

FACILITATION AMONG PISCIVOROUS PREDATORS: EFFECTS OF PREY HABITAT USE

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Abstract. The combined effects of predators on prey may substantially differ from that of each predator species alone because of alterations in prey behavior. Using enclosures within a pond, we examined experimentally the effects of two piscivorous predators on prey mortality and prey resource levels in two habitats. The two predators use two different foraging modes, which also allowed us to examine the behaviorally induced indirect effects of prey on predator growth and prey food resources.

Both perch (*Perca fluviatilis*) and pike (*Esox lucius*) caused significant mortality of roach (*Rutilus rutilus*), and the combined predator mortality was higher than predicted from a multiplicative prey consumption model. Growth rates of perch were similar when enclosures contained only perch and when they contained perch combined with pike. The growth rate of pike was higher when they were together with perch compared to when alone. Growth of roach was similar among treatments. The invertebrate food resources of roach increased by a factor 10 in the open water but remained at similar levels throughout the experiment in the vegetation. Biomass of *Daphnia longispina*, the dominant zooplankton species in the open water, was strongly correlated with mortality of roach, indicating a density-mediated indirect effect of predators on prey resources. There was no indirect effect on *D. longispina* in the vegetation caused by habitat restriction of roach and only a weak relationship in the open water. There was a strong indirect effect of pike predation on macroinvertebrates induced by a habitat shift of roach.

Our results suggest that there was facilitation between predators caused by conflicting antipredator behavior of roach, which resulted in density-mediated indirect effects on prey resources. The behavioral response of roach to the two predators also induced indirect effects on invertebrate prey.

Key words: behavior; *Esox lucius*; habitat choice; indirect effects; macroinvertebrates; multiple predator; *Perca fluviatilis*; piscivorous predators; prey refuge; *Rutilus rutilus*; zooplanktivorous.

INTRODUCTION

The study of predator–prey interactions has been central in community ecology in providing an understanding of species relations in food webs (Brooks and Dodson 1965, Sih et al. 1985, Lima and Dill 1990, Lima 1998). Recently, an extensive literature has demonstrated that species-specific dynamic traits, such as behavior, morphology, and body size, are key elements affecting the outcomes of predator–prey interactions (Lima and Dill 1990, Werner 1992, Eklöv and Diehl 1994, Lima 1998, Eklöv and Werner 2000). In particular, changes in traits of organisms can not only affect the direct consumption of predators, but also have large indirect effects on competitive and predator–prey interactions among other community members (Abrams 1993, 1995, Werner and Anholt 1996, Peacor and Werner 1997, Eklöv and Werner 2000). Although the num-

ber of studies examining the species-specific traits in predator–prey interactions is increasing, there is still little evidence for how these traits may affect species interactions. The effects of traits on species interactions are especially apparent in the presence of multiple predators because different predators may impose conflicting demands on prey behavior, leading to different outcomes compared to pair-wise interactions (Matsuda et al. 1993, Sih et al. 1998, Eklöv and Werner 2000). Because prey typically face more than one predator at a time, the study of multiple predator–prey interactions should provide a more mechanistic and realistic understanding of species interactions in a community (Sih et al. 1998).

A multiple predator effect results when prey face simultaneously several different predators that together cause a nonadditive effect on prey mortality (Sih et al. 1998). The nonadditive effect arises if the encounter rate of prey either increases or decreases with one of the predators when a second predator is added. The nonadditive effect may either be caused by an indirect interaction between predators due to conflicting prey responses (net facilitation) or by interference competition between predators (net inhibition) (Vandermeer et al. 1985, Matsuda et al. 1993). Although conflicting

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prey responses to predators might be quite common because predators forage in different habitats and at different times of the day or use different foraging modes, it is less clear how these responses may affect the magnitude of interaction between prey and the different predators. Furthermore, because predators can regulate the relationships between trophic levels, it is important to evaluate the nonadditive relationships as separate predator-prey links in order to predict community structure.

In aquatic communities, structural complexity is an important factor mediating predator-prey interactions (Savino and Stein 1989, Persson 1991, Diehl and Eklöv 1995, Persson and Eklöv 1995). In general, foraging efficiency of predators decreases in the presence of structural complexity, but structure may affect the foraging rate of predators differently because predators differ in foraging mode and habitat-specific efficiency (Savino and Stein 1989, Eklöv 1992, 1997, Eklöv and Diehl 1994). Perch (*Perca fluviatilis*) and pike (*Esox lucius*) are major piscivorous predators in European lakes and cause major habitat shifts in prey, which can lead to changes in predator-prey and competitive interactions (Eklöv and Diehl 1994, Diehl and Eklöv 1995, Persson and Eklöv 1995). Perch is an active, group-foraging predator that is most efficient in the open water (Eklöv 1992, Eklöv and Diehl 1994). Pike is a sit-and-wait predator that forages mainly close to the littoral vegetation and is more efficient than perch in structurally complex environments (Eklöv and Diehl 1994). As prey generally tend to avoid these predators by a habitat shift, their combined effects might differ substantially from that of each predator species alone. To evaluate the combined predator-prey interactions of perch and pike, we examined both the numerical and behavioral responses of a common prey, roach (*Rutilus rutilus*), and how these responses, in turn, affected predator growth and invertebrate resource levels. Using treatments with each predator singly and with both predators combined, we estimated the (1) additive effect of each predator species on prey behavior and mortality, (2) nonadditive effect of the two predators on prey mortality and behavior, and (3) indirect effects of predators on their own growth and on prey resource levels.

MATERIALS AND METHODS

We performed the experiment in 1997 in a rectangular pond (22 × 77 m) at Röbbäcksdalen, Umeå University's pond facility for aquatic research in Sweden. The pond is fed with well water and the water level can be adjusted between 0 and 170 cm. In May, we drained the pond to ~5 cm to allow invertebrates to survive. We divided the pond into 20 enclosures (7 × 10 m). The walls consisted of nylon reinforced plastic attached to stiff propylene plastic sheets that were buried to ~15 cm into the mud. The water was thereafter set to a depth of 80 cm. The distribution of vegetation

(*Carex rostrata* and *Myriophyllum* sp.) in the enclosures was adjusted to a strip of vegetation extending 3 m from the shore. The rest of the enclosure had open water.

At the beginning of May we electrofished age 1+ yr roach in a nearby lake. The fish were brought to an adjacent pond and held until the start of the experiment. Two weeks before the experiment started we electrofished or angled predatory perch and pike from nearby lakes. The predators were fed a mixture of age 0+ yr perch and roach and were held in 1000-L tanks with circulating water placed on the bank of the pond. The experiment started on 16 August, when 80 age 1+ yr roach (wet mass, 1.88 ± 0.077 g, mean \pm 1 SD) were stocked into each enclosure. For 3 d the enclosures were checked for mortalities and fish were replaced if necessary. On the third day, perch (wet mass, 104.4 ± 36.4 g) and pike (wet mass, 110.9 ± 50.6 g) were added to the enclosures forming the following treatments: 4 perch, 4 pike, 4 perch + 4 pike, and a control with no predators. The predators were matched by size to establish a similar size distribution of predators among enclosures. The predators were then individually marked with Floy Tags before stocking (Floy Tag & Manufacturing, Seattle, Washington, USA) to enable individual recognition. The treatments (including control) were replicated four times and distributed among four blocks that differed slightly in vegetation abundance, making up 16 enclosures in total.

Invertebrate densities were estimated immediately prior to the start of the experiment. In each enclosure, one sample was taken in the vegetation and one in the open water with a plankton net (diameter 23 cm, mesh size 75 μ 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 open water samples included zooplankton only. Microcrustaceans 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 in Botrell et al. (1976) or by using our own length-mass relationships (macroinvertebrates).

We estimated roach behavior 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 used binoculars to continuously report the positions of the fish and the other recorded position and behavior on a lap-top computer. We followed all individual predators and a focal prey for 10 min, respectively, and the recorded behavior was proportion of prey active and proportional use of refuge and open water by both prey and predators. We also recorded more detailed behavior of the predators and

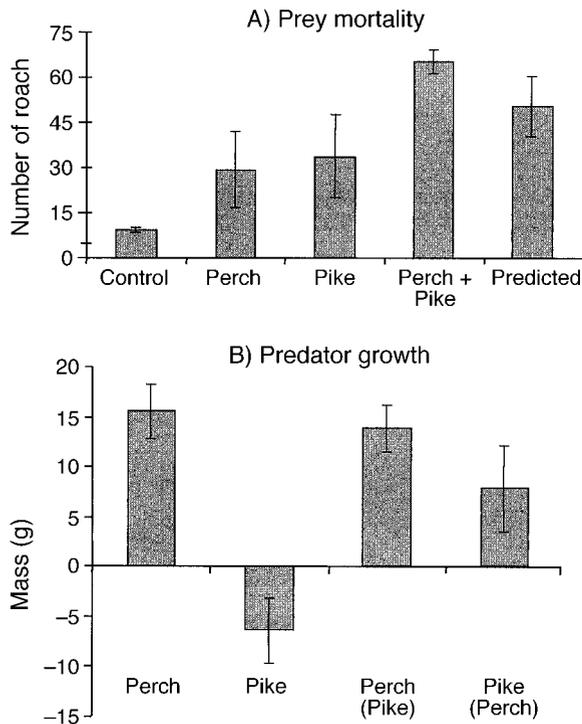


FIG. 1. (A) Number of roach that died during the experiment in the control, perch, pike, and perch + pike treatments (means \pm 1 SE). The predicted value is calculated from a multiplicative prey consumption model (see *Materials and Methods*). (B) Mass increase of perch and pike during the experiment in the perch, pike, and perch + pike treatments (means \pm 1 SE).

the prey but the description of methods and results of those behaviors will be reported elsewhere (P. Eklöv and T. VanKooten, *unpublished data*). Behavioral recordings were conducted during the first and last weeks of the experiment with the same procedure on both occasions.

At the end of the experiment (17–18 September) we sampled invertebrates both in the vegetation and open water with the same methods used earlier. We then removed the fish from the enclosures with a seine, determined the wet mass of roach and piscivores (perch and pike), and the piscivores were immediately frozen for later gut-content analysis. Final mass of roach was based on the sum of all individuals retrieved in each enclosure whereas the mass of piscivores was determined individually. One replicate was discarded from the analysis due to a hole that we found in the wall of one enclosure (four perch). The enclosure was situated at the end of the pond, and, therefore, the hole did not affect other enclosures.

Statistical analyses were conducted using ANOVA, with perch and pike as factors, on mortality, growth, activity, and habitat use of roach, and total biomass of invertebrates. Predator growth was analyzed using predator species and predator density as factors. Linear

regression was used to estimate the relation between *Daphnia longispina* and abundance of roach in the two habitats. Proportions were square-root arcsine-transformed and the other data were $\ln(x + 1)$ -transformed to stabilize variance. Because there was no significant block effect in any of the analyses, blocks were pooled. The experiment was designed to test for deviations from additive-model predictions concerning the consumption rate of the predators. Total prey consumption was estimated from prey mortality at the end of the experiment. If the predators have independent (i.e., additive) effects on roach mortality, the proportion of roach killed at the end of the experiment would be the following (after Soluk 1993):

$$P_{ab} = N_p(P_a + P_b - P_aP_b)$$

where P_{ab} is the predicted combined consumption for the initial prey density N_p , and P_a and P_b are probabilities of being consumed by perch or pike, respectively, over the experimental period. The model is derived from the additive theorem of probability and assumes that the capture probability of one predator lowers the capture probability of the other predator. The model is referred to as a multiplicative risk model and has the advantage that the predicted consumption P_{ab} cannot exceed the total number of prey introduced (Wilbur and Fauth 1990, Wootton 1994). To test the multiplicative mortality hypothesis we performed a two-way ANOVA on log-transformed mortality of roach. A significant interaction term would suggest nonadditive predation effects of perch and pike on roach mortality.

RESULTS

Roach mortality and growth of piscivores

Both perch and pike caused significant mortality of roach of similar magnitude (Fig. 1A, Table 1). However, the combined predation mortality was nonadditive, indicated by the significant interaction term (Table 1). This suggests that there was an interaction between the two predators that led to higher prey mortality with combined predators compared to the prediction from an additive consumption model.

The nature of the interaction was examined in an ANCOVA of mass change of the predators during the experiment. Overall, pike had a lower growth than perch (Fig. 1B, Table 2). However, pike gained more

TABLE 1. ANOVA for the effect of perch and pike on the mortality of roach in an experimental pond at Röbbäcksdalen, Umeå University, Sweden.

Source of variation	SS	df	F	P
Perch	2.609	1	14.146	0.003
Pike	4.297	1	23.298	0.001
Perch \times Pike	0.852	1	4.62	0.055
Error	2.029	11		

TABLE 2. ANCOVA for the effect of predator species and predator density on mass change of perch and pike using initial perch and pike mass as covariates.

Source of variation	ss	df	F	P
Species	749.384	1	19.015	0.001
Density	107.861	1	2.737	0.129
Species × Density	223.207	1	5.664	0.039
Initial mass	69.14	1	1.754	0.215
Error	394.108	10		

than perch in the combined predator treatment compared to the single predator treatment, as indicated by the significant species × density interaction (Table 2). Pike mass was higher in the combined predator treatment than in the single predator treatment whereas perch mass was similar in both treatments (Fig. 1B).

Roach growth

There was no difference in roach growth between treatments despite both roach density and food resource levels differing among treatments at the end of the experiment (Fig. 2, ANOVA on roach growth: effect of perch, $F_{1,8} = 1.230$, $P = 0.3$; effect of pike, $F_{1,8} = 0.012$, $P = 0.915$; effect of perch × pike, $F_{1,8} = 0.342$, $P = 0.575$).

Macroinvertebrates and zooplankton

Prior to the start of the experiment, ephemeropterans, hemipterans, and zygopterans dominated the macroinvertebrate fauna, and the total biomass was marginally higher in the pike treatment (Fig. 3, ANOVA on macroinvertebrate biomass: perch effect, $F_{1,11} = 0.129$, $P = 0.73$; pike effect, $F_{1,11} = 4.422$, $P = 0.057$; perch × pike, $F_{1,11} = 1.702$, $P = 0.216$). Macroinvertebrate biomass decreased over time and decreased more in the pike treatment compared to the other treatments, as indicated by the significant time × pike interaction effect (Table 3A, Fig. 3). Ephemeroptera dominated the macroinvertebrates remaining at the end of the experiment. Low numbers of *Chironomidae* spp., *Chaoborus* spp., *Asellus aquaticus*, and *Pisidium* spp. were also found (other category).

In the vegetation, the zooplankton community was dominated by *Daphnia longispina*, cyclopoid copepods, and *Eurycerus* sp. and there were no differences in zooplankton biomass between treatments before the start of the experiment (Fig. 4A, ANOVA on zooplankton biomass in the vegetation: perch effect, $F_{1,11} = 0.691$, $P = 0.424$; pike effect, $F_{1,11} = 0.257$, $P = 0.622$; perch × pike effect, $F_{1,11} = 0.933$, $P = 0.355$). Zooplankton total biomass did not change over time (Table 3B), and there were no treatment differences at the end of the experiment (Fig. 4B, ANOVA on zooplankton biomass: perch effect, $F_{1,11} = 2.261$, $P = 0.158$; pike effect, $F_{1,11} = 1.721$, $P = 0.214$; perch × pike effect, $F_{1,11} = 1.747$, $P = 0.211$).

In the open water the zooplankton community was

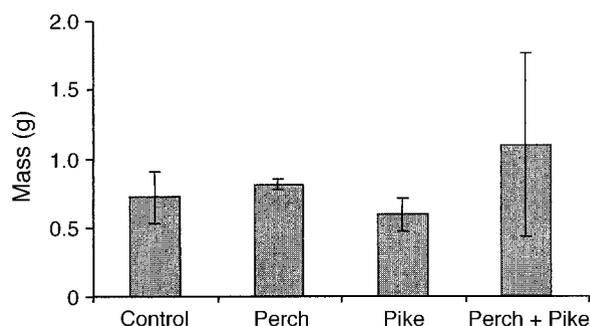


FIG. 2. Mass increase of roach during the experiment in the control, perch, pike, and perch + pike treatments (means ± 1 SE).

dominated by *D. longispina*, cyclopoid copepods, and *Eurycerus* sp., and there were no differences among treatments before the start of the experiment (Fig. 4C, ANOVA on open water zooplankton biomass: perch effect, $F_{1,11} = 0.063$, $P = 0.807$; pike effect, $F_{1,11} = 0.541$, $P = 0.477$; perch × pike effect, $F_{1,11} = 0.282$, $P = 0.606$). Zooplankton biomass increased strongly during the experiment, but there was no interaction effect of time with treatment (Table 3C, Fig. 4D), and there were no treatment differences at the end of the experiment (ANOVA on zooplankton biomass: perch

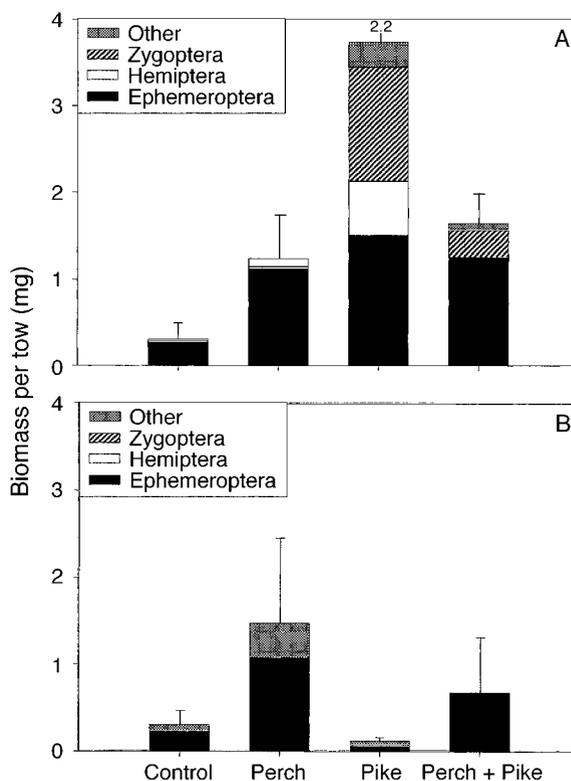


FIG. 3. Biomass per tow of macroinvertebrates in the vegetation in the control, perch, pike, and perch + pike treatments (A) at the start of the experiment and (B) at the end of the experiment (means ± 1 SE).

TABLE 3. Repeated-measures ANOVA for the effect of perch and pike on (A) macroinvertebrate biomass, (B) zooplankton biomass in the vegetation, and (C) zooplankton biomass in the open water using August and September as repeated measures.

Source of variation	SS	df	F	P
A) Macroinvertebrate biomass				
Perch	0.384	1	0.956	0.347
Pike	0.337	1	0.837	0.378
Perch × Pike	0.469	1	1.167	0.301
Error	4.824	12		
Time	1.615	1	6.331	0.027
Time × Perch	0.103	1	0.404	0.537
Time × Pike	1.372	1	5.377	0.039
Time × Perch × Pike	0.161	1	0.633	0.442
Error	3.062	12		
B) Zooplankton biomass in the vegetation				
Perch	0.749	1	1.107	0.315
Pike	0.145	1	0.215	0.652
Perch × Pike	0.008	1	0.012	0.916
Error	7.447	11		
Time	2.032	1	1.516	0.244
Time × Perch	3.813	1	2.844	0.120
Time × Pike	1.09	1	0.813	0.386
Time × Perch × Pike	1.827	1	1.363	0.268
Error	14.747	12		
C) Zooplankton biomass in the open water				
Perch	0.379	1	0.684	0.426
Pike	0.098	1	0.177	0.682
Perch × Pike	0.137	1	0.248	0.628
Error	6.095	11		
Time	6.694	1	9.182	0.011
Time × Perch	0.379	1	0.520	0.486
Time × Pike	0.553	1	0.759	0.402
Time × Perch × Pike	0.007	1	0.010	0.922
Error	8.019	11		

effect, $F_{1,11} = 0.678$, $P = 0.428$; pike effect, $F_{1,11} = 0.499$, $P = 0.495$; perch × pike effect, $F_{1,11} = 0.093$, $P = 0.766$).

There was a strong relation between roach mortality and final *D. longispina* biomass (Fig. 5A; $R^2 = 0.777$, $P < 0.0001$). Regressions on *D. longispina* biomass against numbers of observed roach in the two different habitats showed only a weak relation for *D. longispina* biomass in the open water habitat and none in the vegetation (Fig. 5B; regression on *D. longispina* at the end of the experiment against numbers of prey in the open water, $R^2 = 0.270$, $P = 0.047$; and in the vegetation, $R^2 = 0.001$, $P = 0.919$).

Predator and prey habitat use and prey activity

Both in August and in September, pike predominantly used the vegetation whereas perch predominantly used the open water (ANOVA on proportional use of the vegetation refuge by perch and pike: species effect, $F_{1,26} = 8.923$, $P = 0.007$; effect of time, $F_{1,26} = 0.319$, $P = 0.578$). There was no difference in roach activity between treatments, and activity of roach did not change with time (Fig. 6; ANOVA on prey activity using August and September as repeated measures: perch effect, $F_{1,8} = 1.417$, $P = 0.268$; pike effect, $F_{1,8} = 1.247$, $P = 0.292$; perch × pike effect, $F_{1,8} = 2.078$,

$P = 0.187$; time effect, $F_{1,8} = 1.176$, $P = 0.310$; time × perch effect, $F_{1,8} = 0.102$, $P = 0.757$; time × pike effect, $F_{1,8} = 0.215$, $P = 0.655$; time × perch × pike effect, $F_{1,8} = 0.017$, $P = 0.898$).

Roach primarily used or stayed close to the vegetation in the presence of perch (Fig. 7, Table 4). Essentially no roach entered the vegetation in the pike and control treatments (Fig. 7). Roach use of vegetation did not change with time (Table 4).

DISCUSSION

A growing number of studies demonstrate that the impact of multiple predators cannot be predicted from the sum of pair-wise interactions (reviewed by Sih et al. 1998). To improve our understanding of the consequences of species interactions, we not only have to broaden our focus to include simultaneous interactions between several species but also evaluate the consequences of these interactions to other species in the food web. This study documented strong interactions of two predators; mortality of roach was higher than predicted from additive prey consumption. This appeared to result from a conflicting behavioral response of roach to the two predators. In turn, prey habitat shifts and prey mortality caused by the presence of two different predator species had strong effects both on the growth of predators and on prey's food resources.

Pike and perch differed in their foraging efficiency in the two habitats (Eklöv and Diehl 1994), suggesting that the observed increase in the combined predation rate did not benefit the predators equally. Pike grew considerably more when together with perch compared to when alone whereas perch growth did not differ between the one- and two-predator treatments. Perch occupied primarily the open water habitat, in which they can forage at high rates due to group foraging behavior (Eklöv 1992). In contrast, pike are typically sit-and-wait predators that mainly forage in or close to vegetation (Diana et al. 1977, Eklöv 1997). Foraging efficiency of both piscivores is higher in the absence of structural complexity; however, pike are more efficient than perch at catching prey in the vegetation (Eklöv 1992, Eklöv and Diehl 1994). Thus, it is likely that the difference in growth of the predators when they were combined was because roach used the vegetation more and thus became more susceptible to pike predation. The higher strike efficiency of pike than perch probably also contributes to the increase in pike growth, i.e., perch spend more time chasing prey than pike (Eklöv and Diehl 1994).

Pike also appeared to benefit from the combined treatment because of reduced interference among individuals, which can significantly inhibit pike growth (Eklöv 1992, Eklöv and Diehl 1994). Pike are strongly cannibalistic if size differences are sufficient (Nursall 1973), and two smaller individuals in one enclosure of our experiment were eaten by a larger pike. However, we did not observe any cannibalism in pike in the com-

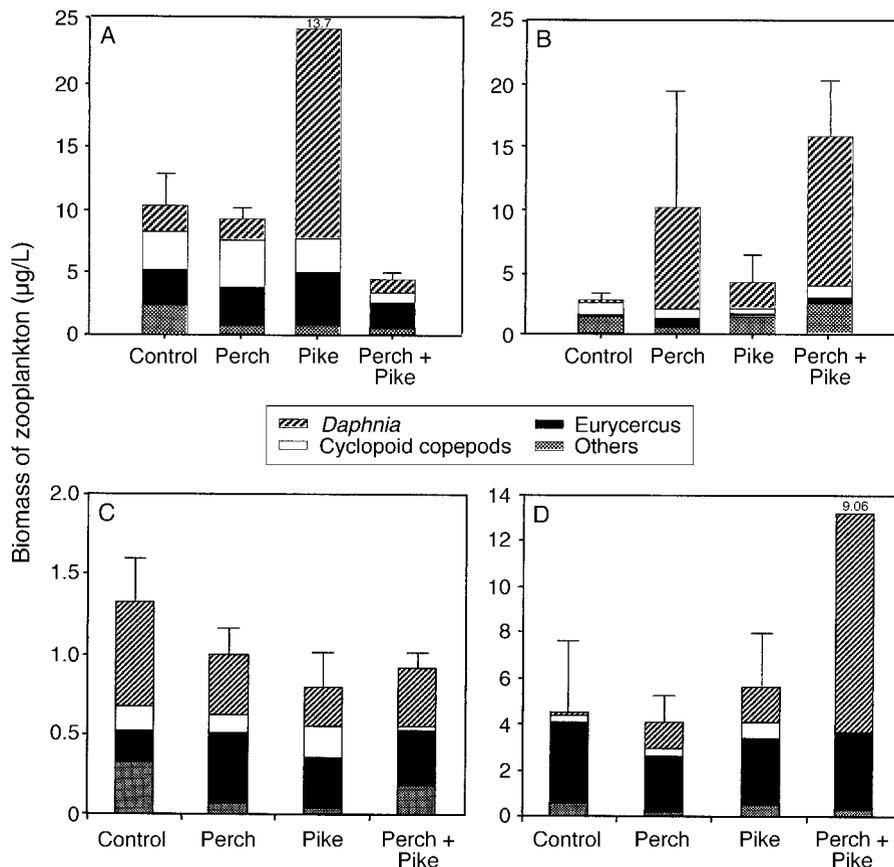


FIG. 4. Top panels: total biomass of zooplankton in the vegetation in the control, perch, pike, and perch + pike treatments (A) at the start of the experiment and (B) at the end of the experiment (means + 1 SE). Bottom panels: mass of zooplankton in the open water in the control, perch, pike, and perch + pike treatments (C) at the start of the experiment and (D) at the end of the experiment (means + 1 SE).

bined predator treatment, suggesting that cannibalism decreased when roach became more available.

Responses of roach to one predator species

In the presence of piscivorous perch, roach moved into or stayed close to the vegetation, likely using the structural complexity to reduce predation (Anderson 1984, Diehl and Eklöv 1995, Persson and Eklöv 1995). However, a shift into structurally complex habitats is often associated with a reduced foraging rate because physical structure interferes with foraging or due to competition with other refuging prey (Persson 1991, Fraser and Gilliam 1992, Diehl and Eklöv 1995, Persson and Eklöv 1995). In contrast to previous experiments (Person and Eklöv 1995), roach growth in our experiment did not decrease by the higher refuge use compared to controls. This was likely because the initial density of roach was low and decreased further through the experiment as indicated by the increase of open water zooplankton during the experiment.

In the presence of pike, which stayed mainly in or close to the vegetation, roach used the open water almost exclusively. The main zooplankton food, *Daphnia*

longispina, decreased with increasing density of roach in the open water, so the structured habitat could have been more profitable. However, total food levels were similar in the two habitats, and therefore, because roach has a higher foraging rate in open water compared to structured habitats (Persson 1991), they should stay mainly in the open water habitat.

Responses of roach to two predators

In general, prey avoid encounters with predators either by reducing activity or by changing habitat (Werner 1992, Persson et al. 1996). Predators did not affect prey activity or prey growth in our experiment (see also Eklöv and Persson 1995, Christensen 1997), suggesting that roach continued to forage efficiently despite the presence of predators. This, in turn, suggests that the risk enhancement for roach in the presence of two predators was dependent on prey habitat choice, predator behavior, or predator density.

It is plausible that there are constraints in roach behavior that caused the nonadditive effects. Such constraints could, for example, involve conflicting responses to different predators, such that responses to

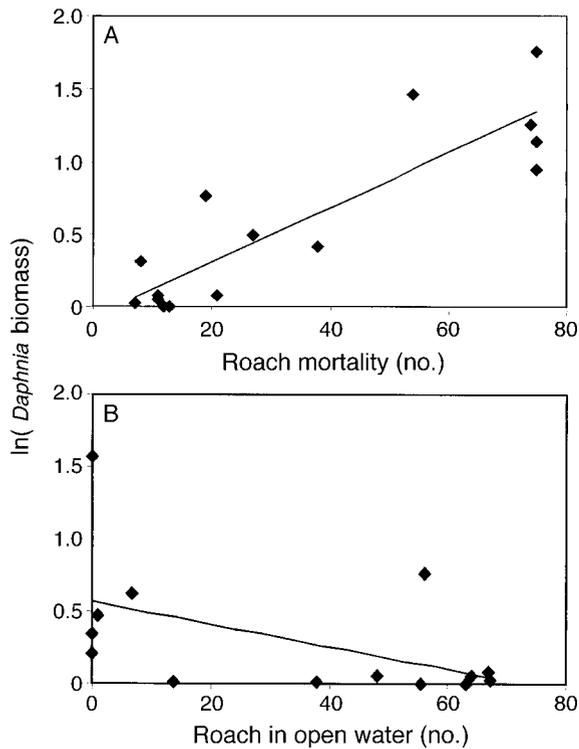


FIG. 5. (A) The relation between total mortality of roach and total biomass (in micrograms per liter) of *Daphnia longispina* at the end of the experiment and (B) the relation between number of prey observed in the open water in September and *D. longispina* biomass at the end of the experiment.

one predator results in a greater risk from another predator (Soluk and Collins 1988, Wissinger and McGrady 1993). Theoretical studies show that an increase in non-specific predator defense can lead to an overall decreased predation risk, whereas conflicting predator-specific defenses should generally lead to increased predation risk (Lima 1992, Matsuda et al. 1993). In the presence of the two predators, switching between habitats probably increased dramatically the risk to roach from pike because roach were repeatedly chased into the refuge where they were at risk from pike predation.

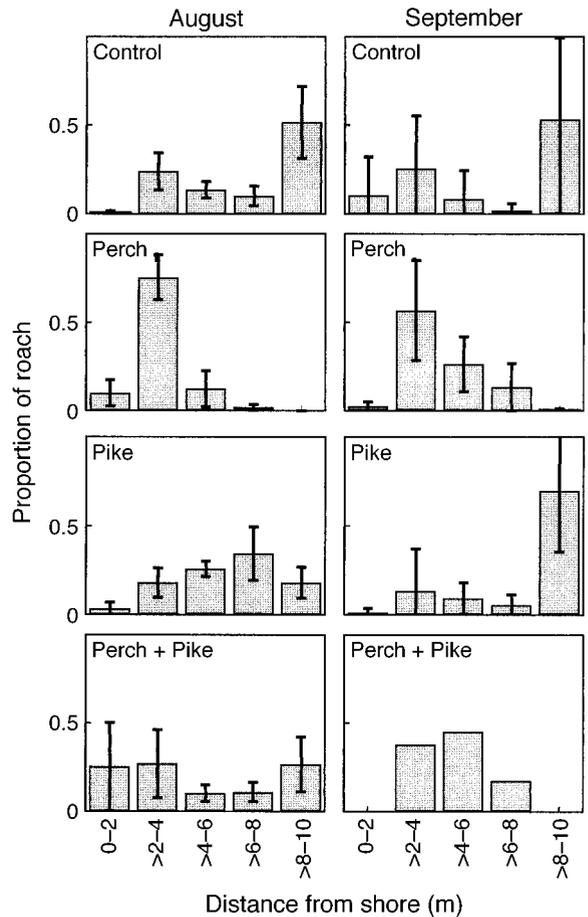


FIG. 7. Proportional use of the enclosure by roach classified at 2-m intervals from the edge of the enclosure in the control, perch, pike, and perch + pike treatments in August and September (means \pm 1 SE). The first distance range, 0–2 m, represents the vegetation refuge. Error bars are missing in September for the perch + pike treatment due to the low numbers of surviving roach.

Direct and indirect effects in piscivore–prey interaction food webs

Our results demonstrated strong effects of the habitat shifts of roach on mortality and on species-specific predator growth. But what were the consequences of

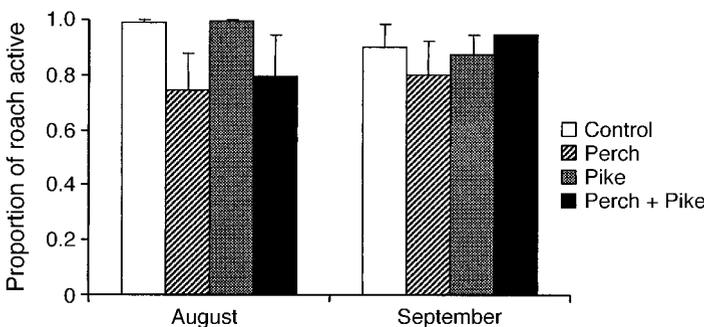


FIG. 6. Proportion by roach active in the control, perch, pike, and perch + pike treatments in August and September (means + 1 SE).

TABLE 4. Repeated-measures ANOVA for the effect of perch and pike on (A) prey proportional refuge use and (B) prey distance to refuge using August and September as repeated measures.

Source of variation	ss	df	F	P
A) Proportional refuge use				
Perch	0.213	1	7.988	0.018
Pike	0.001	1	0.002	0.961
Perch × Pike	0.008	1	0.318	0.585
Error	0.267	10		
Time	0.030	1	3.407	0.095
Time × Perch	0.029	1	0.101	0.101
Time × Pike	0.015	1	1.735	0.217
Time × Perch × Pike	0.001	1	0.106	0.751
Error	0.088	10		
B) Distance to refuge				
Perch	71.650	1	14.303	0.004
Pike	0.346	1	0.069	0.798
Perch × Pike	0.521	1	0.104	0.754
Error	50.095	10		
Time	1.563	1	0.919	0.360
Time × Perch	0.173	1	0.102	0.757
Time × Pike	2.867	1	1.686	0.223
Time × Perch × Pike	0.664	1	0.390	0.546
Error	17.005	10		

the predator-induced habitat shifts of roach on other species in the food web? The overall decrease in roach density due to predation had an indirect positive effect on *Daphnia* biomass whereas roach had no or only weak indirect effects due to habitat shifts on *Daphnia* biomass in the vegetation and the open water. Instead, roach caused a strong negative indirect effect on macroinvertebrates by shifting to the open water in the presence of pike, forcing pike to shift from a diet of roach to macroinvertebrates. Thus, both behaviorally mediated and density-mediated interactions are important in this system.

As noted, one plausible mechanism to explain the weak effects on resources in the vegetation is the poor foraging ability of roach in this habitat. Alternatively, the similarity in growth of roach among treatments could be because they switched frequently between habitats (P. Eklöv and T. VanKooten, *unpublished data*) and thus compensated for food deprivation in the vegetation with a higher food intake in the open water (see also Eklöv and Persson 1996). This could also explain why there was only a weak negative relationship between the numbers of roach and *Daphnia* biomass in the open water (see also Diehl and Eklöv 1995). In contrast, other studies have shown strong indirect effects of a predator on prey resource levels mediated by changes in the behavior of an intermediate consumer (Werner et al. 1983, Turner and Mittelbach 1990, Peacor and Werner 1997).

In the presence of pike, roach mainly used the open water and were thus unavailable to pike predation. Consequently, pike decreased macroinvertebrate biomass to very low levels. Other studies of pike diet support our results and demonstrate that pike will feed to a

large extent on macroinvertebrates when fish prey are at low abundance (Chapman et al. 1989, Eklöv and Hamrin 1989, Beaudoin et al. 1999). For example, Beaudoin et al. (1999) showed that 90% of the pike in lakes lacking other fish species consumed only macroinvertebrates, compared to ~30% of the pike in lakes with mixed fish species. Pike living only on macroinvertebrates also appear to grow more slowly than pike in mixed-species assemblages (see Beaudoin et al. 1999).

Our enclosure experiment demonstrated strong effects of two piscivores on prey mortality, which led to effects on prey resource levels. What is the evidence that these effects also occur in natural, larger scale systems? Presently there are no larger scale studies that have explicitly tested the effects of the suggested mechanisms. Nevertheless, there are strong indications that these effects are real and important in natural systems. For example, several studies have manipulated the pike density in lakes and have thereby been able to estimate both the direct effect of pike on prey mortality and the indirect effect on prey resources in the presence of piscivorous perch (Persson et al. 1996, Berg et al. 1997, Søndergaard et al. 1997). However, because prey behavior and fitness is driven by the trade-off between predation mortality and foraging activity, which varies between habitats (see Gilliam and Fraser 1987), the next important step would be to identify factors that determine the magnitude of multiple predator interactions. How does predation risk vary with predator density in different habitats and how does that affect the trade-off between predation risk and foraging intake of prey in different habitats?

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