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ORIGINAL PAPER

Predator-induced changes in morphology of a prey fish: the effects of food level and temporal frequency of predation risk

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Abstract In a series of experiments, we investigated the effects of food availability and risk frequency on the dynamics of predator-induced changes in growth and morphology of prey fish using goldfish (*Carassius auratus*) as our test species. In experiment 1, we fed goldfish high or low food rations and exposed them to either alarm cues from conspecifics, cues from swordtails or a water control. After 60 days, goldfish in the alarm cue treatment significantly increased their body depth and body weight but had smaller body length than goldfish exposed to swordtails cues or water, likely reducing their vulnerability to gape-limited predators. Importantly, food level had an impact on the amplitude of the morphological changes. In experiment 2, goldfish were exposed to two different frequencies of predation cues or a water control for 50 days. The cues were either continued or discontinued from day 51 to 100, and all cues were resumed from day 101 to 150. We found that goldfish exposed to predation cues increased their depth and weight at a faster rate than did the goldfish exposed to water, and of particular significance was the fact that frequency of risk had an effect on the amplitude of the change. When the cues were interrupted, the increase in growth rate parameters was reduced to the level of the goldfish exposed to water. However, when the cues were resumed, the rate increased to match the growth rate of the goldfish that were continuously exposed to the cues. Finally, we staged encounters between goldfish of differing morphologies and yellow perch (*Perca flavescens*) and found that deep-bodied goldfish had better survival than the shallow-bodied ones. These experiments illustrate the dynamic nature of inducible morphological defences.

Keywords Predator/prey interactions · Morphological defences · Inducible defences · Chemical cues · Goldfish

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Introduction

Due to the unforgiving nature of predation, prey animals are under intense selection to detect and avoid predators (Lima and Dill 1990; Wisenden and Chivers 2005). The means by which they do so is highly variable and has been the subject of considerable study. Anti-predator defences are generally placed into three categories: behavioural defences, morphological defences and defences that involved changes in the life history of prey animals (Chivers and Smith 1998; Hoverman et al. 2005). Upon encountering a predator, for example, prey animals may show dramatic changes in their behaviour by fleeing or seeking refuge. Behavioural responses to predators can also include subtle changes in habitat choice and alterations in the timing of foraging and reproduction (Lima 1998). Life history changes include alterations in the timing of metamorphosis, changes in growth and reproductive patterns and changes in longevity (Crowl and Covich 1990; Chivers et al. 1999, 2001). Morphological defences often involve such things as the presence of protective spines and armour and the presence of cryptic and aposematic colouration (Edmunds 1974; Appleton and Palmer 1988).

A wide array of aquatic organisms exhibit changes in morphology when exposed to stimuli associated with predation risk. Due to their costs, such morphological changes are reduced, or absent under low risk. Examples are particularly common among invertebrate taxa, including protozoans (Kuhlman and Heckmann 1985; Kusch 1993; Wiackowski et al. 2003), cladocerans (Grant and Bayly 1981; Laforsch 2004), rotifers (Beauchamp 1952a, b; Stemberger and Gilbert 1984), bryozoans (Yoshioka 1982), gastropods (Appleton and Palmer 1988; Hoverman et al. 2005) and insects (Hershey and Dodson 1987; Johansson and Samuelsson 1994; Johansson 2002). For vertebrates, the diversity of taxa studied to date is small, but the in-depth nature of the studies is impressive.

The pioneering work on predator-induced morphological traits in vertebrates, published by Brönmark and Miner (1992), showed that in lakes and ponds containing fish predators, like northern pike (*Esox lucius)*, low densities of large-sized crucian carp (*Carassius carassius*) were common, whereas in other ponds and lakes without fish predators, high densities of small-sized carp were found. Twelve weeks after stocking pike into one side of a divided pond, carp from the two sides diverged in shape, with carp from the pike side being deeper bodied. Subsequent laboratory tests demonstrated that the preferential growth in body depth, which was caused by alarm cues from piscivores (Stabell and Lwin 1997), made the carp less vulnerable to gape-limited predators (Nilsson et al. 1995). However, the defence was costly. Individuals with the induced morphological defence suffer a hydrodynamic cost and are out competed by individuals without the induced morphology (Pettersson and Brönmark 1997, 1999; Andersson et al. 2006).

Following from the work of McCollum and Van Buskirk (1996), Van Buskirk, Relyea and their colleagues have published a number of excellent papers on predator-induced changes in morphology of various tadpoles, most notably gray treefrogs (*Hyla versicolor*) and woodfrogs (*Rana sylvatica*). In response to larval predators, tadpoles develop relatively deep tail fins and shorter bodies. These traits make the tadpoles less vulnerable to predation but at the same time appear to reduce the tadpoles growth (Van Buskirk and Relyea 1998; Relyea 2002a, b, 2004; Van Buskirk 2002; Schoeppner and Relyea 2005). Since this work there has been an explosion of research on predator induced phenotypic plasticity in tadpoles (e.g. LaFiandra and Babbit 2004; Kishida and Nishimura 2004; McIntyre and Flecker 2004; Teplitsky et al. 2005; Tsukasa et al. 2005; Kraft et al. 2005, 2006).

The importance of spatial and temporal variability in predation pressure in driving anti-predator defences is reasonably well established in ecology (Lima and Bednekoff 1999). This is particularly evident when considering morphological defences. For example, fixed defences, like protective spines, are often favoured where predation pressure is permanent while inducible morphological defences are favoured where predation pressure is variable and unpredictable (Harvell 1990; Clark and Harvell 1992). One question that arises from studies of morphological defences is whether the traits are reversible. If the prey suffers a cost of possessing or maintaining the defence, and the predation pressure is removed, then prey may have an advantage if they can reverse their morphological defence. For tadpoles, Relyea (2003) showed that changes in tail depth, and body depth were highly reversible early in ontogeny but less reversible later in ontogeny. For crucian carp, the morphological effect is somewhat reversible, but even after being held for 180 days in the absence of predation, carp do not return to the same body depth as control fish (Brönmark and Petterson 1994). Besides the work on crucian carp, only one study has examined the ecology of induced morphological defences in fishes. Januszkiewicz and Robinson (2007) recently demonstrated that pumpkinseeds (*Lepomis gibbosus*) increased body depth and dorsal spine length in response to predatory walleye (*Sander vitreus*).

In a series of three experiments we test another member of the genus *Carassius*, the common goldfish, *Carassius auratus*, for changes in morphology in response to predation cues. Although there are no comprehensive studies on goldfish, there are anecdotes that commercial goldfish introduced in the wild gain a deep-bodied morphology when coexisting with predators (Codieux 1953). In the first experiment we addressed whether goldfish exhibit a change in morphology in response to alarm cues from injured conspecifics, and if so, whether food level influenced the ability to change morphology. Induced changes in growth may be constrained under limited food conditions. Studies with tadpoles have shown that induced defences are weaker under low resource conditions (e.g. Relyea 2002a, b; Teplitsky et al. 2005). The second experiment was an examination of the effects of temporal variability on the presence and reversibility of morphological responses. We exposed fish to predation cues at two different frequencies (once per day or once every 3 days) for 50 days, then stopped treating the fish for 50 days and finally resumed treating them for the last 50 days. Our final experiment tested the survival consequences of the morphological defences during encounters with predatory yellow perch (*Perca flavescens*). Perch do not naturally co-occur with goldfish, thus any survival effects could be attributed to the morphological differences of the goldfish.

Methods

Fish collection and maintenance

The goldfish used in experiment 1 were obtained from a commercial supplier in Saskatoon, SK, in April 2004. The fish were fed daily with commercial fish pellets and kept in the lab at about 16°C on a 14:10 h L:D photoperiod for 20 days prior to the start of the experiment. Goldfish used for experiment 2 were obtained from the same supplier in January 2005 and kept under the same conditions described above for 15 days prior to the start of the experiment. Fish for experiment 3 were the same fish used in experiment 1 (see below for details).

Experiment 1: Predation risk and the morphology of goldfish

The purpose of this experiment was 2-fold. First, to test whether goldfish exhibit an adaptive change in growth and morphology in response to chemical alarm cues of injured conspecifics (i.e. do goldfish raised under predation risk situations have a deeper body and higher growth rate than those raised in no predation risk situations?). Second, to test whether varying food level influences the ability of goldfish to exhibit an adaptive change in growth and morphology.

Stimulus preparation

In order to prepare the goldfish and swordtail (*Xiphophorus helleri*) cues, we humanely killed the fish with a single blow to the head in accordance with the guidelines set by the Canadian Council on Animal Care. A fillet of skin was removed from each side of each fish and placed in chilled glass-distilled water. A total of 479.3 cm^2 of goldfish skin and 253.2 cm^2 of swordtail skin were collected. Each skin solution was homogenized with a Polytron homogeniser, filtered through filter floss to remove larger particles and then diluted in distilled water to make a solution of 14 cm^2/l. Stimulus solutions were pipetted into sample bags in 100 ml aliquots and frozen at −20°C until used.

Experimental protocol

In this experiment we used a 2 × 3 full factorial design, testing the effects of two levels of food and three types of chemical cues. Food level was manipulated by providing goldfish either low food (5% fish wet weight of commercial flake food, fed each day at 1000 h) or high food (5% fed at 1000 and 3% at 1600 h). The effects of cue were tested by exposing the fish daily to 10 ml of either (1) skin extract from conspecifics (GF), (2) skin extract from heterospecific swordtails (SWT) or (3) distilled water (DW). Swordtails were used to control for fish skin odour as their skin is known to lack alarm cues recognized by Ostariophysian fishes (Chivers and Smith 1998). The chemical stimuli were added to the aquaria each day at approximately 1100 h. We used a total of 97 aquaria with 15–17 replicates in each of the six treatments.

Experiments were performed in 74-l aquaria (60 × 30 × 40 cm) which were wrapped in black plastic on three sides so that fish in adjacent aquaria were not visible to each other. Each aquarium was filled with dechlorinated tap water and provided with a corner box filter. The bottoms of all the aquaria were covered with two cm of gravel. The aquaria were maintained under a 14:10 h L:D dark regime, at a water temperature of 18 ± 2°C for the 60-day duration of the experiment. To maintain water quality, one third of the water was changed in each aquarium each week.

Prior to the start of the experiment, goldfish were anaesthetized with MS 222, weighed (to the nearest mg) using an electronic scale and were randomly assigned to each aquarium. On day 30, 45 and 60, goldfish were again anaesthetized, weighed and measured for both length and maximal body depth (to the nearest mm) using digital callipers. The experimenter was blind to the treatments at the time of measuring the fish. At this time we readjusted the food level to the new mass of the fish. Data from the three fish in each aquarium were always averaged for all statistical analyses, thus the aquarium, not the fish was considered the replicate. To assess the effect of time, food level (low or high) and type of cue injected (goldfish cues, swordtail cues or distilled water), we performed a repeated-measures MANOVA (Zar 1999, pp 312–323) on the three morphological variables. We conducted multivariate analyses to account for dependency between the morphological measures. Since a significant interaction was found between food level and cue, we analysed the effect of cues for high food and low food independently using a MANOVA on the data for the last day of the experiment (day 61). Post-hoc LSD tests were performed to assess the difference between cues. All analyses were performed using SPSS 15 (SPSS Inc.)

Experiment 2: Temporal variation in risk and the morphology of goldfish

The purpose of this experiment was 2-fold. First, to understand the effects of predation risk frequency on the adaptive change in goldfish morphology, and second, to determine whether morphological responses to predation risk cues are reversible. As we were interested only in the effects of perceived risk, not the specific source of the risk, predator odour and tap water were used as the experimental and control cues.

In this experiment goldfish were exposed to chemical cues of pike fed goldfish or dechlorinated tap water at two different frequencies (once per day or once every third day). Fish in the experimental (pike) treatment were exposed to the cues for the 150-day duration of the experiment (cue continued treatment) or alternatively were exposed to the predator cues for the entire duration except for 50 days in the middle of the experiment (days 51–100; cue discontinued treatment). This was done to test for a possible reversal in the morphological change following the cessation of the predator cue. Fish in the control treatment were always exposed to the tap-water treatment. The tap water controls were not discontinued between day 50 and 100 like half of the pike odour treatments. This was a result of physical space constraints and sample size concerns. Thus we had two frequencies (low and high) and three treatments (water, cue continued and cue discontinued). It is important to note that we did not have a fully factorial design, using frequency (high or low), cue type (water or cue) and continuity. However, we considered each exposure type as an exposure treatment.

We used the same general experimental protocol as described above in experiment 1. Fish were fed 5% wet weight per day at 1230 h and were measured on day 0, 50, 100 and 150 of the experiment. The pike odour was water from a 74 l aquarium that contained two pike (approximately 20 cm in length). The pike were held under our standard laboratory conditions. They were fed every three days with goldfish (approximately 2% of their body weight) and routine water changes were done to maintain water quality.

In order to assess the effect of time and treatment on each of the three morphological factors, we performed repeated-measures MANOVAs. Due to the interaction between frequency and treatment, we subsequently analysed the data for high and low frequency independently. We investigated the effect of treatment using a MANOVA on the data for the last day of the experiment (day 150). Post-hoc LSD tests were performed to assess the difference between the treatment responses. To investigate in detail the effect of the discontinuity of the predation treatments, we performed three repeated-measures ANOVAs between day 0 and 50, day 51 and 100 and day 101 and 150 on the two predator cues treatments (cue continued vs. cue discontinued). If the discontinuity has an effect on the rate of increase of any of the morphological measures, then we should see an interaction between time and continuity. Once the cues are resumed, we expect the rate of increase to be similar between the two treatments (no interaction between time and continuity). This analysis allowed us to compare the growth rates (slopes) among treatments.

Experiment 3: Morphological defences and goldfish survival during encounters with predators

The purpose of this experiment was to test whether changes in goldfish morphology have significant effects on survival during staged encounters with predators. We used yellow perch as the predator in our experiments (Mean ± SD, standard length = 11.2 ± 2.1 cm). The perch were collected from Blackstrap Lake in central Saskatchewan and prior to the experiment were housed in a 4000-l pool were they were fed goldfish and minnows.

During each trial we staged an encounter between a single yellow perch and six goldfish, two from each of the three treatments in experiment 1: goldfish skin extract, swordtail skin extract and distilled water (low food treatment only). The experiment began within three days of the end of experiment 1 and was completed within 2 weeks.

Trials ($N = 24$) were conducted in 148-l glass aquaria (92 × 46 × 39 cm). Each aquarium was provided with two cm of gravel substrate and was divided with a translucent Plexiglas barrier into a large and small compartment. The small compartment (measuring one third of the aquarium length) was used as an acclimation chamber for the predator, and the large compartment was used as an acclimation chamber for the prey. Predators were allowed to acclimate in the experimental aquaria 3 days before the trials began. To standardize hunger level, the perch were not fed during this period. Prey were added 60 min before the trials began, and all trials were run for 60 min. To minimize disturbance during the trials, the observer completed the trials from behind a black mesh curtain 1 m from the aquarium. During each trial we recorded which fish was the first to be captured. To assess the effect of morphology on survival, we used three Fisher Exact tests comparing the proportion of fish eaten from each treatment.

Results

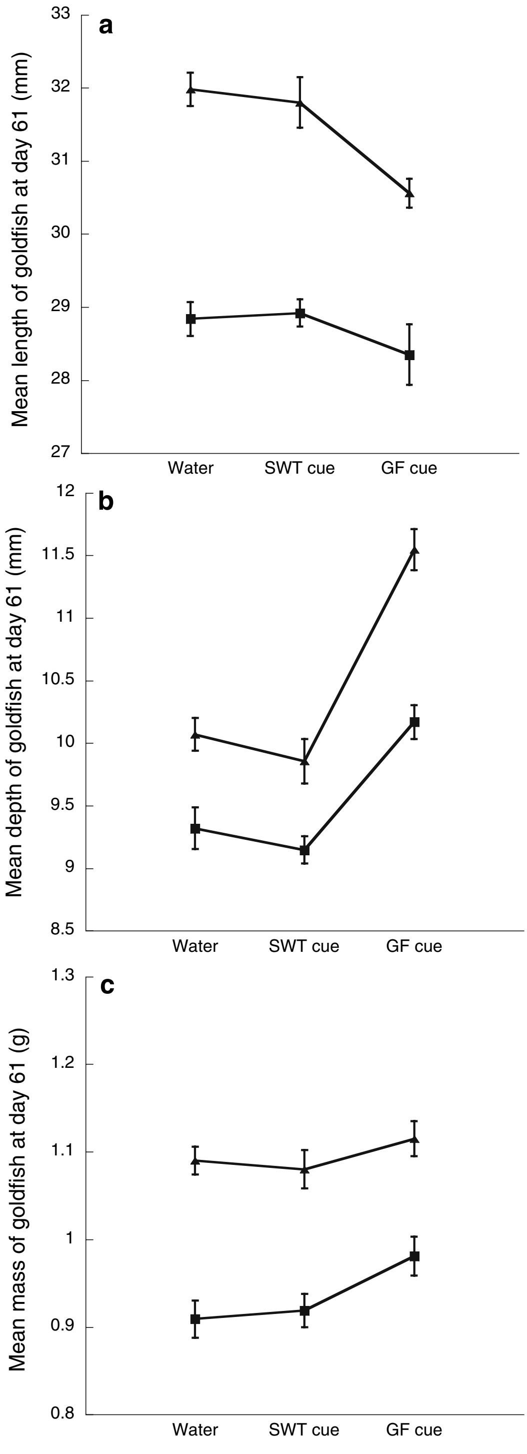
Experiment 1

The results of the repeated-measures MANOVA revealed a significant effect of time on the morphological measures (Table 1, Fig. 1a–c). We found significant time × food and time × cue interactions, demonstrating that food and cue both had significant effects on the growth of fish. As predicted, fish in the high food treatment grew more than fish in the low food treatment (Fig. 1a–c). The two MANOVAs performed in each food level revealed a

Table 1 Results of the repeated-measures MANOVA performed for experiment 1, examining the effect of time, food level (low and high) and cue (water, swordtail skin extract, goldfish skin extract) on goldfish morphology (length, depth and mass)

Effect		*F*	Hypothesis df	Error df	Sig.
Between subjects	Food	33.1	3	64	<0.001
	Cue	14.3	6	130	<0.001
	Food × Cue	4.8	6	130	<0.001
Within subjects	Time	629.0	9	58	<0.001
	Time × Food	18.2	9	58	<0.001
	Time × Cue	5.0	18	118	<0.001
	Time × Food × Cue	.9	18	118	0.556

Fig. 1 Mean (±S.E.) of (**a**) standard length (mm), (**b**) body depth (mm) and (**c**) body mass (g) on day 61 of experiment 1 for goldfish maintained on a low (*squares*) or high (*triangles*) food level and exposed to distilled water (Water), swordtail skin extract (SWT cue) or goldfish skin extract (GF cue)



significant effect of cue on the three morphological measures in low food ($F_{6,68} = 7.0$, $P < 0.001$) and high food ($F_{6,60} = 8.5$, $P < 0.001$) conditions. Univariate analyses revealed that cue had an effect on depth and mass in both food conditions (all $P < 0.043$), but length was only affected by cues in the high food treatment (low food: $P = 0.336$; high food: $P = 0.003$). The post-hoc LSD tests all indicate that, when exposed to goldfish cues, fish had higher body depth and mass than fish exposed to water or swordtail cues (all $P < 0.031$) and there were no significant difference between the depth and mass of fish exposed to water or swordtail cues (all $P > 0.169$). In high food conditions, fish exposed to alarm cues were significantly shorter than those exposed to water or swordtail cues ($P < 0.005$), but fish exposed to water or swordtail cue did not differ in their length ($P = 0.664$). These results provide strong evidence that the detection of high risk alarm cues induces dramatic changes in the growth and morphology of goldfish.

Experiment 2

The results of the repeated-measures MANOVA are presented in Table 2. We found a significant effect of time and time × treatment interaction, as well as an overall effect of frequency and cue on the morphological measures of the goldfish. The subsequent MANOVAs revealed that treatment had a significant effect on the three morphological measures for both high ($F_{6,\ 88} = 11.8$, $P < 0.001$) and low ($F_{6,90} = 10.9$, $P < 0.001$) frequency. The univariate analyses revealed a significant effect of treatment on length, depth and mass in both frequency treatments (all $P < 0.018$). Post-hoc LSD tests performed on the high frequency data revealed that fish exposed to water were significantly longer than fish exposed to cue discontinued treatment ($P < 0.001$), and those in the discontinued treatment were longer than fish exposed to cue continued treatment ($P = 0.001$). It also shows that fish exposed to continued cues are deeper bodied than fish exposed to discontinued cues ($P < 0.001$), and those in the discontinued treatment were deeper bodied than those exposed to water ($P = 0.001$). Fish exposed to goldfish cues were heavier than fish exposed to water (both $P < 0.002$), but fish exposed to goldfish cues continuously were marginally heavier than those exposed to goldfish cues in the discontinued treatment ($P = 0.053$). Post-hoc tests performed on low frequency data showed that fish exposed to water were significantly longer than fish exposed to goldfish continued cues ($P = 0.005$), but fish exposed to water and discontinued cues ($P = 0.098$) and fish exposed to continued

Table 2 Results of the repeated-measures MANOVA performed for experiment 2, examining the effect of time, cue frequency (low and high) and cue type (water, pike odour continued, pike odour discontinued) on goldfish morphology (length, depth and mass)

Effect		*F*	Hypothesis df	Error df	Sig.
Between subjects	Frequency	5.4	3	89	0.002
	Cue	20.9	6	180	<0.001
	Frequency × Cue	1.4	6	180	0.222
Within subjects	Time	2749.6	9	83	<0.001
	Time × Frequency	2.4	9	83	0.020
	Time × Cue	11.8	18	168	<0.001
	Time × Frequency × Cue	1.2	18	168	0.249

and discontinued ($P = 0.195$) did not differ in their length. Regarding depth and mass, fish exposed to continued cues were deeper bodied and heavier than fish exposed to discontinued cues (both $P < 0.001$), which were deeper bodied and heavier than fish exposed to water ($P < 0.011$).

The results of the three repeated measures MANOVAs revealed that prior to the discontinuation of the skin extract (day 0–50), fish in continued and discontinued treatments had the same growth pattern (both frequencies: no effect of continuity [both $P > 0.777$], a significant effect of time [both $P < 0.001$] and no time × continuity interaction [both $P > 0.117$]). However, during the discontinuation period (day 50–100), we found a significant effect of time, discontinuity and an interaction between the two factors (all three $P < 0.020$). This indicated that the rate of change of the morphological measures was lower when the cue was discontinued. Univariate analyses indicate that, for the two frequencies data, the interaction was significant for depth (both $P < 0.013$) and mass (both $P < 0.047$). However, length was not affected (high frequency: $P = 0.053$, low frequency: $P = 0.393$). When the cues were re-administered (day 100–150), a significant effect of time and cue discontinuity was found (all $P < 0.001$) but there was no interaction between time and discontinuity (both $P > 0.498$). This indicates that the growth pattern of fish in the continued and previously discontinued treatments were similar after the predator cues were re-administered (i.e. all the slopes were the same). These results provide very strong evidence that the adaptive change in morphology is reversible (Fig. 2).

Experiment 3

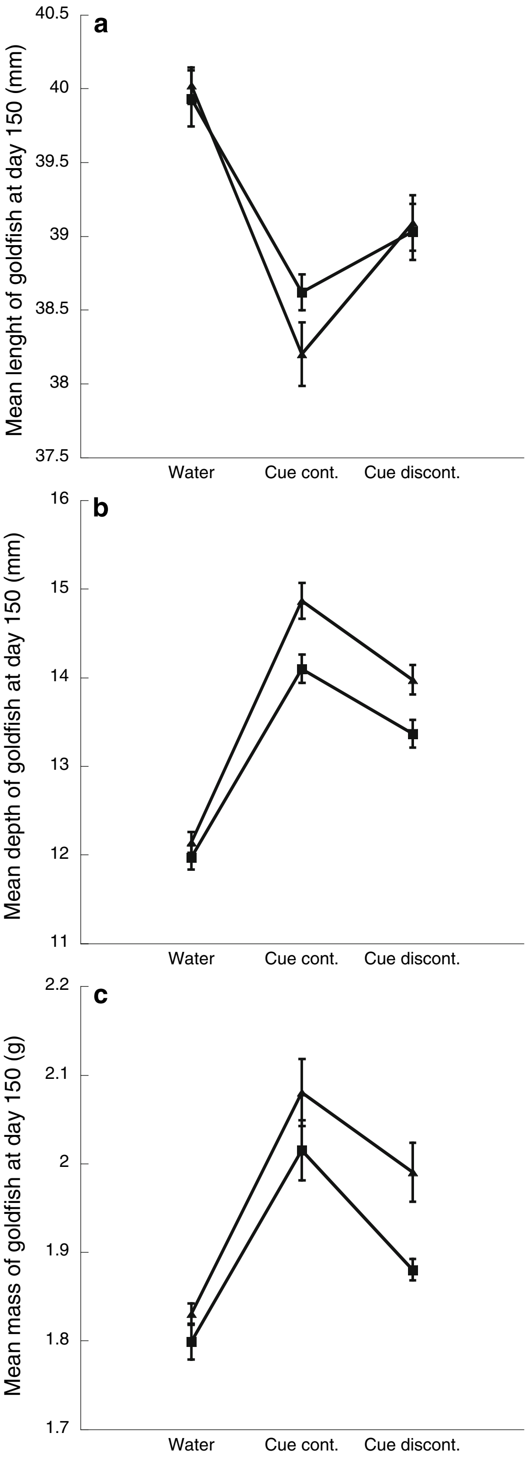
The results of the Fisher Exact tests revealed that the first fish eaten during the staged encounters was less often a fish from the goldfish skin extract treatment than a fish from the swordtail treatment (two-tailed Exact $P = 0.003$) or the distilled water treatment (two-tailed Exact $P = 0.017$). There was no difference in the probability of the fish from the swordtail and distilled water treatments being eaten (two-tailed Exact $P = 0.772$).

Discussion

The results of our experiments illustrate the dynamic nature of morphological defences in a prey fish. This is only the third species of fish for which induced morphological defences have been reported. We anticipate that other fish species may likewise show such adaptive flexibility when dealing with variable predation risk.

In our first experiment we documented that the induced morphological change (an increase in depth and mass) could result from exposure to alarm cues from injured conspecifics. Brönmark and Pettersson (1994) demonstrated that crucian carp failed to exhibit a change in morphology in response to carp that were injured by scratching their sides, but they did respond to predators fed carp. Stabell and Lwin (1997) confirmed that predator odours were responsible for inducing the change in morphology. However, the predator needs to be fed carp in order to induce the change in morphology. Such diet dependent anti-predator responses are widespread in aquatic predator/prey systems (review Chivers and Mirza 2001). Stabell and Lwin (1997) also showed that alarm cues from injured carp alone can induce the change in morphology. It seems likely that the concentration of cues used by Brönmark and Pettersson (1994) was not sufficient to elicit the morphological change. For tadpoles, Schoeppner and Relyea (2005) documented that crushed prey alone

Fig. 2 Mean (±S.E.) of (**a**) standard length (mm), (**b**) body depth (mm) and (**c**) body mass (g) on day 150 of experiment 2 for goldfish exposed to a high (*square*) or low (*triangles*) frequency of distilled water (Water), pike odour continuously (Cue cont.) or pike odour discontinued between day 51–100 (Cue discont.)



did not induce a change in morphology but odours of predators consuming prey did induce the change in morphology. In experiment 2, we likewise documented that the change in morphology could result from exposure to predators fed goldfish.

When trying to understand the ecology and evolution of induced defences, we need to consider all of the costs and benefits of the defence. While there are clear survival advantages to the prey, the prey also suffer considerable costs particularly in term of reduced growth and competitive ability (Pettersson and Brönmark 1997, 1999; Van Buskirk and Relyea 1998; Relyea 2004; Schoeppner and Relyea 2005). One of the costs that have to be considered is that related to the resources required to induce the change in morphology. We hypothesized that the ability of prey to exhibit a change in growth and morphology should be constrained by resources. In our first experiment we compared the ability of goldfish fed two different food levels to exhibit a change in morphology and found that fish fed the lower food ration were less able to exhibit a change in morphology (differential growth in depth) than those fed the higher food diet. Several studies of larval amphibians have likewise shown that induced morphological defences are weaker under low resource conditions (Relyea 2002a, b; Teplitsky et al. 2005).

When weighing the costs and benefits of exhibiting an induced defence, we need to consider the survival effects associated with the defence. For a prey animal the survival benefits should be proportional to the number of encounters with the predator. The more often the prey comes into contact with the predator, the more benefit the defence should offer. Consequently, in experiment 2 we altered the frequency with which the prey were exposed to the predator cues, predicting that the induced morphological defence should be more pronounced in the high frequency treatment than the low frequency treatment. Our data supports these predictions. Future researchers examining induced defences should carefully consider the frequency of risk in their experiments.

We have strong evidence that induced morphological defences are highly reversible in goldfish. Fish exposed to predation risk emphasized more growth in depth compared to control fish. The fish that had their predation cues discontinued during day 51–100 in experiment 2 showed the same pattern as the controls, but recovered to show the same growth rate as the predator exposed fish when we re-administered the predator cues on day 101–150. Brönmark and Pettersson (1994) suggested a limited ability of crucian carp to exhibit reversibility. Although direct comparisons are not possible, we seem to see more flexibility in reversibility in goldfish than crucian carp. This may represent a species difference or may reflect that reversible changes are much easier earlier in ontogeny, as has been shown in tadpoles (Relyea 2003). Brönmark and Pettersson (1994) used fish approximately 130 mm in length while our fish were only about 26 mm in length at the start of the experiment. The difference in reversibility for fishes of different sizes may reflect differential investment in gonadal versus somatic growth as the fishes mature. Predators are known to come and go on seasonal and yearly cycles. Future work should consider whether repeated reversals are possible in the life of a given individual.

Our final experiment addressed the survival benefits associated with the predator induced change in morphology of goldfish. We exposed goldfish from experiment 1 to yellow perch and then quantified which was the first individual eaten. We have clear evidence that perch capture the small shallow-bodied goldfish from the swordtail and water control treatments first more often than they catch the large deep-bodied goldfish from the goldfish cue treatment first. The capture difference could result from a change in the overall size of the goldfish (i.e. a mass difference) or a difference in morphology (i.e. a shape difference). Either of these differences could alter the foraging behaviour of the perch or alter the behaviour of the prey, which could make the prey less conspicuous to the perch (Anderson et al. 2006). Nevertheless, the results show a quantifiable survival benefit. These results are consistent with those of Nilsson et al. (1995) who showed that northern pike prefer shallow-bodied to deep-bodied crucian carp.

The comprehensive series of experiments that we present in this paper have considerably extended our understanding of the ecology of predator-induced morphological changes in vertebrates. We showed that both chemical alarm cues and predator odours alter the overall morphology of the goldfish. We clearly showed that fish under higher food level were able to invest in a greater depth than those under low food conditions. Moreover, we found that the frequency of risk (exposure daily vs. once every 3 days) did influence the ability to alter growth. This variable should be examined in future studies. Likewise, researchers should continue to examine the reversibility of induced morphological changes. It may be particularly informative to raise fish under different risk levels, with different frequencies and predictabilities of risk to address the costs and benefits of reversibility. Despite the selective breeding that goldfish have experienced as a result of the pet trade, they still show amazing phenotypic flexibility. The fact that such flexibility still exists may be a reminder of the power that predation pressure might have had in shaping the morphology of prey fishes. We encourage other researchers to consider phenotypic plasticity in other fish systems as has been the case in amphibian systems. The pioneering work of Brönmark and his colleagues has not received the attention that it deserves. Understanding the physiological mechanisms underlying this plasticity should prove to be a challenging but intriguing mystery.

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