

Genetic variation and phenotypic plasticity: causes of morphological and dietary variation in Eurasian perch

Richard Svanbäck^{1,2*} and Peter Eklöv²

¹*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå*
and ²*Department of Limnology, Evolutionary Biology Centre, Uppsala University,*
SE-752 36 Uppsala, Sweden

ABSTRACT

Question: What is the importance of genetic variation and phenotypic plasticity in forming the morphological difference between littoral and pelagic perch?

Organism: Juveniles of Eurasian perch (*Perca fluviatilis* L.).

Site: Enclosures (2 × 2 m) in a pond, Röbäcksdalen, Umeå, Sweden.

Methods: Adults from the littoral and pelagic habitats were bred separately and their offspring were raised in enclosures with either open water or vegetation in an artificial pond.

Results: Offspring from littoral parents had a higher proportion of littoral prey types in their diet than pelagic offspring even though there were no differences in prey community between treatments. Littoral offspring had a deeper body than pelagic offspring raised in the same environment. However, most of the phenotypic variation in this experiment was explained by phenotypic plasticity: offspring from both parental types raised in open water displayed pelagic-type characteristics, whereas offspring raised in vegetation displayed littoral-type characteristics.

Conclusion: Previous long-term studies on perch show that they experience a fluctuating environment due to population dynamics. The plasticity in perch could therefore be important as fluctuating environments favour plasticity.

Keywords: adaptive variation, genetic variation, perch, phenotypic plasticity, trophic polymorphism.

INTRODUCTION

In forming a phenotype, two interacting factors act on the developmental programme – the genome and the environment (Scheiner, 1993). Genetic variation for a fixed phenotype has been hypothesized to be favoured in stable environments (Hori, 1993; Smith, 1993). Besides genetic

* Address all correspondence to Richard Svanbäck, Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada. e-mail: svanback@zoology.ubc.ca
Consult the copyright statement on the inside front cover for non-commercial copying policies.

variation for a canalized phenotype, phenotypic plasticity, an environmental-induced phenotypic change that occurs within an organism's lifetime (Stearns, 1989), is also likely to play an important role in the process of diversification (West-Eberhard, 1989). Phenotypic plasticity was once thought to result primarily from developmental accidents, but recent evidence suggests that much environmentally induced phenotypic variation exhibited by organisms is selectively advantageous (e.g. Brönmark and Miner, 1992; Day *et al.*, 1994; Robinson and Wilson, 1996). Thus, phenotypic plasticity has recently come to be viewed as a trait subject to selection, just like any other phenotypic character (Schlichting and Levine, 1986; Scheiner, 1993; Schlichting and Pigliucci, 1998). Such plasticity can often be an important adaptive strategy to help cope with environmental variability (Stearns, 1989; Scheiner, 1993). Further evidence that phenotypic plasticity is heritable is the apparent genotype-by-environment interaction (genetic variation for phenotypic plasticity) in many natural populations (e.g. Scheiner, 1993; Day *et al.*, 1994; Newman, 1994; Gotthard and Nylin, 1995).

Many cases of adaptive morphological variation within species have been related to trade-offs in foraging efficiency on different resources in different habitats (e.g. Smith, 1987; Schluter, 1993; Bolnick *et al.*, 2003; Svanbäck and Eklöv, 2003). Once adaptive morphological variation has been detected in a population, it becomes important to know if the foraging specialists are the product of genetically different individuals or if a single genotype has the capacity to produce a range of morphologies dependent on local conditions. This knowledge could then have important implications for speciation (West Eberhard, 1989; Stearns, 1989; Skúlason and Smith, 1995) and the evolution of individual specialization (Bolnick *et al.*, 2003). Even though our understanding of resource polymorphisms has increased of late, there are few studies at the earliest stages of divergence that test the relative contribution and interaction among genetic variation and phenotypic plasticity (but see Robinson and Wilson, 1996).

In this study, we attempt to measure the relative importance of genetic variation and plasticity on phenotypic variation in a population of perch (*Perca fluviatilis*). We do this in a population that has been shown to differ in morphology between the littoral and pelagic habitats in an adaptive way (Svanbäck and Eklöv, 2002, 2003). In this population, perch from the littoral zone have a deeper body than perch from the pelagic zone. In previous studies, we have shown that habitat choice by perch is associated with a trade-off in foraging efficiency between the littoral and pelagic habitats (Svanbäck and Eklöv, 2003, 2004). Furthermore, the morphological variation has been shown to have important consequences for a fitness proxy, measured in terms of growth rate (Svanbäck and Eklöv, 2003). The morphological difference between littoral and pelagic perch is not dramatic but the pattern in morphology and habitat use is highly replicable (P. Eklöv and R. Svanbäck, unpublished data), and the same pattern is found in other morphologically variable fish species (e.g. Ehlinger and Wilson, 1988; Robinson *et al.*, 1993, 2000). In this study, we address two fundamental questions about the ecology and evolution of adaptive morphological variation: (1) What is the relative importance of genetic variation and plasticity on phenotypic variation in this perch population? (2) Various biologists (e.g. Mayr, 1963; Price *et al.*, 2003) have suggested that adaptive divergence of behavioural traits will precede that of morphological or less flexible traits. We therefore examine whether that heritable behavioural divergence is stronger than morphological divergence between ecomorphs. We answer these questions in a common garden experiment in which we raised juvenile perch from littoral and pelagic parents in either open water or in vegetation habitats.

METHODS

Experimental design

We performed the experiment in a rectangular pond (22×77 m) at Röbbäcksdalen, Umeå, central Sweden. The pond is fed with well water and the water level was adjusted to a depth of 80 cm. The flow rate was set to about $5 \text{ litres} \cdot \text{min}^{-1}$. The pond was previously divided into ten equally sized compartments (7×10 m) by plastic curtains reaching from the bottom to above the water surface (see Eklöv and VanKooten, 2001). Water was allowed to flow between compartments through mesh-covered openings (30×30 cm) in the plastic walls. The experiment was carried out in enclosures (2×2 m) and we placed four enclosures in each of ten compartments. At the beginning of May we drained the pond but left about 5 cm of water to allow invertebrates to survive. The enclosures were constructed using a 1 m high plastic screen (grid size 2.5 mm) that was attached to a wooden frame (5×5 cm). At the bottom the screen was attached to stiff propylene plastic sheets that were buried into the mud (~ 15 cm). After constructing the enclosures we raised the water level to a depth of 80 cm so that the walls of the enclosures reached about 20 cm above the water surface. Both the bottom and the top of the enclosures were open. The mesh size of the enclosure walls was large enough to allow passage of water and small invertebrates, but was too small for young fish to swim through. However, to avoid the small perch larvae escaping early on, the inside of each enclosure was covered with a plastic curtain for the first 4 weeks of the experiment. Two randomly selected enclosures in each compartment were cleared of emerging macrophytes ('open water enclosures') at the beginning and after the first sampling, while in the other two enclosures vegetation was allowed to grow freely ('vegetation enclosures'). Originally, 40 enclosures were set up but four of them were excluded from the experiment due to wind damage. One hundred perch larvae from either littoral or pelagic parents were stocked into each enclosure, thus replicating each parental and environmental combination nine times. After 52 days of the experiment we randomly sampled five individuals from each enclosure, and at the end of the experiment (day 72) the remaining individuals in each enclosure were removed for length, dietary and morphological measurements. The five individuals collected at day 52 were chosen after all individuals from an enclosure were collected. The remaining individuals were thereafter put back into the enclosure.

Experimental fish

In the late summer and fall (end of August to beginning of September) the year before the experiment, live adult perch from the littoral and pelagic habitats of Lake Trehörningen ($64^{\circ}00'50''\text{N}$, $20^{\circ}08'00''\text{E}$) were collected with seine-nets or barbless hooks. Perch (male and female) from the two habitat types were stocked into separate, previously fishless, ponds nearby the experimental pond. The following spring after spawning, fertilized eggs from 10 egg-strands (each female lays a single strand) in each pond were collected and hatched in the laboratory. Three days after hatching, about 100 offspring of each female perch from either the littoral or pelagic habitat were randomly transferred to either open water or vegetation enclosures. That is, each enclosure had the offspring of a single female. The perch larvae were fed zooplankton collected in a nearby fishless pond for the first 4 weeks to prevent them from starving until the zooplankton proliferated in the experimental pond.

Resource sampling

On days 52 and 72, we sampled invertebrate densities. In each enclosure, one sample was taken with a plankton net (diameter 23 cm, mesh size 75 μm) pulled horizontally 2 m through the water (sample volume 82 litres), at a depth of 40 cm. The invertebrate samples were preserved with Lugol's solution for later analysis. Samples from the vegetation enclosures included both vegetation-attached and free swimming microcrustaceans (zooplankton) as well as macroinvertebrates, whereas samples from the open water enclosures included only zooplankton. Microcrustaceans and macroinvertebrates were identified to genus or species and the first ten individuals from each taxa were measured for length. Lengths were transformed to dry mass using length–mass relationships given in Bottrell *et al.* (1976) or by using our own length–mass relationships.

Morphometric and dietary analysis

We analysed the morphology using landmarks digitized with TPS-digit (Rohlf, 2001a) from digital images of each specimen and used 16 landmarks on the left side of each specimen (Fig. 1). We used the digitized landmarks to analyse the relative position of each landmark and variation in body shape using TPSRW [Thin-Plate Spline Relative Warp (Rohlf, 2001b)]. We used TPSRW to calculate partial warp and uniform scores of the individuals. The uniform shape components parameterize all shape variation that is uniform throughout the whole geometry, meaning the variation is large scaled and neither spatially localized nor spatially disproportionate. A common example of uniform shape variation is a general extension/contraction of a whole animal along some axis. In contrast, the partial warps measure non-uniform shape variation that is localized to particular regions of the geometry and is smaller scaled. A common example would be a local extension/contraction that does not occur in other parts of the animal (Bookstein, 1991, 1996).

The partial warp and uniform scores were then analysed with a multivariate discriminant function analysis of all individuals pooled and classified by the treatment (sampling date, parent and environment). This technique combines all partial warp and uniform scores into discriminant functions (morphological indexes) for each fish that maximally discriminate between the treatments. Shape changes associated with the discriminant functions were visualized as deformations by using the TPSREGR program (Rohlf, 2000) to display the regression of the original coordinates on the discriminant function.

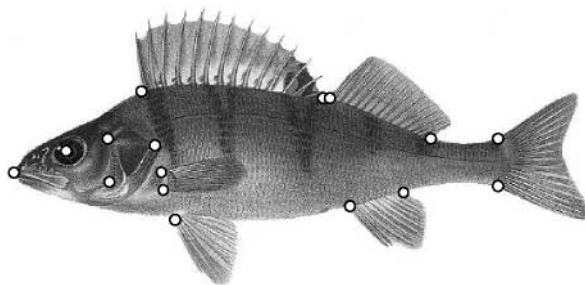


Fig. 1. Landmark configuration on perch for the morphological analysis. The results of the morphological analysis of the landmarks are visualized as deformation grid plots with the landmarks in Fig. 3.

The stomach contents of each fish were analysed under a dissecting microscope and the zooplankton and macroinvertebrates were identified to the lowest taxonomic level possible, counted and measured to the nearest 0.1 mm. The length of all prey items was then converted to biomass (dry weight) using our own length–weight relationships. The proportions of different prey in individual perch diets were calculated by dividing the mass (dry weight) of each diet taxa by the total biomass of the gut contents. We calculated the proportion of littoral taxa in the diet by summarizing the proportions of all littoral taxa, which in this study included chironomids, Ephemeroptera, Trichoptera, Zygoptera, *Sialis*, *Asellus*, *Notonecta*, Hirudinea, and benthic cladocerans such as *Euryercus* and *Chydorus*.

Statistical analysis

All results are analysed using three-way analysis of variance (ANOVA) with sampling time, parental type and environment as factors, thus ignoring the block effect. Since there was a size difference between the first and second samplings, we linearly regressed each shape measurement (discriminant function scores) against total length for all fish combined to remove the effect of size on morphology (Hjelm *et al.*, 2001; Svanbäck and Eklöv, 2002) and we then analysed the residual variation in morphology. Since we sampled several individuals from each enclosure, we used the average from those individuals in the analysis and in the figures. We arcsine square root transformed proportions of diet scores before analysis.

RESULTS

Survival and size

There was no difference in survival between the treatments (two-way ANOVA: environment: $F_{1,32} = 2.45$, $P = 0.13$; parental type: $F_{1,32} = 0.14$, $P = 0.72$; environment \times parental type: $F_{1,32} = 0.31$, $P = 0.58$). Average survival for all treatments was 17.5%.

There was a difference in the length of the perch between the sampling dates. Perch had a mean (\pm standard error) length of 45.2 ± 0.4 mm at the first sampling, but a mean length of 53.5 ± 0.7 mm at the second sampling. Environment had a small but non-significant effect on growth, as perch raised in open water tended to grow more than those raised in vegetation (Table 1). However, there was no difference in growth between perch from littoral and pelagic parents, and there was no interaction effect between parental type and environment (Table 1).

Resources and diet

Littoral resource biomass differed between open and vegetation enclosures and between sampling dates (Table 2). Littoral resource biomass was higher in vegetation enclosures and decreased between the first and the second sampling date. Parental type had no effect on littoral prey biomass. The change in littoral resource biomass over time depended on the environment, as indicated by the interaction (Table 2). There was no effect of parental type and environment on pelagic resource biomass. The only difference in pelagic resource biomass was a decrease between the first and second samplings.

The diet differed between parental types and environment but not between sampling dates (Table 1). Perch from littoral parents had a higher proportion of littoral prey types in

Table 1. Results of the two analyses of variance of the effect of treatment on size and diet, indicated by mean square (MS) and *F*-values for each independent factor

	Size		Diet	
	MS	<i>F</i>	MS	<i>F</i>
Date	1250	56.3***	486	1.51
Environment	66	2.99 [#]	40584	126***
Parental type	0.97	0.04	5085	15.8***
Date × environment	6.5	0.29	353	1.09
Date × parental type	2.0	0.09	820	2.54
Environment × parental type	0.32	0.02	27	0.08
Date × environment × parental type	0.18	0.01	197	0.6
Error	22		322	

Note: The degrees of freedom in both models are 1,64. [#]*P* < 0.1, ****P* < 0.001.

Table 2. Results of the two analyses of variance of the effect of treatment on the littoral and pelagic biomass, indicated by mean square (MS) and *F*-values for each independent factor

	Littoral biomass		Pelagic biomass	
	MS	<i>F</i>	MS	<i>F</i>
Date	0.51	12.8***	1.1	5.47*
Environment	0.59	14.8***	0.17	0.83
Parental type	0.025	0.64	0.016	0.08
Date × environment	0.45	11.4***	0.037	0.18
Date × parental type	0.017	0.44	0.052	0.25
Environment × parental type	0.028	0.70	0.18	0.89
Date × environment × parental type	0.020	0.51	0.15	0.75
Error	0.040		0.21	

Note: The degrees of freedom in both models are 1,64. **P* < 0.05, ****P* < 0.001.

their diet than those from pelagic parents. The environment also determined the variation in diet, as perch raised in vegetation had a higher proportion of littoral prey types in their diets (Fig. 2). Calculations of variance components for diet showed that 78% of variance was explained by the environment, and 9% by parental treatment.

Morphology

The discriminant function analysis indicated that the eight treatment groups were distinct in multivariate space (Wilks' $\lambda = 0.023$, $F_{28,419} = 635.7$, $P < 0.001$). The discriminant function analysis correctly classified 296 of the 448 perch (66.1%) into their respective groups, compared with a random expectation of 12.5% correctly classified. Most misclassifications were to the same environmental treatment but to the other parental origin. The discriminant function analysis gave us seven functions, the first two of which explained 77 and 18.6% of the variance respectively; none of the other functions explained more than 2% of the

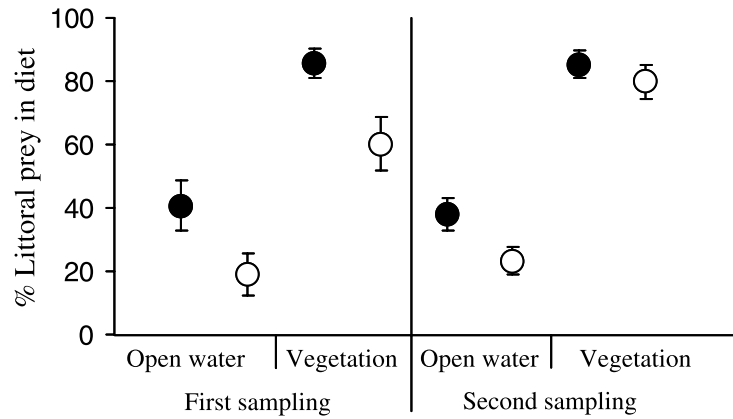


Fig. 2. Percentage of littoral prey types in the diet of the treatment groups at the two sampling dates (mean \pm standard error). Solid symbols indicate treatments with littoral parents; open symbols indicate treatments with pelagic parents.

Table 3. Results of the two analyses of variance of the effect of treatment on the first two morphological functions from the discriminant function analysis, indicated by mean square (MS) and F -values for each independent factor

	Function 1		Function 2	
	MS	F	MS	F
Date	29	102***	28	156***
Environment	424	1450***	3.7	21.0***
Parental type	0.39	1.34	1.7	9.59**
Date \times environment	51	173***	0.089	0.50
Date \times parental type	0.032	0.11	0.024	0.14
Environment \times parental type	0.007	0.02	0.010	0.06
Date \times environment \times parental type	0.002	0.01	0.003	0.02
Error	0.292		0.178	

Note: The degrees of freedom in both models are 1,64. ** $P < 0.01$, *** $P < 0.001$.

variance. Because the third factor added little additional discriminant power, we limit our analyses to the first two functions, except where noted.

A separate ANOVA on the variation in the first function showed effects of date and environment on perch morphology (Table 3). The first function describes variation in the bending of individuals, with a downward bending of the body for negative scores and an upward bending of the body for positive scores. Described by the first discriminant function, perch raised in open water enclosures had their bodies bent slightly upwards, whereas perch raised in vegetation enclosures had their bodies bent slightly downwards (Fig. 3). Furthermore, as indicated by the first function, the difference due to environment increased with time, and this increase was due mostly to the morphological change in the vegetation treatments.

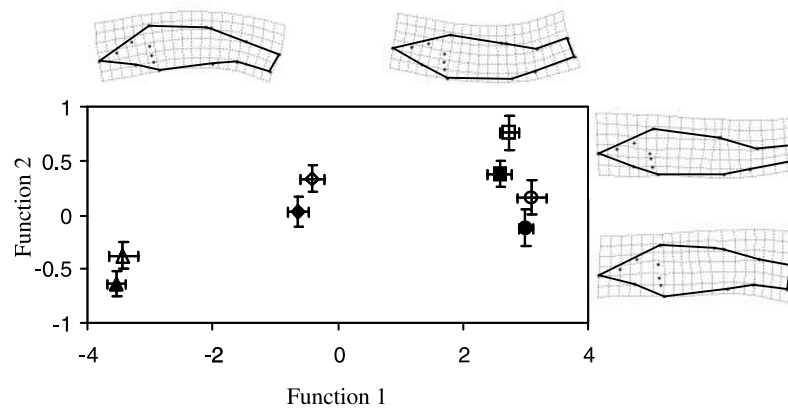


Fig. 3. Means (\pm standard error) of the function scores from the discriminant function analysis on the eight parent–environment–date groups for the first two functions. The first function describes a bending of the body, with negative scores representing a downward bending of the body and positive scores an upward bending of the body (see grid-plots above the graph for visualization of function 1). The second function describes the depth of the body, with negative scores representing a deeper body and positive scores a more streamlined body (see grid-plots to the right of the graph for visualization of function 2). The outlined form is a guide to locate landmarks, and does not represent the location of the true body outline. Solid symbols represent treatments with littoral parental types and open symbols represent treatments with pelagic parental types. From the left to the right on the graph, triangles represent second sampling in the vegetation treatments, diamonds represent first sampling in the vegetation treatments, squares represent first sampling in the open water treatments, and circles represent second sampling in the open water treatments. The deformation grid plots for both morphological axes have been extended to represent individuals of scores -10 and 10 respectively to make the visualization clearer.

A separate ANOVA showed that the variation in the second function described differences in perch morphology that were due to both environment and parental type (Table 3). The second function describes variation in the depth of the body. Individuals with negative scores have a deeper body, especially laterally, and their head is also a little more compressed compared with individuals with a positive score. Individuals with a positive score, on the other hand, are larger anteriorly and have a more streamlined body. Described by the second discriminant function, perch raised in vegetation enclosures had a deeper body than those raised in open water (Fig. 3). Furthermore, individuals with littoral parents had a deeper body than individuals from pelagic parents. The perch also attained a deeper body with time, as indicated by the difference between sampling dates. The depth of perch is normally related to the size of individuals (Svanbäck and Eklöv, 2002), but in this case we had already corrected for size (see Methods). This would indicate that fast-growing perch at the first sampling would have a more streamlined body than equally sized but slower-growing individuals at the second sampling.

We calculated the relative importance of genetic versus phenotypic plastic difference using the variance explained by each discriminant function adjusted by the variance components from the ANOVA to reflect the treatment variance components (Sokal and Rohlf, 1981). The adjusted variance components due to environment, time, the environment \times time interaction and parental type are 62, 15, 7 and 2% respectively. The effect of environment

is thus about 34.5 times more powerful than the genetic differences between offspring types. Similarly, no other interaction explained more than 0.3% of the morphological variation.

DISCUSSION

Most of the morphological and dietary variation in this experiment was due to phenotypic plasticity, and only to a small extent to genetic differences between the parental types. The results show that the foraging behaviour and diet choice of perch might have a genetic basis, as perch from littoral parents had a higher proportion of littoral prey types in their diet than perch from pelagic parents independent of the environment they were grown in. This might suggest that the behavioural differences between littoral and pelagic perch reported by Svanbäck and Eklöv (2003, 2004) have a genetic basis. The behavioural differences between parental types could be the cause of the 'heritable' effect on body form, but it might also be the other way around – that is, the body form is a plastic response to diet and that diet choice is heritable. The stronger parental effect on diet choice (9%) than that on morphology (2%) suggests that genetic differences in behaviour would precede genetic differences in body form. To our knowledge, no empirical work has been done on this subject, but behavioural changes followed by morphological evolution have been hypothesized to be a potent force in driving evolution in novel directions (Price *et al.*, 2003). This difference in parental effect between diet and morphology might also suggest that structure has a stronger effect on morphology than diet. Correspondingly, in an experiment that combined structural complexity and diet, Olsson and Eklöv (2005) showed that structure had more of an effect on morphological development in perch than diet. However, with this experimental design, we cannot answer the question of what comes first, behaviour or morphology.

Even though the genetic variation contributed very little to the morphological variation, it might have some significance for individual habitat and diet choice in nature, but this needs further investigations before any conclusions can be drawn. Due to the experimental protocol, we cannot be certain that the effect of parental type is not just one of maternal effects. However, Gerlach *et al.* (2001) found genetic differences in perch from different localities in Lake Constance (Germany), indicating that perch possess some kind of genetic structuring. Regardless of maternal effects or genetic differences, the differences we found were in a predictable direction and would certainly have an effect on diet and habitat choice in the wild. Furthermore, we found indications in this experiment that individual growth rate might affect the morphological development of perch. This fact might also be important in the ecology and evolution of morphological variation in perch, as differences between years in intra- and/or inter-specific competition will translate into differences in growth rates (Persson *et al.*, 2000, 2003, 2004).

In a field survey, we found that a discriminant function analysis correctly classified 83% of the perch from the littoral and pelagic habitats of Lake Trehörningen (Svanbäck and Eklöv, 2003). These morphology–habitat correlations are common in all perch populations we have surveyed (P. Eklöv and R. Svanbäck, unpublished data), and are also found in many other fish species as well as in many other animal taxa (Skúlason and Smith, 1995; Smith and Skúlason, 1996; Bolnick *et al.*, 2003). In Lake Trehörningen, littoral perch have a deeper and more downward bending body than pelagic perch, which have a more streamlined and upward bending body (Svanbäck and Eklöv, 2002, 2003). The bending of the body shown by our first function is probably an adaptation to searching for food towards the water surface

(upward bending) and towards the bottom (downward bending). However, although speculative, we have found this bending pattern in all perch populations that we have surveyed (Svanbäck and Eklöv, 2002, 2003; P. Eklöv and R. Svanbäck, unpublished data), as well as in roach (R. Svanbäck *et al.*, unpublished data) and in bleak (R. Svanbäck *et al.*, unpublished data). Furthermore, other experimental studies on perch and other fish species have shown that individuals raised on a benthic diet develop a downward bending body, whereas individuals raised on a pelagic diet develop an upward bending body (Hjelm *et al.*, 2001; Andersson, 2003; Olsson and Eklöv, 2005; P. Eklöv and R. Svanbäck, unpublished data). Our second morphological function describes the body depth of individuals. A deeper body is thought to be better for manoeuvring in structured habitats, whereas a streamlined body is thought to be adapted for minimizing drag while searching for food in open water (e.g. Webb, 1984).

Although not always investigated, the morphology–habitat correlations found within populations are probably due to foraging efficiency trade-offs and diversifying selection (Skúlason and Smith, 1995; Smith and Skúlason, 1996; Bolnick *et al.*, 2003). In perch we have shown that the deeper-bodied littoral perch are better foragers in complex structured environments, such as in the littoral zone, than the more streamlined pelagic perch. The pelagic perch, on the other hand, are superior foragers on pelagic prey types in open water environments (Svanbäck and Eklöv, 2003, 2004). Many studies have shown that adaptive variations and resource polymorphisms may have a genetic basis or that phenotypic plasticity is involved in forming them (Skúlason and Smith, 1995; Smith and Skúlason, 1996; Bolnick *et al.*, 2003), but only a few studies have tried to evaluate the relative importance of genetic variation and phenotypic plasticity (but see Robinson and Wilson, 1996).

So what makes phenotypic plasticity dominate genetic variation in forming perch body morphology? Phenotypic plasticity would be favoured if the environment varies such that the selection on the phenotype varies. In the case for resource polymorphisms, phenotypic plasticity would be favoured if the resources vary through time. The profitability of a given resource type generally changes with consumer body size and will thus induce diet shifts with size. The resources could also fluctuate through time due to abiotic (environmental variation) or biotic factors (population- and community-dynamics).

Variation in resources in both habitats will influence the diet choice of individuals. Such variations in resources can be the result of zooplankton and benthic invertebrate species varying in density during a season, due to differences in life history (Sommer *et al.*, 1986). Variations in resources might also be due to abiotic environmental variations, such as unpredictable environmental variation that changes relative prey abundances (e.g. Grant, 1986; Grant and Grant, 2002; Stenseth *et al.*, 2002). Furthermore, fluctuating intra- and inter-specific competition might also result in variations in resources (Persson *et al.*, 2000). Previous studies have shown that perch density in a single-species lake fluctuates with time, due to internally driven predation and competitive interactions (Persson *et al.*, 2000). With these fluctuations in density, both the habitat and diet choice of perch changed as a response to differences in habitat-specific resource densities (Persson *et al.*, 2000; Svanbäck and Persson, 2004). Most lakes, however, are not single-species lakes and the density fluctuations of all species with time will influence available resources and the selective regime (P. Eklöv and R. Svanbäck, unpublished data). Furthermore, perch potentially undergo two niche shifts during their lifetime, from zooplanktivory to benthivory and then from benthivory to piscivory (e.g. Persson, 1988; Hjelm *et al.*, 2000; Svanbäck and Eklöv, 2002), that is influenced by foraging rate and predation risk. With such habitat shift, juveniles might change morphology to adapt to their new environment (Eklöv and Svanbäck, in press).

In conclusion, we found that most of the morphological variation in this perch population was due to phenotypic plasticity. We also show that the response to the environment was relatively fast (see also Hjelm *et al.*, 2001) and conforms to functional expectations. The reason for the high degree of plasticity in perch might be due to fluctuations in competitive and predatory interactions acting on available resources and mortality risk. With such fluctuations, the optimal habitat for an individual will change with time and size favouring phenotypic plasticity.

ACKNOWLEDGEMENTS

We would like to thank G. Svanbäck, K. Bergström and M. Sundbom for logistic help during the experiment. The manuscript was greatly improved by valuable comments on previous drafts by J. Olsson, M. Quevedo, B. Robinson and A. Hendry. This study was supported by grants from Stiftelsen Oscar and Lili Lamms Minne to R. Svanbäck, and The Swedish Research Council for Environment, Agricultural Science and Spatial Planning (Formas) to P. Eklöv.

REFERENCES

- 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.
- Bookstein, F.L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. New York: Cambridge University Press.
- Bookstein, F.L. 1996. A standard formula for the uniform shape component in landmark data. In *Advances in Morphometrics* (L.F. Marcus, M. Corti, A. Loy, G. Naylor and D. Slice, eds), pp. 153–168. New York: Plenum Press.
- Bottrell, H.H., Duncan, A., Gliwich, Z.M., Grygierik, E., Herzig, A., Hillbrich-Ilkowska A. *et al.* 1976. A review of some problems in zooplankton production studies. *Norveg. J. Zool.*, **24**: 419–456.
- Brönmark, C. and Miner, J.G. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science*, **258**: 1348–1350.
- Day, T., Pritchard, J. and Schluter, D. 1994. A comparison of two sticklebacks. *Evolution*, **48**: 1723–1734.
- Ehlinger, T.J. and Wilson, D.S. 1988. Complex foraging polymorphism in bluegill sunfish. *Proc. Natl. Acad. Sci. USA*, **85**: 1878–1882.
- Eklöv, P. and Svanbäck, R. in press. Predation favors phenotypic divergence in sympatric perch populations. *Am. Nat.*
- Eklöv, P. and VanKooten, T. 2001. Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, **82**: 2486–2494.
- Gerlach, G., Schardt, U., Eckmann, R. and Meyer, A. 2001. Kin-structured subpopulations in Eurasian perch (*Perca fluviatilis* L.). *Heredity*, **86**: 213–221.
- Gotthard, K. and Nylin, S. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos*, **74**: 3–17.
- Grant, P.R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton, NJ: Princeton University Press.
- Grant, P.R. and Grant, B.R. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**: 707–711.

- 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.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.
- Newman, R.A. 1994. Genetic-variation for phenotypic plasticity in the larval life-history of spadefoot toads (*Scaphiophus couchii*). *Evolution*, **48**: 1773–1785.
- Olsson, J. and Eklöv, P. 2005. Habitat structure, feeding mode and morphological reversibility: factors influencing phenotypic plasticity in perch. *Evol. Ecol. Res.*, **7**: 1109–1123.
- 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., De Roos, 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.
- Persson, L., Claessen, D., De Roos, A.M., Byström, P., Sjögren, S., Svanbäck, R. *et al.* 2004. Cannibalism in a size-structured population – energy extraction and control. *Ecol. Monogr.*, **74**: 135–157.
- 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.
- Robinson, B.W. and Wilson, D.S. 1996. Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gibbus*). *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 Margosian, A.S. 2000. A pluralistic analysis of character release in pumpkinseed sunfish (*Lepomis gibbosus*). *Ecology*, **81**: 2799–2812.
- Rohlf, F.J. 2000. *Tps Regression v. 1.25*. Department of Ecology and Evolution. State University of New York, Stony Brook, New York (free computer software available online at: <http://life.bio.sunysb.edu/morph/>).
- Rohlf, F.J. 2001a. *Tps-digit: Basic Digitizing Software v. 1.31*. Department of Ecology and Evolution. State University of New York, Stony Brook, New York (free computer software available online at: <http://life.bio.sunysb.edu/morph/>).
- Rohlf, F.J. 2001b. *TPSRW: Thin-Plate Spline Relative Warp Analysis v. 1.24*. Department of Ecology and Evolution. State University of New York, Stony Brook, New York (free computer software available online at: <http://life.bio.sunysb.edu/morph/>).
- Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.*, **24**: 35–68.
- Schlichting, C.D. and Levine, D.A. 1986. Phenotypic plasticity: an evolving plant character. *Biol. J. Linn. Soc.*, **29**: 37–47.
- Schlichting, C.D. and Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland, MA: Sinauer Associates.
- Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecology*, **74**: 699–709.
- Skúlason, S. and Smith, T.B. 1995. Resource polymorphisms in vertebrates. *Trends Ecol. Evol.*, **10**: 366–370.
- Smith, B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature*, **329**: 717–719.

- 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 Skúlason, S. 1996. Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.*, **27**: 111–133.
- Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. New York: W.H. Freeman.
- Sommer, U., Gliwicz, Z.M., Lampert, W. and Duncan, A. 1986. The PEG*-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.*, **106**: 433–471.
- Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *BioScience*, **39**: 436–445.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. and Lima, M. 2002. Ecological effects of climate fluctuations. *Science*, **297**: 1292–1296.
- 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.
- Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.*, **24**: 107–120.
- West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.*, **20**: 249–278.

