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## Effects of fish chemical cues on the interactions between tadpoles and crayfish

Per Nyström and Kajsa Åbjörnsson

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We studied the effects of predatory crayfish (*Pacifastacus leniusculus*), the non-lethal effects of fish chemical cues (*Oncorhynchus mykiss*), and the combined effects of crayfish and fish chemical cues on the performance of tadpoles of two co-existing anuran species, *Rana temporaria* and *Bufo bufo*, in experimental pools. We also examined grazing effects on periphyton, the main food source for the tadpoles. Crayfish significantly reduced tadpole survival, particularly by feeding on *Bufo*. *Rana* benefited from reduced numbers of competitors, resulting from crayfish predation, by increased growth rate, whereas the growth rate of *Bufo* was unaffected by crayfish. The proportion of *Rana* in refuges (in relation to the number of survivors at the end of the experiment) was unaffected by crayfish, whereas proportionally more *Bufo* stayed in refuges in the presence of crayfish, relative to controls. Fish cues had no effect on tadpole survival of either species. During the entire larval period, *Rana* responded to fish cues by increasing the use of refuges relative to controls, whereas *Bufo* did not show any significant behavioural response to fish cues. In accordance with these observations, the proportion of *Rana* in refuges at the end of the experiment was high in the presence of fish cues, whereas the use of refuges by *Bufo* was not affected by fish cues. Predatory crayfish and fish chemical cues had additive effects on tadpole survival, growth and refuge use.

Tadpoles in all treatments reduced periphyton biomass. Both crayfish and fish cues had positive indirect effects on periphyton biomass. The positive indirect effect of fish cues on periphyton was likely an effect of reduced grazing from *Rana*. Thus lethal, as well as non-lethal, predator effects on prey populations can influence lower trophic levels.

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Both empirical and theoretical work suggests that predators may structure communities through direct and indirect trophic interactions (e.g. Carpenter et al. 1985, Fretwell 1987). Multiple factors affect the strength of direct and indirect interactions in food chains including behavioural interactions among predators, subsidies to consumers from other habitats, spatial heterogeneity, omnivory and the ability of prey to reduce predation (e.g. Polis and Strong 1996). Prey have evolved a variety of adaptations to reduce predation risk such as morphological structures, chemical repellents, crypsis and avoidance behaviours (Endler 1986, Sih 1987, Kats et al. 1988). As a consequence

these adaptations may result in predators having weak effects on prey abundance, and thus result in weak direct interactions in the food chain. In the presence of predators, prey may alter their behaviour so that they are more difficult to capture, detect, or encounter (Lima 1998). Many prey species reduce their general activity levels when predators are detected (e.g. Lima and Dill 1990). These avoidance behaviours are common in aquatic ecosystems, and may strongly affect predator-prey interactions and top-down control of community structure (Scheffer 1997). In nature, however, prey often encounter multiple predators with different foraging strategies, and behavioural responses to

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different types of predators may produce conflicting alternatives to prey (Sih et al. 1998). Thus, when many types of predators are present, prey mortality may ultimately increase (Rahel and Stein 1988, Wooster and Sih 1995, Kurzava and Morin 1998).

In most predation studies in aquatic systems the strength of direct and indirect interactions are estimated by measuring densities or biomass of trophic levels in food chains. Hence, the impact of predators on prey populations has often focused on the direct lethal effects of predators; however, predators may also have strong indirect effects on prey populations through non-lethal effects on prey life-styles (e.g. Sih 1987, Lima 1998). Even when aquatic predators are not allowed to consume prey there may be behaviourally transmitted indirect effects on prey resources (Peacor and Werner 1997, Turner 1997, Peckarsky and McIntosh 1998). Many prey species in aquatic ecosystems have the ability to estimate predation risk by assessing the presence of predator chemical cues (e.g. reviewed in Dodson et al. 1994). Prey respond to predator associated chemical cues in a number of ways, most often by reduced activity level and increased refuge use (for a recent review, see Kats and Dill 1998). Prey responses to chemical cues may strongly affect food chain dynamics in freshwater communities. For example, predator released chemical cues may indirectly increase periphyton biomass by altering the foraging activity of grazers (Peacor and Werner 1997, Turner 1997, Peckarsky and McIntosh 1998).

It is well established that many amphibian larvae use chemical cues to detect and avoid predators (Petranka et al. 1987, Kats et al. 1988, Bridges and Gutzke 1997). Nevertheless unpalatable species with chemical repellents in the skin, such as bufonids, often show weak antipredator behaviour to predator cues (Kats et al. 1988, Semlitsch and Gavasso 1992, Laurila et al. 1997; but see Hews 1988). During the aquatic stage, amphibian larvae may encounter both vertebrate and invertebrate predators. Species specific traits, such as palatability and activity level, affect vulnerability to different types of predators (Werner and McPeck 1994). If predators selectively reduce the number of tadpoles, and/or if some amphibian larvae alter their feeding behaviour, lower trophic levels as well as the strength of inter- and intraspecific competition can be affected (e.g. Wilbur and Fauth 1990, Wilbur 1997).

Organisms in freshwater ecosystems are exposed to a wide range of chemical signals (Dodson et al. 1994). Yet there have been few attempts to evaluate the long term influence of predator released chemical cues on prey behaviour and food chain interactions in chemically complex environments (Chivers and Smith 1998, Kats and Dill 1998). Here, we studied the lethal

effects of crayfish, non-lethal effects of fish chemical cues, and the combination of these predator impacts on the performance of the larval stages of two amphibian species, *Rana temporaria* and *Bufo bufo*, that often co-exist. In natural breeding ponds predation and intraspecific competition can strongly influence sympatric populations of *R. temporaria* and *B. bufo* (Bardsley and Beebee 1998). Periphyton is the main food source for the tadpoles of both species (Harrison 1987, Bardsley and Beebee 1998), but the two amphibian species differ with respect to palatability, activity level and responses to predator cues. *Bufo bufo* is the more active species, being distasteful to several aquatic predators, such as fish, while tadpoles of *R. temporaria* are less active but palatable (Henrikson 1990, Lardner and Loman 1995, Laurila et al. 1997). Moreover *R. temporaria* tadpoles have been shown to modify their behaviour more strongly than *B. bufo* to chemical cues released from dragonfly larvae feeding on tadpoles (Laurila et al. 1997).

We expected *Rana* tadpoles to be more vulnerable to crayfish predation than the chemically defended *Bufo* tadpoles. Further, *Rana*, but not *Bufo*, should respond to chemical cues released from fish by reducing their overall activity level. Reduced activity was then expected to affect *Rana* food intake, growth rate and vulnerability to crayfish. Indirectly, reduced grazing by *Rana* was expected to affect periphyton biomass; *Bufo* was expected to benefit from increased periphyton biomass as grazing from *Rana* decreased.

## Methods

### Study organisms

*Rana temporaria* and *B. bufo* are two widespread and common anurans in Europe, often found in the same permanent or semi-permanent ponds (Bardsley and Beebee 1998). In Sweden, *R. temporaria* and *B. bufo* sometimes breed in ponds with signal crayfish (*Pacifastacus leniusculus*) and rainbow trout (*Oncorhynchus mykiss*) (P. Nyström pers. obs.). Laboratory experiments have shown that signal crayfish consume both *Rana* and *Bufo* tadpoles, although *Bufo* is less preferred (Axelsson et al. 1997). Rainbow trout readily consume *Rana*, but not *Bufo* (B. Lardner pers. comm.). The impact of crayfish on amphibian larvae is not well known, but in contrast to fish, crayfish are considered to be inefficient predators on swimming amphibian larvae (Lefcort 1996). Signal crayfish feed mostly on less mobile invertebrates, such as snails, and on macrophytes (Nyström et al. 1999). The diet of rainbow trout typically includes larger invertebrates and tadpoles (Cooper 1988).

## Experimental set-up

We had four treatments, each replicated five times: controls with tadpoles of both species and no predators (hereafter control pools), tadpoles with a caged rainbow trout (fish cue pools), tadpoles with signal crayfish (crayfish pools), and tadpoles with both signal crayfish and a caged trout (crayfish + fish cue pools). Treatments were randomly assigned to 20 circular wading pools (volume: 1000 l, area: 2.6 m<sup>2</sup>). The experiment was conducted during May–July 1998 on the roof of the Ecology Building in Lund. On 13 April, a mixture of sediment free from macro-invertebrates from a eutrophic lake and sand was added to a depth of 2 cm in each pool. Each pool contained ground water, an inoculum of pond water (10 l), allochthonous detritus (15 g dry mass of alder and beech leaves) and macrophytes (200 g wet mass each of *Elodea canadensis* and *Chara contraria*). Macrophytes and detritus increased habitat complexity and served as alternative food sources for crayfish throughout the experiment. The addition of five plastic pipes (20 cm long, 5 cm in diameter) and 80 smaller pipes (3 cm long, 5 cm in diameter) further increased habitat complexity and the number of refuges for crayfish and tadpoles. On 27 April a commercial plant nutrient solution (percentages: PO<sub>4</sub>-P, 1%; NH<sub>4</sub>-N, 2%; NO<sub>3</sub>-N, 3.1%; by weight) was added to all pools corresponding to nutrient levels found in eutrophic ponds in southern Sweden (total phosphorus concentration of 50 µg/l and total nitrogen concentration of 260 µg/l). Water temperature (15.5°C ± 3.6 SD) was measured weekly in each pool at noon and did not differ between treatments (repeated measures ANOVA, Treatment:  $P = 0.82$ , Time:  $P < 0.0001$ , Time × Treatment:  $P = 0.81$ ).

## Tadpoles

On 24 April, eggs from multiple *Rana* egg masses and *Bufo* egg strings were collected from two ponds close to Lund. Both ponds were devoid of crayfish and fish. Eggs were placed in two smaller plastic wading pools (250 l) containing sediment, macrophytes and a mixture of ground and pond water. These pools were kept in a non-heated greenhouse. Tadpoles hatched on 30 April and were fed commercial rabbit food. On 8 May, 90 *Rana* tadpoles (stages: 28–29 (Gosner 1960); dry mass: 2.14 mg ± 0.58 SD,  $N = 10$ ) and 90 *Bufo* tadpoles (stages: 27–28; dry mass: 2.39 mg ± 0.76 SD,  $N = 10$ ) were stocked in each pool, corresponding to a total density of 69 tadpoles/m<sup>2</sup>. This density is well within the range of natural densities of *Rana* and *Bufo* in Swedish ponds (B. Lardner pers. comm.). Refuge use by tadpoles was estimated by counting all visible tadpoles, once per week at noon

in each pool. Two observers were standing close to a pool, but on opposite sides, and counting the number of visible tadpoles for each species in half of the pool area during one minute. Thus the total number of observed tadpoles per pool was the sum of the counts from the two pool halves. This counting procedure was chosen as it did not affect the behaviour of the tadpoles in the pools. The experiment was terminated on 8 June, just before tadpole metamorphosis (*Rana*: stages 38–42, *Bufo*: 37–39). Then the pools were emptied and all surviving tadpoles counted. Average individual tadpole dry mass (tadpole dry mass per pool divided by number of survivors) and growth rate (mean mass divided by larval period) were then determined.

## Predators

Predators were introduced on 11 May. Crayfish were trapped in a pond close to Lund. The rainbow trout in this pond include crayfish in their diet (P. Nyström unpubl.). One adult male signal crayfish (mean carapace length: 45.5 mm ± 3.0 SD,  $N = 10$ ) and one two-year-old male signal crayfish (mean carapace length: 24.2 mm ± 1.2 SD,  $N = 10$ ) were placed in each of the pools assigned to crayfish treatments. The corresponding density of 0.8 crayfish/m<sup>2</sup> has been used in previous pool experiments with signal crayfish and tadpoles (Axelsson et al. 1997) and is well below densities found in ponds with signal crayfish and spawning *Rana* and *Bufo* in southern Sweden (Nyström and Granéli 1996). In each pool we placed one circular plastic cage (volume: 90 l, diameter: 55 cm) along the side of the pool. One trout (≈ 70 g wet-mass), obtained from a local fish farmer, was put in the cage in each of the pools assigned as fish cue treatments. The cage wall had two plastic screen windows (16 × 12 cm, two layers of net, mesh size 1 mm) and the top was covered with a removable net (mesh size 1 mm). This design allowed any water-born cues released from the cage to diffuse into the pool water. Moreover the double net prevented tadpoles from detecting the fish by vision. To ensure water exchange between cages and pools, periphyton was scrubbed off weekly from the screen windows with a brush, and water within the cage was aerated continuously. In each cage we placed one stone and planted 10 strands of *Elodea canadensis* in the sediment covering the cage bottom. To simulate natural feeding behaviour, fish were allowed to feed on a mixed diet of live tadpoles (*Rana* and *Bufo*) and the amphipod *Gammarus pulex*. Tadpoles used as trout food were kept in the greenhouse, and *Gammarus* were caught in a pond close to the Ecology Building in Lund. Fish were fed 10 individuals of each prey species on a weekly basis. Every week prey were counted in each

cage and replaced with new individuals if necessary. At the end of the experiment, all remaining prey in each cage were counted.

### Periphyton

On 1 April, 120 glazed tiles (10 × 10 cm) and 120 polyethylene strips (1.6 × 25 cm) were placed in outdoor tanks receiving water from a eutrophic pond. This allowed periphyton to colonise the substrates before the start of the experiment. In order to keep strips vertical, a nut anchored the lower end of each strip, while a small cork buoyed the top end. On 1 May, we transferred six strips and six tiles into each of the experimental pools. Strips and tiles were evenly distributed over the pool area. By this time these substrates were covered with filamentous green algae (mainly *Mougeotia* and *Zygnema*) and diatoms (mainly *Synedra*, *Fragilaria* and *Diatoma*). In order to quantify the ability of tadpoles to graze periphyton as well as to estimate if nutrients released by crayfish and fish had any effect on periphyton biomass, we included tiles and strips that were exposed and not exposed to grazing. Tiles exposed to tadpole grazing were placed on small pipes (3 cm long, 5 cm in diameter) so that they were three cm above the sediment surface, to reduce any disturbance from crayfish. Tiles that were not to be exposed to tadpole grazing were placed in a pot covered by a plastic net (mesh: 2 mm), and similarly, strips not exposed to tadpole grazing were placed in a small cage made of the plastic net. When the experiment was terminated the strips were put in vials and frozen. Periphyton from the tiles was scraped off with a razor and then put in vials and frozen. Within three months the chlorophyll *a* content was measured spectrophotometrically using ethanol as the extractant (Jespersen and Christoffersen 1987).

### Statistical analyses

We tested whether the single effects of crayfish and fish cue could predict the combined effect of crayfish and fish cue simply by summing their single effects. This was done by testing a multiplicative risk model (on log transformed data) by running factorial ANOVAs or MANOVAs with two factors (crayfish and fish cues) on the response variables (tadpole overall performance and periphyton biomass) (Sih et al. 1998). A significant interaction in the ANOVA indicates that the combined effects of crayfish and fish cues are greater or lower than the sum of their single effects. We tested whether crayfish and fish cues affected tadpole growth using ANCOVA. Because growth rate among tadpoles may be density dependent (e.g. Morin 1983) we introduced the final number of surviving tadpoles (*Rana* + *Bufo*) in each pool as the covariate.

## Results

### Tadpole responses

During the experiment, the caged fish had consumed all *Rana* tadpoles given and most of the *Gammarus*. *Bufo* larvae were rarely consumed, but the variation between individual fish was large. Survivorship for both *Rana* and *Bufo* was nearly 100% in both control and fish cue pools (Fig. 1A). Crayfish, however, significantly reduced tadpole survivorship, particularly by consuming *Bufo* tadpoles (Fig. 1A, Table 1A). The combined effect of crayfish and fish cues on the survival of *Rana* and *Bufo* was not stronger than the single effect of either crayfish or fish cues alone (Fig. 1A, Table 1A). Throughout the experiment the number of visible *Bufo* tadpoles (i.e. not using available refuges) in control and fish cue pools was higher than the number of *Rana* tadpoles (Fig. 2). For both species the number of visible tadpoles was reduced in pools with crayfish. The number of visible *Rana* tadpoles was significantly lower in pools with fish cues than in control pools, whereas the number of visible *Bufo* tadpoles was not significantly affected by fish cues (Fig. 2, Table 2). On the last sampling date, the proportion of visible *Rana* tadpoles (the numbers visible in relation to the number of surviving *Rana* tadpoles) was low in the presence of fish cues relative to controls, whereas crayfish had no significant effect on the proportion of visible *Rana* (Fig. 1B, Table 1B). In contrast, the proportion of visible *Bufo* tadpoles was unaffected by fish cues; however, the proportion of visible *Bufo* tadpoles was significantly reduced in the presence of crayfish (Fig. 1B, Table 1B). The mean mass of *Rana* increased significantly in the presence of crayfish but was unaffected by fish cues (Fig. 1C, Table 1C). The mean mass of *Bufo* was unaffected by either fish cues or crayfish (Fig. 1C, Table 1C). The growth rate of *Rana* tadpoles was mainly affected by changes in tadpole density and did not differ between treatments (ANCOVA,  $F_{3,12} = 1.61$ ,  $P = 0.240$ , Fig. 3). In contrast, the growth rate of *Bufo* did not show the same density dependent growth rate as *Rana*. The growth rate of *Bufo* was low in treatments with crayfish, despite reduced number of survivors, as was indicated by a significant interaction between treatment and the number of surviving tadpoles (ANCOVA,  $F_{3,12} = 3.69$ ,  $P = 0.0431$ , Fig. 3).

### Periphyton

Overall, tadpoles reduced periphyton biomass as indicated by the higher biomass on substrates not exposed to grazing in comparison with exposed substrates (Fig. 4). Periphyton biomass on the substrates not exposed to grazing did not differ between treatments (Table 3, Fig. 4). Periphyton biomass on the exposed substrata in-

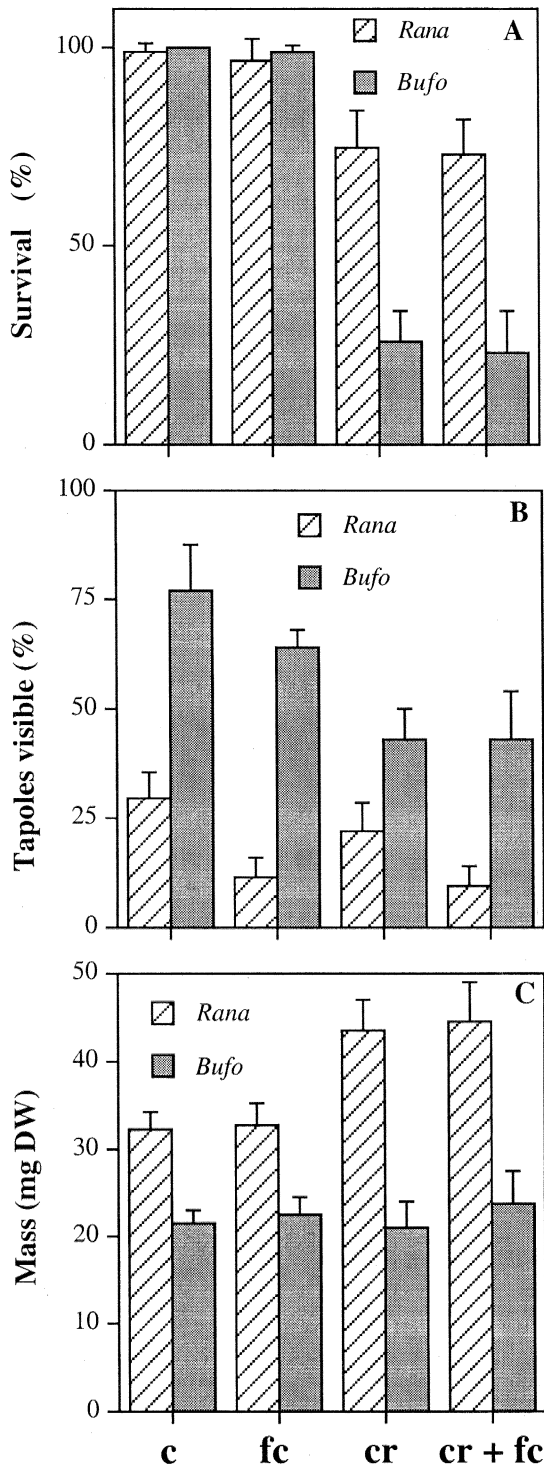


Fig. 1. *Rana* and *Bufo* at the end of the experiment in control pools (c), pools receiving fish cues (fc), pools with crayfish (cr) and pools with crayfish and fish cues (cr + fc). Average percentage survival (A), percentage of the number of visible tadpoles in relation to the number of survivors (B) and average mass of surviving tadpoles (C). Error bars denote 1 SD.

Table 1. Summary of ANOVAs of the effect of crayfish and fish cues on *Rana* and *Bufo* at the end of the experiment; survival (A), percentage of visible tadpoles in relation to the number of survivors (B) and mean mass (C).

A. Survival	df	SS	F	P
<i>Rana</i>				
Crayfish	1	0.4006	45.2251	<0.0001
Fish cue	1	0.0019	0.2170	0.6476
Crayfish × Fish cue	1	0.0000	0.0020	0.9652
Error	16	0.1417		
<i>Bufo</i>				
Crayfish	1	10.7440	136.2477	<0.0001
Fish cue	1	0.0517	0.6562	0.4298
Crayfish × Fish cue	1	0.0389	0.4931	0.4926
Error	16	1.2617		
B. Visible				
<i>Rana</i>				
Crayfish	1	0.2437	1.7655	0.2026
Fish cue	1	4.5613	33.0435	<0.0001
Crayfish × Fish cue	1	0.0350	0.2533	0.6216
Error	16	2.2087		
<i>Bufo</i>				
Crayfish	1	1.2596	41.6750	<0.0001
Fish cue	1	0.0434	1.4361	0.2482
Crayfish × Fish cue	1	0.0336	1.1122	0.3073
Error	16	0.4836		
C. Mass				
<i>Rana</i>				
Crayfish	1	0.4713	69.7828	<0.0001
Fish cue	1	0.0015	0.2255	0.6413
Crayfish × Fish cue	1	0.0000	0.0039	0.9507
Error	16	0.1081		
<i>Bufo</i>				
Crayfish	1	0.0005	0.0352	0.8534
Fish cue	1	0.0303	2.0791	0.1686
Crayfish × Fish cue	1	0.0080	0.5508	0.4688
Error	16	0.2335		

creased, however, in the presence of fish cues and crayfish. The non-significant Crayfish × Fish cue interaction indicates that the observed positive effects on periphyton by crayfish and fish cues were additive (Table 3, Fig. 4).

## Discussion

### Tadpole responses

Results from this study show that crayfish affect tadpole survival and growth, whereas fish cues released from the caged fish influence tadpole behaviour. There were, however, species specific differences of *Rana* and *Bufo* in response to crayfish and chemical cues released by fish. The chemically defended *Bufo* were more vulnerable to predatory crayfish than *Rana*. In a previous aquarium experiment it was observed that adult signal crayfish, although killing *Bufo*, did not consume stages 30–37 to a great extent, suggesting that crayfish were repelled by the presence of toxins (Axelsson et al. 1997).

However, there may be ontogenetic variation in toxicity of bufonids (e.g., Brodie and Formanowicz 1987). Both inter- and intraspecific variations in toxic effects on predators consuming different developmental stages of *Bufo* tadpoles have been found. For example, crayfish (*Cherax quadricarinatus*) consumed all developmental stages of *Bufo marinus* without any apparent ill effect, whereas several bugs (*Lethocerus insulanus*) experienced significant mortality after preying upon mid and late developmental stages of the tadpoles (Crossland 1998). Because we did not observe any dead *Bufo* tadpoles, and there was a gradual decrease in the number of visible *Bufo* tadpoles in pools with crayfish over time, our results suggest that crayfish were not repelled by the toxicity of these tadpoles. Further all crayfish survived the experiment showing no apparent ill effects. It can also be excluded that the tadpoles lacked chemical defence, because most trout did not consume *Bufo* tadpoles in the cages. The higher mortality of *Bufo* than of *Rana* in this study is likely to be an effect of differences in behaviour between the two species, rather than variation in palatability. *Bufo* species are generally continually active and are less manoeuvrable than *Rana* (Wassersug and Hoff 1985, Chovanec 1992). The behaviour of *Bufo* makes the encounter rate and the probability of being captured by crayfish high. Species differences in the activity of tadpoles have been shown to affect their vulnerability to both invertebrate and vertebrate predators (Lawler 1989, Wilbur and Fauth 1990, Semlitsch 1993).

As expected, *Rana* tadpoles increased their time spent in refuges in the presence of fish cues, whereas *Bufo* did not show a significant response. Moreover refuge use by *Rana* in response to fish cues persisted during their entire larval period. These results agree with the general prediction that only palatable amphibians that are at

great risk from predatory fish respond to water conditioned by fish (Kats et al. 1988). Previous experiments have shown that *R. temporaria* tadpoles respond to chemical cues released by predatory invertebrates by lowering activity levels, whereas *B. bufo* show only weak responses (Laurila et al. 1997, 1998). Tadpole responses to predatory crayfish are not well studied, but tadpoles of *Rana utricularia* and *Hyla chrysoscelis* respond to chemical cues from crayfish by increasing use of refuges. This response is not as strong as to predatory fish (Lefcort 1996, Bridges and Gutzke 1997). A field experiment indicates that *R. temporaria* tadpoles respond to the presence of signal crayfish by increasing their activity level and avoiding benthic refuges. In contrast when trout or both crayfish and trout are present (i.e. not just cues), tadpoles respond by remaining in refuges (Nyström et al. unpubl.). In this study we did not observe increased activity of *Rana* in crayfish pools, possibly because crayfish density was lower than in the field experiment making the probability of encountering crayfish also lower.

The interaction between predation and competition strongly influences species composition of anurans (Morin 1983). Predators can reduce prey abundance, but mortality due to predators may also reduce inter- and intraspecific competition (Wilbur 1997). Here, the growth rate of *Rana* was strongly density dependent; when the number of tadpoles declined, *Rana* growth rate increased. Similarly, the crayfish *Cambarus bartonii* reduced the number of *Hyla chrysoscelis* tadpoles and the surviving tadpoles grew faster due to diminished intraspecific competition (Fauth 1990). Despite reduced numbers of surviving tadpoles in pools with crayfish, *Bufo* did not show any significant changes in growth rate. Likewise, *Bufo americanus* and *Rana palustris* are competitors when raised together; when *Bufo* and *Rana*

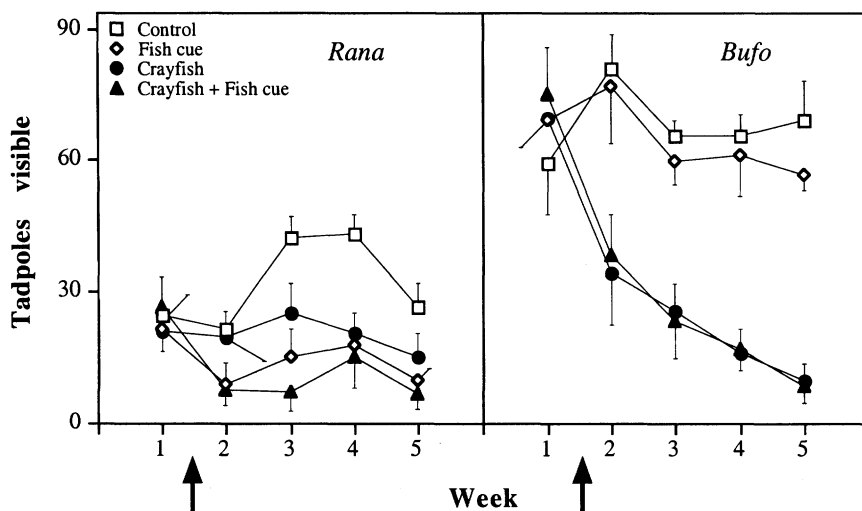


Fig. 2. Average number of visible *Rana* and *Bufo* tadpoles counted weekly in pools during the experiment. Arrows indicate time of predator introductions. Error bars denote 1 SD.

Table 2. Summary of repeated measures ANOVAs of the effects of crayfish and fish cues on the number of visible *Rana* and *Bufo* tadpoles over time.

Source	df	SS	F	P
<i>Rana</i> (Between subjects)				
Crayfish	1	3.1719	7.2159	0.0162
Fish cue	1	12.5939	28.6501	<0.0001
Crayfish × Fish cue	1	0.1152	0.2622	0.6156
Error	16	7.0332		
<i>Rana</i> (Within subjects)				
Time	4	6.4674	14.9220	<0.0001
Time × Crayfish	4	1.6890	3.8970	0.0068
Time × Fish cue	4	4.7727	11.0119	<0.0001
Time × Crayfish × Fish cue	4	0.6033	1.3919	0.2468
Error	64	6.9347		
<i>Bufo</i> (Between subjects)				
Crayfish	1	22.8972	181.3601	<0.0001
Fish cue	1	0.0246	0.1951	0.6646
Crayfish × Fish cue	1	0.0069	0.0546	0.8182
Error	16	0.4836		
<i>Bufo</i> (Within subjects)				
Time	4	12.4736	94.4099	<0.0001
Time × Crayfish	4	10.8856	82.3910	<0.0001
Time × Fish cue	4	0.2799	2.1187	0.0887
Time × Crayfish × Fish cue	4	0.0696	0.5267	0.7165
Error	64	2.1139		

were reduced by predators only *Rana* benefited by growing more rapidly (Wilbur and Fauth 1990). However, as the mortality of *Bufo* larvae was high in our crayfish pools it is possible that crayfish may have selectively consumed the most active, and largest tadpoles, making the interpretation of *Bufo* growth rate and final size complicated. Recent field observations indicate that predation and intraspecific competition are the dominant structuring forces in breeding ponds with *R. temporaria* and *B. bufo* (Bardsley and Beebe 1998). Predators, such as insects and fish, consume less *Bufo* than *Rana* and *Rana* is therefore found only in small numbers, making competition with *Bufo* negligible. In contrast, intraspecific competition may be intense in populations of *Bufo* when there are few invertebrate predators, as in ponds with fish (Bardsley and Beebe 1998). Our results indicate that in ponds with crayfish, *Bufo* may suffer heavier predation than *Rana*, and the latter may benefit from reduced inter- and intraspecific competition.

*Rana* responded to fish cues by increasing the use of refuges but this behaviour did not affect the growth of the tadpoles as has been shown for some other species (e.g., Skelly 1992, Werner and Anholt 1996). A field experiment indicates however that *Rana* stay in refuges in the presence of trout and this has strong negative effects on their growth rate (Nyström et al. unpubl.). The impact of predators on tadpole growth depends strongly on the food availability during the larval period. Van Buskirk and Yurewicz (1998) showed that resource availability played a critical role in determin-

ing the relative importance of direct predation (reduced density) and predation risk (reduced activity) for the growth of *Rana sylvatica*. Tadpoles decreased their time spent feeding when exposed to cues from a caged dragonfly, but when tadpoles were small, and food sources not were limited, growth declined only due to reduced activity and not to reduced density. In contrast, when tadpoles were large and food sources were depleted, growth rate increased when tadpole density was reduced, but was unaffected by predation risk. In our study, periphyton levels were comparatively low, although within the natural range of periphyton levels found in wetlands (Goldsborough and Robinson 1996). In the field experiment the periphyton chlorophyll *a* levels in enclosures with trout, measured just before metamorphosis, averaged 0.6 µg/cm<sup>2</sup> (on strips) and 0.4 µg/cm<sup>2</sup> (on tiles) (Nyström et al. unpubl.). In this study, the periphyton levels were much lower in the fish cue pools (strips: 0.03 µg/cm<sup>2</sup>, tiles: 0.01 µg/cm<sup>2</sup>), and thus growth rate for *Rana* was density dependent and less affected by activity suppression due to fish cues.

### Food chain interactions

The most important result of this study is that direct lethal effects as well as chemically induced behavioural effects can strongly influence lower trophic levels. Tadpoles had strong effects on periphyton biomass and when crayfish reduced tadpole numbers periphyton biomass increased. There are several examples of tadpoles of the genus *Rana* reducing algal biomass in lakes



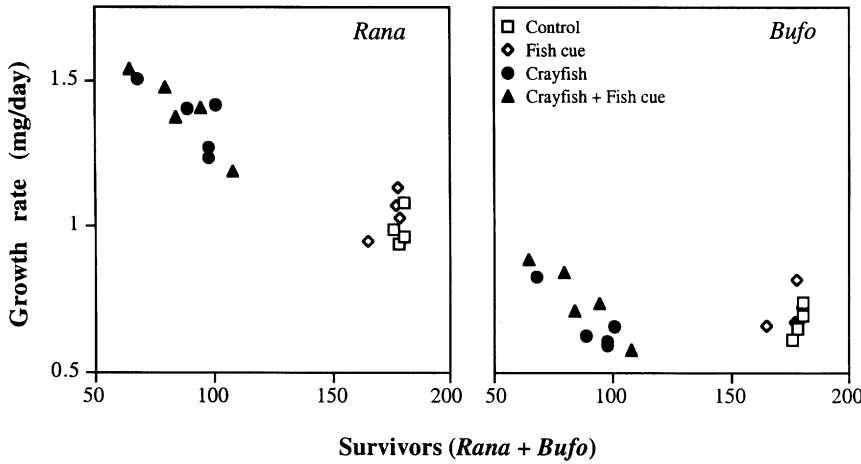


Fig. 3. Average growth rate of *Rana* and *Bufo* tadpoles in relation to the total number of surviving tadpoles in the different treatments.

Holomuzki 1998), but few studies have shown that predation on tadpoles may indirectly have positive effects on periphyton (but see Leibold and Wilbur 1992,

Wilbur 1997). We found that periphyton biomass also increased in the presence of fish cues. Because periphyton biomass on the substrates not exposed to tadpole grazing did not differ between treatments, this indicates that nutrients released by crayfish and fish had no apparent effect on periphyton biomass. Thus, the increase in periphyton biomass in fish cue pools was probably a consequence of reduced grazing from *Rana*, as they responded to fish cues by staying in refuges, or possibly by feeding in other habitats than on the periphyton substrates. In accordance with this observation chemical cues released by fish caused *Rana* spp. to spend less time in patches of food (Horat and Semlitsch 1994). It cannot be excluded that *Bufo* grazing on periphyton was affected by fish cues because these cues affect aggregation behaviour in *Bufo* (Watt et al. 1997). We only counted the number of visible tadpoles, which may not accurately reflect *Bufo* grazing on periphyton in these pools.

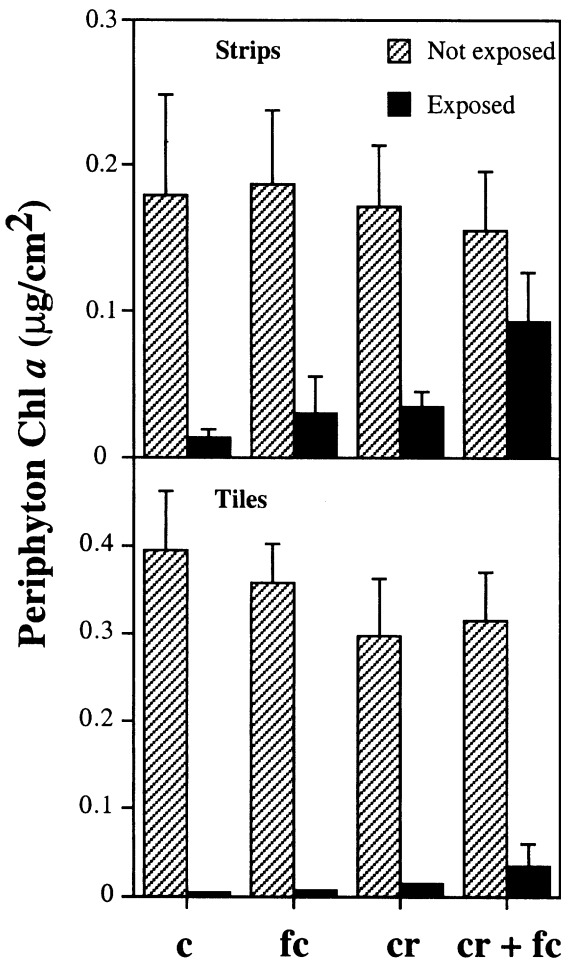


Fig. 4. Average final periphyton biomass expressed as chlorophyll *a* per unit surface area, on strips and tiles that were exposed or not exposed to tadpole grazing. Note the different scales on the *y*-axes. Error bars denote 1 SD.

The presence of predatory crayfish and fish cues had additive effects on all response variables measured (e.g. tadpole survival, growth, and use of refuges and periphyton biomass). Non-additive impact of multiple predators have been found to occur when predation risk is reduced due to predator-predator interactions and when predation risk is increased due to conflicting prey responses to multiple predators (Sih et al. 1998). In this study, *Rana* tadpoles increased the use of refuges in the presence of fish cues but this behaviour did not increase their risk of being consumed by crayfish. Daytime observations confirmed that *Rana* tadpoles spent considerable time in smaller pipes and leaves, whereas crayfish were mainly using the larger pipes and macrophytes. Hence the encounter rate with crayfish in this experiment was probably low. Crayfish may also have responded to trout by decreasing their overall activity level, further decreasing encounter rates with tadpoles. Crayfish behaviour and food consumption

Table 3. Summary of MANOVA of the effect of crayfish and fish cues on periphyton biomass on tiles and strips (dependent variables) not exposed and exposed to tadpole grazing.

Source	df	Wilks' $\lambda$	F	P
Not exposed				
Crayfish	2,15	0.7201	2.9153	0.0852
Fish cue	2,15	0.9969	0.0235	0.9768
Crayfish $\times$ Fish cue	2,15	0.9221	0.6335	0.5444
Exposed				
Crayfish	2,15	0.2412	23.5937	<0.0001
Fish cue	2,15	0.5243	6.8054	0.0079
Crayfish $\times$ Fish cue	2,15	0.9595	0.3164	0.7335

can be affected by the presence of predatory fish (Stein and Magnuson 1976, Blake and Hart 1993, Hill and Lodge 1995).

For food web ecologists population density or biomass are the variables of most interest, but as has been shown in this study, indirect effects such as trophic cascades could be generated by trait-mediated effects or by a combination of density and trait mediated effects (Abrams et al. 1996). Such effects may have strong implications for our understandings and predictions of how communities are structured.

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