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Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr

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Recent models suggest that the existence of environmentally induced polymorphisms within a single population (especially those related to foraging) facilitates the process of evolutionary divergence within a single gene pool by generating distinct phenotypic modes that are exposed to differential selection. In order to test a prediction of the phenotypic plasticity model of divergence, we used a well-documented polymorphism to disentangle the relative effects of morph and rearing environment in generating phenotypic variance. We reared first-generation offspring of two sympatric morphs of Arctic charr *Salvelinus alpinus* in the laboratory and compared their head morphology with that of their wild parents. Morphological characters with a known functional role in foraging were highly plastic. Rearing environment accounted for the largest component of the variation in expressed phenotype, but this environmental effect overlaid a clear (but small) genetic effect. We conclude that phenotypic plasticity has played a significant role in the evolution of this trophic polymorphism, but that the evolutionary process has progressed to the point that the gene pool is now segregated. *Biological Journal of the Linnean Society*, 2004, **81**, 611–618.

ADDITIONAL KEYWORDS: environmental modulation – evolution – phenotypic variation – polymorphism.

INTRODUCTION

Recent models describing the early stages of speciation suggest that inherited differences in phenotype are not essential precursors of evolutionary divergence within a single gene pool. Such models show how divergence may arise prior to any genetic segregation as a result of environmentally induced phenotypic plasticity at the individual level. Where the traits concerned are of strong functional significance, the existence of different forms creates the circumstances in which subsequent genetic divergence is favoured (West-Eberhard, 1986, 1989, 1998; Wimberger, 1994; Skúlason, Snorrason & Jónsson, 1999).

Skúlason and coworkers propose a four-stage process of species divergence based on phenotypic plasticity (Skúlason *et al*., 1999). In the first stage, alternative, adaptive traits are expressed in individuals within a single gene pool. West-Eberhard (1989) argues that behavioural phenotypes are most likely to show discrete alternatives within a population and that those relating to foraging are particularly strong candidates for subsequent divergence due to their strong functional significance (Wimberger, 1994; Smith & Skúlason, 1996). In the second stage, behavioural specialization may result in modification of morphological traits through phenotypic plasticity in anatomical traits (Wimberger, 1994; Skúlason *et al*., 1999). Once this evolutionary stage is reached, reproductive segregation may occur through differential habitat use or through mate selection by different phenotypic variants (stage 3). As a consequence, different forms are exposed to different selection pressures and hence genetic fixing of traits can occur (stage 4) (see West-Eberhard, 1986; West-Eberhard, 1989; Wimberger, 1994; Skúlason *et al*., 1999).

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One key element of this model is that environmental precedes genetic control of phenotypic variation. Thus, this mechanism of evolutionary diversification is most likely to work when two preconditions apply. First, the species concerned must be phenotypically plastic and thus able to express more than one variant of a phenotypic trait within a single gene pool. Secondly, diversifying selection must act on the different phenotypic modes (West-Eberhard, 1989). Thus, species that exhibit discrete polymorphism in phenotype would be strong candidates for this mechanism of evolution.

The role of genetic vs. environmental regulation of phenotype has been examined in a number of polymorphic and recently diverged fish species pairs. Putative species pairs of three-spined stickleback (*Gasterosteus* sp.) from a number of lakes in British Columbia differ in the anatomy of their mouthparts and in foraging ecology, specializing in either zooplankton (the limnetic form) or zoobenthos (the benthic form). Genetic studies have shown clear genetic differences between sympatric species pairs (Taylor & McPhail, 1999, 2000). However, the foraging environment to which sticklebacks are exposed has also been shown to have a direct effect on the expression of the phenotype of the mouthparts (Day & McPhail, 1996).

One difficulty in interpreting the importance of genetic differences between morphs or closely related sister species is that most studies use genetic markers that are presumed to be selectively neutral and have no involvement in the phenotypic variation expressed in related groups. Thus, it is impossible to determine whether genetic differences between related groups are indicative of differences in the genetic control of observable phenotypic variation or if genetic divergence at selection-neutral sites is the result of restricted gene flow following environmentally induced phenotypic divergence. In order to avoid this difficulty, we modify an approach common in selective breeding studies used to segregate genetic and environmental effects on trait expression and apply this in a novel way to the assessment of the relative role of gene and environment to a previously described sympatric polymorphism in Arctic charr *Salvelinus alpinus*.

The Arctic charr is a freshwater fish that displays a high degree of phenotypic variation across the species (Behnke, 1984; Alexander & Adams, 2000). In a considerable number of populations, sympatric polymorphisms have been reported. In some cases these take the form of discrete, multimodal size frequency variants (Savvaitova, 1969; Nyman, Hammar & Gydemo, 1981; Nordeng, 1983; Klemetsen *et al*., 1985). In many, the variants overlap in size range but show distinct variation in the anatomy of feeding apparatus (Walker, Greer & Gardner, 1988; Snorrason *et al*., 1989; Adams *et al*., 1998; Fraser, Adams & Huntingford, 1999). In these trophic polymorphisms, discrete variation in the anatomy of the feeding apparatus is almost always linked with variation in feeding ecology (Snorrason *et al*., 1994; Adams *et al*., 1998; Fraser *et al.*, 1999).

In Loch Rannoch, Scotland, three morphs of Arctic charr can be clearly defined on the basis of head anatomy and feeding ecology: a benthivorous morph with a relatively large, robust head morphology, feeds on bottom-living macro-invertebrates; a planktivorous morph with a delicate mouth structure, feeds in the pelagic zone on zooplankton; and a piscivorous form with an extremely large head and robust mouth anatomy feeds upon fish (Adams *et al*., 1998). This sympatric polymorphism is known to be stable over time (Walker *et al.*, 1988; Adams *et al*., 1998) and behavioural and anatomical features that define the polymorphism persist in laboratory reared individuals (Adams & Huntingford, 2002a, b). The criteria for the definition of a species presented by Kottelat (1997) suggests that there is an argument for these morphs being afforded full species status. However, it is clear that whatever their taxonomic status, in evolutionary terms these morphs are likely to be at a relatively early stage of divergence.

The phenotypic plasticity model predicts that environmentally regulated alternative, discrete and stable morphological traits precede but subsequently promote, genetic differences (West-Eberhard, 1986; Wimberger, 1994; Skúlason *et al*., 1999). If this were true we would predict that for incipient species at an early stage of divergence, the environmental control of phenotypic variability would be significantly greater than the genetic effects. Here we test this prediction by quantifying the relative role of two distinct rearing environments on the head morphology of the two morphs of Arctic charr described above. Specifically, we use a novel combination of a well-established phenotype partitioning technique with a two-way ANOVA to tease apart and quantify the separate effects of rearing environment and morph origin on variation in head morphology.

METHODS

Ten discrete family broods, each comprising the eggs from a single female fertilized by two males, were collected in the wild from each of two morphs of Arctic charr from Loch Rannoch. Sexually mature fish of the benthivorous morph were trapped as they ascended an afferent river to their spawning area in late October. Mature males and females of the planktivorous morph from Loch Rannoch were collected using gill nets at a spawning site on a submerged beach in the main loch in mid-October.

These two forms are easily distinguishable on the basis of colour and head anatomy. They also breed in different areas of the catchment (Adams *et al*., 1998). Eggs were stripped from ovulating females in the field following capture and fertilized immediately. Eggs were allowed to hydrate before being moved to standard incubation facilities at the University Field Station, Loch Lomondside. Following incubation and hatching, alevins from each family were combined to create multifamily morph groups. At first feeding, we transferred each morph group into a separate, 0.6-m-diameter, standard circular tank with tangential through-flow, exposed to ambient water temperature and light for this latitude (56°N).

For three weeks following first feeding, alevins in both groups were fed a mixture of homogenized liver and a dry salmon fry diet (BOCM-Pauls). Subsequently a dry salmon fry diet alone was fed. As the fish grew, their density within each tank was reduced several times by removing at random around half the total number into an identical tank. After 18 months of growth, the charr occupied six 1.3-m-diameter tanks, each containing *c*.150 fish of one of the two forms. At this time fish were removed at random, until *c*.30 fish from across the size range covered by the wild parental group were collected. These fish were anaesthetized, measured (fork length) and photographed in lateral and ventral views for head morphometric analysis. Head morphometric analysis was also conducted on the wild parental group. Approximately 30 sexually mature individuals, comprising both males and females collected for stripping, from each morph group, were killed and photographed in lateral and ventral views on a suitable scale. These included all the parent fish of the two experimental groups, but also additional mature fish collected at the same time.

Morphometric analysis

Ten linear measurements of head anatomy (see Fig. 1 and Adams *et al*., 1998) were made directly on a digitizing pad from photographic prints (×4 enlargement) of lateral and ventral views of the head of each individual fish of both morphs from the wild-collected specimens and their laboratory-reared progeny groups.

Statistical analysis

In order to ensure an overlap in size of all groups, we analysed only charr in excess of 150-mm fork length (the minimum size of fish caught from the wild). Inevitably, laboratory-reared fish grew faster and thus were younger when of a similar size to their wild counterparts.

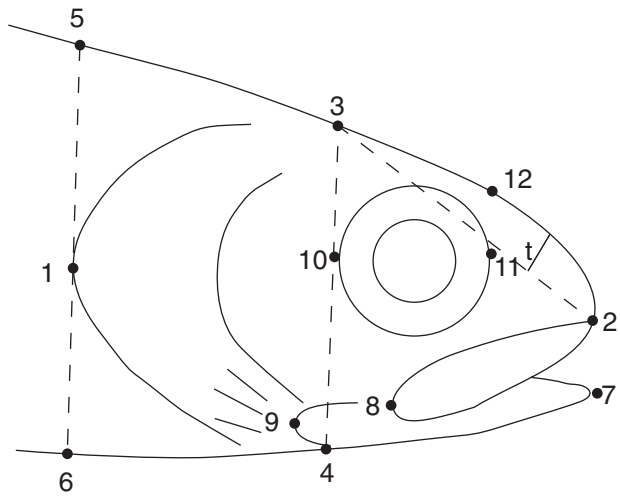

Figure 1. Head morphometric variables measured in charr: LJL, lower jaw length (7–9); HL, head length (1–2); JW, jaw width (not shown); MB, maxillary bone (2–8); HDE, head depth at eye (3–4); ED, eye diameter (10–11); HDO, head depth at operculum (5–6); SB, snout bluntness [curve of snout (2–3 through point 12) divided by the longest tangent from direct line from 2 and 3 (t) to the outer curved edge of snout]; SC, snout curvature (curve of snout point 2–3 through point 12, divided by direct line from 2 to 3).

The head morphometric characters showed a strong relationship with body size (except snout bluntness and snout curvature, which are ratios of two measures). We compared the two morphs and the two rearing environments to which charr were exposed, by obtaining size-independent residuals from pooled regressions of each morphometric character on fork length for both of the morph, rearing–environmental combinations. The effects of morph and rearing environment and their interactions were analysed using two-way ANOVA, with morph (benthivorous and planktivorous) and rearing environment (laboratory and wild) characterized as separate conditions. This approach did not allow us to distinguish between a morph-specific response to the same environment and a morph-dependent choice of microhabitat in the wild condition (as wild fish have access to a heterogeneous environment and can modify the environment to which they are exposed). Similarly, in the wild condition, the morph effect can not be regarded as a simple genetic component as the effect of morph-specific differential mortality prior to sexual maturity cannot be ruled out. Separation of these effects, however, is beyond the scope of the study presented here.

In order to summarize the overall effect of morph and rearing environment on head anatomy, we used Principal Component Analysis (using a correlation

Table 1. A two-way ANOVA on factor scores from the first four derived principal components showing morph (benthivorous/planktivorous) and rearing environment (laboratory/wild) effects and their interaction

Morphometric variable	Morph effect		Rearing environment effect		Interaction	
	F	*P*	*F*	*P*	*F*	*P*
PC1	0.804	0.3720	77.00	0.0000	0.4151	0.5208
PC2	7.350	0.0078	39.47	0.0000	1.3465	0.2485
PC3	0.144	0.7050	2.504	0.1165	29.253	0.0000
PC4	62.07	0.0000	0.2322	0.6308	12.73	0.0005

d.f = 1, 105 throughout

matrix) to derive size-independent factor scores for each group, again using residuals from pooled head morphometric variables regressed on fork length.

To allocate the variance in head anatomy resulting from morph (benthivorous–planktivorous) or rearing environment (laboratory–wild) effects, we employed a modification of the variance partitioning equation presented by Falconer (1989):

$$V_p = V_m + V_{re} + V_i,$$

where V_p = total phenotypic variance expressed, V_m = phenotypic variance resulting from a morph effect, V_{re} = phenotypic variance resulting from the effect of rearing environment (i.e. laboratory or wild) and V_i = phenotypic variance resulting from interaction between morph and rearing environment (these values were derived from ANOVA).

RESULTS

Table 1 shows the results of the two-way ANOVA on the factor scores for the first four principal components (PC1–4) derived from residuals of head anatomy measures on fork length and the untransformed snout bluntness and snout curvature ratios.

Principal components scores for PC1 and PC2 show a significant effect of rearing environment and PC2 and PC4 a significant morph effect. Interaction effects were seen in PC3 and PC4. The total phenotypic variance for each of the principal components and that variance partitioned into morph, rearing environment and interaction effects are shown in Table 2. Rearing environment effects accounted for more of the phenotypic variance than morph effects in three of the four principal components. Interaction effects accounted for the greatest variance in only one of the four principal components (PC3). For PC1 and PC2, rearing environment accounted for the vast majority of the phenotypic variation explained (98% and 82%, respectively). Only for PC4 did the morph effect exceed the explained variance of the rearing-environment effect.

Table 2. Total phenotypic variance (V_p) and variance partitioned (as per cent of total) into morph effect (benthivorous/planktivorous, V_m), rearing environment effect (laboratory/wild, V_{re}) and interaction effects (V_i) on factor scores of principal components 1–4

	V_p	V_m (%)	V_{re} (%)	V_i (%)
PC1	45.72	1.03	98.45	0.52
PC2	34.28	15.26	81.94	2.80
PC3	25.41	0.43	7.87	91.70
PC4	46.75	82.74	0.30	16.96

Two-way (morph and rearing environment) analysis of variance of the residuals derived from the regression of the head anatomy feature on fork length and the two ratio measures (snout bluntness and curvature), showed highly significant effects of rearing environment (wild vs. laboratory) in six of the nine univariate characters examined ($P < 0.0001$). Only head depth at the operculum, head depth at the eye and snout bluntness failed to show a significant effect. (Table 3). Similarly, there were significant morph effects for six of the nine univariate characters examined (Table 3). Only eye diameter, jaw width and head depth at the operculum did not differ significantly between morphs.

Post hoc testing of residual means demonstrated several categories of effect. For six head anatomy characters, a rearing environment effect was present and in the same direction in both morphs. For five of these (eye diameter; jaw length; maxillary bone length; head length and snout curvature) (Fig. 2), length-corrected measures were larger in wild caught fish in both morphs; conversely length-corrected jaw width was smaller in wild fish.

Table 3. Two-way ANOVA on residuals from pooled regressions of charr head morphometric variable on fork length, using morph (benthivorous/planktivorous) and rearing environment (laboratory/wild) as effects

	Morph effect			Rearing environment effect			Interaction		
Morphometric variable[1]	*F*	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
LJL	7.41	1,111	0.008	130.4	1,111	<0.0001	21.8	1,111	<0.0001
HL	13.7	1,110	0.0003	30.2	1,110	<0.0001	0.02	1,110	0.88
JW	0.439	1,111	0.51	26.5	1,111	<0.0001	7.81	1,111	0.006
MB	7.56	1,111	0.007	42.9	1,111	<0.0001	5.60	1,111	0.02
HDE	11.13	1,111	0.001	0.88	1,111	0.35	8.19	1,111	0.005
ED	1.46	1,111	0.23	105.0	1,111	<0.0001	34.1	1,111	<0.000
HDO	2.38	1,111	0.12	1.18	1,111	0.28	0.01	1,111	0.90
SB	27.6	1,111	<0.0001	0.55	1,111	0.46	0.23	1,111	0.63
SC	20.3	1,111	<0.0001	66.7	1,111	<0.0001	17.3	1,111	<0.0001

[1]LJL, lower jaw length; HL, head length; JW, jaw width; MB, maxillary bone; HDE, head depth at eye; ED, eye diameter; HDO, head depth at operculum; SB, snout bluntness; SC, snout curvature.

We found three different kinds of morph effect. For maxillary bone length, morph differences were only found in wild fish, as a consequence of a greater amplifying effect in the planktivorous form. For head length and snout bluntness, we found morph effects that were independent of rearing environment, planktivorous fish having smaller length-corrected head length scores and larger length-corrected snout bluntness scores.

For three head characters – jaw length; head depth at the eye and snout curvature – there was a clear morph effect in laboratory-reared fish. Specifically, laboratory-reared benthivorous fish had longer jaws and less curved snouts and a greater head depth at the eye than laboratory-reared planktivorous fish. These differences were not found in the wild fish due to differential effects of the environment on the two morphs. For eye diameter, a morph difference in laboratory-reared fish (planktivorous fish having larger eyes) is reversed in wild fish due to a greatly enhanced amplifying effect in benthivorous fish.

The total phenotypic variance (derived from the two-way ANOVA) in the residuals of the univariate morphometric variables on body size was greatest in measures of jaw length (Table 4) followed by head length, jaw width and maxillary bone length. In six of the nine univariate variables (maxillary bone, eye diameter, jaw width, lower jaw length, snout curvature and head length) rearing environment accounted for >50% of the total phenotypic variation. For only three morphometric variables did the morph effect account for over half of the total phenotypic variation (head depth at the operculum, head depth at the eye and snout bluntness).

DISCUSSION

In this study we tested a prediction derived from the phenotypic plasticity model of divergence that for incipient species at an early stage of divergence, phenotypic variability is principally modulated through environmental regulation.

In the wild specimens examined here, the phenotypic variation in head anatomy between the two morphs of Arctic charr from Loch Rannoch is discrete, stable over at least 10 years and correlates with alternative feeding ecologies (Walker *et al.*, 1988; Dorucu *et al.*, 1995; Adams *et al.*, 1998); its functional role in foraging suggests it is under strong selection pressure (Adams & Huntingford, 2002b).

Here we have shown that although there is a clear underlying genetic effect influencing the phenotype expressed (i.e. a strong morph effect in the laboratory rearing environment), overall the effect of the rearing environment was considerably greater than the effect of morph (98% and 82% of expressed phenotype explained by environment in PC1 and PC2, respectively; see Table 2). For individual anatomical characteristics, the rearing environment explained more phenotypic variation than did morph in six out of nine head anatomy variables. Of the characteristics examined here, jaw length exhibited the greatest phenotypic variability. This character has been shown to have a strong functional significance for foraging in charr (Adams & Huntingford, 2002b). It is likely that the role of the environment in modulating head anatomy is underestimated in this study. Only two rearing environment conditions were examined, neither of which could be regarded as near the extremes of the range of environmental tolerance for this species.

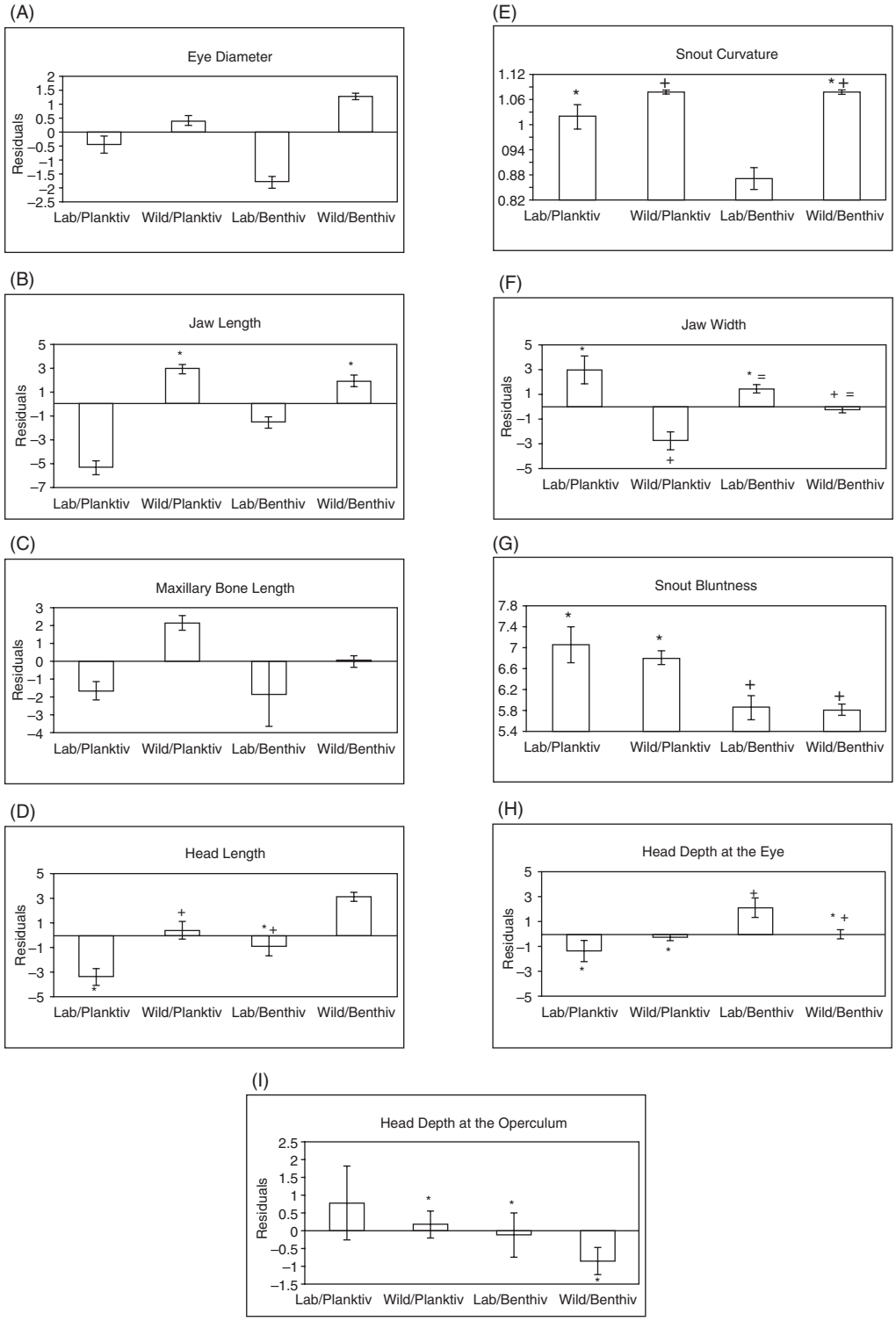

Figure 2. Mean and standard error of residuals of morphometric variables regressed on fork length for benthivorous and planktivorous origin Arctic charr reared in the laboratory and from the wild: (A) eye diameter, (B) jaw length, (C) maxillary bone length, (D) head length, (E) snout curvature, (F) jaw width, (G) snout bluntness, (H) head depth at the eye and (I) head depth at the operculum. (*, + identical symbols indicate no significant post hoc differences within morphometric variable.)

Table 4. Total phenotypic variance in residuals of univariate head morphometric variables regressed on fork length in charr, and total variance (V_p) partitioned (as per cent of total) into morph effect (benthivorous/planktivorous, V_m), rearing environment (laboratory/wild, V_{re}) and interaction effects (V_i)

Morphometric variable[1]	V_p	V_m (%)	V_{re} (%)	V_i (%)
LJL	1157.00	4.64	81.69	13.66
HL	599.80	31.26	68.69	0.05
JW	394.35	1.58	95.60	2.81
MB	281.80	13.48	76.47	10.04
HDE	180.50	55.07	4.38	40.55
ED	140.80	1.21	74.57	24.22
HDO	37.65	66.67	32.93	0.40
SB	34.65	97.26	1.93	0.81
SC	0.84	19.52	64.29	16.67

[1]LJL, lower jaw length; HL, head length; JW, jaw width; MB, maxillary bone; HDE, head depth at eye; ED, eye diameter; HDO, head depth at operculum; SB, snout bluntness; SC, snout curvature.

Thus, it would be reasonable to expect that, presented with a wider range of environmental conditions, the environmentally modulated phenotypic variation might be greater than that expressed here. However, the relative magnitude of the environmental effect on the expression of the discrete phenotypic variation supports the prediction of the phenotypic plasticity model of divergence: namely, that phenotypic plasticity is the principal mechanism creating alternative phenotypic modes upon which diversifying selection may act (West-Eberhard, 1989).

There are two principal mechanisms through which the environment may have influenced the variation in head anatomy shown here. First, environmental variation in head anatomy may be the result of differential mortality within morphs between wild and laboratory environments. If this mechanism is the route to the environmental effect, this requires very strong differential mortality in the wild populations of benthivorous and planktivorous Arctic charr in Loch Rannoch.

A second, but not mutually exclusive, explanation is that phenotypic variation in head anatomy is modulated within each individual's lifetime by environmental exposure, the most likely being through some developmental process such as the heterochronic growth of anatomical features (Meyer, 1987; Eiriksson, Skúlason & Snorrason, 1999). There is evidence that this latter route to head anatomy polymorphism can occur in charr from these morphs (Adams & Huntingford, 2002a; Adams, Woltering & Alexander, 2003).

One consequence of invoking phenotypic plasticity to drive the early stages of evolutionary divergence is that it allows alternative phenotypes to be expressed at a rate higher than would be predicted by mutation rates alone and thus may increase the speed of evolution (West-Eberhard, 1989, 1998; Kirschner & Gerhart, 1998). The discrete nature and functional significance of alternative head anatomy phenotypes examined here would appear to make this polymorphism particularly susceptible to rapid divergence by evolutionary forces (Smith & Skúlason, 1996).

Previous studies into the control of expressed phenotype in sympatric trophic morphs of Arctic charr have variously concluded that phenotype was wholly under environmental control (Nordeng, 1983), mostly under environmental control but with some expressed characteristics influenced by genetic effects (Hindar & Jonsson, 1993), or significantly influenced by genetic effects (Skúlason, Noakes & Snorrason, 1989; Klemetsen *et al*., 2002). One explanation for the differing emphasis on environmental vs. genetic control is that different polymorphisms are at different stages of divergence. However, although both environmental and genetic effects have been documented, no previous studies have attempted to quantify the relative contribution of each to the expression of phenotypes of known functional significance in charr (or in other species). Thus, reported differences between populations remain unclear.

We conclude that the phenotypic plasticity model presents the best explanation for the evolution of the sympatric polymorphism described here from Loch Rannoch. However, clear but small genetic effects on expressed phenotype show that evolution in this polymorphism has proceeded to the point where non-random breeding occurs in the population and that the gene-pool is now segregated.

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