observations) mimicking the feeding mode required when feeding on littoral prey. Four patches of doormat were distributed in each aquarium to minimize aggression, competition and the build up of hierarchies among the fish. Fish with pelagic feeding mode were fed frozen adult brine shrimps suspended in water. During feeding the suspended brine shrimps were distributed in the aquaria using a pipette, allowing the fish to pick the brine shrimps while still in the water column (personal observations), mimicking the feeding mode when feeding on pelagic prey. Since perch do not feed on brine shrimps in nature, we were unable to evaluate the effects on morphological divergence of prey type *per se* by using this set-up. Instead, we focused on the effect of feeding mode of the littoral and pelagic habitats by providing the experimental fish with different prey types in such a way that different feeding modes were required to capture these prey types.

To examine the reversibility of an induced morphology, two reverse treatments (replicated four times) were also included in the set-up. In this part of the study, we followed the morphological trajectories of individuals for which the habitat structure as well as the feeding mode were reversed after half of the experiment. In the first reverse treatment (reverse treatment 1), the fish were first exposed to a structured habitat with littoral feeding mode and then to an open habitat with pelagic feeding mode. The fish in the second reverse treatment (reverse treatment 2) were first exposed to an open habitat with pelagic feeding mode and then to a structured habitat with littoral feeding mode. To elucidate whether an induced morphology could be reversed or not, we compared the final morphology of the fish from the two reverse treatments to that of the fish in the other treatments. If the morphology was reversible for the fish in reverse treatment 1, we expected their final morphology (1) to have departed from the fish experiencing a structured habitat with littoral feeding mode during the whole experimental period, and (2) to have converged to the fish in the treatment with an open habitat with pelagic feeding mode during the whole experimental period. Regarding reverse treatment 2, the opposite was expected if the morphology was reversible. The final morphology should have (1) departed from the fish experiencing an open habitat with pelagic feeding mode during the whole experimental period, and (2) converged to the fish in the treatment with a structured habitat with littoral feeding mode during the whole experimental period. Individual growth was measured midway through as well as at the end of the experiment for all experimental fish to explain possible differences in reversibility between the two reverse treatments. This was done since we know that a high growth rate is needed for a change in morphology to occur (J. Olsson, R. Svanbäck and P. Eklöv, unpublished manuscript).

Experimental procedure

The perch used in the experiment were approximately 2 months old with an average size of 0.82 ± 0.19 g (mean fish weight ± standard deviation). Altogether, 240 fish were randomly chosen from the experimental population and 10 approximately equally sized individuals were placed in one of 24 aquaria. The fish were fed *ad libitum* once a day following a maximum growth rate trajectory at the specific temperature conditions (Lessmark, 1983), and fed the same amount of dry weight food across all treatments. Midway through the experiment (on days 29 and 30), all fish were netted out of the aquaria and weighed to the nearest 0.1 g. The habitat structure and the feeding mode were also changed for the fish in the two reverse treatments. At the end of the experiment, each fish was killed using an overdose of phenoxy-ethanol, weighed, sized and photographed using a digital camera for morphological analyses. Before photographing, each fish was placed on a piece of Styrofoam plastic with their fins fixed with needles. The Styrofoam plastic had a shallow excavation to avoid morphological deformation of the fish. During all experimental procedures, we followed Swedish guidelines concerning the care and welfare of experimental fish.

Morphological analysis

We used landmark-based geometric morphometrics involving thin-plate spline analyses (Adams *et al.*, 2003) to quantify the morphological variation in the experimental material. The photos of the fish were imported into TpsDIG32 (Rohlf, 2003a), and 15 homologous landmarks (Fig. 1) were digitized on the left side of each specimen. The x and y coordinates of the landmarks were captured by TpsDIG32, and individual morphologies were then further analysed using the program TpsRelw (Rohlf, 2003b). This program describes the morphometric shape variation in the material by comparing the landmark coordinates of one individual to those of other individuals (Adams *et al.*, 2003). The components describing this shape variation are then decomposed into uniform and non-uniform scores, and the latter scores can be further decomposed into partial warps. The non-uniform scores (in our case 12 x and 12 y) as well as the uniform scores (one x and one y) can then be used as parameters for statistical analyses of variation in whole body morphology between groups. We used a multivariate discriminant function analysis (DFA) of the partial warps and uniform scores in relation to experimental treatment in order to compare the morphology of the different treatments. The procedure of the DFA was to enter all the independent variables together. The shape variation obtained from the DFA was then visualized using TpsRegr (Rohlf, 2004) based on the regression between the original coordinates captured by TpsDIG32 and individual DFA factor scores.

Statistical analyses

All statistical analyses were performed using SPSS 11.0 for Windows. We used the average morphology, size and growth of the fish in each aquarium as replicates in all of the analyses. We only used parametric tests since all data had homogenous variance and were normally distributed.

When analysing growth differences between treatments, we performed one-way analyses of variance with treatment as a factor. The growth of each treatment was measured at both the midway point and the end of the experiment and was calculated as the weight increase (in %) from the start of the experiment. To determine whether there were possible interaction effects of time, habitat structure and feeding mode on growth, we performed a two-way repeated-measures analysis of variance (ANOVA) with growth at the midway point and the end of the experiment as repeated measures, and habitat structure and feeding mode as factors.

To control for size differences between the treatments, we used the standardized residual values from linear regressions between weight of the fish and the DFA factor scores in all

Fig. 1. The positions of the 15 landmarks used for morphological analyses.

morphological analyses. In the analysis containing effects of habitat structure, feeding mode and the relative contribution of the two on morphological divergence, only the first four treatments were included. Thus, the two reverse treatments were only included in analyses of morphological reversibility. To calculate the influence of habitat structure and feeding mode on morphological divergence, we used two-way analyses of variance with habitat structure and feeding mode as factors. We used one-way analyses of variance with Tukey *post-hoc* tests with treatment as the factor to calculate reversibility of induced morphologies. We used the variance explained by the five functions from the DFA adjusted by the variance components (based on mean square errors) from the ANOVA for each factor (Sokal and Rohlf, 1981) to calculate the relative contributions of habitat structure and feeding mode on morphological divergence.

RESULTS

Survival was high, as only five individuals in two of the chironomide-treatments died during the experiment. Therefore, the results presented here are based on the remaining 235 individuals.

Growth

There was a treatment effect on growth during the experimental period (Fig. 2). At both the midway point and at the end of the experiment, the treatments with pelagic feeding mode had higher growth than the treatments with littoral feeding mode regardless of habitat structure experienced (one-way ANOVA: midway, $F_{1,14} = 23.92$, $P < 0.001$; end of experiment, $F_{1,14} = 29.27$, $P < 0.001$). We found a similar pattern for the individuals in the reverse treatments; the fish initially experiencing pelagic feeding mode (reverse treatment 2) had higher growth midway through the experiment (one-way ANOVA: $F_{1,6} = 14.64$, $P = 0.009$). At the end of the experiment, there was no difference in growth between the two reverse treatments (one-way ANOVA: $F_{1,6} = 2.25$, $P = 0.19$). However, the individuals in reverse treatment 1 (finishing on pelagic feeding mode) had significantly higher growth after the habitat switch than the fish in reverse treatment 2 (one-way ANOVA: $F_{1,6} = 15.23$, $P = 0.008$). When looking at possible interaction effects of time, habitat structure and feeding mode on growth, we found an effect of time on growth, but none of the possible interactions were significant [two-way repeated-measures ANOVA (based on Wilks' λ): time, $F_{1,12} = 390.7$, $P < 0.001$; time × feeding mode, $F_{1,12} = 3.95$, $P = 0.070$; time × habitat structure, $F_{1,12} = 0.004$, $P = 0.951$; time × feeding mode × habitat structure, $F_{1,12} = 0.004$, $P = 0.951$], indicating that the effects of feeding mode and habitat did not change during the experiment. Furthermore, this analysis suggested that the feeding mode experienced affected perch growth at both times regardless of the habitat structure experienced (two-way ANOVA: feeding mode, $F_{1,14} = 28.16$, $P < 0.001$; habitat structure, $F_{1,14} = 0.18$, $P = 0.68$; feeding mode × habitat structure, $F_{1,14} = 0.18$, $P = 0.68$).

Morphology

The DFA correctly classified 56.2% of the individuals into their respective treatment and yielded five morphological functions (Wilks' $\lambda = 0.22$, F statistic = 28.9, $P < 0.001$; Table 1). Since the first two functions alone explained the majority of the total variation (Table 1), we

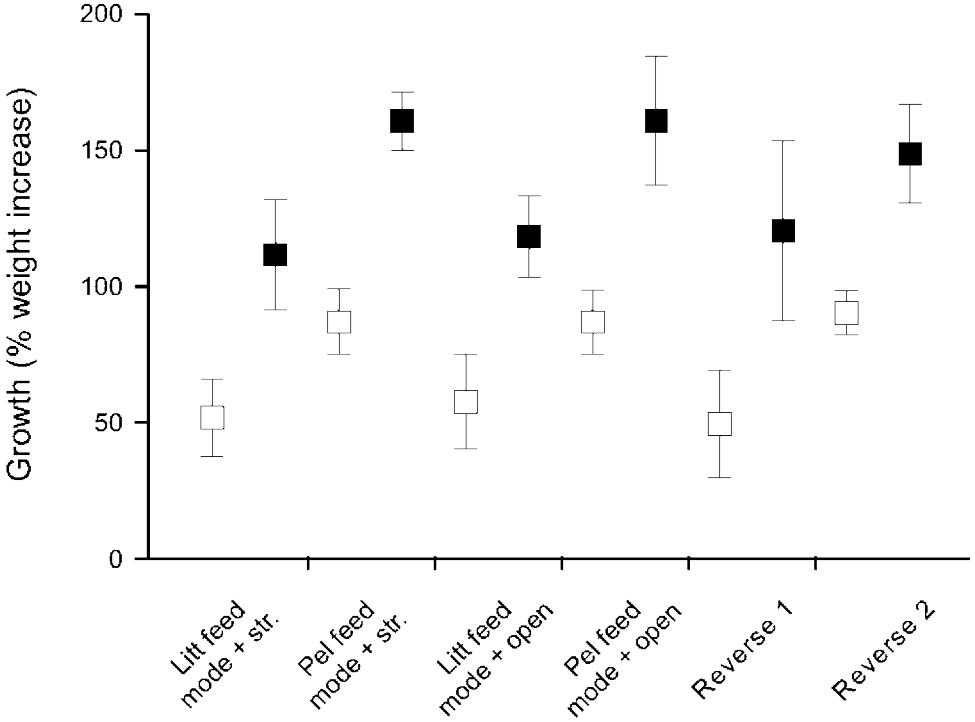

Fig. 2. Growth (% weight increase in grams, mean ± standard deviation) of the different treatments at the midway point (white boxes) and at end of the experiment (black boxes).

Table 1. Results of the five morphological functions yielded by the discriminant function analysis on the morphology of the perch at the end of the experiment

Function	Eigenvalue	% of the total variance explained	Canonical correlation
1	0.758	40.2	0.657
2	0.551	29.2	0.596
3	0.280	14.8	0.468
4	0.195	10.3	0.404
5	0.103	5.5	0.306

hereafter focus on the results from these two functions except where noted. The first function describes a shape variation in body depth and bending. Individuals with positive scores have a deeper body and a more downward pointing snout compared with those with negative scores (Fig. 3). Perch experiencing habitat structure had deeper bodies and more downward pointing snouts regardless of feeding mode, whereas perch experiencing an open habitat where more streamlined (Fig. 3). A two-way ANOVA showed that only the habitat structure influenced morphology for the first function (Table 2).

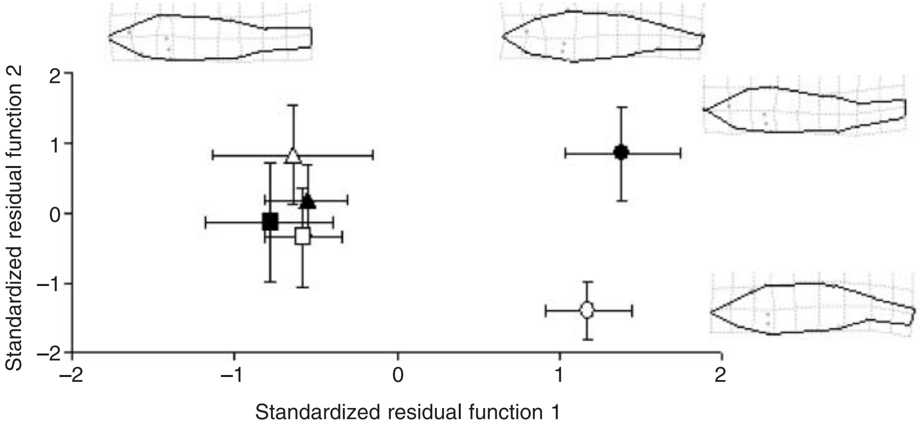

Fig. 3. The standardized residuals of the scores for morphological function 1 and 2 at the end of the experiment. Each observation represents the treatment mean (± standard deviation), and the grid plots are a graphical representation of the function scores obtained from tpsRegr (Rohlf, 2004). Above the figure are graphical representations of the function scores for function 1, and to the right for function 2. The treatments are: littoral feeding mode with structured habitat (●), pelagic feeding mode with structured habitat (○), littoral feeding mode with open habitat (▲), pelagic feeding mode with open habitat (△), reverse treatment 1 (■), and reverse treatment 2 (□).

Table 2. Results of two-way analyses of variance on the different treatments for the first two morphological functions with habitat structure and feeding mode as fixed factors

	Function 1		Function 2	
	F-value	*P*-value	*F*-value	*P*-value
Habitat structure	111.1	<0.001	7.04	0.021
Feeding mode	0.70	0.42	7.41	0.019
Habitat structure × feeding mode	0.11	0.74	23.9	<0.001

Note: The degrees of freedom for both functions are 1,12.

The morphological differences between the treatments for the second function are more difficult to interpret (Fig. 3), but we found a divergence in body form due to both habitat structure and feeding mode (Table 2). There was also a significant interaction effect between habitat structure and feeding mode (Table 2). This function describes a shape variation ranging from slender individuals with an upward bending snout having positive scores, to more deep-bodied fish with a downward pointing snout having negative scores. The interaction between habitat structure and feeding mode is probably due to an effect of both the factors combined. The more downward bending morphology of the perch in the pelagic feeding mode/structured habitat treatment compared with the perch in the pelagic feeding mode/open habitat treatment, for example, is probably due to the presence of structure. The divergence of the pelagic feeding mode/structured habitat treatment from the littoral feeding mode/structured habitat treatment could be due to the growth differences between treatments with different feeding modes.

Table 3. Results of univariate analyses of variance with Tukey *post-hoc* tests on the different treatments for the first two morphological functions with treatment as a fixed factor

	Function 1		Function 2	
	Littoral feed mode with structure	Pelagic feed mode with open	Littoral feed mode with structure	Pelagic feed mode with open
Reverse treatment 1	<0.001	0.95	0.28	0.30
Reverse treatment 2	<0.001	0.99	0.16	0.17

Note: Values represent *P*-values from the *post-hoc* tests. The degrees of freedom for both functions are 1,18.

When comparing the relative contribution of habitat structure and feeding mode on morphological divergence, we included all of the five morphological functions. We found that habitat structure contributed to 40.7%, feeding mode to 4.9% and the habitat structure × feeding mode interaction to 30.2% of the total variation respectively.

Reversibility

Regarding the first function, only the perch in reverse treatment 1 were able to reverse their morphology after the habitat structure/feeding mode switch (Fig. 3). A separate ANOVA with a *post-hoc* test showed that their final morphology had departed from the fish experiencing a structured habitat with littoral feeding mode during the whole experimental period, and converged to the fish in the treatment with an open habitat with pelagic feeding mode (Table 3). No such reversibility, however, was found in reverse treatment 2 (Fig. 3, Table 3). For the second morphological function, an ANOVA with a *post-hoc* test showed that the fish in neither of the two reverse treatments demonstrated a reversible morphology for the second function (Fig. 3, Table 3).

DISCUSSION

In this study, we demonstrate that both habitat structure and the feeding mode play important roles in morphological divergence. To our knowledge, this is the first experimental study to investigate the relative contribution of habitat structure and feeding mode on morphological divergence of fish. Furthermore, the perch in our study were able to respond morphologically to the different treatment effects in as short a time as ~8 weeks, and were to some extent also able to reverse an induced morphology.

Phenotypic plasticity appears to play an important role in the morphological divergence in perch. The fish in this study showed different morphological trajectories depending on the treatment experienced in as short a time as ~8 weeks. Also, in further support of perch morphology being highly plastic, the individuals in one of the reverse treatments were able to reverse their morphology in as short a time as 4 weeks. To our knowledge, only two studies (Meyer, 1987; Proulx and Magnan, 2004) have previously demonstrated that an induced morphology could be reversed during a relatively short time. However, neither of these studies demonstrated such a fast response to changes in the environment as we found in the present study. Proulx and Magnan (2004), for example, demonstrated that juvenile brook charr (*Salvelinus fontinalis* M.) were able to reverse some morphological characters in about 4 months. One reason why perch show such a fast response in morphology compared with, for example, brook charr, could be that perch experience two ontogentic niche shifts during their life, something that brook charr do not. Since each niche is favouring a distinct but different perch morphology (Svanbäck and Eklöv, 2003, 2004) and the first niche shift is usually performed during an individual's first couple of months (Persson, 1988; Hjelm *et al.*, 2000), a faster response to environmental change could be expected for perch than, for example, brook charr. It has been demonstrated previously that phenotypic plasticity plays an important role in morphological divergence in fish (Lindsey, 1981; Meyer, 1987; Wimberger, 1992; Day *et al.*, 1994; Robinson and Wilson, 1995, 1996; Mittelbach *et al.*, 1999), and in a previous field experiment (Hjelm *et al.*, 2001) the morphology of young-of-the-year perch diverged with respect to habitat use in as short a time as 7 weeks. Similarly, in a common-garden experiment with young-of-the-year perch that lasted for 3 months, the vast majority of the morphological variation found (about 84%) could be explained by the environment the fish were exposed to (R. Svanbäck and P. Eklöv, unpublished manuscript).

There are several reasons why it should be adaptive for perch with a plastic phenotype. During their lifetime, perch usually go through two ontogenetic niche shifts (Persson, 1988), first from zooplanktivory to benthivory, and then from benthivory to piscivory (Persson, 1988; Hjelm *et al.*, 2000; Svanbäck and Eklöv, 2002). Since the different niches and diets favour a distinct morphology, perch are likely to experience an ontogenetic trade-off in optimal morphology. For example, Svanbäck and Eklöv (2003) demonstrated that more deep-bodied perch from the littoral zone were more efficient and grew better on littoral macro-invertebrates in a structured habitat, than more streamlined pelagic perch that in turn were more efficient and grew better on zooplankton in an open habitat. The optimal morphology for feeding on macro-invertebrates in a structured habitat is therefore not optimal when feeding on zooplankton in an open habitat (Ehlinger and Wilson, 1988; Ehlinger, 1990; Schluter, 1993). By having a plastic morphology, perch might therefore compromise between these different optimal morphologies and thereby experience a higher fitness during all ontogenetic stages.

Another factor that could influence the plasticity of perch is environmental variations. It has been hypothesized that phenotypic switches in stable environments are under strong genetic control (Hori, 1993; Smith, 1993), whereas plastic responses to the environment are dominant in relatively unstable environments (Stearns, 1989; Pfennig, 1992; Scheiner, 1993). Populations usually fluctuate in density over time in relation to available resources (see, for example, Mittelbach *et al.*, 1995; Smith *et al.*, 1999; Persson *et al.*, 2000, 2003), and recent studies have demonstrated a twenty-fold change in the density of adult perch in a population between years (Persson *et al.*, 2000; Svanbäck and Persson, 2004). These fluctuations have in turn led to variation in resources, and with that a variation in the width of the diet choice of the population (Persson *et al.*, 2000; Svanbäck and Persson, 2004). Svanbäck and Persson (2004) found that all adult perch occupied the littoral zone and fed on littoral prey types at low perch densities, whereas at high adult perch densities a part of the population switched to feed in the pelagic zone. At high population densities, the population therefore consisted of individuals specializing on littoral prey types as well as individuals specializing on pelagic prey types. Since diet is tightly coupled to morphology in perch (Svanbäck and Eklöv, 2002, 2003), the fluctuations in density and thereby also in the level of intraspecific competition, suggests that the fitness landscape in optimal morphology fluctuates with population density in this population. Thus, selection would therefore favour plastic rather than heritable perch morphologies.

In our experiment, it was only the perch in reverse treatment 1 that were capable of reversing their morphology. These individuals were exposed to a pelagic feeding mode during the last part of the experiment and showed significantly higher growth after the habitat switch compared with the perch in reverse treatment 2. It is thus possible that the differences in growth between the treatments could explain the differences in capabilities of reversing morphology, since sufficient growth is probably needed for morphological plasticity to be effective (J. Olsson, R. Svanbäck and P. Eklöv, unpublished manuscript). If the perch in reverse treatment 2 had as high growth as the perch in reverse treatment 1, we would have expected a higher potential for morphological reversibility. Furthermore, since young-of-the-year perch usually migrate from the pelagic to the littoral zone in nature (Persson, 1988; Hjelm *et al.*, 2000), we expected to see morphological reversibility for individuals changing habitats in that direction (i.e. the perch in reverse treatment 2) provided that growth was similar between treatments. We only observed reversibility for the first morphological function. This indicates that perch exhibit high morphological plasticity in some characters (i.e. the ones described by function 1), whereas in others environmental induction seems to be less influential.

Habitat-specific structure and feeding mode

The first two morphological functions explained 79.4% of the total variation, and we found a morphological divergence for both of them. The first function explained a change in body depth and bending, and regardless of feeding mode the perch experiencing a structured habitat had deeper bodies and more downward pointing snouts than perch in treatments with no structure (Fig. 3, Table 2). A frequent observation in lakes is that littoral species of fish (experiencing a structured habitat) usually have deeper and more downward bending bodies than pelagic species, which have a more streamlined morphology with upward bending bodies (Webb, 1984; Webb and Weihs, 1986; Ehlinger and Wilson, 1988; Norton, 1991, 1995; Nemeth, 1997). This pattern is also found among individuals within several fish species inhabiting post-glacial lakes of the northern hemisphere (Malmquist *et al.*, 1992; Schluter and McPhail, 1992, 1993; Robinson *et al.*, 1993; Robinson and Wilson, 1994; Snorrason *et al.*, 1994; Svanbäck and Eklöv, 2002, 2003).

The pattern of the second morphological function is somewhat more difficult to interpret, and the differences between the treatments are not as obvious as for the first function. The extreme morphologies range from perch with somewhat deeper bodies and downward pointing snouts, to perch with more slender bodies and upward pointing snouts (Fig. 3). The morphological divergence for this function was due to both habitat structure and feeding mode, as indicated by the significant effects of these two factors as well as the significant habitat structure × feeding mode interaction (Table 2). Despite that, the morphological divergence for this second function is not totally in line with the results of previous studies, both habitat-specific structure and feeding mode appear to affect morphological development of perch. Moreover, the habitat structure actually contributed much more to the morphological variation than feeding mode (40.5 and 4.9% respectively). Several previous studies have demonstrated that divergent feeding mode itself can trigger a morphological response (see, for example, Robinson and Wilson, 1995; Day and McPhail, 1996; Meyer, 1990; Mittelbach *et al.*, 1999; Hegrenes, 2001; Andersson, 2003; Proulx and Magnan, 2004). However, to our knowledge this is the first study to examine the relative effect of habitat structure and feeding mode on morphological divergence in fish, and to demonstrate that different physical structures of the habitat can have a substantial influence on individual morphology. The relative importance of habitat structure and feeding mode on morphological divergence in this study is likely influenced by the amount of time exposed to the different selection factors. In our study, the perch were fed once a day, and the effects of feeding mode were therefore restricted to a short period once a day, whereas the effects of structure were apparent all of the time. The relative influence of habitat structure and feeding mode on morphological divergence might therefore be biased towards a stronger influence of structure in this study. Under natural conditions, the feeding events of perch span over more extended periods of time, and the influence of habitat structure on morphological divergence in nature is therefore probably not as pronounced as in the laboratory experiment. That the set-up might influence the effects of these two factors is supported by a large-scale enclosure study with young-of-the-year perch (P. Eklöv and R. Svanbäck, unpublished manuscript). Here the feeding duration and intensity were not restricted, and the diet (and thereby probably also the feeding mode) was more important than habitat type for morphological divergence.

The feeding mode but not habitat structure experienced had a significant effect on the growth of the fish at both the midway point and the end of the experiment. However, we did not observe any significant interaction effects between feeding mode, habitat structure and time on the growth of the fish, indicating that the effects of feeding mode and habitat did not change during the experiment. We did, however, find a significant effect of time on growth, something that was expected since the fish increased in size between the midway point and the end of the experiment. Thus, these results suggest that fish in pelagic feeding mode conditions had an overall higher growth than fish in littoral feeding mode conditions.

Conclusions

We have shown that perch morphology is influenced by phenotypic plasticity to such a large extent that an induced morphology might be reversible. The results of this study also suggest that this plastic response might be growth dependent. It is probably adaptive for perch with a plastic morphology for at least two reasons. First, perch face a strong ontogenetic trade-off in optimal morphology and, second, they might experience pronounced temporal fluctuations in intraspecific competition. Furthermore, we showed that not only divergent feeding modes, but also different physical structure of the habitat, can induce a morphological response. Therefore, the role of the physical environment is an important factor driving morphological divergence, especially among aquatic organisms such as fish.

The results of this study suggest that habitat complexity and lake resource abundance might influence the occurrence of morphological adaptations and specializations among fish populations.

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REFERENCES

Adams, D.C., Rohlf, J.F. and Slice, D.E. 2003. Geometric morphometrics: ten years of progress following the 'revolution'. *Ital. J. Zool.*, **71**: 5–16.

Agrawal, A.A. 2001. Pheotypic plasticity in the interactions and evolution of species. *Science*, **294**: 321–326.

Andersson, J. 2003. Effects of diet-induced resource polymorphism on performance in arctic charr (*Salvelinus alpinus*). *Evol. Ecol. Res.*, **5**: 213–228.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. *et al.* 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, **161**: 1–28.

Day, T. and McPhail, J.D. 1996. The effect of behavioral and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). *Oecologia*, **108**: 380–388.

Day, T., Pritchard, J. and Schluter, D. 1994. A comparison of two sticklebacks. *Evolution*, **48**: 1723–1734.

Ehlinger, T.J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology*, **71**: 886–896.

Ehlinger, T.J. and Wilson, D.S. 1988. Complex foraging polymorphism in bluegill sunfish. *Proc. Natl. Acad. Sci. USA*, **85**: 1878–1882.

Hegrenes, S. 2001. Diet-induced phenotypic plasticity of feeding morphology in the orange spotted sunfish, *Lepomis humilis. Ecol. Freshw. Fish.*, **10**: 35–42.

Hjelm, J., Persson, L. and Christensen, B. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. *Oecologia*, **122**: 190–199.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L. and Wahlström, E. 2001. Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos*, **95**: 311–323.

Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science*, **260**: 216–219.

Lessmark, O. 1983. Competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in south Swedish lakes. Doctoral thesis, Institute of Limnology, University of Lund, Sweden.

Lindsey, C.C. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. *Can. J. Fish. Aquat. Sci.*, **38**: 1497–1506.

Malmquist, H.J., Snorrason, S.S., Skulason, S., Jonsson, B., Sandlund, O.T. and Jonasson, P.M. 1992. Diet differentiation in polymorphic Arcitc charr in Thingvallavatn, Iceland. *J. Anim. Ecol.*, **61**: 21–35.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution*, **41**: 1357–1369.

Meyer, A. 1990. Ecological and evolutionary consequences of the trophic polymorphism in *Cichlasoma citrinellum* (Pisces: Ciclidae). *Biol. J. Linn. Soc.*, **39**: 279–299.

Mittelbach, G.G., Turner, A.M., Hall, D.J., Rettig, J.E. and Osenberg, C.W. 1995. Perturbation and resilience – a long-term, whole-lake study of predator extinction and reintroduction. *Ecology*, **76**: 2347–2360.

Mittelbach, G.G., Osenberg, C.W. and Wainwright, P.C. 1999. Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? *Evol. Ecol. Res.*, **1**: 111–128.

Nemeth, H.D. 1997. Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammos. J. Exp. Biol.*, **200**: 2155–2164.

Norton, S.F. 1991. Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology*, **72**: 1807–1819.

Norton, S.F. 1995. A functional approach to ecomorphological patterns of feeding in cottid fishes. *Env. Biol. Fish.*, **44**: 61–78.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. In *Size-structured Populations* (B. Ebenman and L. Persson, eds.), pp. 205–218. Berlin: Springer.

Persson, L., Byström, P. and Wahlström, E. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology*, **81**: 1058–1071.

Persson, L., DeRoos, A.M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S. *et al.* 2003. Gigantic cannibals driving whole lake trophic cascades. *Proc. Natl. Acad. Sci. USA*, **100**: 4035–4039.

Pfennig, D.W. 1992. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionary strategy. *Evolution*, **46**: 1408–1420.

Price, T., Qvarnström, A. and Irwin, D.E. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B*, **270**: 1433–1440.

Proulx, R. and Magnan, P. 2004. Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). *Evol. Ecol. Res.*, **6**: 631–658.

Robinson, B.W. 2000. Trade offs in habitat-specific foraging efficiency and the nascent adaptive divergence of sticklebacks in lakes. *Behaviour*, **137**: 865–888.

Robinson, B.W. and Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. *Am. Nat.*, **144**: 596–627.

Robinson, B.W. and Wilson, D.S. 1995. Experimentally induced morphological diversity in Trinidadian guppies (*Poecilia reticulata*). *Copeia*, **2**: 294–305.

Robinson, B.W. and Wilson, D.S. 1996. Genetic variation and phenotypic variation in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*). *Evol. Ecol.*, **10**: 631–652.

Robinson, B.W., Wilson, D.S., Margosian, A.S. and Lotito, P.T. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evol. Ecol.*, **7**: 451–464.

Robinson, B.W., Wilson, D.S. and Shea, G.O. 1996. Trade-offs of ecological specialization: an intraspecific comparison of pumpkinseed sunfish phenotypes. *Ecology*, **77**: 170–178.

Rohlf, F.J. 2003a. *tpsDIG32* (freeware at: http://life.bio.sunysb.edu/morph/).

Rohlf, F.J. 2003b. *tpsRelw* (freeware at: http://life.bio.sunysb.edu/morph/).

Rohlf, F.J. 2004. *tpsRegr* (freeware at: http://life.bio.sunysb.edu/morph/).

Scheiner, S. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.*, **24**: 35–68.

Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecology*, **74**: 699–709.

Schluter, D. and McPhail, J.D. 1992. Ecological character displacement and speciation in sticklebacks. *Am.Nat.*, **140**: 85–108.

Schluter, D. and McPhail, J.D. 1993. Character displacement and replicate adaptive radiation. *Trends Ecol. Evol.*, **8**: 197–200.

Skulason, S. and Smith, T.B. 1995. Resource polymorphisms in vertebrates. *Trends Ecol. Evol.*, **10**: 366–370.

Smith, G.R., Rettig, J.E., Mittlebach, G.G., Valiulis, J.L. and Schaak, S.R. 1999. The effects of fish on assemblages of amphibians in ponds: a field experiment. *Freshw. Biol.*, **41**: 829–837.

Smith, T.B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch, *Pyrenestes. Nature*, **363**: 618–620.

Smith, T.B. and Skulason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians and birds. *Annu. Rev. Ecol. Syst.*, **27**: 111–133.

Snorrason, S.S., Skulasson, S., Jonsson, B., Malmquist, H.J., Jonasson, P.M., Sandlund, O.T. *et al.* 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogentic niche shifts. *Biol. J. Linn. Soc.*, **52**: 1–18.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. New York: W.H. Freeman.

Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience*, **39**: 436–445.

Svanbäck, R. and Eklöv, P. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia*, **131**: 61–70.

Svanbäck, R. and Eklöv, P. 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos*, **102**: 273–284.

Svanbäck, R. and Eklöv, P. 2004. Morphology in perch affects habitat specific feeding efficiency. *Funct. Ecol.*, **18**: 503–510.

Svanbäck, R. and Persson, L. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J. Anim. Ecol.*, **73**: 973–982.

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Schlichting, C.D. and Van Tienderen, P.H. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.*, **10**: 212–217.

Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.*, **24**: 107–120.

Webb, P.W. and Weihs, D. 1986. Functional locomotor morphology of early life history stages of fishes. *Trans. Am. Fish. Soc.*, **115**: 115–127.

West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.*, **20**: 249–278.

West-Eberhard, M.J. 2002. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

Wimberger, P.H. 1992. Plasticity of fish body shape: the effects of diet, development, family and age in two species of *Geophagus* (Pisces, Cichlidae). *Biol. J. Linn. Soc.*, **45**: 197–218.