Evolutionary Ecology Research, 2005, **7**: 767–778

Behavioural and morphological responses to cannibalism in Arctic charr (*Salvelinus alpinus*)

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ABSTRACT

Question: Does cannibalism lead to resource polymorphism in young Arctic charr (*Salvelinus alpinus*, Pisces)?

Hypothesis: Cannibals should evoke a low-activity morph that is well adapted to benthivory but not planktivory, and which differs in morphology compared with a planktivorous morph.

Methods: We reared young-of-the-year charr in laboratory aquaria with and without larger cannibalistic charr present. Thereafter, we measured foraging efficiency on pelagic and benthic resources, swimming speed when foraging, and morphology of the young charr.

Conclusions: Living among cannibals did not affect the morphology of the young charr. It also did not affect the foraging efficiency of the young charr on the benthic resource. However, individuals from cannibal treatments swam closer and had lower foraging efficiency on the pelagic resource.

Keywords: geometric morphometrics, phenotypic plasticity, predation risk, resource polymorphism.

INTRODUCTION

Resource polymorphism, the occurrence of morphologically different groups (morphotypes) within one species that utilize different resources, is a phenomenon known in many taxa, including amphibians, birds, fish, gastropods and insects (Collins and Cheek, 1983; Smith, 1987; Thompson, 1992; Snorrason *et al.*, 1994; Padilla, 2001). In the study of this phenomenon, a natural question to ask is how different morphotypes might evolve. Resource polymorphism has been shown to depend on both environmental cues (i.e. phenotypic plasticity) and genetic differences between morphotypes (Meyer, 1990). It is often suggested that the morphologies are adaptive responses for an increased foraging efficiency and hence increased competitiveness for a certain resource type. However, several studies have shown that differences in morphology only have a detectable effect on foraging efficiency on one of the resources (Ehlinger, 1990; Thompson 1992; Robinson *et al.*, 1993; Andersson, 2003) and hence there seems to be a lack of a trade-off when one considers only foraging efficiencies as a measure of competitiveness. This lack of trade-offs in foraging efficiency leads to an exploration of alternative costs

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of utilizing different types of resource. Examples of such alternative costs could be decreased success in situations with interference competition or predation risk.

Predation and predation risk themselves are known to have strong effects on both prey behaviour and morphology (Harvel, 1990; Lima, 1998). As for resource polymorphism, the mechanisms include both phenotypic plasticity (inducible defence) (Harvel, 1990) and genetically fixed defences in response to the ecological selection exerted by predation (constitutive defence) (Hoogland *et al.*, 1957). Changes in behaviour attributable to predation risk include decreased activity (Skelly and Werner, 1990; Stoks and Johansson, 2000), altered habitat choice (Eklöv and Diehl, 1995; Van Buskirk and Schmidt, 2000), aggregation (Pitcher, 1986; Elgar, 1989) and increased vigilance (Milinski, 1986). Changes in morphology due to predation risk have been suggested to prevent attacks by causing the predator to reject the prey (Reist, 1980; Kolar and Wahl, 1998; Trussell and Smith, 2000), increase the probability of prey escaping the attack (Havel and Dodson, 1984; Van Buskirk *et al.*, 1997), or increase the probability of the prey escaping during predator handling (Brönmark and Miner, 1992; Reimchen, 2000).

Behavioural and morphological responses to predation have often been studied separately from effects of resource use, although the two may exhibit an interesting interplay. Studies of interactions between predation risk and resource use have found that well-protected morphotypes spent more time foraging in habitats with a high predation risk compared with less protected morphotypes (Sillet and Foster, 2000; Grand, 2000; Vamosi and Schluter, 2002), and that predation risk can induce morphological changes, which in turn seem to be related to resource use (Caldwell, 1986; Van Buskirk and Schmidt, 2000). However, the relationship between behaviour and morphology can be complex and change over the life span of an individual (Dewitt *et al.*, 1999).

In an experimental study, Andersson (2003) showed that resource use in Arctic charr *per se* has a substantial effect on charr performance and morphology. He found that charr fed on zooplankton had a higher swimming speed independent of the resource they forage upon, had a higher foraging rate on zooplankton, but a similar foraging efficiency on chironomids compared with charr fed chironomids. In addition, charr fed on zooplankton developed a different morphology compared with charr fed on chironomids. The aim of the current study was to test the hypothesis that predation risk from cannibals favours the development of benthivores in Arctic charr, in the case where victims can choose their habitat (Andersson, 2003). This laboratory study was performed with groups of young-of-the-year charr kept in the presence and absence of large charr (cannibals), followed by experimental studies of young-of-the-year charr foraging efficiency on planktonic and benthic resources. We measured the morphology on all individuals using geometric morphometrics (Rohlf and Marcus, 1993) to determine whether predation risk by cannibals can induce morphological differences. In addition, we used the morphological data from Andersson (2003) to compare the morphology of resource-induced morphotypes with the charr from the present experiment.

Based on the results of Andersson (2003), we predicted that: (1) swimming speed should be lower for young-of-the-year charr reared in the presence of cannibals because of the cost of high activity when attracting cannibals; (2) young-of-the-year charr reared in the presence of cannibals should have a lower capture rate on zooplankton due to the correlation between swimming speed and zooplankton foraging efficiency; (3) differences in capture rate on chironomids between treatment groups should be small, since high activity is not important for effective benthic foraging; and (4) the morphologies should differ between treatment groups and that charr reared in the presence of cannibals should resemble the benthivores in Andersson's (2003) experiment, whereas charr reared in the absence of cannibals should resemble the planktivores in Andersson's (2003) experiment.

MATERIALS AND METHODS

We collected juvenile charr from the Semlan rearing station in western Sweden. The juveniles originated from wild-caught parents from Lake Håckren (63°11′18″N, 13°35′19″E) and were ~170 days old and non-feeding when moved to Umeå. In Umeå, we kept all juveniles in small aquaria (500 individuals in 30 litres) and fed them with frozen copepods. When all individuals had started feeding exogenously, we picked 400 individuals at random and placed them in four large aquaria with a volume of 500 litres (100 individuals per aquarium). In two of the aquaria we placed one large cannibalistic charr (size ~25 cm). To offer the juveniles an absolute habitat, we placed a plastic net (mesh size 15 × 15 mm) horizontally over the bottom at a depth of 15 cm. The net allowed the juveniles to move freely through the mesh but prevented the large charr from doing so. In addition, to minimize stress we placed PVC-tubes cut into halves on the bottom of the aquaria to offer visual protection to the juveniles.

The water temperature was held at 9°C during the treatment period and water was filtered through biofilters at a flow rate of 6 litres per minute. Twice a week, 10% of the water was exchanged with fresh water and every day the bottom was cleaned of uneaten food. The treatment period lasted for 69 days, during which time we fed the juveniles from above with frozen copepods in suspension two times a day. Due to the water circulation, the copepods spread out and moved freely in the aquaria, imitating live zooplankton fairly well. All aquaria received the same amount of copepods. Cannibalistic charr did not forage on this resource. To avoid starvation in the cannibals, these were replaced with new individuals twice during the treatment period. Behavioural studies during the treatment period consisted of estimating the position of juveniles in relation to depth. The aquaria were divided into two zones – a protected zone under the net and an unprotected zone over the net. We estimated the proportion of individuals in each zone once a week both during feeding and during periods between feeding. All experiments with live animals were approved by the Ethics Committee of Umeå University (Dnr A 17-03).

Foraging experiment

After the treatment period, all individuals were counted. Twelve randomly collected individuals from each aquarium were frozen in water as additional samples for morphometric analyses, and eight juveniles randomly collected from each large aquarium were placed in small aquaria (volume 30 litres) for behavioural and foraging experiments. The aquaria's sides and back were covered with black plastic, and two individuals were held in each aquarium separated from each other by an opaque plastic sheet. To minimize the short-term behavioural effects (e.g. extremely low or high activity or non-feeding due to stress), the juveniles were allowed to acclimate in the new environment for 6 days (Mittelbach, 1981). During this period, the juveniles were also trained in the experimental procedure of the foraging experiments. To standardize hunger, all fish were deprived of food for 12 h before the start of the foraging experiments. Thirty minutes before the experiment started, each fish was placed behind a plastic sheet at each short side of the aquarium. Then the central plastic sheet was removed, which resulted in two holding areas of 2 litres each and a performance arena of 26 litres. Thereafter, a one-way mirror was placed in front of the aquaria to minimize external disturbance, and a fluorescent tube (11 W) was positioned 35 cm above the bottom to ensure that the environment was as homogeneous as possible with respect to light. Finally, before starting the experiment, a removable grid (squares 2.5×2.5 cm) was fixed to the front of the aquarium.

Two types of prey were used in the foraging experiment, zooplankton and chironomids. In the zooplankton experiments, we used cultured *Daphnia magna*, size 1.2 ± 0.04 mm (mean ± standard error of the mean). The desired density of zooplankton was added from above, and the water was gently stirred until the zooplankton was evenly distributed in the aquaria. Subsequently, one of the plastic sheets was removed and the experiment started when the fish attacked the first prey. We recorded the time between the first and the fifth attack followed by a further 30 s of filming (Panasonic® AG-EZ35E Digital Video Camera) to obtain 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 terminated and the number of prey caught was noted followed by 30 s of filming. After we had finished filming, the fish was once again placed behind a plastic sheet at the short side of the aquarium, and the density of zooplankton was restored. A new foraging experiment was then 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 and 24 individuals per litre).

The capture rate experiments, with chironomids as prey, were performed in a similar way to the experiments with zooplankton, after 6 days of acclimation to the new prey. To imitate benthic structure, we used 5×5 cm patches made out of plastic doormat (Astroturf®). One frozen chironomid of size 9.6 ± 2.4 mm was then placed in one patch and altogether we placed eight patches 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 chironomid densities (0.3, 0.4, 0.5, 0.6, 0.7 and 0.8 individuals per 10 cm^2 of the bottom surface). 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. Finally, each individual was filmed for 30 s after the completed capture of three chironomids. After the foraging experiment, all participating specimens were weighed and frozen in water for morphometric analyses.

We calculated the average swimming speed 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.

Morphometric analyses

All frozen fish were thawed (80 individuals, $12 + 8$ individuals per aquarium), weighed and subjected to geometric morphometrics (Rohlf and Marcus, 1993). We measured the positions of 13 landmarks for each fish (Fig. 1). The landmarks were sampled by viewing the fish in a dissecting microscope (Leica © MZ95) and projecting the image directly onto a digitizing tablet (Wacom © Intous2). The coordinates of the landmarks were collected using ARCVIEW GIS 3.2a software. To minimize measurement errors, each fish was coded to eliminate subjectivity due to known origin. In addition, every fish was sampled twice by measuring landmarks for a second time after the first measurements had been taken and the fish was moved from its position under the microscope (see Arnqvist and Mårtensson, 1998). The

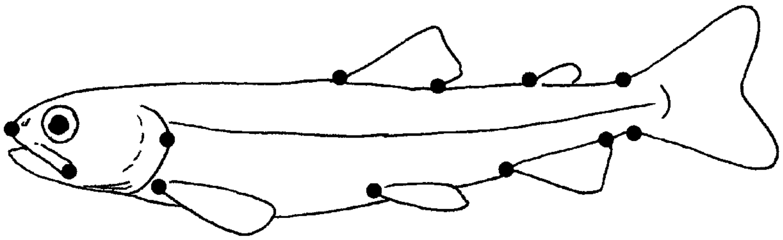

Fig. 1. The 13 landmarks used in the geometric morphometric analysis. Note that one point is in the centre of the eye.

average morphology of each fish was determined by computing orthogonal least-squares procrustes fits with tpsSuper v.1.07 (Rohlf, 2000). The individual's morphology was further analysed by a thin-plate spline analysis using tpsRelw v.1.25 (Rohlf, 2002). The thin-plate spline analysis includes the use of an interpolation function to express morphological variation among specimens. The morphology of each specimen can be characterized by a set of variables, or partial warp scores, which can be viewed as the deviation of that specimen from the average morphology of all specimens. Finally, we performed a principal components analysis on the partial warp scores (i.e. a relative warp analysis with $\alpha = 0$), of which the first nine principal components (explaining more than 90% of all morphological variation) were used to test for overall differences in morphology between treatments.

Statistical analysis

For the analysis of the juveniles' positioning in the large aquaria, we calculated the proportion of juveniles in the bottom zone. These values were then arcsine-transformed and used as independent values in a repeated-measures analysis of variance (ANOVA) with treatment as a fixed factor. To analyse capture rates and swimming speeds, we calculated the mean values of all individuals from each aquaria, for all prey densities, resulting in aquaria as the level of replication. We then performed a two-way ANOVA with treatment and prey density as fixed factors. For the morphology analysis of charr in this experiment, we performed a multivariate analysis of covariance (MANCOVA) with the first nine relative warps scores as dependent variables, aquaria as a fixed factor (four groups) and size (the cube root of weight) as a covariate. All statistical analyses were performed in SPSS 11.00.

To compare the morphology of the charr from this experiment with the charr in Andersson's (2003) experiment, we first computed the average morphology (see above) of all the charr in each aquaria, resulting in four specimens. Then, we included 29 planktonic specimens and 29 benthic specimens from the experiment of Andersson (2003). Since the charr were treated exactly the same in both studies, the comparison was straightforward [for a detailed description, see Andersson (2003)]. Finally, we computed the relative warps for all the 62 specimens above (4 + 29 + 29).

RESULTS

The mortality of juveniles in the absence of cannibals was low (13 and 7 respectively out of 100 individuals) compared with in the presence of cannibals, when more than half of the individuals (52 and 58 respectively out of 100) were cannibalized. The juveniles' positioning in the aquaria during the treatment period differed between the cannibal present and cannibal absent treatments (repeated-measures ANOVA: $F_{1,4} = 974.1$, $P < 0.001$) (Fig. 2). Juveniles in the presence of cannibals almost exclusively remained under the net, whereas the juveniles in the absence of cannibals were found at all depths. Furthermore, a larger proportion of the juveniles was found in the unprotected zone when foraging compared with midday observations (repeated-measures ANOVA: $F_{1,4} = 7.86$, $P = 0.049$). The presence of cannibals increased the proportion of juveniles in the protected zone over the course of the experiment, in contrast to the juveniles in the absence of cannibals, when the proportion of protected juveniles in the protected zone decreased (repeated-measures ANOVA: treatment × time, $F_{6,24} = 3.22$, $P = 0.018$).

We observed no difference in size between juveniles from different treatments participating in the capture rate experiments (cannibal present 0.69 ± 0.02 g, cannibal absent 0.64 ± 0.02 g, mean ± standard error of the mean; *t*-test $P = 0.10$). Individual juveniles generally had a higher swimming speed when feeding on zooplankton than when feeding on chironomids (*t*-test $P < 0.001$). Juveniles reared in the absence of cannibals swam faster than juveniles reared in the presence of cannibals both when foraging on zooplankton (two-way ANOVA: treatment, $F_{1,14} = 58.0$, $P < 0.001$; density, $F_{6,14} = 0.49$, $P = 0.804$; treatment × density, $F_{6,14} = 0.39$, $P = 0.873$) and when foraging on chironomids (two-way ANOVA: treatment, $F_{1,12} = 38.2$, $P < 0.001$; density, $F_{5,12} = 0.28$, $P = 0.915$; treatment × density, $F_{5,12} = 0.74$, $P = 0.61$) (Fig. 3). Finally, individuals with a high swimming speed when foraging on zooplankton also had a high swimming speed when foraging on chironomids (linear regression, $r = 0.43$, $P = 0.013$).

Capture rates on zooplankton were higher for juveniles reared in the absence of cannibals than for juveniles reared in the presence of cannibals at all densities (two-way ANOVA:

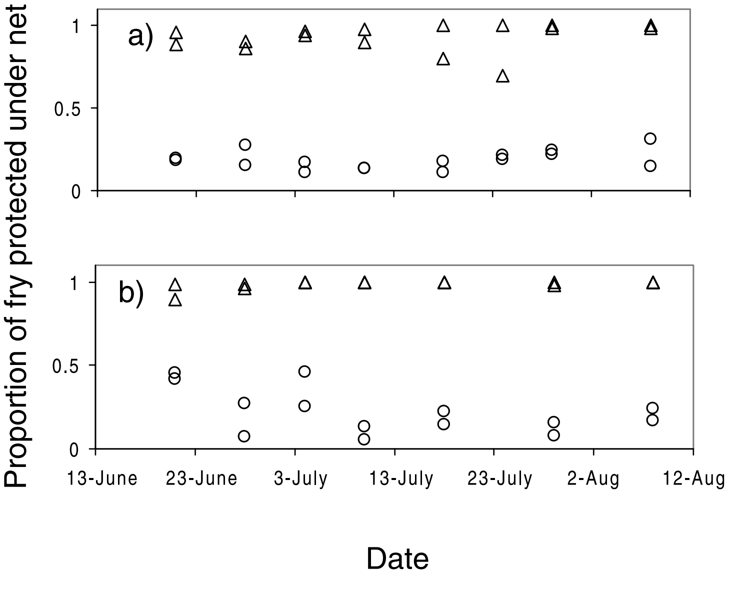

Fig. 2. The proportions of juveniles under the net in each aquarium during the treatment period. (a) The proportions during feeding occasions; (b) the proportions during the midday non-feeding observations. △, aquaria with a cannibal; ○, aquaria without a cannibal.

treatment, $F_{1,18} = 121.6$, $P < 0.001$; density, $F_{8,18} = 91.9$, $P < 0.001$; treatment × density, $F_{8,18} = 3.2$, $P = 0.586$) (Fig. 4a). In contrast, we found no difference in capture rates when feeding on chironomids (two-way ANOVA: treatment, $F_{1,12} = 1.2$, $P = 0.29$; density, $F_{5,12} = 9.0$, $P = 0.001$; treatment × density, $F_{5,12} = 1.0$, $P = 0.45$) (Fig. 4b).

We found no difference in overall morphology between individuals from the different aquaria, and consequently no difference with respect to treatments, although an effect of

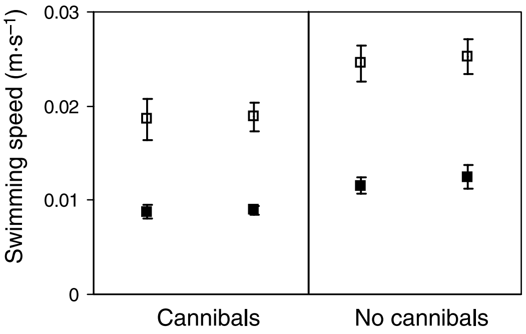

Fig. 3. Mean (± standard error of the mean) swimming speed for charr from each of four aquaria when foraging on zooplankton (□) and chironomids (■).

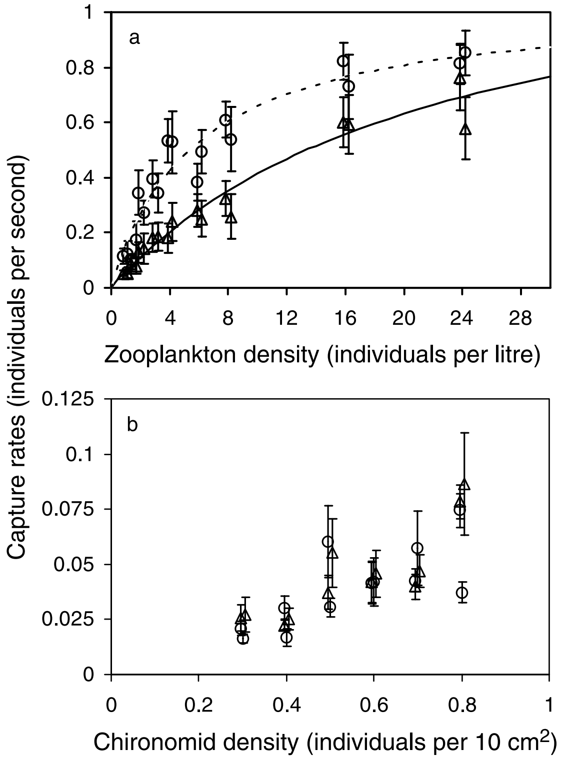

Fig. 4. Mean (± standard error of the mean) aquarium capture rate at different densities of (a) zooplankton and (b) chironomids. △, aquaria with a cannibal; ○, aquaria without a cannibal.

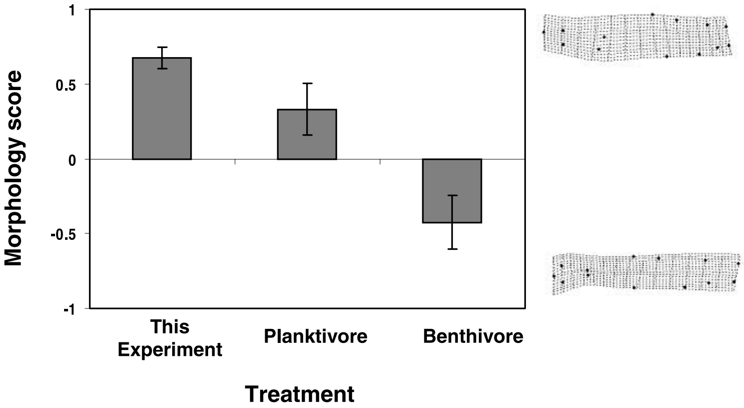

Fig. 5. Morphology described by the residuals after size regression on relative warp 1 scores and corresponding deformation grids for charr in this experiment and the benthivorous and planktivorous charr from Andersson (2003).

size on morphology was observed (MANCOVA: aquaria, Wilks' $\lambda = 0.67$, $F_{27,185} = 1.00$, $P = 0.46$, power = 0.81; size, Wilks' $\lambda = 0.28$, $F_{9,63} = 17.7$, $P < 0.001$, power = 1.0). When comparing the morphology of charr from our experiment with those of Andersson (2003), relative warp 1 (which explained 43% of the variance) suggests that the charr from the present experiment were all of the planktivorous type, with the tip of the mouth more upward pointing and the pelvic fins positioned more posteriorly, compared with the benthivores (Fig. 5).

DISCUSSION

Our results show that cannibalistic charr had a large impact on the juveniles' positioning in the aquaria. As in many other studies, the juveniles spent most of their time in more protected habitats in the presence of predators (Werner *et al.*, 1983; Christensen and Persson, 1993; Sillet and Foster, 2000; Van Buskirk and Schmidt, 2000). We also found that there was an effect of feeding, which suggests that the juveniles were more willing to take risks when food was present, as was reflected by the lower proportion of juveniles remaining close to the bottom during feeding occasions compared with non-feeding occasions. A large proportion of the juveniles in the non-cannibal treatment spent their time in the upper part of the aquaria irrespective of whether food was present or not. In the field, young-of-the-year charr are normally found close to the bottom, which could be an effect of high predation risk and the presence of alternative benthic resources (L'Abée-Lund *et al.*, 1993; Langeland and L'Abée-Lund, 1998; Byström *et al.*, 2004). Finally, the proportion of juveniles at the bottom increased over time in the cannibal treatment. This result indicates that the juveniles either learned that there was a potential risk of predation above the net and adjusted their behaviour to this threat by remaining in the refuge, or that the juveniles that were more active and prone to risk-taking were the ones being consumed by the cannibals and hence were selected against. We cannot exclude either of these two alternative explanations; other studies have provided support for both of these alternatives (Skelly and Werner, 1990; Skelly, 1994).

In the present study, fish swam faster when foraging on zooplankton than when foraging on chironomids, which is line with the results of other studies (Ehlinger, 1990; Andersson, 2003). As predicted, the juveniles in the cannibal treatments swam slower than the juveniles in the non-cannibal treatments, independent of prey type. In addition, we found that a high swimming speed when foraging on zooplankton correlated with a high swimming speed when foraging on chironomids. Taken together, these results suggest that cannibals either induced a less active foraging mode, or that more actively searching juveniles were cannibalized. Discriminating between these two mechanisms is not possible in this experiment due to the lack of a treatment in which small charr could experience the cannibals but still be safe. However, that we found a high predation rate during the experiment, and that the effect of cannibals lasted for 26 days (the duration of foraging experiments without cannibals present), suggests that the difference in swimming speed was an effect of a selective predation on active individuals. Given that previous studies on foraging mode in fish have shown that individuals manage to adapt behaviourally within approximately one week (Mittelbach, 1981; Werner *et al.*, 1981; Andersson, 2003), the 26 days should certainly have been enough to allow changes in swimming speed if this only depended solely on behavioural responses. These results also favour the explanation that the increased proportion of juveniles under the net was an effect of selective predation on active and non-vigilant individuals, rather than flexible behaviour in young-of-the-year charr.

As predicted, juveniles reared in the presence of cannibals had lower capture rates on zooplankton than juveniles reared in the absence of cannibals. In contrast, we did not observe any differences in capture rates on chironomids. Other studies with fish have shown that an individual's foraging efficiency on different resources may depend on several factors, including morphological characters such as number/length of gill rakers (Hjelm and Johansson, 2003), visual ability (Walton *et al.*, 1994), levator muscle size (Mittelbach *et al.*, 1999) and gape width (Hambright, 1991), and behavioural differences such as swimming speed (Andersson, 2003) and vigilance (Milinski, 1986). The capture rate and swimming speed results clearly show that swimming speed in Arctic charr is an important factor for predicting the capture rate on zooplankton, but not as important for predicting the capture rate on chironomids. This is in line with the results of Ehlinger (1990), who found that shorter hover duration (comparable to higher swimming speed) increased the encounter rate with zooplankton for bluegill sunfish (*Lepomis macrochirus*). In addition, Ehlinger (1990) found that longer hover duration increased the encounter rate with macroinvertebrates, whereas we found no such inverse relationship between swimming speed and prey type.

Andersson (2003) found that different diets induced different morphologies as well as different behaviours in Arctic charr juveniles, and that behaviour and morphology were correlated. There are striking behavioural similarities between the plankton feeders in Andersson's (2003) experiment and individuals from the non-cannibal treatment in the present study, and between chironomid feeders in Andersson's (2003) experiment and individuals from the cannibal treatment in the present study. Despite these similarities in behaviour between studies, we found, in contrast to Andersson (2003) and our expectations, no differences in morphology. This result suggests that behavioural differences due to predation risk alone are not enough to induce morphological differences adapted to resource use. Instead, it would appear that the resource itself is important for the development of morphotypes, a conclusion strengthened by the fact that fish in this experiment, which only fed on zooplankton, developed a planktivorous morphology when compared with those studied by Andersson (2003).

Based on the results of the present study and those of Andersson (2003), we suggest that neither resource use nor predation risk alone can explain the observed development of morphotypes in Arctic charr; rather, a combination of the two is necessary to provide an opportunity for the existence of several morphotypes. In the absence of predators, the benthivorous morphotypes are overall competitively inferior, since individuals with a more benthivorous morphology are inferior foragers on zooplankton, but are not better foragers on benthic resources compared with individuals with a more planktivorous morphology (Andersson, 2003). However, the presence of predators may promote the existence of the benthivorous morphotype, as its lower activity will lead to a lower predation mortality compared with the planktivorous morphotype. In addition to the lower activity *per se*, the habitat use of the benthivorous morphotype may also reduce predation risk (Byström *et al.*, 2004).

In summary, we believe that predation as an evolutionary factor selects against high prey activity, which in turn affects the prey's foraging efficiency on different resources. Thus, even though predation itself may not induce morphological changes, it can be a vital factor in facilitating the development of resource polymorphism.

ACKNOWLEDGEMENTS

We would like to thank the staff at Semlan rearing station for help with collecting and holding charr roe until hatching, Stig-Ola Ivarsson for technical assistance, Pär Byström for the illustrations, and Frank Johansson and two anonymous reviewers for valuable comments on previous versions of this manuscript. The study was supported by grants from MISTRA and the Swedish Research Council for the Environment, Agricultural Sciences and Spatial Planning to Lennart Persson, and from the Helge Axson Johnson Foundation to Jens Andersson.

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