

# Predation Risk Influences Adaptive Morphological Variation in Fish Populations

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**ABSTRACT:** Predators can cause a shift in both density and frequency of a prey phenotype that may lead to phenotypic divergence through natural selection. What is less investigated is that predators have a variety of indirect effects on prey that could potentially have large evolutionary responses. We conducted a pond experiment to test whether differences in predation risk in different habitats caused shifts in behavior of prey that, in turn, would affect their morphology. We also tested whether the experimental data could explain the morphological variation of perch in the natural environment. In the experiment, predators caused the prey fish to shift to the habitat with the lower predation risk. The prey specialized on habitat-specific resources, and there was a strong correlation between diet of the prey fish and morphological variation, suggesting that resource specialization ultimately affected the morphology. The lack of differences in competition and mortality suggest that the morphological variation among prey was induced by differences in predation risk among habitats. The field study demonstrated that there are differences in growth related to morphology of perch in two different habitats. Thus, a trade-off between foraging and predator avoidance could be responsible for adaptive morphological variation of young perch.

**Keywords:** adaptive morphological variation, indirect effects, phenotypic plasticity, predation, resource polymorphism.

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The phenotypic modification of an organism is often a response to a heterogeneous environment. Both habitat gradients of physical structure and differences in ecological interactions such as competition and predation are im-

portant representatives of such heterogeneity. Predation is suggested to be especially important because predators are a major structuring force in natural communities, and predation has been shown to have strong direct effects on ecological interactions (Sih et al. 1985; Lima and Dill 1990; Lima 1998). Furthermore, recent studies have shown that predator-prey interactions could be involved in diversification of species because predators have the ability to affect both the abundance and the distribution of phenotypes (Abrams 2000; Rundle et al. 2003; Vamosi 2003; Langerhans et al. 2004). In particular, there are good examples of how predation may contribute to species sorting along environmental gradients in freshwater habitats where predators may constrain the distribution and success of prey species, leading to local adaptation (McPeck 1995; Wellborn et al. 1996).

Besides direct effects through natural selection, predation can cause a variety of indirect effects that likely could produce evolutionary shifts. However, theoretical exploration of the evolutionary effects of indirect interactions is still in its infancy, and empirical examples are strongly needed (Abrams 2000). Examples of such indirect effects are apparent competition and keystone predation, but there are several other ecological indirect effects that potentially have evolutionary consequences (reviewed in Schoener 1993; Menge 1995; Abrams 2003). In particular, predators should be important for adaptive shifts of species that use different habitats and are subjected to a trade-off between foraging and predator avoidance by switching between these habitats. In such a case, high predation risk in one habitat may cause prey to shift to another habitat with the benefit of a lower risk but a cost in terms of reduced foraging efficiency. However, if the prey demonstrates phenotypic plasticity in relation to the new environment, the cost of habitat shift might be mitigated. The relationship between phenotypic plasticity and habitat-specific resource use has been shown in numerous studies (Smith and Skúlason 1996), but the role of ecological interactions, such as the effects of predators on trophic polymorphism of prey species, has not been investigated.

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In this study, we tested whether behavioral shifts due to a variation in predation risk among different habitats cause adaptive morphological changes in a fish population. In aquatic communities, indirect effects of predators have been found to be of major importance for prey habitat preference because the predation risk may vary in both littoral and pelagic habitats (Eklöv and Van Kooten 2001). However, evolutionary consequences of such indirect effects have not been tested. Thus, we combine two different models of community and evolutionary ecology: habitat preference is determined by a trade-off between predation risk and foraging return (e.g., Werner et al. 1983; Eklöv 1995), and the morphological response is determined by the diet in the new habitat, that is, phenotypic plasticity (Via and Lande 1985). We hypothesize that the relative strength of competition and predation mediates a habitat shift that, in turn, leads to an adaptive morphological shift of the prey fish. The evidence for the adaptiveness of such morphological shifts has experimentally been tested, showing strong correlations between morphology and resource-specific foraging efficiency (Svanbäck and Eklöv 2003, 2004). We combined morphological data from a field enclosure experiment with data from a natural population to test whether the morphological expression of the fish in the experiment was in the same direction as in the field. It has been argued that the mutual depletion of resources is the major ecological mechanism to the evolutionary divergence of organisms living sympatrically (Schluter 2000b). Nevertheless, several lines of evidence demonstrate that indirect effects of predators on prey resource use can produce divergence not only at the population level but also at the individual level by affecting individual morphological variation (see Abrams 2000). Thus, in order to evaluate the correlation between individual morphological variation and resource use, we analyzed individual specialization on resources rather than focusing on mean population resource use. This is important in order to detect intrapopulation differences in resource use and whether such variation could result in a morphological variation (see Bolnick et al. 2003 for review).

We addressed the following three predictions: differences in predation risk induce behavioral shifts of the prey that in turn affect individual diet specialization; differences in food resource use of the prey in turn lead to a morphological change, that is, a resource polyphenism; and variation in the prey morphology expressed in an experimental population explains fitness differences among individuals in a natural population. We experimentally tested the two first predictions and then used the experimental results to test the third prediction in a natural field population.

## Methods

### *Pond Experiment*

We performed the experiment in a rectangular pond (22 m × 77 m) at Umeå University's pond facility, Röbbäcksdalen. The pond was divided into 20 enclosures (7 m × 10 m) and fed with well water. The water depth could be adjusted between 0 and 170 cm. The enclosure walls consisted of nylon-reinforced plastic attached to stiff polypropylene plastic sheets that were buried ~15 cm into the mud. At the end of May, we drained the pond to approximately 5 cm to allow invertebrates to survive and checked the walls for potential damages caused during the winter. The water was thereafter set to a depth of 80 cm. The distribution of the vegetation (*Carex rostrata* and *Myriophyllum* sp.) in the enclosures was adjusted to 50% of each enclosure. The rest of the enclosure had open water. Between the vegetation and open water habitats, a net (mesh size 2.5 cm × 2.5 cm) was raised that allowed prey fish to pass through but restricted the predators to one of the habitats.

At the end of June, we angled predatory perch (*Perca fluviatilis*) from a nearby lake and stocked them into an adjacent pond. The predators were sustained on available bottom fauna resources before the start of the experiment. At the end of July, we electrofished young-of-the-year perch, and the fish were held in 1,000-L tanks with circulating water placed on the bank of the pond. The experiment started on August 7, when 120 young-of-the-year perch (wet mass  $0.30 \pm 0.042$  g, mean  $\pm 1$  SD) were stocked into each enclosure. For 2 days, the enclosures were checked for mortalities, and fish were replaced if necessary. On the third day, predatory perch (wet mass  $29.71 \pm 3.56$  g, mean  $\pm 1$  SD) were added to the two habitats at varied densities, making up five treatments (table 1). Because we manipulated predator density in the two habitats, the design allowed us to test for both direct (equal predator densities) and indirect (unequal predator densities) effects of predators on prey morphological responses. The treatments were replicated four times and distributed among four blocks that differed slightly in vegetation abundance, making up 20 enclosures in total. However, because there was no significant block effect in subsequent analyses, blocks were pooled.

Invertebrate densities were estimated immediately before the start of the experiment. In each enclosure, two samples were taken in the open water and in the vegetation, respectively, with a plankton net (diameter 23 cm, mesh size 75  $\mu$ m) pulled horizontally 2 m through the water (sample volume 82 L). Samples were preserved with Lugol's solution. Vegetation samples included both vegetation-attached and free-swimming microcrustaceans (zooplankton) and macroinvertebrates, whereas

**Table 1:** Number of predators in each experimental treatment (four replicates), prey survival, and prey final mass

Treatment	No. predators in open water	No. predators in vegetation	No. prey surviving	Prey final mass (g)
Control	0	0	105 ± 6.5	.86 ± .06
Equal low	3	3	95.2 ± 11.6	.74 ± .06
Equal high	6	6	83 ± 8.1	.72 ± .08
High open water	5	1	86.2 ± 14.8	.77 ± .03
High vegetation	1	5	92.2 ± 3.3	.79 ± .04

Note: Survival and mass values are replicate means ( $\pm$ SE) of recaptured fish of the initial 120 individuals in each treatment.

open-water samples included zooplankton only. Macrocrustaceans and macroinvertebrates were identified to genus or species, and individuals were measured to obtain length-frequency data. Lengths were transformed to dry mass using length-mass relationships given by Bottrell et al. (1976) or by using our own length-mass relationships (macroinvertebrates).

We estimated perch prey habitat use by direct observation from a mobile platform raised 5 m above the water surface. To facilitate the recordings, we divided each enclosure into 1 × 1-m squares by plastic sticks that were pressed into the sediment. Two people performed the recordings: one person used binoculars to continuously report the positions of the fish, and the other recorded position and behavior on a laptop computer. We followed a focal prey for a 10-min period and recorded proportional use of vegetation and open water.

At the end of the experiment (September 13), we sampled invertebrates both in the vegetation and in the open water with the same methods used earlier. We then removed all fish from the enclosures with a seine. We seined each enclosure repeatedly until we had three empty hauls in a row and then considered the enclosure empty. We determined the wet mass of the predators, and the prey and the fish were immediately frozen for later morphometric and gut content analysis.

#### *Morphological Analyses*

We analyzed the morphology of 50 haphazardly selected prey individuals from each enclosure using landmarks digitized with TPS-digit (Rohlf 2001a) from digital images of each specimen. We digitized 16 landmarks on the left side of each specimen. We used the digitized landmarks to analyze the relative position of each landmark and variation in body form using TPSRW (Rohlf 2001b). We used TPSRW to calculate partial warp and uniform scores of the individuals. The uniform shape components parameterize all shape variation that is uniform throughout the whole geometry, meaning the variation that is large scaled and neither spatially localized nor spatially disproportionate. A common example of uniform shape variation is a

general extension/contraction of a whole animal along some axis. In contrast, the partial warps measure non-uniform shape variation that is localized to particular regions of the geometry and is smaller scaled. A common example would be a local extension/contraction that does not occur in other parts of the animal (Bookstein 1991, 1996).

Both experimental fish and fish from the field survey came from the same lake, Lake Trehörningen. We recalculated mass (wet weight) and morphology of 1-year-old perch from field data (Svanbäck and Eklöv 2002, 2003). We caught perch from both the littoral and the pelagic habitats by using gillnets (see Svanbäck and Eklöv 2002, 2003 for details). We used body size (mass) of the individuals as an estimate of fitness. Body size is a reasonable estimate of fitness if individuals are of the same age, as was the case in our field survey. The morphology of the fish (field and enclosure) was combined into a single data set to calculate partial warps.

The partial warp and uniform scores were analyzed with a multivariate discriminant function analysis. We performed the discriminant function analysis on the basis of the separation (classification) of the wild-caught littoral and pelagic perch. This technique combines all partial warp and uniform scores for each fish into one function (morphological index [MI]) that maximally discriminates between the two habitats. To be able to test whether the morphological response was quantitatively of the same magnitude and in the same direction in the experimental study as in the field, we projected the partial warp and uniform scores from the experimental data on to the MI from the wild-caught perch. This allowed us to determine whether the variation in morphology of the experimental fish was correlated to growth rate in the field fish. Body form changes associated with MI were visualized as deformations by using the TPSREGR program (Rohlf 2000) to display the regression of the original coordinates on MI.

We used the MI of the 1-year-old perch in the field survey to relate differences in growth patterns between the two habitats. We analyzed the differences between littoral and pelagic perch in the relationship between the wet

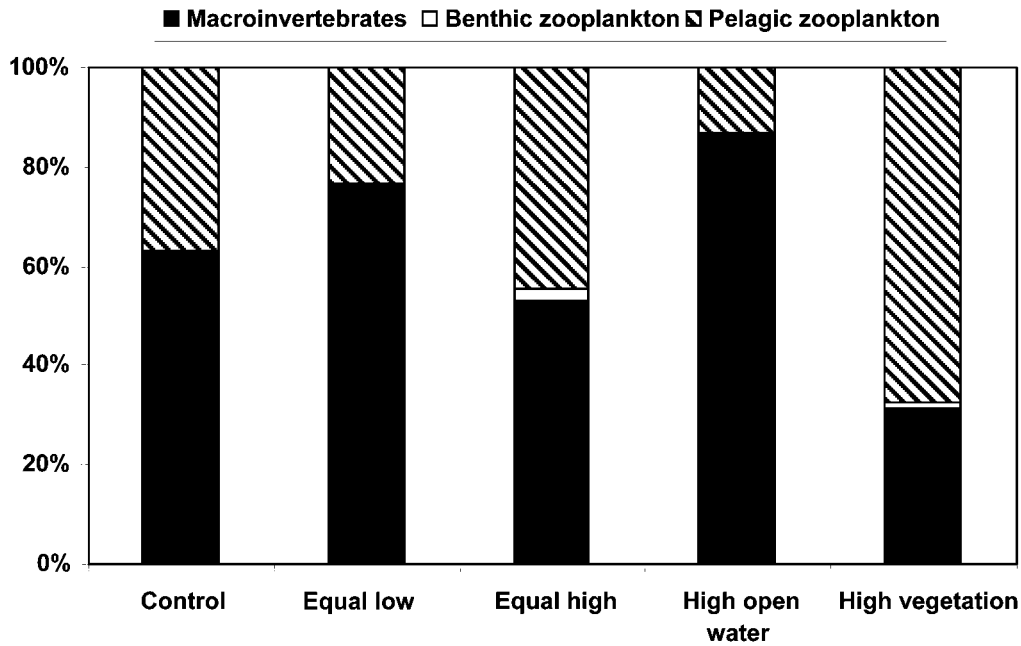


Figure 1: Percentage of prey types in the diet of the juvenile perch in each treatment at the end of the experiment.

weight of the fish and their morphology using ANCOVAs with the MI as a covariate to test for homogeneity of slopes.

#### Diet Data Analyses

The stomach contents were analyzed under a dissecting microscope and were identified to order, family, or species, and lengths of the first 10 prey of each group were measured to the nearest 0.1 mm. If there were <10 prey from a group, then all prey in that group were measured. The lengths of all prey types were then converted to biomass (dry weight) using published length-mass relationships for zooplankton (Bottrell et al. 1976) or by using our own length-mass relationships (macroinvertebrates). The biomass-based diet was separated into five different diet categories. The diet categories were cladocerans, copepods, pelagic macroinvertebrates, predator-sensitive macroinvertebrates, and chironomid larvae. Pelagic macroinvertebrates mainly consisted of chironomid pupae and *Chaoborus* larvae.

There are several methods to measure within-population or within-replicate variation in diet (Bolnick et al. 2002). To assess the within-replicate diet variation, we compared the resource use distribution of an individual to that of its population (replicate) by using a proportion similarity index (PS; Schoener 1968; Feinsinger et al. 1981; Bolnick et al. 2002). The diet overlap between an individual *i* and the replicate is

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j), \quad (1)$$

where  $p_{ij}$  is the frequency of diet category *j* in the individual *i*'s diet and  $q_j$  is the frequency of diet category *j* in the replicate as a whole. For individuals that specialize on a single diet item *j*,  $PS_i$  will be equal to the value of  $q_j$ . For individuals that consume resources in direct proportion to the population as a whole,  $PS_i = 1$ . The overall prevalence of individual specialization (IS) in the replicate can be expressed by the average  $PS_i$  value:

$$IS = \frac{1}{N} \sum_i PS_i. \quad (2)$$

Note that a high degree of individual specialization is indicated by a low value of IS, whereas if  $IS = 1$ , then all individuals have the same diet and there is no individual specialization. If resource-dependent morphological variation is mediated by predation risk, we would expect to see a correlation between morphological variation and diet. For example, if predators cause an increased use of vegetation of the prey, we expect prey to include a higher proportion of littoral prey in their diet and respond morphologically in a direction that potentially favors foraging of littoral prey. Furthermore, we would expect individual specialization to decrease (higher IS value) with increasing induced habitat restriction by predators. Also, if individ-

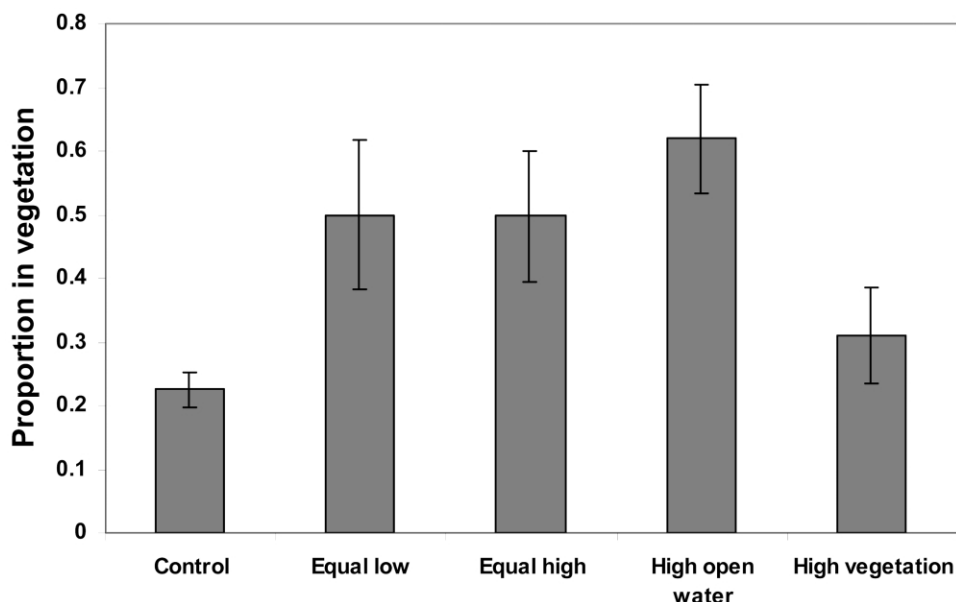


Figure 2: Average ( $\pm$  SE) proportional use of the vegetation habitat of juvenile perch in each treatment.

uals respond morphologically to differences in individual specialization, we would expect to see a larger variation in morphology among individuals that are subjected to no predation or equal predator densities among habitats.

## Results

### *Young Perch Survival and Growth*

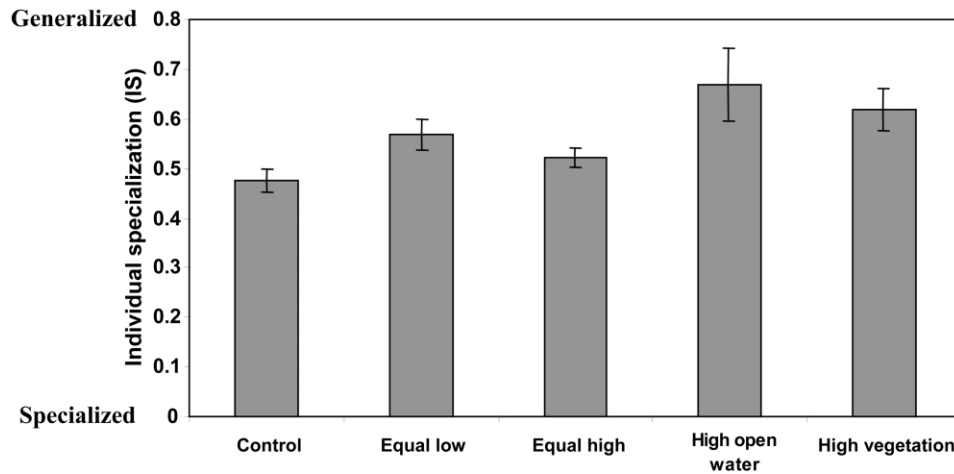
Survival of young perch was high during the experiment (70%–89%), and there was no significant difference in survival across treatments (table 1; ANOVA on young perch survival,  $F = 0.76$ ,  $df = 4, 15$ ,  $P = .56$ ). Comparing young perch survival in the control treatment with the other treatments separately did not show any significant difference (ANOVA on young perch survival, control vs. the other treatments:  $F = 2.22$ ,  $df = 4, 15$ ,  $P = .15$ ). There was no treatment effect on mass increase of young perch, suggesting that there was no difference in competition among treatments (table 1; ANOVA on young perch mass increase,  $F = 0.94$ ,  $df = 4, 15$ ,  $P = .47$ ). That resources were not limiting was supported by the fact that final individual mass was highest in the control treatment despite the highest density of young perch in this treatment.

### *Resources, Diet, and Habitat Use of Young Perch*

Before the experiment started, the zooplankton biomass differed between both habitats and treatments (tables A1,

A2 in the online edition of the *American Naturalist*; ANOVA on zooplankton biomass, habitat:  $F = 11.83$ ,  $df = 1, 30$ ,  $P = .02$ ; treatment:  $F = 3.69$ ,  $df = 4, 30$ ,  $P = .027$ ; treatment  $\times$  habitat:  $F = 3.05$ ,  $df = 4, 30$ ,  $P = .032$ ). The zooplankton biomass strongly decreased similarly in the different treatments during the experiment (repeated-measures ANOVA for the littoral habitat, time:  $F = 84.57$ ,  $df = 1, 30$ ,  $P < .001$ ; time  $\times$  treatment:  $F = 1.86$ ,  $df = 4, 30$ ,  $P = .143$ ; for the pelagic habitat, time:  $F = 165.5$ ,  $df = 1, 30$ ,  $P < .001$ ; time  $\times$  treatment:  $F = 2.12$ ,  $df = 4, 30$ ,  $P = .103$ ). Benthic zooplankton biomass was at very low levels in all treatments (tables A1, A2). The biomass of the macroinvertebrates differed significantly between treatments at the start of the experiment (tables A1, A2; ANOVA on macroinvertebrate biomass, treatment:  $F = 3.05$ ,  $df = 4, 15$ ,  $P = .05$ ) and decreased similarly among treatments during the experiment (repeated-measures ANOVA, time:  $F = 12.09$ ,  $df = 1, 15$ ,  $P = .003$ ; time  $\times$  treatment:  $F = 2.90$ ,  $df = 4, 15$ ,  $P = .058$ ).

Young perch diet consisted primarily of pelagic zooplankton and macroinvertebrates and differed among treatments (fig. 1; ANOVA on proportion of macroinvertebrates, treatment:  $F = 24.42$ ,  $df = 4, 15$ ,  $P < .0001$ ). The proportion of macroinvertebrates in the diet was higher in the treatment with a high density of predators in the open water (HOW treatment;  $P = .002$ ) and lower in the treatment with high predator density in the vegetation (HV treatment;  $P = .004$ ) than in the control (C). The pro-



**Figure 3:** Average ( $\pm$  SE) degree of individual specialization of juvenile perch in each treatment. Note that a high individual specialization (IS; IS close to 1) means individuals have generalized diet, whereas low IS means that individuals have specialized diet.

portion of macroinvertebrates in the diet was also higher in the treatment with equal low predator density (EL treatment) than in the HV treatment ( $P < .0001$ ) and lower in the treatment with equal high predator density (EH treatment) than in the HOW treatment ( $P < .0001$ ).

Young perch predominately used the vegetation in the HOW treatment and used the vegetation to the lowest proportion in the HV treatment and in C (fig. 2; ANOVA on proportion of time in vegetation, treatment:  $F = 3.37$ ,  $df = 4, 15$ ,  $P = .037$ ).

#### *Individual Specialization and Morphological Variation*

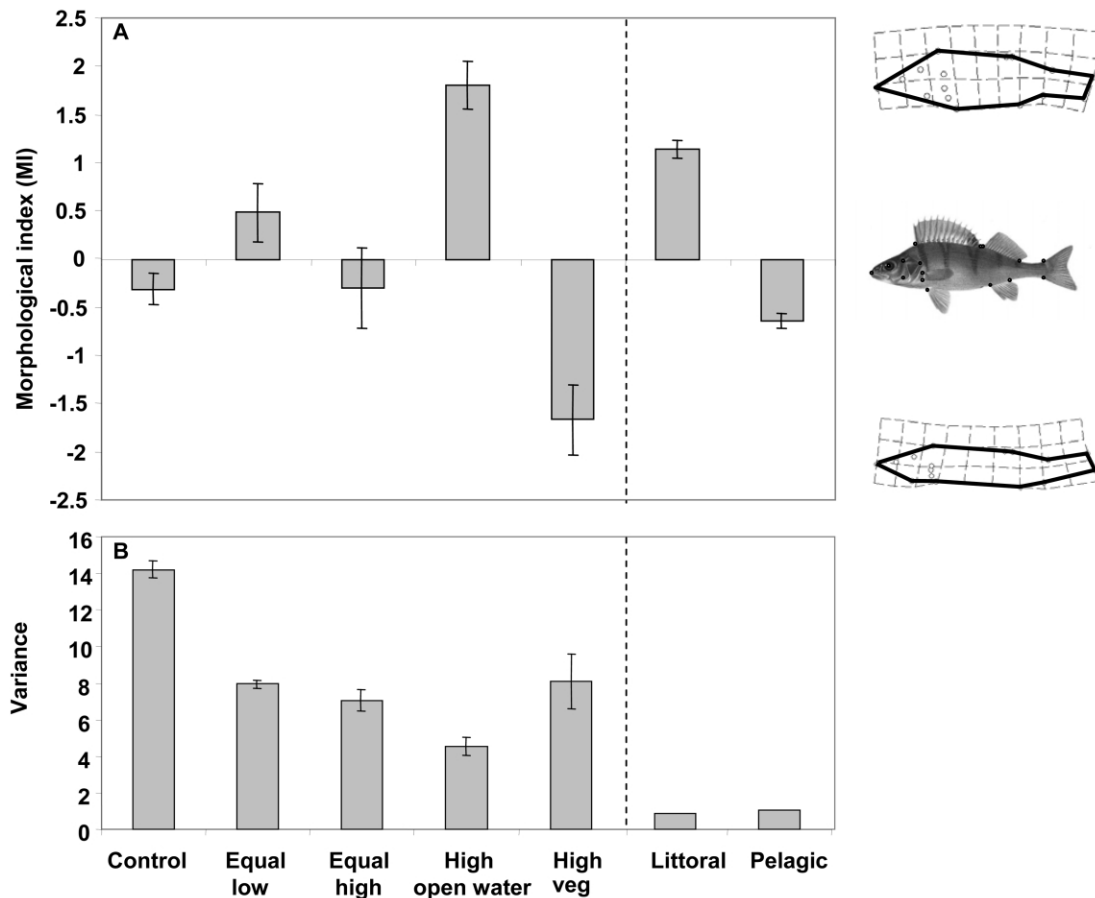
There were differences in individual specialization among the different treatments, and the lowest individual specialization occurred in treatments with unequal predator densities among habitats (HOW and HV treatments; fig. 3; ANOVA on individual specialization index,  $F = 3.411$ ,  $df = 4, 19$ ,  $P = .036$ ). Fish from the field showed a significant difference in morphology between habitats: littoral fish were more downward bent and had a slightly deeper body form, whereas pelagic fish were more upward bent and slightly shallower ( $t$ -test,  $df = 50$ ,  $t = 6.36$ ,  $P < .0001$ ). A similar pattern of habitat and morphology correlation was observed in the experiment: there was a significant morphological response of the prey across treatments, and the strongest response occurred in the unequal predator density treatments (HOW and HV treatments; fig. 4A; ANOVA on MI,  $F = 17.62$ ,  $df = 4, 19$ ,  $P < .0001$ ). When predators were at high densities in the open water, prey moved into the vegetation and responded morphologically with a body form that was bent downward and slightly deeper than prey fish in the other treatments (Tu-

key HSD test on MI and C, EL, and EH treatments vs. HOW treatment,  $P = .05$ ). Conversely, when predators were at high densities in the vegetation, prey were observed to a larger proportion in the open water, and they responded morphologically with a body form that was bent upward and slightly shallower than the prey in the other treatments (Tukey HSD test on MI and C, EL, and EH treatments vs. HV treatment,  $P = .043$ ). Prey fish in the C, EL, and EH treatments showed intermediate morphology. The within-replicate variance differed between treatments and was lowest in the HOW treatment (fig. 4B; ANOVA on morphological variance,  $F = 20.51$ ,  $df = 4, 19$ ,  $P < .0001$ ).

We used linear regression to evaluate two potential mechanisms of predator-induced disruptive selection, diet and habitat. First, the degree to which the typical littoral body form was expressed was positively correlated to the proportion of littoral prey items in the diet, suggesting that there is a strong relationship between morphology and a particular diet of the fish ( $R^2 = 0.459$ ,  $P = .001$ ; fig. 5). Second, regressing morphological variation (MI) against proportional use of vegetation showed a much weaker and nonsignificant relationship ( $R^2 = 0.103$ ,  $P = .168$ ). Third, variation in morphology (SD) decreased with a decreasing individual diet specialization ( $R^2 = 0.198$ ,  $P = .049$ ; fig. 6). Thus, the much stronger relation between morphology and diet suggests that diet has a stronger influence on the morphological variation of young perch than other potential environmental variables.

#### *Morphology and Fitness in the Field*

We evaluated whether there is a relationship between cost in terms of retarded growth and morphology in a partic-



**Figure 4:** Morphology of juvenile perch in each treatment expressed as the average ( $\pm$  SE) morphological index (MI; A) and the average ( $\pm$  SE) variance in MI in each treatment (B). The visualizations of the morphological scores to the right of the graph are deformation grid plots that describe shape changes associated with the MI. The deformation grid plots have been extended to represent individuals of scores  $-4.1$  and  $4.1$ , respectively, to make the visualization easier.

ular habitat of 1-year-old perch in the field by testing the relationship between mass and morphological variation (MI). Littoral 1+ perch showed a positive relationship between mass and the littoral morphology, whereas pelagic 1+ perch showed a negative relationship between mass and the littoral morphology (ANCOVA on mass of 1+ perch, habitat  $\times$  morphological index:  $F = 21.26$ ,  $df = 2, 51$ ,  $P < .0001$ ; fig. 7). Thus, if we consider mass to be positively related to fitness, this suggests that individuals having a more littoral body form would have a higher fitness in the littoral environment, whereas individuals having a more pelagic body form would have a higher fitness in the pelagic environment.

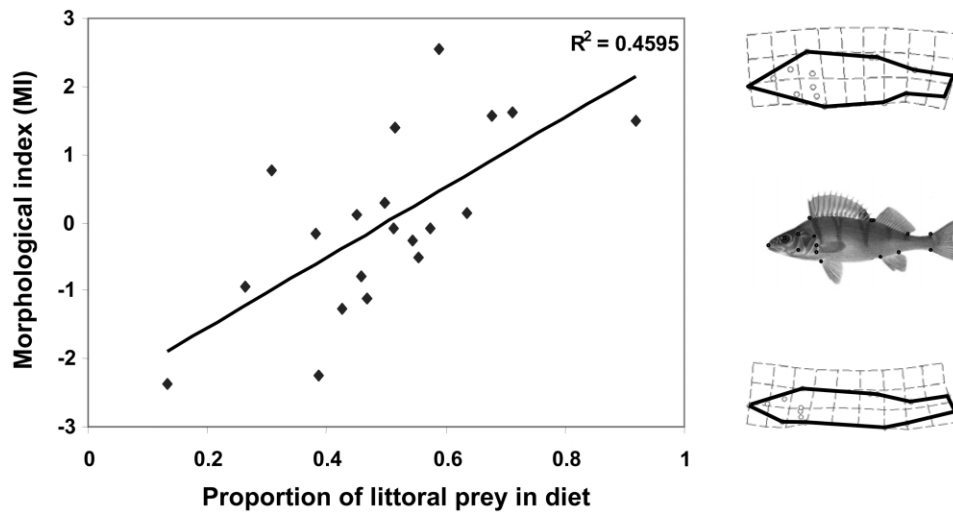
We also tested the relationship between mass and morphological variation (MI) of the experimental fish. However, the analysis did not reveal any significant difference between littoral and pelagic perch prey in the HOW and

HV treatments (ANCOVA on mass of 0+ perch, habitat  $\times$  MI:  $F = 0.125$ ,  $df = 2, 399$ ,  $P = .883$ ).

## Discussion

### *Trophic Polyphenism and Predation Risk*

Our study supports the two first predictions that predation can indirectly cause a shift in morphology of fish populations. Our experimental results demonstrate that the presence of predators may alter the habitat and food resource use of young fish. This predatory effect seemed to ultimately have indirect morphological effects on the prey fish: fish occupying the littoral habitat developed a more littoral morphology (deep body and downward bent), whereas fish occupying the pelagic habitat developed a more pelagic morphology (shallow body and upward



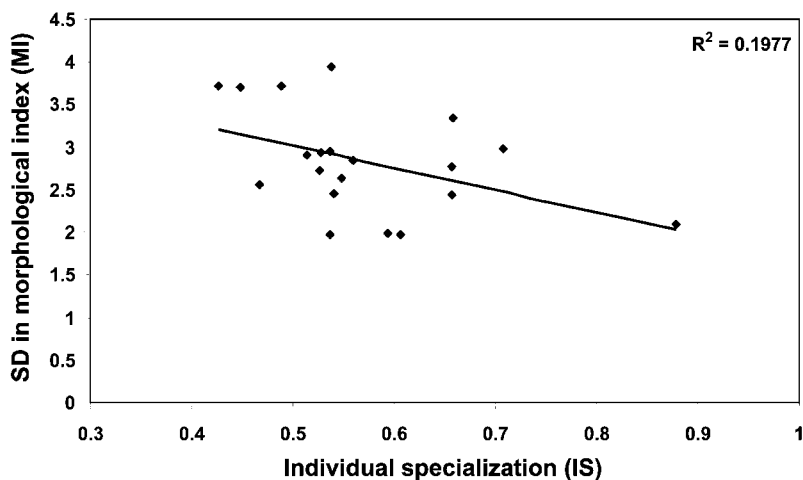
**Figure 5:** Relation between proportion of littoral prey in the diet and morphology (morphological index [MI]) at the end of the experiment. Each dot represents one replicate. The visualizations of the morphological scores to the right of the graph are deformation grid plots that describe shape changes associated with the MI. The deformation grid plots have been extended to represent individuals of scores  $-4.1$  and  $4.1$ , respectively, to make the visualization easier.

bent). This morphological dichotomy seems to be a general pattern among populations of freshwater fish (Robinson and Parsons 2002; Svanbäck and Eklöv 2002). The habitat-correlated morphological variation in the experiment was consistent with the morphological pattern of young fish in the field, supporting the third prediction. Furthermore, the individual morphological variation among perch in the field population was highly correlated to mass, suggesting that there is a cost of having an intermediate morphology. We have used growth as a proxy for fitness because in many organisms with size-structured populations, size is correlated with a number of fitness components such as reproductive success, vulnerability to predation, overwinter survival, and competition (Mittelbach 1981; Post and Evans 1989; van den Berghe and Gross 1989; Merrett 1994; Lundvall et al. 1999). To our knowledge, this is the first empirical result showing that predator-induced habitat shifts in prey can drive morphological variation, that is, a resource polyphenism (but see also Van Buskirk and Schmidt 2000). We use the term “polyphenism” here because the prey response to predators led to the expression of different phenotypes and not to different genotypes. However, in a longer time perspective, it is plausible that such plasticity can be a foreshadowing of future adaptations and possibly speciation (West-Eberhard 2003). By combining experimental and field results, our study demonstrates that predators can induce morphological variation of a species not only at the shorter time scale and at the individual level (the experiment) but also at the longer time scale and the population level (the field).

Although we have no direct quantitative evidence for the magnitude of the predation risk of small fish in the natural environment, we are confident that the risk is substantial because a major food resource of the predators’ diet in the lake we studied consists of small perch (Svanbäck and Eklöv 2002).

It has been suggested that resource polymorphism, an excessive niche-based variation within a population, is due to divergent natural selection (Smith and Skúlason 1996). The general explanation for why this is especially common among northern fish populations is that lakes of previously glaciated regions have depauperate faunas, are environmentally heterogeneous, and allow limited opportunities for dispersal (Robinson and Schluter 2000). Thus, there is good opportunity for strong divergent selection when the contrast in environments between the littoral and pelagic zones in a lake can impose strong selection on various traits related to resource use and defense against predation (Robinson and Wilson 1994; Schluter 1995; Svanbäck and Eklöv 2002). Although the examples of trophic polymorphism in freshwater fishes exist in abundance, we know less about the mechanisms that drive this pattern. Our previous work has demonstrated that there is a strong relationship between morphological variation and behavioral performance of perch (Svanbäck and Eklöv 2003, 2004). The behavioral performance is highly related to feeding efficiency on different food resources and further to fitness (Svanbäck and Eklöv 2003, 2004). The most common explanation for trophic polymorphism is that it is caused by a release in interspecific competition (Rob-





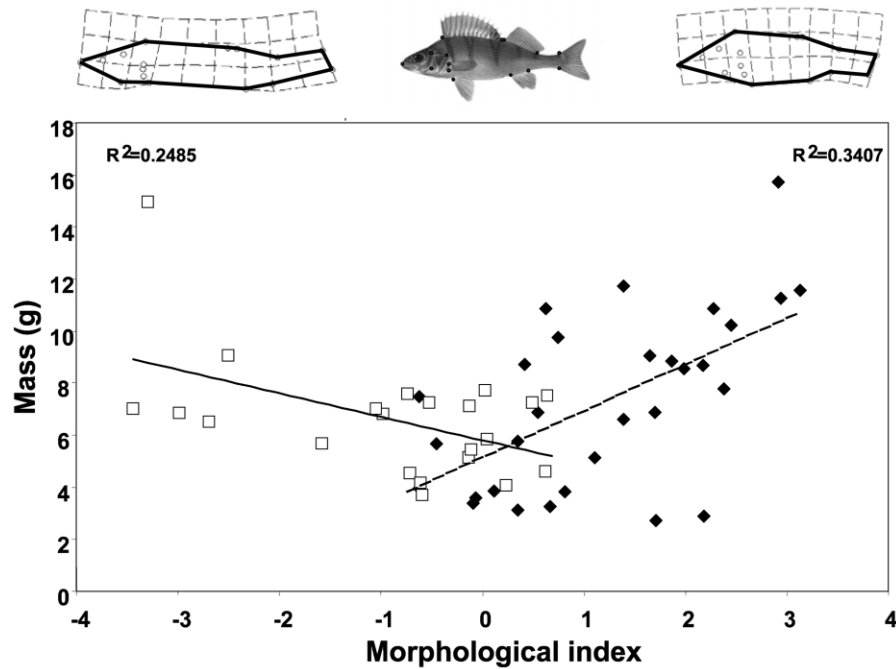
**Figure 6:** Relation between the index of individual diet specialization (IS) and morphological variation (SD) at the end of the experiment. Each dot represents one replicate. Note that a high IS (i.e., IS close to 1) means low degree of specialization.

inson and Wilson 1994; Schluter 1994). Our results suggest that the indirect effects of predators may be an important driver for trophic polyphenism. When the predation risk was higher in one habitat, the prey fish shifted to the other habitat and fed on food resources specific for this habitat. The restricted diet in turn affected the morphology of the prey fish. The evidence for the fact that the direction of the polyphenism is adaptive was demonstrated by the correlations between morphology and mass in the field populations. In the natural environment, both predation and competition are probably involved as important ecological factors affecting the morphology, and it is likely that the morphological response is affected by a trade-off between foraging and predator avoidance.

#### *The Role of Diet and Structure for Morphological Variation*

Changes in the morphology that result from habitat shifts may arise either as a response to the structure of the environment or a response to the use of specific resources. Other studies have shown that predation risk alone can induce morphological change through prey responses to chemical cues (Brönmark and Miner 1992; Eklöv 2000). However, such responses were probably of lesser importance in our study because there was apparently no directional change in morphology as a result of presence or absence of predators (compare *control*, *equal low*, and *equal high* in fig. 4A). The experiment demonstrated a response to diet, but in a natural lake, many other components of the habitat may induce a plastic response. For example, in a laboratory experiment, young perch showed high plas-

ticity to both structure and food (Olsson and Eklöv 2005). Still, the strong correlation between morphology and proportion of littoral prey in the diet in our experiment showed that the diet was of high importance for the morphological variation of young perch. Furthermore, a decrease in the variation in morphology with an increase in diet similarity also indicated that there is a connection between morphological variation and diet. Whole-lake manipulations have demonstrated that there is a strong connection between resource fluctuations and individual diet specialization (Svanbäck and Persson 2004). Svanbäck and Persson (2004) showed that when the preferred prey types of perch (macroinvertebrates and small fish) were common, all adults had the same diet. However, when the preferred prey types were scarce because of increased intraspecific competition, a part of the population switched to feed on zooplankton whereas others kept a diet of macroinvertebrates. Such specialization on certain resources may have strong implications for morphological adaptations because the foraging efficiency of perch is strongly related to individual morphology (Svanbäck and Eklöv 2003, 2004). The morphological difference between littoral and pelagic perch has been found to be driven by a functional trade-off between body forms that optimize different foraging tasks such as feeding on zooplankton and macroinvertebrates (Svanbäck and Eklöv 2004). Similar connections between habitat-specific foraging efficiencies and morphological adaptations have also been found for other species (see reviews in Smith and Skúlason 1996; Bolnick et al. 2003). For example, Ehlinger and Wilson (1988) showed that bluegill sunfish show an adaptive intraspecific variation in morphology and foraging behaviors



**Figure 7:** Mass of 1-year-old perch from the field sampling in relation to morphological index (MI) from the discriminant function analysis. Filled symbols and dotted line represent perch from the littoral zone, whereas open symbols and solid line represent perch from the pelagic zone. The visualizations of the morphological scores above the graph are deformation grid plots that describe shape changes associated with the MI. The deformation grid plots have been extended to represent individuals of scores  $-4.1$  and  $4.1$ , respectively, to make the visualization easier.

that is related to specialized feeding in either the littoral or the pelagic habitats.

#### *Ecological Interactions and Morphological Differentiation*

The role of ecological interactions for the phenotypic differentiation of species in natural communities is not yet known (see Schluter 2000a). Most evidence comes from closely related sympatric species showing exaggerated differences in morphological traits that are explained by disproportionately strong competition for resources (Schluter 2000a, 2000b). The field results in our study indicate that this process is potentially also important for the differentiation of two morphological types within a fish species. In our study, the predator and the prey are the same species, and therefore it is difficult to conceive of them as being evolutionarily independent so that selection will ultimately lead to speciation. However, we can still regard this system as a model for how such a process could work in a system where predator and prey are different species.

We found that being intermediate of littoral and pelagic morphological types had negative effects on individual growth. It is not clear whether the proximate mechanism for differences in specific growth of the phenotypes was

competition between them or whether growth was affected by individual habitat choice dependent on differences in predation risk. However, there is strong evidence that habitat shifts in small fish are driven by trade-offs between foraging and predator avoidance when foraging in the open water is more profitable but also riskier than foraging in the littoral (Werner et al. 1983; Persson and Eklöv 1995). The trade-off between foraging and predator avoidance has been shown to be the major factor influencing species interactions in ecological communities (Werner and Anholt 1993; Lima 1998), and theoretical analyses show that this trade-off also may lead to evolutionary branching and ultimately speciation (Abrams 2003). There are several potential ways that predation can lead to evolutionary branching, including apparent competition (Abrams 2000; Abrams and Chen 2002), predator selection on vulnerable forms of a species (Vamosi and Schluter 2002), and potentially intraguild predation. We did not examine the effects of predator selection on morphological diversification in our study, but our results suggest that habitat and diet selection of the prey due to predation risk alone can cause strong morphological responses. That predation risk alone can be responsible for morphological differentiation was evident in the experiment in which perch differentiated

morphologically depending on the predation risk despite no differences in competition. Furthermore, the morphological variance was lowest in the predator treatments and especially in the treatment with high predator density in the open water, in which young perch showed a strong morphological response. Thus, the presence of predators affects not only the direction of morphological development indirectly but also the variance among prey, which suggests that the mere presence of predators can have substantial directional effect on prey morphology.

Although both competition and predation are probably involved in trophic polyphenism in the natural environment, it is possible that competition is important only for morphological diversification in combination with predation when individuals trade-off between foraging and predator avoidance by moving between different habitats. If individuals should choose the behavioral option that minimizes the rate of mortality per unit increase in growth rate (Gilliam 1982; Werner and Gilliam 1984), predators would potentially have an impact on those individuals that have a lower fitness in a structured habitat and should take a higher risk to increase their foraging rate in the open-water habitat. For example, Vamosi and Schluter (2002) showed that in a stickleback species pair, the limnetic form survives better than the benthic form in the absence of predators. In contrast, in the presence of predators, the benthic form survives better because predators selectively prey on limnetic forms. Thus, contrasting predation pressures in different habitats could promote further divergence than would otherwise be expected. In our study, there was no difference in prey mass increase across treatments, indicating that the competition for resources was probably weak and that the differential resource use of the prey fish probably resulted from the restricted habitat use due to predation risk. It could be argued that the experimental test provides a relatively limited explanation for the fitness consequences in the field because there was no correlation between individual growth and morphology, as there was in the field. However, this was probably a result of the relatively short experimental time and the fact that it probably takes a longer time for differences in morphology to affect individual growth. The relation between morphological development and individual growth over time and how predators may affect this relationship is still unknown and would require further experiments.

### Conclusions

Our findings provide support for the prediction that predation risk is important for adaptive morphological variation of young fish. Character displacement or predator selection is commonly used as an explanation for adaptive morphological variation, but this was not the most likely

explanation for the morphological variation of perch in our experiment. Predators caused prey to shift to a lower-risk habitat in which they increased their use of habitat-specific resources, ultimately leading to alterations in the morphology. Such behavioral-mediated indirect effects by predators are widespread and important in ecological food webs, but their evolutionary consequences still remain poorly explored (see Werner and Peacor 2003). Rundle et al. (2003) showed a similar pattern to ours, that divergent selection may be enhanced by predation despite weak competition. This demonstrates that morphological divergence of individuals probably involves a richer array of ecological interactions than competition for resources only. Thus, exploring the evolutionary consequences of more complex ecological interactions will be a challenge for future studies.

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### Literature Cited

- Abrams, P. A. 2000. Character shifts of prey species that share predators. *American Naturalist* 156(suppl.):S45–S61.
- . 2003. Can adaptive evolution or behaviour lead to diversification of traits determining a trade-off between foraging gain and predation risk? *Evolutionary Ecology Research* 5:653–670.
- Abrams, P. A., and X. Chen. 2002. The evolution of traits affecting resource acquisition and predator vulnerability: character displacement under real and apparent competition. *American Naturalist* 160:692–704.
- Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanbäck. 2002. Measuring individual-level trophic specialization. *Ecology* 83:2936–2941.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161:1–28.
- Bookstein, F. L. 1991. *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, New York.
- . 1996. A standard formula for the uniform shape component in landmark data. Pages 153–168 *in* L. F. Marcus, M. Corti, A. Loy, G. Naylor, and D. Slice, eds. *Advances in morphometrics*. Plenum, New York.
- Bottrell, H. H., A. Duncan, Z. M. Gliwich, E. Grygierik, A. Herzig, A. Hillbrich-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24:419–456.
- Brönmark, C., and J. G. Miner. 1992. Predator-induced phenotypical

- change in body morphology in crucian carp. *Science* 248:1348–1350.
- Ehlinger, T. J., and D. S. Wilson. 1988. Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences of the USA* 85:1878–1882.
- Eklöv, P. 1995. Effects of behavioural flexibility and habitat complexity on predator-prey interactions in fish communities. PhD diss. Umeå University.
- . 2000. Chemical cues from multiple predator-prey interactions induce changes in behavior and growth of anuran larvae. *Oecologia (Berlin)* 123:192–199.
- Eklöv, P., and T. Van Kooten. 2001. Facilitation among piscivorous predators: effects of prey habitat use. *Ecology* 82:2486–2494.
- Feinsinger, P., E. E. Spears, and R. W. Poole. 1981. A simple measure of niche breadth. *Ecology* 62:27–32.
- Gilliam, J. F. 1982. Foraging under predation risk in size-structured populations. PhD diss. Michigan State University, East Lansing.
- Langerhans, R. B., C. A. Layman, A. M. Shokrollahi, and T. J. DeWitt. 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* 58:2305–2318.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215–289.
- Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lundvall, D., R. Svanbäck, L. Persson, and P. Byström. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1285–1292.
- McPeck, M. A. 1995. Morphological evolution mediated by behavior in the damselflies of two communities. *Evolution* 49:749–769.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21–74.
- Merrett, N. R. 1994. Reproduction in the North-Atlantic ichthyofauna and the relationship between fecundity and species sizes. *Environmental Biology of Fishes* 41:207–245.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Olsson, J., and P. Eklöv. 2005. Habitat structure, feeding mode and morphological reversibility: factors influencing phenotypic plasticity in perch. *Evolutionary Ecology Research* 7:1109–1123.
- Persson, L., and P. Eklöv. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76:70–81.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1958–1968.
- Robinson, B. W., and K. J. Parsons. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1819–1833.
- Robinson, B. W., and D. Schluter. 2000. Natural selection and the evolution of adaptive genetic variation in northern freshwater fishes. Pages 65–94 in T. Mousseau, B. Sinervo, and J. A. Endler, eds. *Adaptive genetic variation in the wild*. Oxford University Press, New York.
- Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: a neglected literature. *American Naturalist* 144:596–627.
- Rohlf, F. J. 2000. TPS regression. Version 1.25. Department of Ecology and Evolution, State University of New York, Stony Brook. Free software available online at <http://life.bio.sunysb.edu/morph/>.
- . 2001a. TPS-digit: basic digitizing software. Version 1.31. Department of Ecology and Evolution, State University of New York, Stony Brook. Free software available online at <http://life.bio.sunysb.edu/morph/>.
- . 2001b. TPSRW: thin-plate spline relative warp analysis. Version 1.24. Department of Ecology and Evolution, State University of New York, Stony Brook. Free software available online at <http://life.bio.sunysb.edu/morph/>.
- Rundle, H. D., S. M. Vamosi, and D. Schluter. 2003. Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. *Proceedings of the National Academy of Sciences of the USA* 100:14943–14948.
- Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* 266:798–801.
- . 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* 76:82–90.
- . 2000a. Ecological character displacement in adaptive radiation. *American Naturalist* 156(suppl.):S4–S16.
- . 2000b. *The ecology of adaptive radiation*. Oxford University Press, New York.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- . 1993. On the relative importance of direct versus indirect effects in ecological communities. Pages 365–411 in H. Kawanabe, J. E. Cohen, and K. Iwasaki, eds. *Mutualism and community organization: behavioral, theoretical and food web approaches*. Oxford University Press, Oxford.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:296–311.
- Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* 27:111–133.
- Svanbäck, R., and P. Eklöv. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia (Berlin)* 131:61–70.
- . 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos* 102:273–284.
- . 2004. Morphology in perch affects habitat-specific feeding efficiency. *Functional Ecology* 18:503–510.
- Svanbäck, R., and L. Persson. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *Journal of Animal Ecology* 73:973–982.
- Vamosi, S. M. 2003. The presence of other fish species affects speciation in threespine sticklebacks. *Evolutionary Ecology Research* 5:717–730.
- Vamosi, S. M., and D. Schluter. 2002. Impacts of trout predation on fitness of sympatric sticklebacks and their hybrids. *Proceedings of the Royal Society of London B* 269:923–930.
- Van Buskirk, J., and B. R. Schmidt. 2000. Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology* 81:3009–3028.
- van den Berghe, E. P., and M. R. Gross. 1989. Natural selection

- resulting from female breeding competition in a pacific salmon (Coho: *Oncorhynchus kisutch*). *Evolution* 43:125–140.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242–272.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford University Press, Oxford.

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