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# Plastic resource polymorphism: effects of resource availability on Arctic char (*Salvelinus alpinus*) morphology

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Resource polymorphism has been suggested to be a platform for speciation. In some cases resource polymorphism depends on phenotypic plasticity but in other cases on genetic differences between morphotypes, which in turn has been suggested to be the ongoing development of a species pair. Here we study environmentally induced morphological differences in two age classes of Arctic char (*Salvelinus alpinus*) influencing char performance and diet in relation to resource availability. We found that structurally complex habitats with relatively lower zooplankton densities gave rise to individuals with a deeper body, and a downward positioned tip of the snout compared with individuals from structurally simple habitats with relatively higher zooplankton densities for both age classes. Environment also had an effect on foraging efficiency on zooplankton, with fish from structurally simple habitats had a higher foraging rate than fish from structurally complex habitats. Diet analyses showed that resource use in char mainly depends on the relative abundance of different resources. Therefore, to gain further understanding of resource polymorphism we suggest that future studies must include population dynamic feedbacks by the resources on the consumers.  *Biological Journal of the Linnean Society*, 2005, **85**, 341–351.

ADDITIONAL KEYWORDS: diet – foraging efficiency – geometric morphometrics – habitat – planktivory – resource densities.

## INTRODUCTION

Resource polymorphism, i.e. the presence of individuals within a species displaying different morphologies and utilizing different resources, is commonly found in many taxa (Robinson & Wilson, 1994; Skúlason & Smith, 1995). Resource polymorphism may result from either genetic differences (Harris *et al*., 1990; Smith, 1993; Skúlason *et al*., 1996; Bernatchez, Chouinard & Lu, 1999) or phenotypic plasticity (Meyer, 1987; Walls, Belanger & Blaustein, 1993; Mittelbach, Osenberg & Wainwright, 1999; Padilla, 2001). The existence of genetically diverged morphotypes foraging on different resources has been suggested to be the first step in the process of speciation (Smith & Skúlason, 1996). In this process, phenotypic plasticity may act as a first step in the development of resource polymorphism, which could then result in genetic divergence and finally speciation (West-Eberhard, 1989; Price, Qvarnström & Irwin, 2003).

Studies on resource polymorphism have used a number of approaches: (1) laboratory experiments in which individuals are reared on different resources followed by measurements on morphological differences and sometimes also measurements on foraging efficiency (Thompson, 1992; Padilla, 2001; Andersson, 2003); (2) field experiments in which individuals are reared in different habitats followed by measurements on morphological differences and sometimes also measurements on growth (Hjelm *et al*., 2001); and (3) sampling of individuals from different natural habitats in order to compare morphology and resource use or

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performance (Gosler, 1986; Robinson *et al*., 1993; Jónsson & Skúlason, 2000; Hjelm & Johansson, 2003). A common aim of these studies on resource polymorphism is the search for links between morphology and habitat use, diet and performance. Sometimes the link is straightforward and intuitively easy to understand, e.g. that gill raker spacing influences a planktivorous fish's foraging rate on zooplankton (Hjelm & Johansson, 2003) or that a bird's bill size affects its foraging rate on hard vs. soft seed (Smith, 1987). In other studies, the links between morphology and performance are more diffuse, although we find morphologically different groups, e.g. that planktivorous fish have more slender bodies than benthivorous fish (Webb, 1984) or that larger head and mandibles in grasshoppers increase their foraging capacity on hard plants (Thompson, 1992).

The purpose of our study was to examine the effects of habitat-specific resource densities on morphological variability in Arctic char (*Salvelinus alpinus*). The Arctic char is well known for displaying resource polymorphism in many lakes over its entire range of distribution (Ekman, 1912; Adams *et al*., 1998; Gíslason *et al*., 1999; Riget *et al*., 2000; Alekseyev *et al*., 2002; Klemetsen *et al*., 2002). Commonly found in such lakes is a littoral/benthic morph foraging on benthic macroinvertebrates and a pelagic morph foraging on zooplankton (Nilsson & Filipsson, 1971; Sandlund *et al*., 1992; Bjøru & Sandlund, 1995). In some lakes, the morphs have diverged genetically (Gíslason *et al*., 1999) and in others the differences between morphs seem to reflect phenotypic plasticity (Nordeng, 1983; Adams, Woltering & Alexander, 2003). Finally, Andersson (2003) showed in a laboratory study that young-of-the-year (henceforth YOY) char reared on different resources developed different morphologies and that the developed morphologies affected foraging efficiency.

In this study, we extended the laboratory experiment of Andersson (2003) to the level of field experiments by combining two pond experiments and one lake experiment in which we kept char in different habitats. As response variables we measured morphology, performance and diet of the char, but in addition we also monitored resource densities. In addition, we investigated the effect of time on the development of morphological traits and if morphological plasticity varied over ontogeny by using two different age classes of char.

## MATERIAL AND METHODS

Our study was based on three experiments (hereafter pond experiment 1, pond experiment 2 and lake experiment) in which we compared morphological divergence in Arctic char as a function of habitat type and resource availability. In all experiments, one group of fish was kept or caught in structurally complex habitat initially with high densities of macroinvertebrates compared with zooplankton densities. The other group of fish was kept in structurally simple habitats initially with lower densities of macroinvertebrates compared with zooplankton densities. In pond experiment 1 we measured foraging efficiency on zooplankton of fish from both habitats and resource densities in addition to morphology. In pond experiment 2 we measured diet and resource densities and in the lake experiment we measured diet and zooplankton densities in addition to morphology.

### POND EXPERIMENT 1

Two adjacent ponds (length 32 m, width 10.8 m and depth 0.9 m, separated by a 2-m-wide soil wall) in Umeå were divided into 12 enclosures by a net (mesh size 2 mm) of which half were used in our experiment. Owing to the prior presence of crayfish (*Astacus astacus*) in one pond, this pond had a very low density of vegetation, resulting in a habitat with a simple structure. The other pond had a dense submerged vegetation (*Potamogeton* sp.), resulting in a complex structure. On 6 July 2001, we stocked 50 hatchery-reared YOY char originating from wild-caught parents from Lake Torrön (63°49′13″N, 13°6′19″E). After 55 days, the fish were caught by electro fishing and seine netting. We measured resource densities at the start and the end of the experiment. Zooplankton was sampled by pulling a net (mesh size 100 μm, diameter 25 cm) for 5 m at an approximate speed of 0.5 m $s^{-1}$ in open water. All samples were preserved in Lugol's solution and analysed in the laboratory. The macroinvertebrate fauna was sampled by pulling a net (4.4 $dm^2$ mesh size of 0.5 mm) at an approximate speed of 0.5 m $s^{-1}$ in the upper 2 cm of the sediment layer. The samples were taken in two transects (5 m apart) and macroinvertebrates attached to vegetation were thus included where vegetation existed. The samples were preserved in ethanol and analysed in the laboratory.

From the fish sampling, eight individuals from each of the two ponds (three, three and two individuals from each enclosure) were transported to the laboratory and acclimatized in aquaria for 10 days during which they were fed live plankton collected from a small pond in Umeå. Thereafter, we performed attack rate estimates on each individual. During the foraging experiments, the fish were kept in 30-L aquaria which had the back and the sides covered with black plastics and a semi-transparent mirror and a grid in the front. A fluorescent tube (11 W) was positioned 50 cm above the bottom and all experiments were performed at 12 °C. To standardize hunger, all fish were deprived of food for 12 h before the start of the foraging experi-

ments. Before the foraging trials started, the fish was placed behind a non-transparent plastic sheet that created a holding chamber (2 L) and a performance arena (28 L). Thereafter, we poured the desired densities (1, 2, 4, 6, 8 and 16 $L^{-1}$) of zooplankton (*Daphnia magna* of size $1.2 \pm 0.04$ mm, mean ± 1 SE) from above, the water was gently stirred until the zooplankton was evenly distributed, and the plastic sheet was then removed. Measurements started when the char captured their first zooplankton and ended when the fifth capture was recorded. The capture rate measurements at the different densities were fitted to a Holling type II functional response:

$$C = aR/(1 + ahR)$$

where $C$ is capture rate, $a$ is attack rate, $R$ is zooplankton density and $h$ is handling time. From this function, individual attack rate and handling time were estimated

### Pond experiment 2

The experiment was performed in 2002 using the same ponds as for pond experiment 1. Each pond was divided into eight enclosures by a plastic wall with a small connection (area of 0.2 $m^2$) covered by a net (mesh size 3 mm). On 4 and 5 June, hatchery reared 1-year-old and YOY char from Lake Torrön were stocked in the ponds in different density combinations: (i) 50 YOY, (ii) 50 YOY and 20 1-year-old, (iii) 25 YOY and ten 1-year-old, and (iv) 20 1-year-old char. After 35 days, the fish were caught by seine netting, and deep frozen in water for morphological and diet analyses in the laboratory. Resource densities were sampled three times during the experiment (start, middle and end of the experiment). Zooplankton sampling was carried out in the same way as in pond experiment 1. Macroinvertebrates were sampled at the same dates as for zooplankton with a net ($290 \times 190$ mm, mesh size 0.5 mm) drawn 2 m along the shoreline horizontally with the edge of the net at the bottom substrate through the littoral vegetation. Samples were preserved in ethanol. In order to measure the total macroinvertebrate density at enclosure level, the area covered by vegetation was estimated and further used to calculate the average macroinvertebrate density for the whole enclosure.

### Lake experiment

On 4 July 2002, 24 individuals of 1-year-old char were caught in Ella traps and via electro fishing in the nearshore habitat and thereafter placed in four large circular enclosures (six individuals per enclosure) in the pelagic zone of a small subalpine lake, Lake Vuorejaure, in northern Sweden (see Byström *et al*., 2004, for details). The enclosures (diameter 1.6 m and depth 4 m) were constructed of net (mesh size 3 mm), which allowed zooplankton to pass through freely. Owing to the positioning of the enclosures, the fish had no access to benthic macroinvertebrates. During the experiment, zooplankton densities in the pelagic and the littoral zones were sampled in the lake three times (start, middle and end of the experiment) and two times in the enclosures (middle and end of the experiment). The pelagic samples were taken by pulling a 100-μm-mesh net (diameter 25 cm) vertically at an approximate speed of 0.5 m $s^{-1}$ from 4 m depth to the surface (in the enclosures from 3 m depth). Littoral samples were taken with a net (mesh size 100 μm, diameter 25 cm) drawn 12 m parallel to the shore at an approximate speed of 0.5 m $s^{-1}$. Zooplankton samples were preserved in Lugol's solution. At the same time as the sampling of resources, ten 1-year-old char were caught by electro fishing in the littoral zone and frozen for later diet analyses. After 57 days, the enclosures were emptied and all fish were killed and frozen in water for later diet and morphological analyses in the laboratory. At the same time, 20 individuals caught by electro fishing in the littoral zone of the lake were deep frozen for later diet and morphological analyses.

### Laboratory analyses

Analyses of resource densities and morphology for all experiments together with diet analyses in pond experiment 2 and the lake experiment were performed in the laboratory following the procedures below.

#### *Resources*

Zooplankton was classified to species level, counted and the lengths of 15 individuals (or all if fewer were found) of each species from each sample were measured in an inverted microscope. Lengths were transformed to dry biomass using regressions relating body length to dry weight (Dumont, Van de Velde & Dumont, 1975; Botrell *et al*., 1976). The macroinvertebrate samples were stained with Rose Bengal, classified to family level, counted and the lengths of all individuals of each group from each sample were measured. Lengths were transformed to dry biomass by regressions relating body length to dry weights using our own length–weight relationships (see Persson *et al*., 1996).

#### *Diet*

Diet of char at the end of pond experiment 2 was estimated by analysing stomach contents of ten individuals (or all if fewer were available) from each size class and enclosure. In the lake experiment, stomach content of all char was analysed. Prey items in stomachs were identified to suborder, family or genus level. If possible, ten prey of each category were measured for

length. Lengths of prey were transformed to dry weights by using weight–length relationships (zooplankton: Dumont *et al.*, 1975; Botrell *et al.*, 1976; macroinvertebrates: Persson *et al.*, 1996).

*Morphology*

To analyse the morphology of the fish we used geometric morphometrics, a method based on landmarks (Marcus *et al.*, 1996; Hjelm *et al.*, 2001; Rüber & Adams, 2001). The advantages of using geometric morphometrics over traditional methods (i.e. measurements of distances between landmarks tested with multivariate statistics) are that geometric morphometrics are more effective in capturing information regarding the shape of an individual and that morphological differences are possible to visualize, which makes it possible to compare and interpret morphologies of different groups more easily. In addition, geometric morphometrics also provide more powerful statistical analyses of differences and relationships between the morphology of groups of individuals and morphologies vs. other parameters (e.g. environmental or taxonomic parameters) (Rohlf & Marcus, 1993).

In the laboratory, the fish were thawed and total length was measured to the nearest millimetre. Thereafter, each individual (538 in total) was photographed with a digital camera (Minolta Dimage 7). Twelve landmarks (Fig. 1) were recorded from the images by using TPSDigit (Rohlf, 2001a) followed by calculations of the individual's centroid size (Bookstein, 1991, p. 93). To explore differences between treatments (structurally complex habitat vs. structurally simple habitat) we used the following procedure in each experiment. All individuals from the experiments (pond experiment 1, 89 individuals; pond experiment 2, 230 individuals; lake experiment, 45 individuals) were superimposed by using generalized procrustes superimposition, which scales and rotates all the individuals so that they line up as closely as possible, resulting in an average morphology in each experiment (consensus shape) (Rüber & Adams, 2001). We thereafter generated shape variables, so-called partial warp scores, which are decomposed descriptions of the deviation of one specimen relative to the consensus shape. Differences in overall morphology between habitats in each experiment were thereafter tested by a MANCOVA with the partial warps along with uniform components as dependent factors and centroid size as the covariate (Bookstein, 1996).

In order to compare morphologies between the different experiments, we used the average morphology for each enclosure in the two pond experiments and the average morphology of the fish from each enclosure and four randomly produced littoral groups in the lake experiment. In addition, we also separated the two year classes in pond experiment 2 and treated them as replicates although they sometimes coexisted in some enclosures. Because of the small number of replicates, we were not able to perform tests on the effects on morphology by different age classes living allopatrically vs. sympatrically. The chosen level of replication resulted in six samples (three from structurally complex habitat and three from structurally simple habitat) from pond experiment 1, 24 samples (12 from structurally complex habitat and 12 from structurally simple habitat) from pond experiment 2, and eight samples (four from structurally complex habitat and four from structurally simple habitat) from the lake experiment. Average morphology and partial warp scores were computed as discussed above. Thereafter, we performed a principal component analysis on the partial warps (i.e. relative warp analyses with $\alpha = 0$) (Rohlf, 1993). Because of the low sample size we approximated the overall morphology by using the first eight relative warps, which explained more than 95% of the morphological variation. Differences in overall morphology between structurally complex and simple habitats were thereafter tested by a MANCOVA with the first eight relative warps as dependent factors and centroid size as the covariate (Bookstein, 1996). The trends in morphology along the first four relative warps were thereafter interpreted by studying the corresponding deformation grids. All morphological analyses were performed in TPSRelw v.1.29 (Rohlf, 2001b).

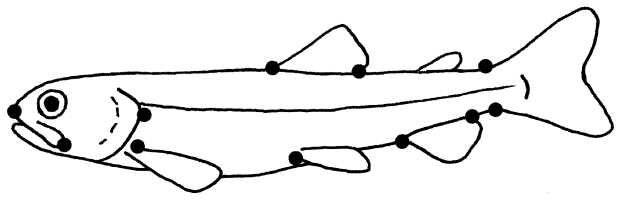

**Figure 1.** The 12 landmarks used in the morphological analyses. Note that one landmark is positioned in the centre of the eye.

### Statistical analyses

All statistical analyses were performed in SPSS 11.0 and all estimates were Ln-transformed when performing analyses of variance, except for morphology analyses and when testing proportions of prey types in diet. In the latter case we arcsin-transformed all data before performing the ANOVA.

## RESULTS

### Resources

In pond experiment 1, the density of macroinvertebrate fauna was higher in the structurally com-

plex habitat than in the structurally simple habitat both at the start and at the end of the experiment (start, $t$-test, $t = 3.31$, $P = 0.03$; end, $t = 2.91$, $P = 0.04$) (Fig. 2A). We found no difference between treatments in zooplankton densities at the start of the experiment ($t$-test, $t = 0.34$, $P = 0.77$) (Fig. 2B). Zooplankton densities decreased in both treatments over time. Based on the prediction that char in the structurally simple habitat would decrease the zooplankton to lower densities than in the structurally complex habitats owing to the lack of alternative resources, we used a one-tailed $t$-test and the zooplankton densities were thus higher in the structurally complex habitat than in the structurally simple habitat at the end of the experiment (one tailed $t$-test, $t = 2.24$, $P = 0.044$) (Fig. 2B).

In pond experiment 2, macroinvertebrate densities increased over time in both habitats and was higher in the structurally complex habitat than in the structurally simple habitats (repeated-measures ANOVA sphericity assumed; time $F_{2,28} = 20.0$, $P < 0.001$; time*habitat, $F_{2,28} = 0.10$, $P = 0.91$; habitat, $F_{1,14} = 151.3$ $P < 0.001$) (Fig. 3A). For zooplankton, one replicate in the structurally simple habitat differed more than 20-fold from the average in that treatment, which led us to consider that replicate as an outlier (Fig. 3B). Excluding this outlier, we found that zooplankton densities increased over time and that the increase was higher in the structurally complex habitat (repeated-measures ANOVA using Greenhouse–Geisser correction for degrees of freedom due to heterosphericity; time, $F_{1.4,17.7} = 7.2$, $P = 0.01$; time*habitat, $F_{1.4,17.7} = 4.5$, $P = 0.037$; habitat, $F_{1,13} = 2.6$, $P = 0.13$) (Fig. 3B).

In the lake experiment, zooplankton densities differed between habitats and enclosures at the two last sampling occasions (one-way ANOVAs; at time 2, $F_{2,7} = 27.5$, $P < 0.001$; at time 3, $F_{2,7} = 202.3$, $P < 0.001$) (Fig. 4). Zooplankton densities were high-

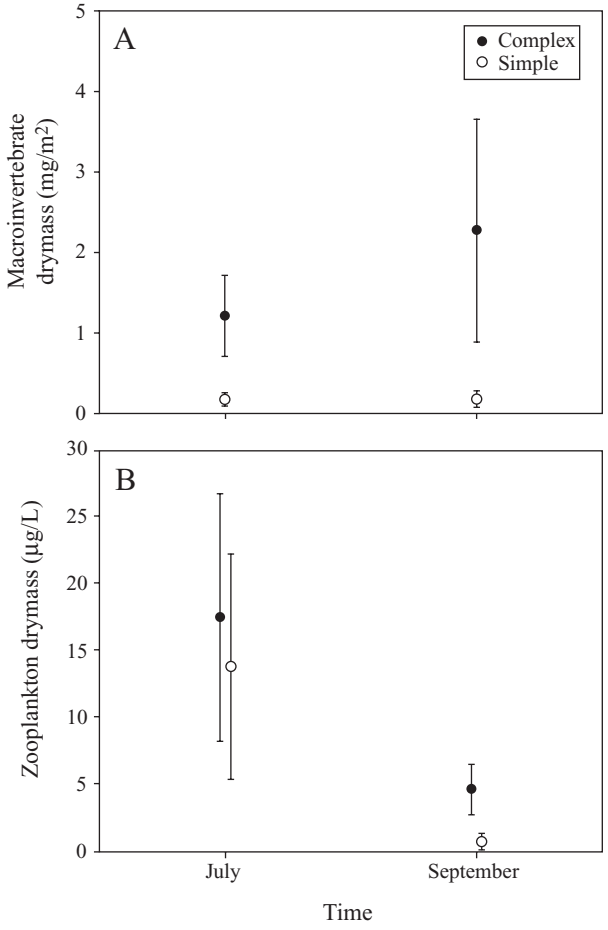


**Figure 2.** The average resource densities in pond experiment 1. Open symbols represent structurally simple habitat, closed circles structurally complex habitat, and error bars SE. A, macroinvertebrates; B, zooplankton.

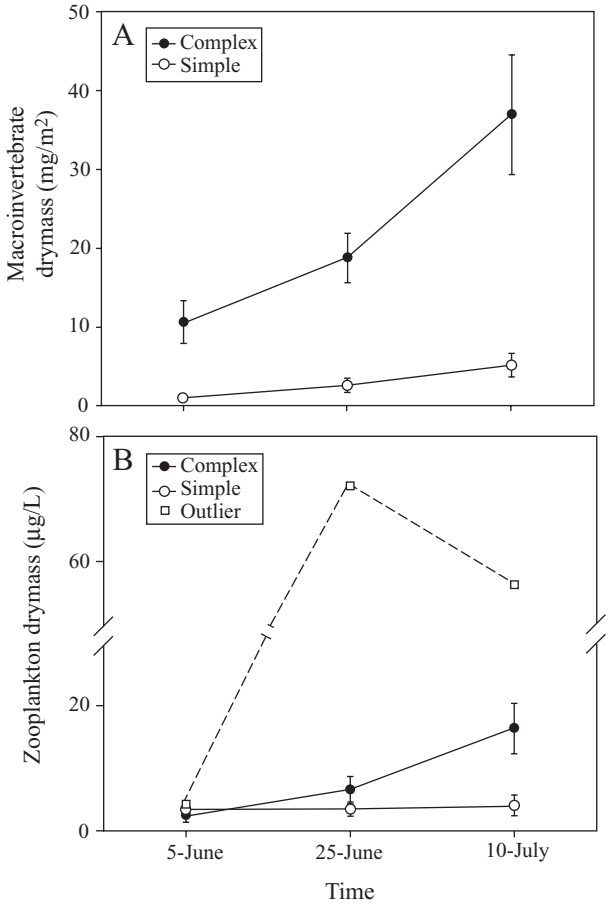


**Figure 3.** The average resource densities in pond experiment 2. Open symbols represent structurally simple habitat, closed circles structurally complex habitat, and error bars SE. A, macroinvertebrates; B, zooplankton.

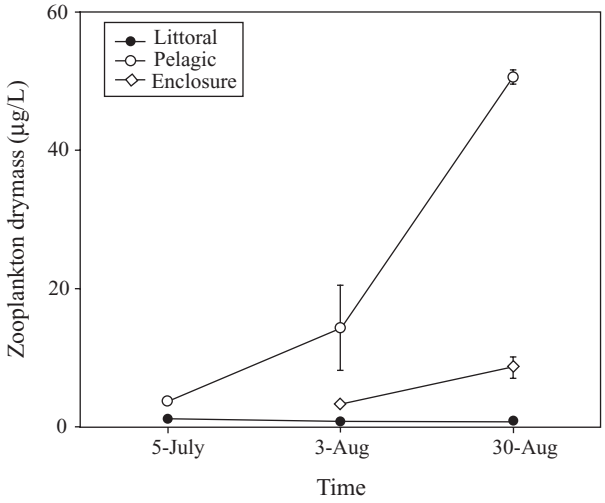


**Figure 4.** Zooplankton densities in the lake experiment. Open symbols represent the pelagic habitat, closed symbols the littoral habitat and diamonds inside the enclosures.

**Table 1.** Average size (total length in mm) ± 1 SD of arctic char in the different habitats or treatments at the end of the three experiments

| | Habitat/treatment | |
|---|---|---|
| Experiment | Simple habitat/ pelagic | Complex habitat/ littoral |
| Pond experiment 1 | 69.3 ± 6.1 | 72.6 ± 6.2 |
| Pond experiment 2 | | |
| YOY | 52.9 ± 1.7 | 55.6 ± 2.6 |
| 1-year old | 95.6 ± 3.0 | 97.8 ± 2.7 |
| Lake experiment | 91.0 ± 5.2 | 93.6 ± 5.8 |

est in the pelagic, lowest in the littoral zone and intermediate in the enclosures at both sampling occasions (Tukey's *post-hoc* test; time 1, pelagic vs. enclosure, $P = 0.019$, enclosure vs. littoral, $P = 0.009$; time 2, pelagic vs. enclosure, $P < 0.001$, enclosure vs. littoral, $P < 0.001$).

## MORPHOLOGY

On average, fish from structurally simple habitat were smaller than fish from structurally complex habitat (Table 1). Individuals from the two different pond types differed in morphology in both pond experiments whereas no difference in morphology between treatments in the lake experiment was found (Table 2). Taking all experiments into account and using the average morphology from each pond enclosure (and age-class in pond experiment 2) and lake enclosures as samples, we found a difference between fish from structurally simple habitat compared with fish from structurally complex habitat. Thus independent of the approach, the fish developed consistent differences in morphology as a result of habitat type. This latter result shows that, although not significant, the morphologies in the lake experiments developed in similar directions but could not be statistically confirmed because of low sample size. To interpret the most important morphological differences we present the first four relative warps, which explained 83% of the morphological variation (RW1–RW4; 39.7, 21.4, 16.6 and 5.4%, respectively) (Fig. 5). Considering RW1 and RW2, fish from structurally simple habitats developed a slender body, the tip of the snout directed more downward, and the pelvic fin being positioned more anterior compared with fish from the structurally complex habitat (Fig. 5A). RW3 and RW4 mainly describe the change from deep-bodied fish when going from structurally complex habitat to slender fish from the structurally simple habitat (Fig. 5B).

**Table 2.** MANCOVAs on morphology in each experiment and the overall morphology with all experiments included

| Experiment | Wilk's λ | *F*-value | *P*-value |
|---|---|---|---|
| Pond experiment 1 | | | |
| Size | 0.43 | $F_{20,67} = 6{,}35$ | < 0.001 |
| Habitat | 0.52 | $F_{20,67} = 3.08$ | < 0.001 |
| Pond experiment 2 | | | |
| Size | 0.16 | $F_{20,382} = 103.2$ | < 0.001 |
| Habitat | 0.72 | $F_{20,382} = 7.42$ | < 0.001 |
| Lake experiment | | | |
| Size | 0.62 | $F_{20,23} = 1.87$ | 0.08 |
| Habitat | 0.45 | $F_{20,23} = 1.38$ | 0.23 |
| Overall | | | |
| Size | 0.157 | $F_{8,28} = 18.8$ | < 0.001 |
| Habitat | 0.461 | $F_{8.28} = 4.10$ | 0.002 |

## PERFORMANCE AND DIET

We found that individuals from the structurally simple habitat had a higher attack rate ($L\ s^{-1}$) on zooplankton than individuals from structurally complex habitat (structurally simple habitats, 0.30 ± 0.04; structurally complex habitat, 0.13 ± 0.05, mean ± 1 SE) (*t*-test, $t = 3.53$, $P = 0.004$) (Fig. 6). We found no differences in handling time (s per prey item) between individuals from the structurally simple habitat and individuals from structurally complex habitat (structurally simple habitats, 0.73 ± 0.14; structurally complex habitat, 1.31 ± 0.50, mean ± 1 SE) (*t*-test, $t = 0.61$, $P = 0.55$).

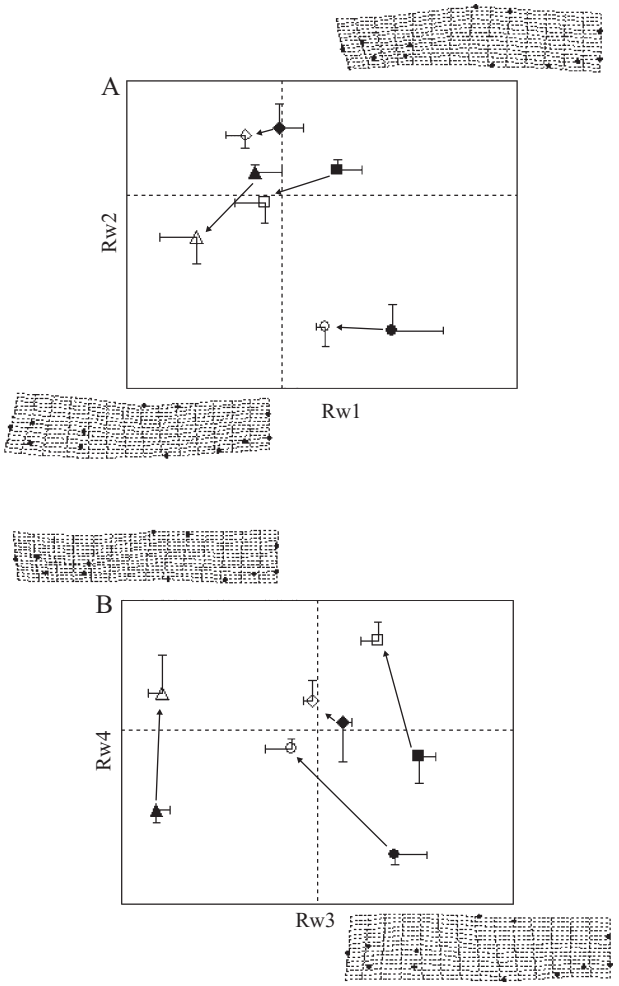


**Figure 5.** Residuals on size for relative warp scores from each experiment. The deformation grids correspond to the morphological changes along the diagonal. Each score is the mean of all replicates in that treatment and error bars represent SE. Open symbols represent habitats of low structural complexity and closed symbols habitats of high structural complexity. Diamonds represent YOY from pond experiment 2, squares 1-year-old char from pond experiment 2, circles pond experiment 1, and triangles the lake experiment.

The diet analyses in pond experiment 2 showed that zooplankton constituted a larger fraction of consumed prey in the structurally complex habitat than in the structurally simple habitat and that zooplankton constituted a larger fraction of consumed prey in YOY char than in 1-year-old char (two-way ANOVA, habitat, $F_{1,20} = 6.96$, $P = 0.016$; age, $F_{1,20} = 20.0$, $P < 0.001$; habitat*age $F_{1,20} = 0.72$, $P = 0$)(Fig. 7). Diet analyses in the lake experiment showed that zooplankton was the main resource in the pelagic enclosures and that benthic prey were the main resource for free-living char (Fig. 8).

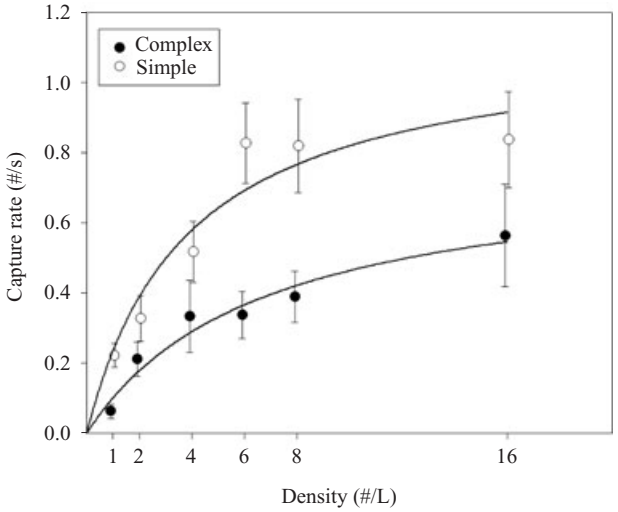


**Figure 6.** The average capture rates at different zooplankton densities where error bars represent SE. Open symbols represent habitat of low structural complexity and closed symbols habitat of high structural complexity. The curve represents fitted average Holling type II functional response.

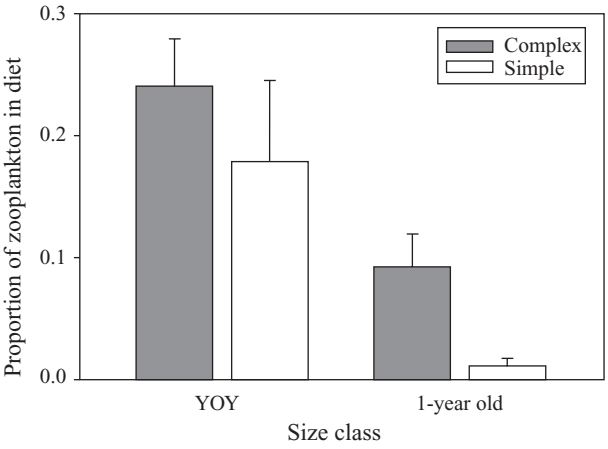


**Figure 7.** Proportion of zooplankton in the diet in YOY and 1-year-old char from each habitat. Error bars represent SE.

## DISCUSSION

Initially, zooplankton densities were similar in both habitats in all experiments, whereas macroinvertebrate densities were higher in the structurally complex habitat. These differences in resources meant that char was more dependent on zooplankton as a resource in the structurally simple habitat than in the structurally complex habitat. This, in turn, paralleled the development in morphological differences between fish from the two habitats. The fish from the structur-

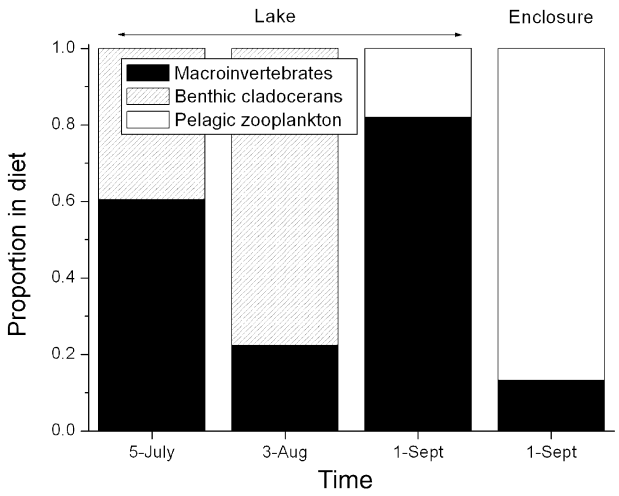


**Figure 8.** Proportion of different food items in the lake experiment. Three occasions in the littoral zone and one occasion in the enclosures are shown.

ally complex habitat, which was relatively rich in macroinvertebrates, developed deeper bodies and a downward positioned tip of the snout compared with fish from structurally simple habitat, which was relatively rich in zooplankton. Deeper bodies have been suggested to characterize a benthivorous foraging type (Hjelm *et al*., 2001) whereas a slender body has been suggested to characterize a planktivorous foraging type (Webb, 1984). We also found that the pelvic fin was positioned more anteriorly in fish from the structurally complex habitat, which is in accordance with Andersson (2003). Correspondingly, a relatively higher availability of one prey type has been shown to induce a morphology adapted for that prey (Gosler, 1986; Meyer, 1990; Mittelbach *et al*., 1999). Interestingly, the morphological changes developed quite rapidly (30 days in pond experiment 2). These rapid changes in morphology are among the fastest recorded for fish in relation to the species' lifetime (see Meyer, 1987; Robinson & Wilson, 1995; Day & McPhail, 1996; Mittelbach *et al*., 1999; Hjelm *et al*., 2001). We cannot determine whether this reflects a unique trait of Arctic char or whether this is merely a consequence of most experiments being conducted in such a way that morphological changes are given sufficient time to develop and that morphological differences might have occurred earlier without having been measured (but see Day & McPhail, 1996).

We also found that fish of different initial size (age) developed similar morphologies in response to the environment. This result can be compared with those of Meyer (1987), who showed that morphological differences can result from heterochrony and that they can disappear as a result of environmental conditions such as changes in resource availability when fish age. It has also been proposed that resource polymorphism in Arctic char is an effect of heterochrony and that the maintenance of morphological differences depends on time and location of spawning for different morphs, resulting in different resource use (Skúlason, Noakes & Snorrason, 1989). Although we only studied YOY and 1-year-old char, our results show that resource-induced morphological changes in Arctic char are not constrained to an early stage, and that morphological trajectories may be altered later during an individual's life.

We found that fish from the structurally simple habitat had a substantially higher attack rate on zooplankton than fish from the structurally complex habitat. This result is in accordance with laboratory studies by Andersson (2003), who found that char fed on zooplankton had a higher attack rate on zooplankton than fish fed a mixture of zooplankton and chironomides, which, in turn, had a higher attack rate than fish only fed chironomides, suggesting that variation in attack rate on zooplankton is a function of the encounter rate of zooplankton. Our study shows that the results of Andersson (2003) are valid also at larger spatial scales where both prey types are present and that the char's foraging rate on zooplankton is a function of the relative availability of zooplankton also in more natural systems.

Searching for a trade-off, we did not find any differences between fish from the different sections when foraging on chironomides (unpublished result because of few replicates from mortality and hence low power). However, the same result was found by Andersson (2003), which suggests that adaptations for planktivory do not incur any (or only very small) costs for foraging efficiency on macroinvertebrates. This result seems to be quite general also for other species (Robinson *et al*., 1993; Schluter, 1995; Robinson, 2000). In addition, corresponding field studies have shown that macroinvertebrates are found in the diet of planktivorous morphs to a much larger extent than zooplankton are found in the diet of benthic morphs (Schluter & McPhail, 1992; Sandlund *et al*., 1992; Robinson *et al*., 1993). Together, these results suggest that the profitability of the zooplankton resource is the driving mechanism behind the development of benthivore–planktivore pairs but that a complete reliance on the zooplankton resource is less likely, which results in the asymmetry in performance often found. Supporting this hypothesis is the fact that the species in the studies above are all benthivores when only one morph exists in a lake (McPhail, 1993; Wainwright, Osenberg & Mittelbach, 1991; Robinson & Parsons, 2002), and that a complete reliance on zooplankton can be fatal as the zooplankton resources available to fish predation often respond strongly negatively in the

presence of fish (Brooks & Dodson, 1965). In accordance, the diet analyses in this study show that only when confined to the pelagic zone (enclosures in the lake) did zooplankton become the dominant resource for char. We therefore propose that morphological adaptations can be a route to reduce competition for macroinvertebrates by expanding the niche under conditions of an increased profitability of an alternative resource (e.g. zooplankton), and that rapid plastic adaptations allow utilization of the zooplankton resource at densities that are unprofitable for individuals not adapted to forage on zooplankton. Planktivore morphs may thereafter switch back to benthic resources during periods of low zooplankton densities without a high cost. Correspondingly, use of the pelagic resource has been shown to be density dependent in young Arctic char (Klemetsen & Dahl-Hansen, 1995; Byström *et al*., 2004). At the end of the pond experiments, zooplankton densities were generally higher in the structurally complex habitat than in the structurally simple habitat. However, we cannot conclude whether these differences between habitats are due to habitat-specific zooplankton production or to different predation pressure because of the higher foraging rate on zooplankton by char in the structurally simple habitats. It has been shown that physical structure itself can reduce the foraging efficiency on zooplankton (Winfield, 1986; Persson, 1991) and hence the higher zooplankton densities in the structurally complex habitat may just be an effect of a low efficiency of the char in the structurally complex habitats.

In contrast to our expectations, char from the structurally complex habitat in pond experiment 2 included zooplankton in their diet to a larger extent than char from the structurally simple habitat at the end of the experiment, despite their benthic morphology and lower efficiency on zooplankton. We believe that this is most likely an effect of the higher densities of zooplankton in the structurally complex habitat than in the structurally simple habitat at the end of the experiment. With available data, we cannot conclusively show that char fed more on zooplankton in the structurally simple habitat during the experiment. However, the reliance on the zooplankton resource by char in the structurally simple habitat should have been higher in the structurally simple habitat than in the structurally complex habitat due to the low densities of the alternative resource (macroinvertebrates). The strongest support for the char having utilized zooplankton as a resource to a larger extent in the structurally simple habitat is the differences in foraging efficiency of the char from different habitats. Taken together, these results indicate that the utilization and adaptation to one resource may lead to a reversed selection as a feedback of the decreased density of that resource. The result in such a case would be fluctuating frequencies of certain morphologies over time. Correspondingly, it has been shown that the gillraker spacing in roach (*Rutilus rutilus*) changes over time as a response to fluctuating zooplankton densities (Hjelm & Johansson, 2003).

Based on the results from this study, we suggest that to gain further insight to the mechanisms behind the development of resource polymorphism, future studies need to take into account the effect of the consumer on its resources. Although there are several examples of stable resource polymorphism, the absence of discrete morphs in systems even of a single or few species seems to be more common. We therefore suggest that the absence of stable resource polymorphism may be an effect of an increased selectivity for one prey, potentially followed by morphological adaptations, leading to a decrease of that resource and resulting in an increased use of the alternative resources. By using alternative resources the forager would then be subjected to reversed selection preventing further divergence and maintenance of two discrete morphs.

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## REFERENCES

**Adams CE, Frazer D, Huntingford FA, Greer RB, Askew CM, Walker AF. 1998.** Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. *Journal of Fish Biology* **52:** 1259–1271.

**Adams CE, Woltering C, Alexander G. 2003.** Epigenetic regulation of trophic morphology through feeding behaviour in Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society* **78:** 43–49.

**Alekseyev SS, Samusenok VP, Matveev AN, Pichugin MY. 2002.** Diversification, sympatric speciation, and trophic polymorphism of Arctic char, *Salvelinus alpinus* complex, in Transbaikalia. *Environmental Biology of Fishes* **64:** 97–114.

**Andersson J. 2003.** Effects of diet-induced resource polymorphism on performance in Arctic char (*Salvelinus alpinus*). *Evolutionary Ecology Research* **5:** 213–228.

**Bernatchez L, Chouinard A, Lu G. 1999.** Integrating molecular genetics and ecology in studies of adaptive radiation:

whitefish, *Coregonus* sp., as a case study. *Biological Journal of the Linnean Society* **68:** 173–194.

**Bjøru B, Sandlund OT. 1995.** Differences in morphology and ecology within a stunted Arctic char population. *Nordic Journal of Freshwater Research* **71:** 163–172.

**Bookstein FL. 1991.** *Morphometric tools for landmark data*. Cambridge: Cambridge University Press.

**Bookstein FL. 1996.** Combining the tools of geometric morphometrics. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, eds. *Advances in morphometrics.* New York: Plenum Press, 131–151.

**Botrell HH, Duncan A, Gliwicz ZM, Grygierek E, Herzig A, Hillbricht-Illkowska A, Kurasawa H, Larsson P, Weglenska T. 1976.** A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* **24:** 419–456.

**Brooks JL, Dodson SI. 1965.** Predation, body size, and composition of plankton. *Science* **150:** 28–35.

**Byström P, Andersson J, Persson L, De Roos AM. 2004.** Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. *Oikos* **104:** 109–121.

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

**Dumont HJ, Van de Velde I, Dumont S. 1975.** The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* **19:** 75–97.

**Ekman S. 1912.** Om Torne träsks röding, sjöns natyrförhållande och dess fiske. *Vetenskapliga och praktiska undersökningar i Lappland* 1–54.

**Gíslason D, Ferguson MM, Skúlason S, Snorrason SS. 1999.** Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic charr. *Canadian Journal of Fisheries and Aquatic Sciences* **56:** 2229–2234.

**Gosler AG. 1986.** Pattern and process in the bill morphology of the Great Tit *Parus major*. *Ibis* **129:** 451–476.

**Harris RN, Semlitsch RD, Wilbur HM, Fauth JE. 1990.** Local variation in the genetic basis of paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution* **44:** 1588–1603.

**Hjelm J, Johansson F. 2003.** Temporal variation in feeding morphology and size-structured population dynamics in fishes. *Proceedings of the Royal Society* **270:** 1407–1412.

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

**Jónsson B, Skúlason S. 2000.** Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlídarvatn, a shallow Icelandic lake. *Biological Journal of the Linnean Society* **69:** 55–74.

**Klemetsen A, Dahl-Hansen GAP. 1995.** Disruption of the ontogenetic habitat shift pattern in a population of Arctic char, *Salvelinus alpinus* as a result of intensive fishing. *Nordic Journal of Freshwater Research* **71:** 324–332.

**Klemetsen A, Elliott JM, Knudsen R, Sörensen P. 2002.** Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. *Journal of Fish Biology* **60:** 933–950.

**Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE. 1996.** *Advances in morphometrics*. New York: Plenum Press.

**McPhail JD. 1993.** Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of the species pairs. *Canadian Journal of Zoology* **71:** 515–523.

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

**Meyer A. 1990.** Ecological and evolutionary consequenses of the trophic polymorphism in *Cichlasoma citrinellum* (Pisces: Cichlidae). *Biological Journal of the Linnean Society* **39:** 279–299.

**Mittelbach GG, Osenberg CW, Wainwright PC. 1999.** Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? *Evolutionary Ecology Research* **1:** 111–128.

**Nilsson N-A, Filipsson O. 1971.** Characteristics of two discrete populations of Arctic char (*Salvelinus alpinus* L.) in a north Swedish lake. *Report from Institute of Freshwater Research in Drottningholm* **51:** 90–108.

**Nordeng H. 1983.** Solution to the 'char problem' based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40:** 1372–1387.

**Padilla DK. 2001.** Food and environmental cues trigger an inducible offence. *Evolutionary Ecology Research* **3:** 15–25.

**Persson L. 1991.** Behavioral response to predators reverses the outcome of competition between prey species. *Behavioral Ecology and Sociobiology* **28:** 101–105.

**Persson L, Andersson J, Wahlström E, Eklöv P. 1996.** Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* **77:** 900–911.

**Price TD, Qvarnström A, Irwin DE. 2003.** The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society* **270:** 1433–1440.

**Riget FF, Jeppesen E, Landkildehus F, Lauridsen TL, Geertz-Hansen P, Christoffersen K, Sparholt H. 2000.** Landlocked Arctic charr (*Salvelinus alpinus*) population structure and lake morphometry in Greenland – is there a connection. *Polar Biology* **23:** 550–558.

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

**Robinson BW, Parsons KJ. 2002.** Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **59:** 1819–1833.

**Robinson BW, Wilson DS. 1994.** Character release and displacement in fishes: a neglected literature. *American Naturalist* **144:** 596–627.

**Robinson BW, Wilson DS. 1995.** Experimentally induced morhological diversity in Trinidan Guppies (*Poecilia reticulata*). *Copeia* **2:** 294–305.

**Robinson BW, Wilson DS, Margosian AS, Lotito PT. 1993.** Ecological differentiation of pumkinseed sunfish in

lakes without bluegill sunfish. *Evolutionary Ecology* **7:** 451–464.

**Rohlf FJ. 1993.** Relative warp analysis and an example of its application to mosquito wings. In: Marcus LF, Bello E, Garcia-Valdecasas A, eds. *Contributions to morphometrics.* Madrid: Consejo Superior de Investigacíones Científicas, 133–159.

**Rohlf FJ. 2001a.** tps DIGIT v.1.31. Freeware at http://life.bio.sunysb.edu/morph/

**Rohlf FJ. 2001b.** tpsRELW v.1.29. Freeware at http://life.bio.sunysb.edu/morph/

**Rohlf FJ, Marcus LF. 1993.** A revolution in morphometrics. *Trends in Ecology and Evolution* **8:** 129–132.

**Rüber L, Adams DC. 2001.** Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *Journal of Evolutionary Biology* **14:** 325–332.

**Sandlund OT, Gunnarsson K, Jónasson PM, Jonsson B, Lindem T, Magnússon KP, Malmquist HJ, Sigurjónsdóttir H, Skúlason S, Snorrason SS. 1992.** The Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Oikos* **64:** 305–351.

**Schluter D. 1995.** Adaptive radiation in sticklebacks: tradeoffs in feeding performance and growth. *Ecology* **76:** 82–90.

**Schluter D, McPhail JD. 1992.** Ecological character displacement and speciation in sticklebacks. *American Naturalist* **140:** 85–108.

**Skúlason S, Noakes DLG, Snorrason SS. 1989.** Ontogeny of trophic morphology in four sympatric morphs of Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biological Journal of the Linnean Society* **38:** 281–301.

**Skúlason S, Smith TB. 1995.** Resource polymorphism in vertebrates. *Trends in Ecology and Evolution* **10:** 366–370.

**Skúlason S, Snorrason SS, Noakes DLG, Ferguson MM. 1996.** Genetic basis of the life history variations among sympatric morphs of Arctic char; *Salvelinus alpinus*. *Canadian Journal of Fisheries and Aquatic Sciences* **53:** 1807–1813.

**Smith TB. 1987.** Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature* **329:** 717–719.

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

**Smith TB, Skúlason S. 1996.** Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* **27:** 111–133.

**Thompson DB. 1992.** Consumption rates and evolution of diet-induced plasticity in the head morphology of *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Oecologia* **89:** 204–213.

**Wainwright PC, Osenberg CW, Mittelbach GG. 1991.** Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. *Functional Ecology* **5:** 40–55.

**Walls SC, Belanger SS, Blaustein AR. 1993.** Morphological variation in a larval salamander: dietary induction of plasticity in headshape. *Oecologia* **96:** 162–168.

**Webb PW. 1984.** Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* **2469:** 107–120.

**West-Eberhard MJ. 1989.** Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20:** 249–278.

**Winfield IJ. 1986.** The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Ruilus rutilus*, rudd, *Scardinius erythrophtalmus*, and perch *Perca fluviatilis*. *Journal of Fish Biology* **29:** 37–48.