Temporal variation in feeding morphology and size-structured population dynamics in fishes

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Considerable variation in morphology associated with resource use is a classic example of local adaptation to the environment. We demonstrate that a temporal change in feeding morphology might occur within a population. In a 5-year natural field experiment, we estimated gill raker morphology, resource density and population dynamics of the roach and its competitor, the perch. Despite a variation in density of zooplankton resources and perch across years, no change in roach density was observed. However, gill raker morphology in roach covaried with size structure of the zooplankton resource across years. A laboratory experiment confirmed that gill raker morphology has a great effect on roach foraging efficiency on zooplankton and that there is a functional trade-off with regard to zooplankton foraging. We suggest that the response in gill raker structure is an adaptation to deal with the rapid population dynamics of zooplankton, which are in turn mediated by changes in the size structure of the competing perch.

Keywords: feeding morphology; phenotypic plasticity; size structure; functional trade-off; population dynamics

1. INTRODUCTION

Many organisms show variation in feeding morphology associated with resource use (Wimberger 1994). Similarly, the dynamics of size-structured populations are strongly influenced by resource densities and resource use (Ebenman & Persson 1988; Polis *et al.* 1996). While these two topics have received a great deal of interest during recent years, there are very few studies linking the two. For example, we have limited knowledge of how feeding morphology is influenced by the size-structured population dynamics of resources and competitors, and how the changes in morphology affect the dynamic properties of size-structured populations.

Fishes are well represented in studies of feeding morphology. Several studies have shown that fishes' feeding apparatus, including gill raker structure, is strongly correlated with feeding strategy and environmental conditions (Svärdson 1979; Day *et al.* 1994; Robinson & Wilson 1994; Mittelbach *et al.* 1999). These studies have shown that variation in feeding morphology occurs as a result of adaptation to local resource conditions both within (Robinson & Wilson 1994; Mittelbach *et al.* 1999) and between (Svärdson 1979) systems. Nevertheless, many systems show large temporal variations in resource conditions between years (Boag & Grant 1981; Post *et al.* 1997) but, to the best of our knowledge, few studies have quantified how variation in feeding morphology is related to temporal variations in resource conditions (but see Grant & Grant 2002).

Phenotypic plasticity can be seen as a change in a character in response to the current environmental conditions, i.e. an adaptation. In the case of feeding morphology, each phenotype has a specific morphology adapted to a particular resource type. In order to show

that phenotypic plasticity is adaptive compared with specialization, it is important to show that there is a functional trade-off, i.e. that a morphological adaptation to one resource type causes a disadvantage with respect to another resource type (Robinson *et al.* 1996).

The implications of competition and predation for interactions among size-structured populations have been recognized in both terrestrial and aquatic systems (Mittelbach & Osenberg 1993; Persson *et al.* 1996a; Polis *et al.* 1996), and the dynamics of a given population are likely to depend on the co-occurrence and magnitude of factors such as intra- and inter-cohort competition, predation and cannibalism. One particular well-studied aquatic system is the Eurasian perch–roach system, where a large variation in the size structure and abundance of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and their zooplankton resource is evident across years (Persson *et al.* 1996b, 1999, 2000a,b; Claessen *et al.* 2000). Since the population dynamics of perch are driving the size structure and population dynamics of zooplankton (Persson *et al.* 1996b; 2000a,b), and clear evidence exists that young roach and perch compete over zooplankton (Byström & Garcia-Berthou 1999), it can be suggested that perch influence zooplankton conditions, which in turn affect feeding morphology or population dynamics in roach.

The main purpose of this study was to evaluate how population dynamics in zooplankton, the most important resource of roach, affect morphology in the feeding apparatus and population dynamics of young-of-the-year (YOY) roach. Since gill rakers are used for retaining zooplankton in roach and other planktivorous fishes (Robinson & Wilson 1994), we propose that gill raker morphology should covary with the size structure of zooplankton across years. In addition, we investigated whether there is a functional trade-off between gill raker morphology and capture efficiency of various zooplankton sizes. Moreover, we estimated how roach population size structure was related to zooplankton dynamics, and esti-

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mated the correlation between perch and zooplankton dynamics.

(a) Study system

Perch larvae hatch in the littoral zone and thereafter switch to the pelagic zone (Treasurer 1988, 1989; Persson *et al.* 2000a,b). After 2–3 weeks, when they become juveniles (size *ca.* 20 mm), they do, however, revert to the littoral habitat, where they spend the rest of the year (Persson *et al.* 2000a,b). Young perch feed mainly on zooplankton, switch to benthic macro-invertebrates when they become older and larger, and finally include fishes in their diet when large enough (Persson 1988). Juvenile and young roach spend all their time in the littoral zone and as adults they gradually shift to a more pelagic habitat (Rheinberger *et al.* 1987; Persson 1988; Persson *et al.* 2000a,b). Roach feed mainly on zooplankton and eat benthic invertebrates when they become large enough (Persson 1988; Hjelm & Persson 2001).

2. MATERIAL AND METHODS

The study was performed in Lill-Häggsjön, an oligotrophic lake, 8.5 ha in size, situated *ca.* 25 km northwest of Umeå, northern Sweden. Fishes were annually sampled every September from 1995 to 1999 using survey-link benthic gill nets (see Hjelm *et al.* (2000) for details). Six nets were used, three in the pelagic zone (depth of 4–5 m) and three in the littoral zone (depth of 1–2 m). Fishes caught (perch and roach) were measured (total length and weight). Perch and roach in the study area grow to a size of *ca.* 3–7 cm during their first year (Byström 2000), and therefore the smallest size class in our analysis of 30–70 mm is represented by YOY perch and roach. Since part of our focus was on the population dynamics and size structure of fishes, results are presented as the size structure of the fish population rather than as results relating to YOY fishes only.

Zooplankton were sampled every September both in the pelagic and in the littoral zones. A 60 µm mesh hand net (240 mm in diameter) was used for sampling the littoral zone. The hand net was towed 3 m (total volume filtered of 138 dm³) at a speed of 0.5 m s⁻¹ ($n = 3$). Pelagic zooplankton were collected with a 100 µm mesh tow net (250 mm in diameter), drawn vertically from 1 m above the bottom to the surface, again at 0.5 m s⁻¹ ($n = 3$) (see Hjelm & Persson (2001) for details). Zooplankton size and density sampled in September should reflect past predation pressure and current resource availability to the zooplankton-eating roach and perch populations since growth of perch and roach occur during this period (Byström 2000).

To determine diet, the whole intestines of YOY roach were analysed under a dissecting microscope, and crustacean zooplankton were counted and measured to the nearest 0.01 mm. The gill raker distance was measured on a subset of roach from each cohort ($n = 20$ –30 each year). All inter-raker distances were measured on the medial side of the first left gill arch using a stereomicroscope (Leica MZ8) with an ocular micrometer.

To determine whether variation in gill raker distance is a morphological adaptation to variation in zooplankton size, and whether there is a functional trade-off, we compared the capture rates of zooplankton by YOY roach cohorts born in 1995 and 1997. These cohorts differed in gill raker distance. Capture rate was determined in the laboratory using small and large zooplankton size classes. Roach were sampled by electrofishing and

Figure 1. The relationship between gill raker distance in YOY roach and zooplankton size in their diet in Lill-Häggsjön lake. Error bars are maximum and minimum values.

the mean (± 1 s.d.) size of individuals used in the experiments was 40 mm (± 2.78 mm, and ± 1.21 mm, 1995 and 1997, respectively). The mean $\pm$ s.d. gill raker distance was 0.20 ± 0.002 mm in 1995 and 0.18 ± 0.003 mm in 1997. The foraging experiments were carried out with two size classes of zooplankton (0.25 and 1.0 mm). These size classes occur in the lake and represent somewhat extreme values but since we had no *a priori* reason to expect a discontinuous relationship between gill raker distance and capture rate of different zooplankton sizes we used these two sizes in order to increase our statistical power. The experiments were carried out in plastic aquaria (size of 50 cm $\times$ 30 cm $\times$ 25 cm) filled with 20 l of non-chlorinated tap water. The densities given were 2, 4, 8, 16, 32 and 64 zooplankton per litre. For a further description of the experimental set-up used see Hjelm & Persson (2001). All foraging experiments were replicated six to eight times for each prey density with different fishes for each trial.

3. RESULTS

All YOY roach were collected in the littoral habitat while other age and size classes of roach were found in both littoral and pelagic habitats. Gill raker distance of YOY roach was not related to their size ($r^2 = 0.002$, $F_{1,62} = 0.10$, $p = 0.72$) and therefore we excluded size in further analyses on gill raker distance in roach. Gill raker distance in YOY roach collected in the littoral zone varied across years and was positively related to zooplankton biomass in the littoral zone ($r^2 = 0.98$, $F_{1,4} = 87.3$, $p = 0.003$) and mean size of zooplankton in the diet ($r^2 = 0.88$, $F_{1,4} = 10.1$, $p = 0.05$; figure 1). The mean size of the roach population and the abundance of YOY roach varied little across years (figure 2a). The variation in mean roach size was not related to zooplankton biomass ($r^2 = 0.05$, $F_{1,4} = 0.16$, $p = 0.72$) or zooplankton size in the littoral zone ($r^2 = 0.11$, $F_{1,4} = 0.37$, $p = 0.58$; figure 3a). In addition, the abundance of YOY roach was not related to zooplankton size in the littoral zone ($r^2 = 0.003$, $F_{1,4} = 0.008$, $p = 0.93$). Similarly, roach biomass was not related to zooplankton size or biomass ($p > 0.05$). The

Figure 2. Size distributions of (a) roach and (b) perch for (i) 1995; (ii) 1996; (iii) 1997; (iv) 1998 and (v) 1999 in Lill-Häggsjön lake given as number per catch effort. The smallest size class of each species is the YOY fishes.

variation in zooplankton size across years did not cause YOY roach to grow more slowly in years when zooplankton were small (one-way ANOVA: $F_{4,18} = 1.52$, $p = 0.24$). Roach have relatively short gill rakers compared with many other planktivores and the average length of the gill rakers was not related to zooplankton average size or total biomass.

Since we collected fishes in September, all YOY perch were collected in the littoral zone where they had been since mid-June (Persson *et al.* 2000a,b). In contrast to

roach, the mean size of the perch population and the abundance of YOY perch varied greatly across years (figure 2b). The variation in mean size of the perch population was related to zooplankton biomass ($r^2 = 0.87$, $F_{1,4} = 19.6$, $p = 0.02$) and zooplankton size in the littoral zone ($r^2 = 0.99$, $F_{1,4} = 211$, $p < 0.001$; figure 3b). In addition, there was a positive significant relationship between YOY perch abundance and zooplankton size in the littoral zone ($r^2 = 0.84$, $F_{1,4} = 15.46$, $p = 0.03$). Perch biomass was also related to zooplankton biomass and size

Figure 3. The relationship between (a) mean roach size and (b) mean perch size and zooplankton size in the littoral zone each year in Lill-Häggsjön lake.

to a similar extent. YOY perch grew more slowly in years when zooplankton were small (one-way ANOVA: $F_{4,22} = 11.61$, $p < 0.001$). These results suggest that the variability in the density of zooplanktivorous perch affected zooplankton biomass and size structure, which, in turn, produced a response in the gill raker distance in YOY roach.

Capture rates differed between the two different YOY roach cohorts (figure 4). When feeding on 0.25 mm zooplankton roach with closely spaced gill rakers (born 1997) had a higher attack rate than roach with widely spaced gill rakers (born 1995) (two-way ANOVA: zooplankton density: $F_{5,62} = 166$, $p < 0.001$; roach cohort: $F_{1,62} = 15.7$, $p < 0.001$; cohort $\times$ density: $F_{5,62} = 0.1$, $p = 0.98$; figure 4). The converse was found for 1 mm zooplankton, i.e. roach with closely spaced gill rakers had a lower capture rate than roach with widely spaced gill rakers (two-way ANOVA: zooplankton density: $F_{5,62} = 824$, $p < 0.001$; roach cohort: $F_{1,62} = 39.1$, $p < 0.001$; cohort $\times$ density: $F_{5,62} = 2.1$, $p = 0.075$; figure 4). These results imply that gill raker distance affects roach capture rate of zooplankton and that there is a functional trade-off in the ability to retain zooplankton: being adept at capturing small zooplankton means the fishes are not good at capturing large zooplankton. The effect of gill raker spacing was especially strong at low prey density, where differences in gill raker spacing doubled the capture rate of zooplankton.

Figure 4. The capture rates of roach with narrow (circles) and wide (inverted triangles) gill raker morphology when preying on (a) small (0.25 mm) and (b) large (1.0 mm) zooplankton.

4. DISCUSSION

This study showed that gill raker distance in roach covaried with the size structure of zooplankton, which in turn was related to the perch size structure during the 5 years of the study. Despite large variation in the basic food resource, no variation in the size structure of roach occurred across years. We attribute the lack of variation in size structure of roach to variation in feeding morphology. Roach responded to changes in zooplankton size structure by corresponding changes in gill raker morphology, and roach may thereby maintain a similar population structure and growth rate across years despite the variation in the size range of resources.

Few studies have focused on short-term temporal changes in feeding morphology. Past studies have shown that changes in morphology might occur as an adaptation to resource use. These examples include planktonic and benthic forms of fishes (Robinson & Wilson 1994; Day *et al.* 1994; Schluter 1995) and forms of fishes feeding on hard-bodied and soft-bodied invertebrates (Mittelbach *et al.* 1999) within a system. Prior studies have also shown that species differ in feeding morphology between systems (Svärdson 1979; Lindsey 1981). For example, Lindsey (1981) found that ciscoe (*Leucichthys*) have allopatric benthic and planktivorous lake forms as a consequence of character displacement. Our result shows that variability in feeding morphology may also occur on a short temporal

scale. It is one of the few examples showing that fast temporal changes in feeding morphology might occur as an adaptation to rapid changes in resource conditions. Not only did morphology of the feeding apparatus change in one direction as zooplankton size structure decreased, but it also reverted to the original morphology as mean zooplankton size increased again 4 years later, i.e. an example of temporal character displacement.

Temporal changes in feeding morphology have been shown in a few other systems. Grant & Grant (1995) showed changes in feeding morphology of Galapagos finches as a function of resource conditions. Another example is evident in the scale eater *Perissodus microlepis* in lake Tanganyika (Hori 1993). In this fish, the direction of mouth opening seems to depend on frequency-dependent natural selection driven by the prey resource. However, both these examples of temporal changes in feeding morphology are believed to be genetic effects, where natural selection is acting on fitness components of the fittest morphs. By contrast, we suggest that the response of roach in our study is a phenotypic-plasticity response.

Admittedly, our results are correlative. Nevertheless, to support our view that the observed pattern in gill raker morphology is caused by phenotypic plasticity and not genetic differences across years, we can present five lines of evidence. (i) Phenotypic plasticity in response to variation in resource use has been found in other fish species (Robinson & Wilson 1996; Mittelbach *et al.* 1999). (ii) Our results suggest that gill raker distance is set the year YOY are born. (iii) The results show that the initial difference found between cohorts disappears as roach grow, and at an age of 3 years and above, cohorts from the lake no longer differed in gill raker distance (one-way ANOVA: $F_{4,55} = 0.455$, $p = 0.77$). (iv) Since the size structure of competing perch fluctuates across years (Persson *et al.* 2000a,b) natural selection would favour genotypes with plasticity in gill raker structure that is determined by resource availability (Gavrilets & Scheiner 1993; Mittelbach *et al.* 1999). (v) Selection pressures such as mortality not caused by predation during the larval or juvenile stage, or selective predation on different morphs in different years, is unlikely because it would result in some overlap in gill raker structure across years, which we did not find. Given these facts, we suggest that the difference in gill raker distance across years in YOY roach is caused by phenotypic plasticity, mediated by variation in zooplankton size structure. However, further investigations, including experiments, are needed to support this view fully.

Even though we do not know the explicit cause of the variation in gill raker structure, our capture-rate experiments clearly illustrate that the response in gill raker morphology provides an advantage for resource uptake when the size structure of the resource varies. For example, an advantage in attacking small zooplankton caused a disadvantage in attacking large zooplankton. Consequently, we found a functional trade-off in retaining ability of zooplankton, and a clear link between morphology and ecological function. Experiments have also shown that YOY roach with closely spaced gill rakers can maintain their metabolism on almost 20% lower zooplankton biomass than can YOY roach with widely spaced gill rakers when resources are limited (Hjelm & Persson 2001). Because we wanted to use roach with different gill raker spacings,

the functional response experiments were carried out in two different years (1995 and 1996). We cannot exclude the possibility that roach differed in other aspects besides gill raker spacing and that such other differences caused the observed functional trade-off. For example, pharyngeal muscles or buccal capacity could covary with gill raker spacing. Nevertheless, gill raker spacing could still be important although gill raker structure could covary with other traits (van den Berg *et al.* 1992).

Perch size structure showed variation across years. Similar patterns in perch size structure have been found in both empirical and theoretical studies, and the mechanism behind this pattern is a combination of intraspecific resource competition and cannibalism (Persson *et al.* 1996b, 2000a,b; Claessen *et al.* 2000). We suggest that the population dynamics of perch caused the variations in biomass and size structure in zooplankton across years, because perch size covaried with the two zooplankton variables. Persson *et al.* (1999, 2000a,b) have shown that the size structures of perch populations have strong effects on zooplankton dynamics in lakes situated in the same geographical area. YOY perch and roach feed mainly on zooplankton, and therefore compete for their main resource. Though roach have a higher attack rate (foraging rate) on zooplankton than do perch, the zooplanktivorous perch have a stronger effect on zooplankton density owing to their larger handling capacity (digestion capacity and larger mouth) than do zooplanktivorous roach (Hjelm *et al.* 2000; Hjelm & Persson 2001). In addition, perch larvae hatch earlier in the season than roach larvae suggesting that YOY perch have a larger overall impact than roach on the zooplankton community. Given that juvenile perch is a stronger competitor than juvenile roach, we should expect roach to covary in size structure with their basic food resource, zooplankton, but we did not observe this. The absence of such roach dynamics is surprising because in years with low perch recruitment (1995 and 1999) roach fed on large zooplankton, and in years with high perch recruitment (1996–1998) roach were forced to feed on small zooplankton, which were low in abundance. We suggest that the variation in feeding morphology observed in roach may stabilize their population dynamics. Since the morphological response acts on a rapid time-scale, roach can track resource changes effectively, and growth of individual roach is maintained despite variations in zooplankton size across years.

Since variation in size structure is a common phenomenon in natural systems (Ebenman & Persson 1988), and since resource gain is important for fitness, it is probable that this kind of local morphological adaptation to resource dynamics is very common. Our study shows that ecological factors such as variations in population size structure can promote the evolution of morphological variation, and our study also shows that variation in feeding morphology may stabilize population dynamics. Most models of population dynamics, including models with size structure, have ignored the impact of size-structured population dynamics on the expression of different phenotypes or the converse, i.e. that phenotypic variation is an important factor determining overall population patterns.

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