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Effects of diet-induced resource polymorphism on performance in arctic charr (*Salvelinus alpinus*)

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ABSTRACT

Resource polymorphism is found in many taxa and its presence can be a result of both genetic factors and phenotypic plasticity. The aim of this study was to estimate the effect of diet-induced resource polymorphism on individual performance in Arctic char (*Salvelinus alpinus*). I reared 90 young-of-the-year individuals separately on one of three different diets: a pure zooplankton diet, a pure chironomid diet and a mixture of zooplankton and chironomids. Attack rate and swimming speed were estimated for 10 individuals from each treatment group at the start and the end of the experiment. Morphologies were measured for all 90 individuals at the end of the experiment. I found effects of the treatments on both morphology and performance, and morphology and performance variables correlated at the individual level, suggesting that the morphological changes were adaptive. The zooplankton feeders had the highest attack rate and swimming speed when foraging on zooplankton, followed by the mixed-diet feeders and the chironomid feeders. In contrast, there were no differences in attack rate between treatment groups when foraging on chironomids, although the zooplankton feeders had a higher swimming speed regardless of type of prey. The results suggest that diet itself is not enough to induce different specialists and that other factors, such as population dynamics or predation risk, may act as substrates for the development of resource polymorphism in Arctic charr.

Keywords: competition, geometric morphometrics, performance, phenotypic plasticity, resource polymorphism, *Salvelinus alpinus*, trade-off.

INTRODUCTION

Resource polymorphism, or the occurrence of individuals within the same species with different morphologies and patterns of resource utilization, is a phenomenon found in many taxa, including amphibians, birds, fish, gastropods and insects (Collins and Cheek, 1983; Smith, 1987; Thompson, 1992; Snorrason *et al.*, 1994; Padilla, 2001). Although resource polymorphism is common, the mechanisms behind the development of different morphotypes are still not well understood. It has been suggested that resource polymorphism may develop where there are 'open' or under-utilized niches and a relaxation of interspecific competition (Smith and Skúlason, 1996). By using an alternative resource, individuals will be less affected by competition and will thus increase their fitness than if

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they had continued to forage on the primary resource. This idea has been suggested as the explanation for resource polymorphism in recently colonized habitats, such as islands and deglaciated lakes (Smith and Skúlason, 1996).

The existence of species developing different morphotypes naturally raises questions about the mechanisms behind the development of morphotypes. One common observation is that individuals develop different morphologies as a result of environmental cues – that is, phenotypic plasticity. Thus, it has been shown that in some species resource polymorphism can be a response to different diets (Meyer, 1990; Walls *et al.*, 1993; Mittelbach *et al.*, 1999; Padilla, 2001). In other species, differences in morphology have a genetic basis (Harris *et al.*, 1990; Smith, 1993; Skúlason *et al.*, 1996) and morphotypes may show different life-history traits, have partly isolated reproduction and exploit different resources. In cases of genetically diverged morphotypes, the origin of the morhpotypes is debated. In some cases, the genetic pattern suggests that they have evolved in allopatry and that the co-existence of different morphotypes is due to multiple invasions (McPhail, 1993). In other cases, the genetic pattern suggests that the morphotypes have evolved in sympatry and that competition for food may be the driving force (Smith, 1993; Gíslason *et al.*, 1999). The genetic patterns, however, are usually complex and can support both hypotheses for the same species in a region (Pigeon *et al.*, 1997). There are also indications that factors other than resource utilization may drive the development of different morphotypes, leading to resource polymorphism in populations. Examples of such factors are sexual selection and predation risk (Van Buskirk and Schmidt, 2000; Wilson *et al.*, 2000). In the latter case, predation risk may force individuals to forage in a certain habitat where specific prey is to be found, leading to the development of a morphology specialized for utilizing that prey.

The existence of sympatrically diverged morphotypes raises the question of how they have evolved. West-Eberhard (1989) suggested that phenotypic plasticity may be the underlying mechanism for polyphenic divergence followed by speciation. Whether or not this is possible with respect to sympatric divergence should depend on the quantitative effects of phenotypic plasticity on performance and the rate of change of morphology and thus performance. In addition, to explore in depth whether phenotypic plasticity can form a substrate for sympatric divergence, one would also have to consider the nature of the population dynamics of the resources, for example whether they are stable or fluctuating. As an example one could consider individuals that adapt to a specific prey and hence increase their efficiency on that prey but simultaneously decrease the density of the same prey. In such a case, there are no obvious advantages in developing a morphology specialized for that prey.

To my knowledge, few studies have assessed the quantitative effect of diet-induced morphology on performance (but see Thompson, 1992; Robinson and Wilson, 1995; Day and McPhail, 1996), although there have been many studies on either diet-induced differences in morphology or differences in performance in individuals, caught in the wild, with different morphologies. The results of these studies can, of course, be used to estimate the quantitative effect of phenotypic plasticity on performance. However, in doing this, the effects of genetic variation on morphology cannot be excluded. The aim of this study was to examine the effect of different diets on morphology and performance at an individual level in Arctic charr (*Salvelinus alpinus*).

The Arctic charr is a suitable species to study, since one to four different, more or less discrete, morphotypes have been found in the same lake (Ekman, 1912; Nilsson and Filipsson, 1971; Sandlund *et al.*, 1992; Bjøru and Sandlund, 1995; Adams and Huntingford,

1997; Riget *et al.*, 2000). Theories about the internal relationship between different morphotypes in charr also range over the whole spectrum mentioned above – phenotypic plasticity (Nordeng, 1983), allopatric divergence and multiple invasion (Nyman *et al.*, 1981), and sympatric divergence (Gíslason *et al.*, 1999). The study was performed in the laboratory with individuals from a full sib brood held in separate enclosures. Capture rate for two different types of prey at different densities was measured before and after the diet treatments. At the end of the experiment, the morphology of each individual was measured. I predicted that individuals that fed on one type of prey would develop a morphology adapted to foraging on that particular prey and that these individuals would have a higher foraging rate on that prey than individuals from the other treatment groups. I also predicted that individuals receiving the mixed-diet treatment would have an intermediate morphology and foraging rate compared with the extreme groups.

MATERIALS AND METHODS

Experimental set-up

I collected roe from one wild-caught female from Lake Torrön (63°49′13″N, 13°6′19″E). The roe was artificially fertilized with sperm from one male to minimize the effects of genetic variation. The fertilized roe was placed in a hatching box at the Semlan rearing station to develop. The fry were moved to Umeå 175 days after fertilization and kept in an aquarium until the individuals started to feed exogenously. To stimulate exogenous feeding, I fed them with frozen copepods and chironomids. Thereafter, 90 individuals weighing 0.16 ± 0.0016 g (mean ± standard error) were placed in aquaria (volume 20 and 30 litres). Two individuals were held in each aquarium separated from each other by a non-transparent plastic sheet. The aquaria were kept in a controlled climate at 12°C and connected to a flow-through system (flow 6 litres $\cdot h^{-1}$). Each pair of individuals was allocated to one of three treatments: (i) a pure zooplankton diet consisting of live zooplankton from ponds and lakes around Umeå; (ii) a pure chironomid diet consisting of frozen chironomids placed on 5×5 cm patches made out of plastic doormat (Astroturf®); and (iii) an evenly mixed diet consisting of live zooplankton and frozen chironomids. The fish were fed twice a day and the individuals in the mixed-diet treatment were fed one of the two prey types on each occasion.

After 6 days of acclimatization, 10 individuals from each treatment were used to conduct foraging experiments. Before these experiments began, the fish were trained in the experimental procedures and the specific prey type for 5 days (Fig. 1). The experiments were performed in the aquarium in which the fish were kept (only 30-litre aquaria were used for the foraging experiments). To standardize hunger, all fish were starved for 12 h before the start of the foraging experiments. One hour before the experiment began, each fish was placed behind a plastic sheet along each short side of the aquarium; thus two holding areas of 2 litres and a performance arena of 26 litres were created. Thereafter, the central plastic sheet was removed, a dark grey plastic sheet was placed at the back of the aquarium and a fluorescent tube (11 W) was positioned 50 cm above the bottom to ensure that the environment was as homogeneous as possible. Finally, a removeable grid (squares 2.5×2.5 cm) was fixed to the front of the aquarium. The fish did not show any signs of stress during the foraging experiments. In the zooplankton experiments, I used cultured *Daphnia magna* of size 1.2 ± 0.04 mm. The desired density of zooplankton was added from above and the

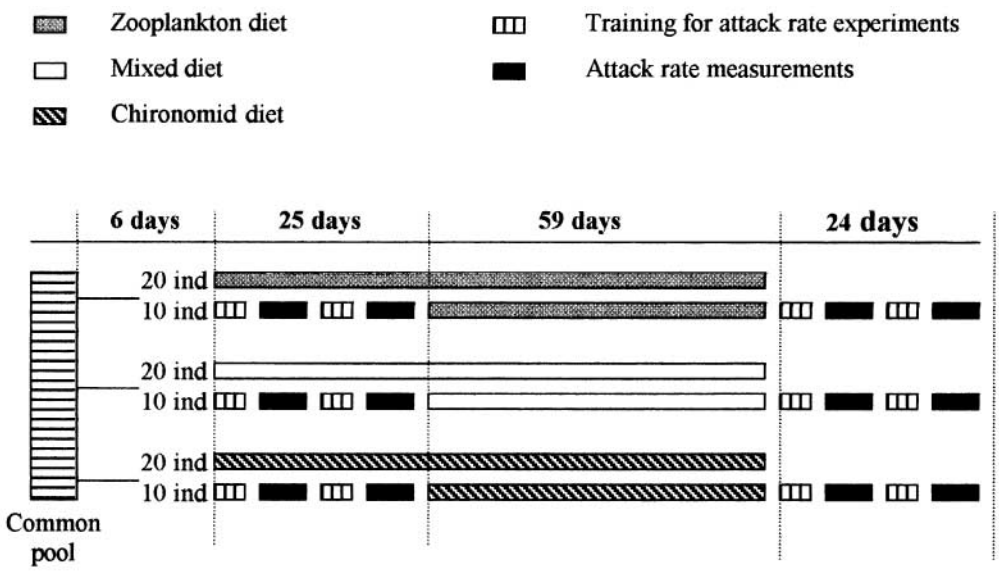

Fig. 1. Schematic representation of the design of the experiment. The different diets show periods when the fish were fed prey according to the treatments. Training includes the time when individuals were customized to the prey and the experimental procedures involved in the following attack rate measurements.

water was gently stirred until the zooplankton was evenly distributed. Subsequently, one of the plastic sheets was removed and the experiment started when the fish attacked the first prey. The time between the first and the fifth attack was recorded followed by a further 30 s of filming (Panasonic® AG-EZ35E Digital Video Camera) to allow estimates of swimming speed. If the fish had not managed to capture five zooplankton within 2 min of the plastic sheet being removed, the capture rate experiment was considered to have ended and the number of prey caught was noted followed by 30 s of filming. After filming had ended, the fish were placed behind a plastic sheet along the short side of the aquarium and the zooplankton consumed was replaced. A new foraging experiment was conducted with the other fish in the aquarium. In total, each individual was involved in nine different trials with various zooplankton densities (1, 1.5, 2, 3, 4, 6, 8, 16, 24 individuals per litre). To avoid systematic errors, the internal order of foraging experiments was different from aquarium to aquarium.

The capture rate experiments with chironomids as prey were performed in a similar way to the experiments with zooplankton. One chironomid of size 9.6 ± 2.4 mm was placed in one patch and the patches were evenly distributed on the bottom. To minimize predator saturation, the number of chironomid prey to be eaten was restricted to three. Capture rates were estimated for six different densities (0.3, 0.4, 0.5, 0.6, 0.7, 0.8 individuals per dm^2). The handling time for chironomids was estimated directly in the aquarium and was defined as the time between a successful attack and the moment when the fish started searching again.

After the first foraging experiments, all 90 individuals were kept on their specific treatments for a further 59 days. Mortality was low during the experimental period and only three individuals died. At the end of this period, 57 individuals were killed due to a shortage

of zooplankton (total treatment time for these 57 individuals was 90 days) and preserved frozen in water (Fig. 1). The remaining 30 individuals were used for a second round of foraging experiments. Due to mortality during the treatment period, 28 of these 30 individuals were the same as those used in the first foraging experiments and two were taken from the group that was not involved in the first experiments. To minimize the effect of short-term behavioural effects, the fish were allowed to train on the prey before assessing attack rates. During the training period, I also assessed capture rates using one prey density to determine when the capture rate became asymptotic, which occurred after 5 days (see Werner *et al.*, 1981). I then began the foraging experiments, using the same methods as described above. After the attack rate experiments were conducted, the remaining 30 individuals were killed and frozen in water.

Procedure

All frozen fish were thawed, weighed and subjected to geometric morphometrics (Zelditch *et al.*, 1992; Rohlf and Marcus, 1993; Arnqvist and Johansson, 1998). I measured the positions of 13 landmarks for each fish (Fig. 2). The landmarks were sampled by viewing the fish in a dissecting microscope (Leica© MZ8) and projecting the image directly onto a digitizing tablet (Summasketch© III). The coordinates of the landmarks were collected using DS-DIGIT (Slice, 1994). To minimize measurement errors, every fish was sampled twice (see Arnqvist and Mårtensson, 1998). To remove variation in landmark position due to measurement errors, the average morphology of each fish was determined by computing orthogonal least-squares procrustes fits with TPSSUPER (Rohlf, 2000). The individual morphologies were further analysed using a thin-plate spline analysis performed with TPSRW (Rohlf, 2001a). The thin-plate spline analysis includes the use of an interpolation function that maps the landmark coordinates of one specimen to coordinates of the landmarks in another specimen. The parameters for this mapping can thereafter be decomposed into uniform and non-uniform components where the non-uniform components can be further decomposed into partial warps. Together, partial warps and the uniform shape components can be used as variables for statistical comparisons of within- and between-groups variability. To explore the general trends of the morphological changes, I also computed relative warps based upon the partial warps. Relative warps are the same as the principal components of a distribution of shapes (Adams, 1999). To examine correlations between individual traits and morphology, I used TPSPLS (Rohlf, 2001b). TPSPLS is designed to explore the relationships between variation in the individual's morphology and

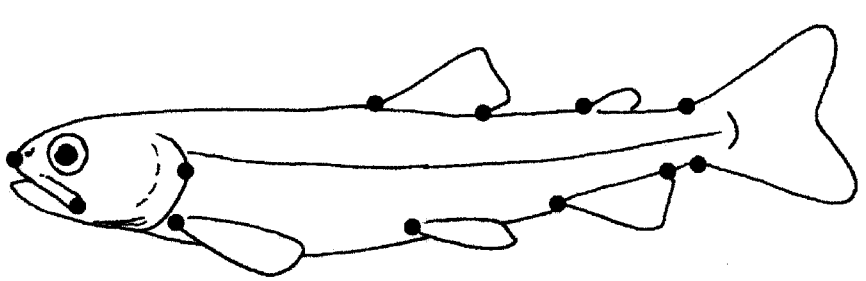

Fig. 2. The landmarks used for the morphology analyses.

a set of other variables (e.g. performance size) by a partial least-squares analysis of the covariation between morphology and the other variables. This results in a set of linear combinations of variables (variable vectors) and a set of partial warps (shape vectors). The vectors are paired, which results in i dimensions consisting of one shape vector and one variable vector. In this analysis, the variables were attack rate on zooplankton, handling time on zooplankton, swimming speed when foraging on zooplankton, attack rate on chironomids and swimming speed when foraging on chironomids.

The average swimming speed was calculated for each foraging trial by determining the individual's position in a two-dimensional coordinate system every second for 30 s. The sum of all distances between two consecutive positions was divided by the total time. Attack rate and handling time for zooplankton were estimated by fitting a type-II functional response curve to the capture rates on different prey densities using non-linear regressions:

$$C = \frac{aR}{1 + ahR} \tag{1}$$

where C is capture rate, a is attack rate, h is handling time and R is resource density (non-linear regression in SPSS 10.01, Levenberg-Marquardt method). The attack rates and handling times were estimated at an individual level. Attack rate and handling time estimates were then used in the partial least-squares analysis. Attack rates on chironomids were estimated using the same function but with h being measured directly during the experiments.

Statistical analysis

For the overall morphological analysis, I performed a multivariate analysis of covariance (MANCOVA; SPSS 10.01) with all partial warp scores and the uniform component as dependent variables, treatment as a fixed factor and size (the cube root of weight) as the covariate (Bookstein, 1996). For the more detailed analysis of morphology, I used one-way analyses of covariance (ANCOVA; SPSS 10.01) on relative warps and univariate characters with size as the covariate. In the partial least-squares analysis, I performed permutation tests included in the TPSPLS program. Swimming speed and capture rates were analysed using a nested analysis of variance (ANOVA) with treatment and prey density as fixed orthogonal factors and individuals nested under treatment.

RESULTS

Morphology

The individuals reached a similar size during the treatment period (chironomid feeders 1.43 ± 0.024 g, mixed feeders 1.50 ± 0.038 g and *Daphnia* feeders 1.42 ± 0.037 g; mean $\pm$ standard error). The overall morphology described by partial warps based upon 87 individuals differed between treatments and was also correlated with size (MANCOVA: treatment, Wilks' $\lambda = 0.427$, $P = 0.044$; size, Wilks' $\lambda = 0.532$, $P = 0.003$). The general trends of morphological changes based on the computed relative warps (RW) showed that there was a significant difference in RW1 due to treatment and a significant effect of size in RW1 and RW2 (Table 1). One useful aspect of using relative warps is that they make it possible to interpret the geometric deformations related to different scores (Fig. 3). The differences in

Table 1. One-way ANCOVA with size (cubic root of weight) as the covariate for the first four relative warps

Relative warp	% Variation explained	*F* (size)	*P* (size)	*F* (treatment)	*P* (treatment)
RW1	29.0	7.56	0.007	4.79	0.011
RW2	12.5	5.70	0.019	2.78	0.68
RW3	10.8	0.35	0.55	0.11	0.90
RW4	7.1	1.79	0.19	1.70	0.19

Note: % Variation explained shows the morphological variation explained by each relative warp.

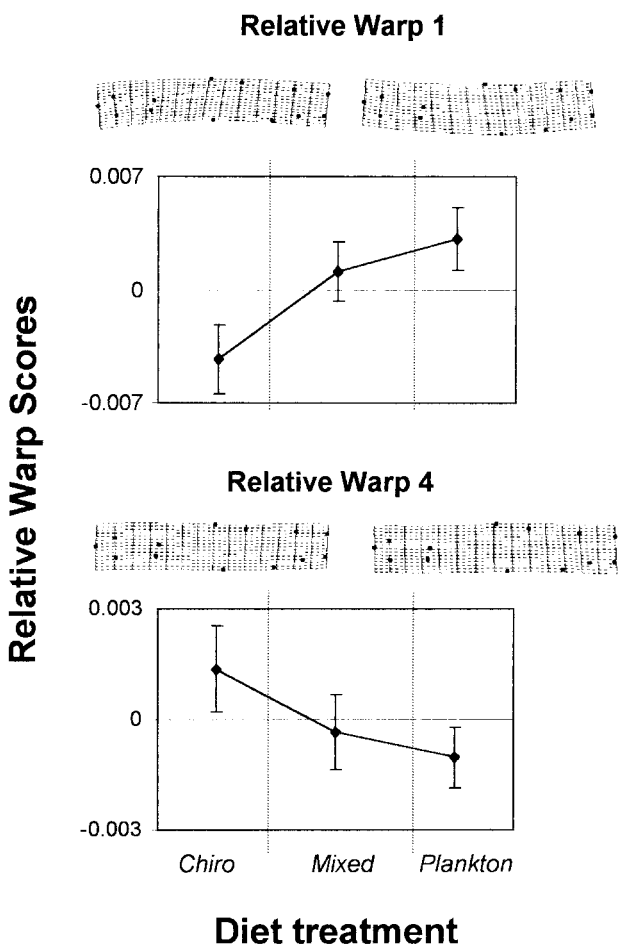

Fig. 3. The scores (mean ± 1 standard error) of relative warps 1 and 4 and graphical representation of scores. In RW1, the pictures show the morphology associated with the RW-score: 0.025 for the zooplankton treatment and −0.025 for the chironomid treatment. In RW4, the RW-scores are 0.01 and −0.01, respectively. The values of the scores were chosen to generate an illustrative picture but are still within the range of values found for individual fish.

morphology between plankton feeders and chironomid feeders are mainly expressed by the positions of the pelvic fin and the tip of the snout. The pelvic fins of the chironomid feeders were positioned more anterior and closer to the dorsal fin, and the tip of the snout was more downward pointing than in the plankton feeders. These differences result in chironomid feeders having an overall concave shape and plankton feeders a convex shape (Fig. 3). Although the other relative warps did not differ significantly between treatments, RW4 showed a pattern that accorded with treatment-induced effects. The trend in RW4 is mainly due to a longer head in chironomid feeders than in plankton feeders (Fig. 3).

The partial least-squares analysis based upon the 30 individuals involved in the foraging experiments showed that there was a correlation at an individual level between shape and performance in the second dimension (correlation coefficient 0.76; permutation test, $P = 0.027$) (Fig. 4). These vectors also showed an unusually high concentration in covariation (permutation test, $P = 0.029$), which indicates that this result is important (it is possible for a pair of vectors to have a high correlation but be unimportant since it explains very little of the covariation). The variables correlated with the variable vector are mainly influenced by measurements of zooplankton foraging (Table 2). Shape changes along the

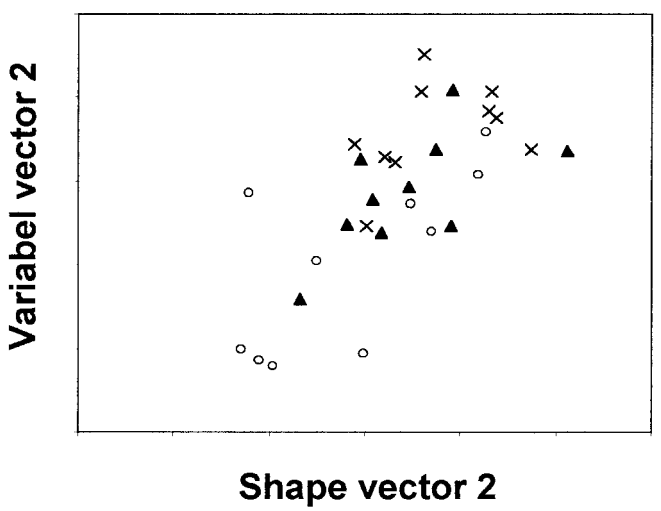

Fig. 4. The correlation between shape and variables in the partial least-squares analysis for the second pair of vectors. ×, an individual on the zooplankton diet; ▲, an individual on the mixed diet; ○, an individual on the chironomid diet.

Table 2. Correlations between the variable vector in the second dimension and size and the five variables related to foraging

Size	0.34
Attack rate, zooplankton	0.87
Handling time, zooplankton	0.77
Swimming speed, zooplankton	0.74
Attack rate, chironomids	0.14
Swimming speed, chironomids	0.54

shape vector indicate that chironomid feeders have a longer head and that the pectoral fin is in a more anterior position compared with plankton feeders, which corresponds to the results of the relative warp analysis described above.

Performance

As expected at the start of the experiment, the individuals in the various treatment groups did not differ in performance (Figs 5, 6 and 7). In contrast, after the treatment period, there was a difference in swimming speed between groups due to prey type (Fig. 5). Individuals from the plankton treatment group swam faster than those in the other two groups

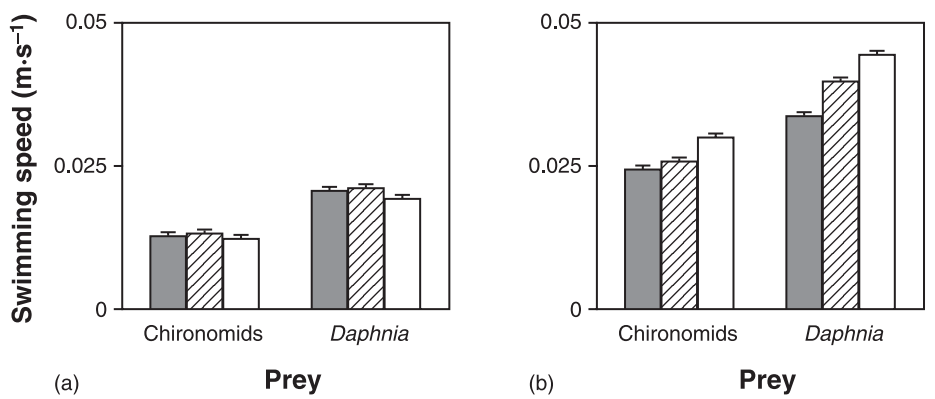

Fig. 5. Swimming speeds (mean ± 1 standard error) before (a) and after (b) the treatment period. ■, chironomid diet; ▨, mixed diet; □, zooplankton diet.

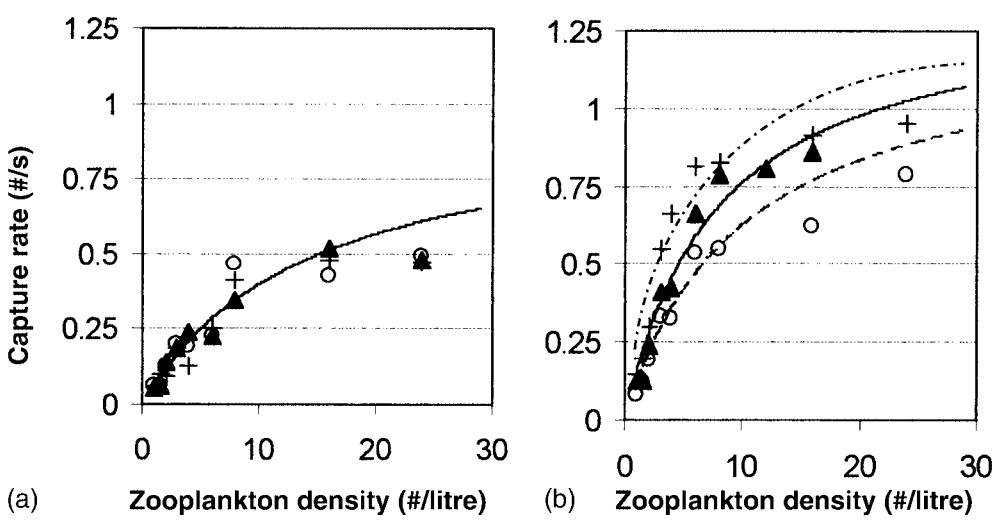

Fig. 6. Average capture rates on zooplankton before (a) and after the treatment period (b) for zooplankton feeders (+), mixed-diet feeders (▲) and chironomid feeders (○). Lines represent the fitted regression of Holling's type II functional response for each treatment.

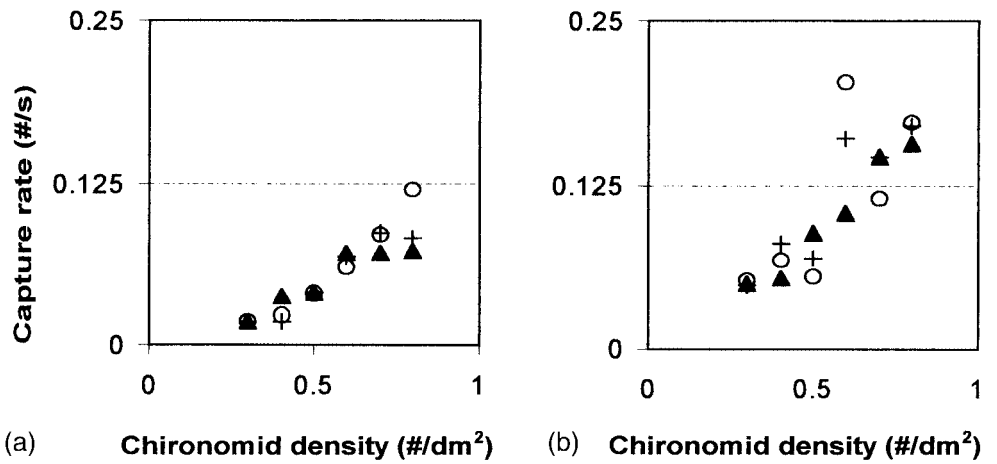

Fig. 7. Average capture rates on chironomids before (a) and after the treatment period (b) for zooplankton feeders (+), mixed-diet feeders (▲) and chironomid feeders (○).

when foraging both on zooplankton (ANOVA: $F_{2,27} = 20.21$, $P < 0.001$) and chironomids (ANOVA: $F_{2,27} = 3.73$, $P = 0.037$). No difference in swimming speed was noted between individuals from the mixed-diet and the chironomid treatment groups for fish foraging on chironomids (Tukey *post-hoc* test, $P = 0.64$), but individuals in the mixed-diet treatment swam significantly faster than individuals in the chironomid treatment when foraging on zooplankton (Tukey *post-hoc* test, $P < 0.001$). Also, capture rates on zooplankton differed between groups after the treatment period (ANOVA: $F_{2,27} = 127.5$, $P < 0.001$) (Fig. 6). The plankton feeders had a higher capture rate than the mixed-diet feeders, which, in turn, had a higher capture rate than the chironomid feeders. Capture rates also increased with zooplankton density (ANOVA: $F_{2,27} = 255.1$, $P < 0.001$) and were higher overall during the second experiment (ANOVA: $F_{1,477} = 92$, $P < 0.001$). Capture rates on chironomids did not differ among groups after the treatment period (Fig. 7). The capture rate increased with prey density (ANOVA: $F_{2,27} = 24.5$, $P < 0.001$) and was higher overall during the second experiment than during the first (ANOVA: $F_{1,358} = 122$, $P < 0.001$).

DISCUSSION

Diet and morphology

Differences in the diet-induced morphologies could be explained in part by the position of the pelvic fin and the fact that the mouth of the chironomid feeders pointed in a more downward direction than that of the plankton feeders. There was also a tendency for chironomid feeders to have a bigger head than plankton feeders. Irrespective of the fish taxa or the cause of resource polymorphism, one common feature is the occurrence of benthic and limnetic morphs (Robinson and Wilson, 1994). Typical characteristics of benthic morphs are deep bodies, large mouths and long pelvic fins, which are all assumed to be adapted traits for foraging on benthic macroinvertebrates (Webb, 1984). In contrast, the typical characteristics of limnetic morphs are a slender elongated body, a narrow mouth

and many long gill rakers (Hjelm *et al.*, 2001). The trend towards a larger head in the chironomid feeders in the present experiment is in line with the results of Skúlason *et al.* (1989), who examined the head morphology of different morphs of Arctic charr from Lake Thingvallaváth during early ontogeny. However, I did not find that the frequently reported trait of limnetic forms, (i.e. an elongated slender body) was induced by a zooplankton diet. Instead, the individuals in the zooplankton treatment group developed a deeper body, mainly as a result of the position of the pelvic fin.

The effects of diet on morphological traits have been reported in several studies (Meyer, 1987; Thompson, 1992; Walls *et al.*, 1993; Day *et al.*, 1994; Robinson and Wilson, 1995; Mittelbach *et al.*, 1999; Padilla, 2001). Although it is well known that a certain diet may induce a certain morphology, the physiological mechanisms behind this are unclear. The induced changes in morphology may result from nutritional differences or from differences in the mechanics of prey searching or prey handling (Day *et al.*, 1994). Although determining the mechanisms behind morphological changes was not the main aim of this study, it is worth considering some results which may increase our understanding of the mechanisms. The morphological traits that changed in accordance with the different treatments (RW1 and RW4) were the same traits that correlated with performance, especially attack rate on zooplankton and swimming speed. These results indicate that the induced morphologies are due to the mechanics of different types of movement when searching for prey. A fish foraging on zooplankton has to swim more and hence develops muscles that are more adapted to cruising, whereas a fish foraging on chironomids has to explore potential patches thoroughly, which includes fine-tuned movement for searching the benthic surface, which, in turn, demands a downward bending of the head. This argumentation is in line with the results of studies on phenotypic plasticity in pumpkinseed sunfish, in which individuals that fed on hard prey developed a much larger levator posterior muscle than individuals fed soft prey (Mittelbach *et al.*, 1999). Further evidence that foraging mode has an effect on morphologies comes from Robinson and Wilson's (1995) study of morphology in Trinidadian guppies (*Poecilia reticulata*). Since all treatments in the experiment of Robinson and Wilson (1995) were based on the same type of food, the effects of nutritional differences between prey could be ruled out, which further emphasizes the effect of foraging mode on morphology. Overall, these results suggest that morphological changes due to phenotypic plasticity are a continuous function of the time spent foraging on different prey.

Foraging performance and morphology

There was clear evidence that the diet during early ontogeny strongly influences capture rate on zooplankton and that the overall morphology correlated with performance; hence the morphological changes appear to be adaptive. Individuals fed zooplankton showed a substantial increase in efficiency in foraging on zooplankton and swimming speed compared with individuals from the other treatment groups. This is in line with the results of Malmquist (1992), who measured performance of wild-caught adult individuals from two genetically diverged morphs of Arctic charr when foraging on zooplankton. Interestingly, the differences in foraging rates between morphs in my study were as large as those found by Malmquist (1992), which suggests that it is possible to induce a difference in foraging ability through phenotypic plasticity that is as large as the differences between genetically different morphs.

In contrast to the zooplankton experiments, I found no evidence for a treatment effect on capture rates on chironomids. It could be argued that this result was an experimental artifact. For example, the chironomids I used were dead, which could make a difference when compared with natural systems. Although I have not conducted any detailed experiments of the differences in capture rates on frozen and live chironomids, I have carried out some qualitative studies. The results of these studies did not indicate any differences in detection rate or handling time between dead and live chironomids (personal observation). Another explanatory factor for the lack of differences in capture rates for chironomids could be the absence of sediment. In natural systems, chironomid larvae are often found in the fine-grained bottom sediments, although they may also inhabit other habitats, such as periphyton (Jones *et al.*, 1997). The capture rate on chironomids could then be limited by handling time when separating sediment and food (Werner *et al.*, 1981), which, in turn, could give benthic specialists an advantage over others. However, the environment of young-of-the-year charr – that is, the littoral zone of oligotrophic lakes (P. Byström and J. Andersson, in prep.) – is often characterized by gravels and rocks, which are probably better imitated by the plastic patches used in this experiment than by soft sediments. To conclude, the lack of a treatment effect on the capture rates on chironomids can hardly be explained as an artifact.

Trade-offs in foraging on different prey types

I found no trade-off in foraging capacities for different prey. In contrast, individuals whose diets included zooplankton appeared to have a competitive advantage over other individuals, since they did not lose any foraging capacity for macroinvertebrates. A lack of a trade-off in foraging capacities on different prey is not restricted to the present study. Similar results showing a clear effect of morphology on foraging capacity on only one of the available resources were reported for Bluegill sunfish by Ehlinger and Wilson (1988), pumpkinseed sunfish by Robinson *et al.* (1996) and grasshoppers by Thompson (1992). Although Schluter (1995) showed for sticklebacks that the benthic morph had a higher foraging efficiency on benthic resources than the limnetic morph and vice versa for pelagic resources, there were indications that the limnetic morph did just as well on benthic as on pelagic resources. Thus, taking the existing evidence together, the suggestion is that an effect of morphology on foraging is often only seen for one of the available resources, resulting in one specialized morph and the other morph functioning more or less as a generalist, with the ability to exploit both resources. There are also field data from small charr lakes which suggest that when there are two morphs, one is more of a benthic specialist and the other more of a generalist (Bjøru and Sandlund, 1995; Jónsson and Skúlason, 2000).

At least three different explanations can be advanced for this pattern. First, resources are divided into discrete habitats, for example pelagic and benthic. If one considers consumption rate as a function of time spent in each habitat multiplied by the attack rate on the prey in that habitat, it will be described by a linear consumption constraint curve *sensu* Tillman (1982). A linear consumption constraint curve with substitutable resources results in switching behaviour in the forager depending on resource densities. However, if a change in diet includes time to move between habitat patches or if there are behavioural constraints (e.g. different foraging tactics for different prey), the consumption constraint curve will have a concave shape. A concave consumption constraint curve gives rise to a trade-off and specialization on either prey depending on resource densities. Like costs of movement

and behavioural constraints, plastic adaptations may also yield concave consumption constraint curves, which could result in a specialist morph unable to compete for one prey and a generalist morph changing prey dependent on resource densities.

Since foraging capacity only deals with exploitative competition, a second explanation for the lack of a foraging trade-off may involve interference competition. Mikheev *et al.* (1996) found that progeny from a benthic morph of charr were more aggressive than progeny from a pelagic morph from the same lake. They suggested that the benthivores were more aggressive due to resource defence. In the present experiment, by holding benthic territories, the benthivores could have gained a competitive advantage over planktivores for benthic resources.

A third explanation is that the trade-off works in other dimensions than competitive ability for different resources. In the present study, morphology was correlated with both attack rate on zooplankton and swimming speed, and the individuals foraging on zooplankton and mixed diets had a higher swimming speed and foraging rate on zooplankton than the individuals in the chironomid treatment group. In many cases, a high foraging rate and activity are associated with a high mortality rate due to predation (Anholt and Werner, 1995; Stoks and Johansson, 2000; Relyea, 2001). These results suggest that an individual who becomes more planktivorous will suffer from a higher predation risk. In this scenario, there could be two different strategies: (i) a benthivorous specialist – low predation risk strategy; and (ii) a generalist – high predation risk strategy. Such a predator-induced resource polymorphism has also been proposed for amphibians and birds (Caldwell, 1986; Van Buskirk and Schmidt, 2000).

Given that diet can induce morphological changes and have substantial effects on performance, it will be important to examine the outcome of phenotypic plasticity in relation to ontogeny and predation risk. Finally, considering phenotypic plasticity over ontogeny, it is also important to determine whether morphologies become fixed, or at least whether the rate of morphological change differs from that of ontogeny – that is, whether one individual placed on one morphological trajectory can change to another morph or not.

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