Interactions between predator- and diet-induced phenotypic changes in body shape of crucian carp

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Predator cues and diet, when studied separately, have been shown to affect body shape of organisms. Previous studies show that the morphological responses to predator absence/presence and diet may be similar, and hence could confound the interpretation of the causes of morphological differences found between groups of individuals. In this study, we simultaneously examined the effect of these two factors on body shape and performance in crucian carp in a laboratory experiment. Crucian carp (*Carassius carassius*) developed a shallow body shape when feeding on zooplankton prey and a deep body shape when feeding on benthic chironomids. In addition, the presence of chemical cues from a pike predator affected body shape, where a shallow body shape was developed in the absence of pike and a deep body shape was developed in the presence of pike. Foraging activity was low in the presence of pike cues and when chironomids were given as prey. Our results thereby suggest that the change in body shape could be indirectly mediated through differences in foraging activity. Finally, the induced body shape changes affected the foraging efficiency, where crucians raised on a zooplankton diet or in the absence of pike cues had a higher foraging success on zooplankton compared to crucian raised on a chironomid diet or in the presence of pike. These results suggest that body changes in response to predators can be associated with a cost, in terms of competition for resources.

Keywords: morphology; induced defence; diet; behaviour; *Carassius carassius*; phenotypic plasticity

1. INTRODUCTION

Phenotypic plasticity is the ability of an organism to express different phenotypes in response to distinct biotic or abiotic environments, an ability that also can be adaptive (Travis 1994; Dudley & Schmitt 1996; Pigliucci 2001). In general, ecologists have focused on how one variable affects plasticity. In natural situations, however, several environmental variables may interact in shaping patterns of plasticity (Sih 2003). Understanding the way different, simultaneously acting, environmental variables affect phenotypic plasticity is important to gain a better understanding of environmental influences on phenotypic variation and their ecological consequences.

In order to survive, organisms are faced with two important challenges: obtain energy and avoid predators. The presence of potential predators has been shown to induce morphological changes in many prey organisms, and the induced change results in a higher survival probability of the prey (Tollrian & Harvell 1999). Similarly, food resource use has been shown to affect the morphology of organisms (Smith & Skúlason 1996). These induced morphological changes have been shown to increase foraging efficiency on the corresponding resource and hence the competitiveness for that particular resource (Collins & Cheek 1983; Andersson 2003).

Since predators induce both morphological shifts and behavioural changes that result in diet shifts (Turner & Mittelbach 1990; Tollrian & Harvell 1999), the effect of predator-induced morphological changes and diet-induced changes may depend on each other (Caldwell 1986; Walker 1997; Vamossi & Schluter 2002; Chipps *et al.*

2004). For example, consider a system where the presence of a predator chemically induces a change in body shape in a prey, and at the same time causes a shift in prey habitat use because of predator avoidance behaviours. This habitat change results in a change in diet, which in turn affects prey body shape. In this scenario it might be difficult to determine whether predator cue induction or diet choice has the strongest impact on body shape.

Morphology also affects foraging success, which is an important fitness component (Arnold 1983; Webb 1984; Schluter 1995; Svanbäck & Eklöv 2003; Waltzek & Wainwright 2003; Carroll *et al.* 2004). For example, in fishes, a deep body shape is predicted to be beneficial in the littoral zone and when preying on sedentary benthic prey, since it allows a higher precision in manoeuvrability (Webb 1984; Domenici 2003). In contrast, a shallow body shape is predicted to be beneficial when foraging on planktonic prey (Webb 1984; Domenici 2003). Some support for these predictions has been found since individuals with morphology related to a certain habitat use or diet usually have a higher foraging success on the particular food item found in that habitat or in the diet (Ehlinger 1990; Andersson 2003; Svanbäck & Eklöv 2003). However, few studies have looked at how predator-induced morphological changes affect foraging success. If a predator-induced morphological change results in lower foraging success on a preferred diet, this morphological beneficial adaptation in one dimension (predation risk) is connected with a considerable cost in another dimension (competition), an aspect which has not received much attention however, see Pettersson & Brönmark (1997).

The crucian carp (*Carassius carassius*) is a common cyprinid fish in Eurasia (Lelek 1987). Laboratory and field

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studies have shown that chemical cues from pike predators induce a deeper body shape in crucians (Brönmark *et al.* 1999). The deeper body shape has been suggested as developing as a protection against pike predators, since pike have a longer handling time for a deep body shape, and pike prefer the shallow body shape in prey choice experiments (Nilsson *et al.* 1995). However, field and laboratory experiments show that crucians also prefer the littoral zone and avoid open areas in the presence of fish predators (Pettersson & Brönmark 1993; Holopainen *et al.* 1997), which in turn has been shown to affect diet (Paszlowski *et al.* 1996). Paszlowski *et al.* (1996) showed that crucian carp, when shifting to an inshore habitat in the presence of predators, included more benthic cladocerans in their diet compared with those in the absence of predators. In relation to previous studies, the crucian carp system, thus, seems to be ideal for studying the interaction between predator and diet-induced morphological changes. Additional evidence from other fish species show that individuals in the littoral zone have a higher proportion of benthic prey in their diet compared to open water living individuals, and that littoral individuals have a deeper body shape (Ehlinger 1990; Schluter 1993; Svanbäck & Eklöv 2003). Since the presence of predators as well as diet and foraging mode affect body shape in a similar way, one cannot be sure how much diet choice, habitat use and predation risk contributes to the body shape changes previously found in crucian carp.

In this study, we examine how benthic prey and pelagic prey, and the presence and absence of predatory pike cues affect body shape of crucian carp. We predict that (i) crucian carp will develop a deep body shape in the presence of pike, (ii) benthic prey will induce a deep body shape and (iii) individuals with a deep body shape will have a low foraging success on planktonic prey compared to individuals with a shallow body shape. With our approach we will also be able to distinguish between a scenario where the two effects are additive (e.g. individuals from the pike cue treatment fed on chironomids should have the deepest bodies) or if one effect can overrule the other (e.g. if diet does not have an effect on body shape in the presence of pike cues).

2. MATERIAL AND METHODS

(a) *Sampling*

Crucian carp (size range 8–12 cm) were caught with traps in a small pond, lacking piscivores, located on Lund University campus in southern Sweden, and thereafter transferred to the laboratory at Umeå University in northern Sweden where all experiments were performed. Past studies on populations in the area have shown that the carp develop a deeper body in the presence of pike predators (Brönmark & Pettersson 1994).

(b) *Experimental setup*

To examine the effect of chemical cues from a pike predator and the effects of diet on carp morphology, crucians were raised in 65 l circular tanks (height 35 cm, bottom diameter 43 cm) for 70 days. The bottoms of the tanks were covered with a plastic doormat (Astroturf) to provide a simulated 'natural' bottom substrate. Four stones the size of a fist kept the carpet piece in place. The crucians were subjected to two diet treatments, zooplankton and benthic chironomids, and

two predator treatments, chemical cues from a pike predator and no chemical cues from a pike predator, in a 2 × 2 factorial design. Dead chironomid larvae bought from a commercial dealer were added through removable tubes. The chironomids were poured into the tube, and when they had sunk to the bottom the tubes were removed and the fish was allowed to feed on this benthic prey. Live zooplankton were added by pouring them from a cup into the tanks. Zooplankton were collected from a fish-free pond in Umeå and consisted mainly of daphnids. Chironomids and zooplankton were added daily at an amount corresponding to 6% of the body weight of the crucian carp. The crucians subjected to chemical cues from a pike predator received water from a large tank containing 150 l of water that held one northern pike (*Esox lucius*). The pike was fed one crucian carp every third day. Pike were replaced three times due to mortality. The size range of the pike used was 30–60 cm.

Three crucian carp were held in each tank, which were ordered in eight blocks of four tanks, giving a total of 32 tanks and 96 crucian carp. Within each block, fishes in two tanks were fed chironomids, while fishes in the other two tanks were fed with zooplankton. Each block was connected to a fifth tank from which water was pumped out to the four tanks. Water was automatically poured back to this fifth tank through a drainpipe. Half of the blocks received chemical cues from a pike predator. These blocks were connected through the pike tank via the fifth tank, and water was pumped from the pike tank and then drained back to the pike tank. It could be argued that the predation treatment is pseudoreplicated since only one pike tank was used. However, three pike in total were used in the tank and assuming that pike cues are left in the water for some time, then more than one pike was used to induce the observed changes in body shape. In addition, the body shape changes induced by pike on the crucian carp were the same as has been shown in many other laboratory experiments (e.g. Brönmark & Miner 1992; Brönmark & Pettersson 1994; Holopainen *et al.* 1997). Hence, we are confident that the use of only a few pike in one tank did not bias our result due to some particular property of this one predation cue source.

The experiment was performed in a laboratory with a transparent glass roof allowing natural light conditions, and water temperature varied between 20 and 22 °C. Five crucian carp, randomly distributed between treatments, died during the experiments. After 70 days, all crucians were taken out of the tanks and given anaesthetic. They were then placed on a styrofoam plate with the fins fixed to the plate, and photographed with a digital camera which provided digital photos used for morphological analysis.

(c) *Morphological analyses*

Body shape was analysed with geometric morphometrics, where landmarks were sampled from the digital photos using the software Tps-Dig (Rohlf 2003a). Ten landmarks were taken from each fish (figure 1). All individuals were superimposed using generalized procrustes superimposition, which scales and rotates all the individuals so that they line up as closely as possible, resulting in a consensus body shape of all individuals (Rüger & Adams 2001). We thereafter generated shape variables for each individual fish, so-called partial warps and uniform components, which are decomposed descriptions of the deviation of the mean fish relative to the consensus shape for all fishes. All geometric morphometrics were performed using Tps-Relw software (Rohlf 2003b).

Figure 1. Landmark configuration (dots) on crucian carp used for the morphometric analysis. Note that one landmark is positioned at the centre of the eye.

The effects of the treatments on body shape were tested with a nested MANCOVA using the following model

$$\text{body shape} = \text{predator treatment} + \text{diet treatment} + \text{size} \\ + (\text{predator} \times \text{diet}) + \text{tanks}(\text{predator} \times \text{diet}),$$

where the 14 partial warps and the two uniform components were denoted as dependent variables, diet and predator presence as independent factors, centroid size (Bookstein 1991, p. 93) as a covariate, and tanks nested within the interaction of diet and predation (Langerhans & DeWitt 2004). No significant interactions between size and predation or diet were found, and, consequently, we dropped these interaction terms from the model. Finally, in order to visualize the differences in shape between treatments, we produced deformation grids using the Tps-Spline software (Rohlf 2003c). In order to interpret main effects, we produced deformation grids describing the consensus shape for the two main factors by pooling all individuals from one group to be compared to the individuals from the other group (i.e. all individuals from zooplankton versus all individuals from chironomid treatments, and all individuals from pike cue versus all individuals from no pike cue treatments). In addition, to be able to study the interaction terms we also produced the deformation grids based on the consensus shape of each of the four treatment combinations (i.e. chironomid feeders with and without pike cues and zooplankton feeders with and without pike cues). For more detailed descriptions of the logistics and methods of geometric morphometrics, see Rohlf & Marcus (1993) and Andersson (2003).

(d) Behaviour

We measured two behaviours, swimming speed in the tank experiments and foraging success in consecutive aquaria experiments. Swimming speed in the tank was estimated on four occasions; day 1, 21, 47 and 54. We randomly chose one individual out of three in each tank and noted the distance it swam during 1 min. Swimming speed was estimated as distance swum per second and was estimated 1 min after the prey was added and the fishes were actively feeding. Distance was estimated according to a grid pattern drawn on a transparent Plexiglas plate that was put on the top of each tank. The crucian's position during the minute was recorded by the observer speaking into a tape recorder.

After photographing (i.e. 70 days), the fishes were transferred to four 400 l holding tanks, one for each combination of diet and predation risk. Ten litres of water

Table 1. The results of a MANCOVA examining shape variation between different treatments.

factor	Wilks' λ	F-value	d.f.	p-value
pike	0.48	2.95	16,43	0.002
diet	0.43	3.59	16,43	<0.001
diet $\times$ pike	0.59	1.83	16,43	0.058
tanks (diet $\times$ pred)	0.0003	1.61	448,661	<0.001
size	0.77	0.79	16,43	0.67

from the tank containing the pike were poured every third day into the two tanks containing crucian carp from the pike treatment. All crucian carp were fed the same amount and type of food as prior to the photographing. Foraging success was thereafter estimated as the capture rate on zooplankton in 100 l aquaria (length 100 cm, height 33 cm, depth 30 cm). We chose to use only zooplankton when estimating capture rate because foraging adaptations are more pronounced between different morphological types when consumers forage on zooplankton prey compared to on chironimids (Andersson 2003). Because crucians seem to behave as social feeders, four individuals from a treatment were placed into one aquarium. To acclimatize fishes to the aquaria and to decrease the effect of previous diet due to learning, all crucians were fed zooplankton for 10 days prior to the estimates of capture rate on zooplankton. Daphnids, caught from a fish-free pond in Umeå, were used as prey. To standardize zooplankton size, daphnids were sorted serially through two sieves. Zooplankton which passed through 1 mm, but were caught with 0.75 mm mesh, were used. Two zooplankton densities were used; 2 and 30 individuals per litre. Zooplankton were gently poured into the experimental aquarium so that they were distributed as equally as possible throughout the water. Capture rate was estimated as the time interval between the first and the fifth daphnid captured and was measured sequentially for all individuals, and thereafter the average capture rate of all fishes from one aquarium was used as our replicate unit. Thereafter, another round with new individuals was performed following the same procedure as described above. The foraging success experiments were terminated when we had performed five replicates for each treatment.

Swimming speed during the tank experiment was analysed with a two-way repeated measures ANOVA using observation day as repeated measures. Diet and predator were used as factors and ln-transformed swimming speed was used as the dependent variable. To analyse the capture rate on zooplankton, we performed a three-way ANOVA with capture rate (ln-transformed) as the dependent variable. Diet, predation and zooplankton density were used as independent factors. Finally, we also conducted a test on capture rates in order to look for differences between the four treatments (all six pairwise combination between diet and predation) by performing a Bonferroni corrected *post hoc* test.

3. RESULTS

(a) Morphometrics

There was no difference in consensus size between the different treatments after the experiment was terminated ($p > 0.62$ for all factors). When the shape variables were tested with a nested MANCOVA, a significant effect of predator and diet was found, as was a tendency for an

Figure 2. Deformation grids showing shape changes induced by predation risk and diet. The central landmark configuration represents the consensus fish (mean fish shape). The head of the fish is to the right and the lines between the outer landmark lines were added to help interpretation of fish shape. The vertical central column shows shape changes when going from a zooplankton diet to a chironomid diet independent of the predation effect. The horizontal central row shows shape changes when going from a non-predator treatment to a predator treatment independent of the diet effect. The corners show the actual shape of fish from the no predator+zooplankton, predator+chironomids, predator+chironomids and no predator+chironomids treatments, respectively.

effect of the interaction term between predator and diet (table 1). In addition, the tanks nested within the pike and diet treatment were also significant, whereas centroid size was not (table 1). The graphical interpretation using deformation grids showed that the effect of diet on shape was described by plankton feeders having a more slender and upward-bending body compared to the chironomid feeders, which had a deeper and downward-bending body (figure 2, vertical central column). The deformation grids also showed that crucians in the presence of pike cues mainly differed by having a deeper body compared to crucians in the absence of pike (figure 2, horizontal central row). The interaction term indicates that the effect of treatments on body depth differed depending on treatment combinations. We found that the effect of diet was more pronounced in the absence of pike cues (figure 2, left column), where chironomid feeders were substantially deeper-bodied than zooplankton feeders. In comparison, although there was a difference in body depth between chironomid feeders and zooplankton feeders in the presence of pike cues, it was clearly smaller (figure 2, right column).

(b) Behaviour

Average swimming speed in tank was low in all treatments except for that with zooplankton without pike cues (figure 3). A two-way repeated measures ANOVA showed that crucians feeding on zooplankton had a higher swimming speed than crucians feeding on chironomids ($F_{1,28}=3.99$, $p=0.05$). The predator factor was close to significant ($F_{1,28}=3.77$, $p=0.06$), the interaction between the diet and predator factor was significant ($F_{1,28}=4.90$, $p=0.03$). These results show that crucians in the absence of pike tended to have a higher swimming speed than crucians in the presence of pike and that this pattern was more pronounced when zooplankton was given as prey. The crucians decreased their swimming speed over time and this was supported by a significant effect of observation day (repeated measures). No interaction

Figure 3. Mean swimming speed of crucian carp in the tanks when given zooplankton and chironomids in the presence and absence of pike cues. Error bars are s.d.

between observation day and the main factors was present (all p -values ≥ 0.25).

When testing treatment effects on capture rate, we found that resource density, diet and pike cues all had an effect on capture rates (three-way ANOVA: density, $F_{1,32}=22.7$, $p<0.001$; diet, $F_{1,32}=9.5$, $p=0.004$; pike cues, $F_{1,32}=5.7$, $p=0.02$; figure 4), whereas none of the four interaction terms were significant ($p>0.55$ for all interaction terms). These results suggest that prior feeding experience on zooplankton is an important factor in determining foraging efficiency, but that adaptations to predation risk also have a substantial impact on foraging efficiency. Our *post hoc* test on capture rates showed that only fishes from the zooplankton–non-pike treatment

Figure 4. The effect of diet (chironomids and zooplankton) and predation risk (pike present and pike absent) on capture rate of crucian carp on zooplankton at high and low densities. Error bars are s.d.

differed from the chironomide–pike treatment ($p=0.021$), whereas all other comparisons were non-significant (all p -values >0.3). However, without Bonferroni corrections the zooplankton–non-pike treatment differed significantly from all other three treatments ($p<0.05$) and in the comparison between zooplankton–pike and the chironomide–pike treatment there was a trend for a difference ($p=0.07$).

4. DISCUSSION

Past studies have shown that predation risk and diet as separate factors can affect the body shape of organisms (Brönmark & Miner 1992; Robinson & Wilson 1995), but there is an increasing interest in how these two factors might interact (Walker 1997; Vamosi & Schluter 2002; Chipps *et al.* 2004). However, these studies have been performed on fish caught in different habitats, which precludes any detailed analysis of the separate mechanisms behind the morphological adaptations and the relationship between them. In contrast, our study has taken a more mechanistic approach in which we were able to study the effects of predation risk and diet on morphology and foraging performance both separately and combined.

The presence of chemical pike cues induced a deeper body shape in crucian carp which is in correspondence with field and laboratory results achieved during the last decade (Brönmark & Miner 1992; Brönmark & Pettersson 1994; Holopainen *et al.* 1997). Similarly, crucian carp feeding on benthic prey had a deeper body than crucians feeding on planktonic prey, which is in line with previous studies on diet-induced shape changes in fishes (Day *et al.* 1994). These results suggest that predation risk and benthic resource use have similar effects on body shape. In addition, the upward bending of planktivores and the downward bending of benthivores are also in line with previous laboratory and field studies on diet-induced

adaptive body shape changes in fishes (Hjelm *et al.* 2001; Andersson 2003; Svanbäck & Eklöv 2003).

The deeper body depth of crucian carp in the presence of pike predators has been attributed to be a direct effect of chemical cues from pike, triggering physiological growth and development processes, where more energy is allocated to produce a deeper body depth rather than a shallow one (Brönmark & Miner 1992; Brönmark & Pettersson 1994). Although we cannot exclude their hypothesis, our results suggest that an alternative mechanism mediated indirectly by foraging behaviour could also explain a deeper body in the presence of pike cues.

Our activity estimates (i.e. swimming speed) showed that chironomid foragers in the absence of pike, and the two treatments with pike cues, had a lower activity compared to the zooplankton eaters in the absence of pike cues (figure 3). Behavioural modifications with lower activity in the presence of predator cues have also been shown in other studies on crucian carp (Holopainen *et al.* 1991, 1997; Pettersson & Brönmark 1993; Vøllestad *et al.* 2004). The observed feeding behaviour in our and the reviewed studies (i.e. a low activity and probably benthic feeding in the presence of pike cues) seems to be similar to the feeding behaviour on benthic prey without pike cues, where we also observed a low activity. Thus, we suggest that the effect of predation risk and benthic prey, by causing the same behaviour, also affects body shape in a similar way, i.e. a deeper body shape. The two factors seem to be additive, since the highest activity and most slender bodies were found among crucians feeding on zooplankton in the absence of pike cues, and, correspondingly, the lowest activity and deepest bodies were found in crucians fed chironomids in the presence of pike cues. Interestingly, in the combinations with conflicting factors, the crucians feeding on zooplankton in the presence of pike cues had a higher activity but a deeper body than crucians feeding on chironomids in the absence of pike cues. This result indicates that behaviour alone cannot explain all shape changes and that when these two factors are in conflict, the effect of predator cues overrules the effect of diet. However, whether the conflicting situation with dominating plankton resource use in the presence of pike occurs under natural conditions has still to be explored.

Both Holopainen *et al.* (1997) and Vøllestad *et al.* (2004) also suggested that the deeper body depth found in the presence of predators in their studies were a result of a behavioural reaction and an effect of saving energy. In the experiment by Holopainen *et al.* (1997), the presence of pike and the corresponding decrease in activity resulted in a low respiration rate, and the saved energy was suggested to have been allocated to somatic growth. Similarly, Vøllestad *et al.* (2004) found that crucian carp exposed to chemical cues from pike were less active, grew better and developed a deeper body compared to control fishes, despite the same resource levels being given to both treatments. If this alternative explanation is true, then the predator-induced morphological change is partly mediated by foraging behaviour, and thus partly an indirect effect which is not directly related to defence against predators. The changes in body shape could also facilitate defence against predators, but in our opinion defence might not be the direct cause but a positive consequence of a change in feeding behaviour. This effect

will only be apparent when food is readily available as in our and Völlestad *et al.*'s (2004) laboratory experiment. Food resources might, however, be limited in nature and a shallow body shape might be achieved under such conditions (Holopainen *et al.* 1997).

The change in body depth has also been suggested to depend on resource levels *per se*, because when per capita resource levels are high, a deeper body shape has been observed (Brönmark & Miner 1992; Tonn *et al.* 1994). In our experiment, the per capita resource levels given were the same for zooplankton and chironomid feeders. We never observed any remnants of uneaten prey in the containers, suggesting that all prey were consumed. There could, however, be differences in food quality between chironomids and daphnids, which in turn could affect body shape.

Our alternative explanation is, however, only a result of correlative patterns, and to be able to distinguish between the direct effect of chemical cues and the behavioural-induced indirect hypothesis, additional manipulative experiments are required. In addition, our experiments were performed on only one stage during ontogeny. The phenotypic changes might be different earlier or later on, since developmental windows of plastic responses are known to occur (Wimberger 1992; Stern & Emlen 1999). Morphological changes induced by predators associated with additional behavioural changes are common in other predator-prey systems (e.g. Kush 1993; McCollum & Van Buskirk 1996), and we suggest that our alternative interpretation of the changes in body shape should be sought in these systems as well.

Differences in morphology also have the potential to affect foraging behaviour (Smith 1987; Thompson 1992; Andersson 2003). Comparisons of benthic and pelagic morphs within species show that individuals with a deep body shape have a high foraging efficiency on benthic prey compared to individuals with a shallow body shape. In contrast, individuals with a shallow body shape have a higher foraging efficiency on pelagic prey compared to individuals with a deep body shape (Schluter 1993; Svanbäck & Eklöv 2003). We showed that a zooplankton diet induced a shallow body shape, and that individuals from this treatment had a higher foraging efficiency on daphnids (pelagic prey) compared to individuals fed with chironomids, and hence we believe that a shallow body shape is adaptive when foraging on zooplankton. Analogously to diet, we found that individuals from pike cue treatments (i.e. with a relatively deeper body) had a lower foraging rate on zooplankton than individuals from non-pike treatments, which suggests that the induction of a predator defence could be connected with a cost through the loss of competitiveness. Additional support for this cost is also given by Pettersson & Brönmark (1997), who showed that shallow-bodied crucian carp gained body mass much faster than deep-bodied crucians at high densities of crucians, in an enclosure experiment where zooplankton was the main food resource.

In conclusion, we found that diet and predator cues could have similar impacts on morphology, and that the benefits and costs of each phenotype depend on different ecological factors (i.e. predation risk versus competition). Thus, our study points towards the need for using a multi-factor approach to gain further understanding of the mechanisms behind induced phenotypes in natural

systems, and that the new interest of integrating predation risk and resource use has a great potential for understanding the existence of different types of phenotypic polymorphism in different ecological settings.

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