

THE INFLUENCE OF MULTIPLE INTRODUCED PREDATORS ON A LITTORAL POND COMMUNITY

PER NYSTRÖM, OLA SVENSSON, BJÖRN LARDNER, CHRISTER BRÖNMARK, AND WILHELM GRANÉLI

Department of Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden

Abstract. In a replicated field experiment we studied the effects of natural densities of two exotic consumers, the predatory and herbivorous signal crayfish (*Pacifastacus leniusculus*) and the predatory rainbow trout (*Oncorhynchus mykiss*), on multiple trophic levels of a pond community. The goals were to: (1) determine the individual and combined effects of predators on macroinvertebrates, macrophytes, and periphytic algae; (2) evaluate the strength of direct and indirect interactions in a food web influenced by omnivores; and (3) evaluate the relative importance of direct and indirect predator effects on mortality and growth of a native frog species, *Rana temporaria*.

The experiment showed that both signal crayfish and rainbow trout had strong effects on multitrophic levels of a littoral pond community, through direct consumption and indirect effects on lower trophic levels. Crayfish had weak but significant negative effects on the biomass of predatory invertebrates and greatly reduced the biomass of snails, the most abundant invertebrate grazers. Although the number of active herbivorous tadpoles tended to be higher in crayfish cages relative to control cages, the proportion of surviving froglets was lower in crayfish cages than in control cages, possibly due to crayfish predation on injured tadpoles. The size of surviving froglets did not differ from controls, but tadpoles in crayfish cages often suffered tail injuries. Macrophyte coverage decreased as a result of crayfish consumption and nonconsumptive fragmentation. However, the biomass of periphyton increased in crayfish cages relative to controls, probably due to reduced grazing from snails. In contrast, trout had strong negative effects on the biomass of both predatory invertebrates and insect grazers, whereas trout had less effect on snail biomass than did crayfish. Also, in contrast to crayfish cages, the number of active tadpoles in trout cages was lower than in controls, probably due to a combination of trout predation and trout-induced reduced tadpole activity. Trout had a strong negative impact on froglet survival, and froglets in trout cages metamorphosed at a smaller size and had reduced growth rates compared to froglets in crayfish and control cages. As with crayfish, the biomass of periphyton increased in trout cages relative to controls, which may be due to a combination of both density and trait-mediated trout effects on tadpole grazing.

In treatments with multiple predators the effects of crayfish and trout on caged communities were independent, and there were few interactions. Mostly effects of combined predators reflected those in single predator cages. Our results demonstrate that noninteracting, introduced multiple predators can have strong direct and indirect effects on multiple trophic levels in pond communities. Trophic cascades may develop in aquatic food webs even with omnivores such as crayfish, and in complex habitats with trout. These strong indirect effects are mediated through both predation on important grazers (i.e., the crayfish–snail–periphyton link) and a combination of density and behavioral responses of grazers to predators (i.e., the trout–tadpole–periphyton link). When two noninteracting predators have strong but different effects on prey survival or activity, their combined effects on intermediate trophic levels reflect responses to the more dangerous predator.

Key words: *exotic species; freshwater pond; grazers; growth rate; littoral pond; omnivory; Oncorhynchus mykiss; Pacifastacus leniusculus; predators, multiple; Rana temporaria; Sweden; trophic cascade.*

INTRODUCTION

Predation is one of the major factors influencing prey population dynamics and community structure (e.g., Sih 1987, Lima and Dill 1990). In the joint evolution of prey and predators, prey evolve morphological structures, chemical repellents, crypsis, and antipredator be-

haviors that reduce predation risk (e.g., Lima and Dill 1990, Endler 1991). These adaptations affect the ability of predators to regulate prey abundance (Power 1992a, Polis and Strong 1996, Scheffer 1997). However, introduced predators may have particularly strong effects on native prey that do not recognize new predators, do not show appropriate avoidance behaviors (Shave et al. 1994, Kiesecker and Blaustein 1997), or if the introduced predators have foraging strategies that differ from those of native predators (McIntosh and Town-

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send 1996). Subsequently, introduced predators can potentially affect the distribution and abundance of organisms at multiple trophic levels in a community (e.g., Schoener and Spiller 1999).

In community ecology, both theoretical (e.g., Hairston et al. 1960, Oksanen et al. 1981, Fretwell 1987) and experimental work has traditionally focused on the direct and indirect effects of predators in tightly linked food chains with distinct trophic levels. For example, several studies have revealed the importance of predator-induced trophic cascades (e.g., Spiller and Schoener 1990, Brönmark 1994, Letourneau and Dyer 1998), and studies of introduced predators have further increased our knowledge of how trophic cascades may develop (e.g., McIntosh and Townsend 1996, Schoener and Spiller 1999, Nyström and Åbjörnsson 2000). However, the applicability of the traditional linear food chain theory to species interactions in natural food webs has recently been questioned, because many communities have multiple interacting predators and high connectance due to the prevalence of omnivory (e.g., Polis and Strong 1996, Rosenheim 1998). Further, the mechanism explaining trophic cascades in food chains has traditionally been viewed as a result of prey removal, but recent studies have shown that cascading effects can also be behaviorally transmitted (Lima 1998). Examples from both terrestrial (Schmitz et al. 1997, Gastreich 1999) and freshwater systems (McIntosh and Townsend 1996, Turner 1997, McCollum et al. 1998, Peckarsky and McIntosh 1998) suggest that if herbivores shift their foraging behavior in response to predation risk, basal resources may increase.

Studies of introduced and native predators typically examine the effects of one predator at a time. Many communities, however, have been invaded by multiple predators (Ross 1991, Elvira et al. 1996, Gamradt and Kats 1996, Kiesecker and Blaustein 1998). Results from experimental studies of multiple native predators suggest the combined effects can be very strong, although quite complex due to a combination of direct and indirect trophic effects (Peckarsky and McIntosh 1998), the prevalence of omnivory (the consumption of resources from more than one trophic level; Diehl 1993, 1995, Pringle and Hamazaki 1998), and interactions among predators (Sih et al. 1998). Therefore, to understand the effects of multiple predator invasions, we need to consider all predator types and how they interact directly and indirectly with other trophic levels in the community.

To predict the effects of multiple predators on the structure of natural communities, the traditional approach that examines interactions between individual prey and predator species may not be appropriate (see review in Sih et al. 1998). That approach assumes predators do not interact in their effects on prey, i.e., that interaction modifications are absent (Billick and Case 1994, Wootton 1994). Indeed, work in both terrestrial (e.g., Spiller and Schoener 1994) and freshwater sys-

tems (Pringle and Hamazaki 1998, Van Buskirk 1988) have revealed that multiple predators may have non-interactive effects on prey populations. However, other studies have shown that multiple predators often have complex effects that can not be predicted simply by observing interactions between pairs of species in isolation (Sih et al. 1998). Most often, the combined effects of predators on prey are lower than expected from their individual effects, due to interactions among predators (Soluk and Collins 1988, Soluk 1993, Rosenheim 1998). Less commonly, the combined predation rate of predators is higher than expected from their individual effects (Sih et al. 1998). Facilitation among multiple predators can occur when antipredator responses to one predator increase risk of predation to another predator (Soluk and Collins 1988, Losey and Denno 1998, Kiesecker and Blaustein 1998).

Because many communities have more than one introduced predator species, the resulting effects on these invaded communities may be complex and hard to predict, but potentially very strong (e.g., Kiesecker and Blaustein 1998). The mechanisms behind the strong effects of exotic predators are rarely determined, but may provide results that can be successfully integrated into models of community ecology (Vitousek 1990, Lodge et al. 1998).

In this study, we examined the impact of two exotic predators, the signal crayfish (*Pacifastacus leniusculus*) and the rainbow trout (*Oncorhynchus mykiss*) on trophic interactions in a natural pond community. The signal crayfish is both a herbivore and a predator whereas rainbow trout is a predator on different consumer trophic levels. The goals of this study were to: (1) determine the individual and combined effects of these two commonly introduced exotic predators on multiple trophic levels in a pond; (2) evaluate the strength of direct and indirect interactions in a food web influenced by omnivores; and (3) evaluate the relative importance of direct and indirect predator effects on mortality and growth of a native frog species, *Rana temporaria*.

The introduced predators

The signal crayfish, native to northwestern United States, is resistant to the fungus that causes crayfish plague, and was therefore imported to Sweden in 1960 as a replacement for the susceptible native noble crayfish (*Astacus astacus*) (Lowery and Holdich 1988). The signal crayfish is an omnivore that feeds on invertebrates, macrophytes, periphyton, and detritus (Nyström et al. 1996, Lirås et al. 1998).

Rainbow trout, native to the Pacific coast of North America, was introduced to Sweden and Europe at the end of the 19th century. Although rainbow trout are often the top predators in lakes and ponds where they are introduced, their feeding behavior in lakes and ponds in Europe is not well studied. Data from British lakes suggest that they eat primarily large active prey such as amphipods and water bugs, whereas insect

grazers and snails are consumed to a lesser extent (Hunt and O'Hara 1973). Similarly, data from ~200 fishes caught by anglers in three Swedish lakes, show that rainbow trout feed on the immature and adult stages of predatory invertebrates (e.g., Odonata, Heteroptera, and Coleoptera), and on aquatic insect grazers (e.g., Ephemeroptera and Trichoptera) (Lindqvist 1981).

Many ponds in Sweden are devoid of both native crayfish and predatory fish. In addition, rainbow trout are often introduced, even though they are predators on native and introduced crayfish species (Foster and Slater 1995; P. Nyström, unpublished data).

The natural system

Permanent fishless habitats often have communities composed of large predatory invertebrates and large moderately active prey (Wellborn et al. 1996). In permanent ponds in southern Sweden without predatory fish and crayfish, predatory invertebrates such as bugs, beetles, and leeches are top predators (Nyström et al. 1996, Wagner 1997, Fig. 1A), and the grazer community is dominated by large thin-shelled pulmonate snail species (Brönmark 1994, Brönmark and Weisner 1996). Predatory invertebrates typically have weak effects on these grazers (Brönmark 1992, 1994), and large pulmonate snail species efficiently regulate periphyton biomass (see review in Brönmark 1989). However, insect grazers mostly have a negligible impact on periphyton biomass (Brönmark 1994, Brönmark and Vermaat 1998, Fig. 1A).

During spring and summer, up to seven amphibian species breed in these ponds, including both widely distributed species such as the common frog *Rana temporaria* (Loman 1988) and more rare species (e.g., the European tree frog, *Hyla arborea*, Brönmark and Edenhalm 1994). Experimental studies have shown that common frog larvae have effects on periphyton comparable to those of snails (Brönmark et al. 1991, Fig. 1A). In many ponds predatory invertebrates cause significant mortality of amphibian larvae (e.g., Smith 1983, Wellborn et al. 1996, Fig. 1A).

Predicted impact of the introduced predators

Crayfish typically reduce the biomass of slow-moving benthic invertebrates, particularly snails, but have less impact on mobile nonmolluscan invertebrates (Lodge et al. 1994, Nyström et al. 1996, Perry et al. 1997, Nyström et al. 1999, Fig. 1B). Also, crayfish can have strong direct impacts on primary producers by grazing macroalgae (Hart 1992, Creed 1994), and by grazing and nonconsumptive destruction of macrophytes (e.g., Lodge et al. 1994, Nyström and Strand 1996, Fig. 1B). Effects of crayfish on amphibian larvae are not well known, but experimental studies suggest that while some crayfish species, including signal crayfish, may consume or injure tadpoles (e.g., Axelsson et al. 1997, Nyström and Åbjörnsson 2000), crayfish are generally weak predators on tadpoles (Holomuzki

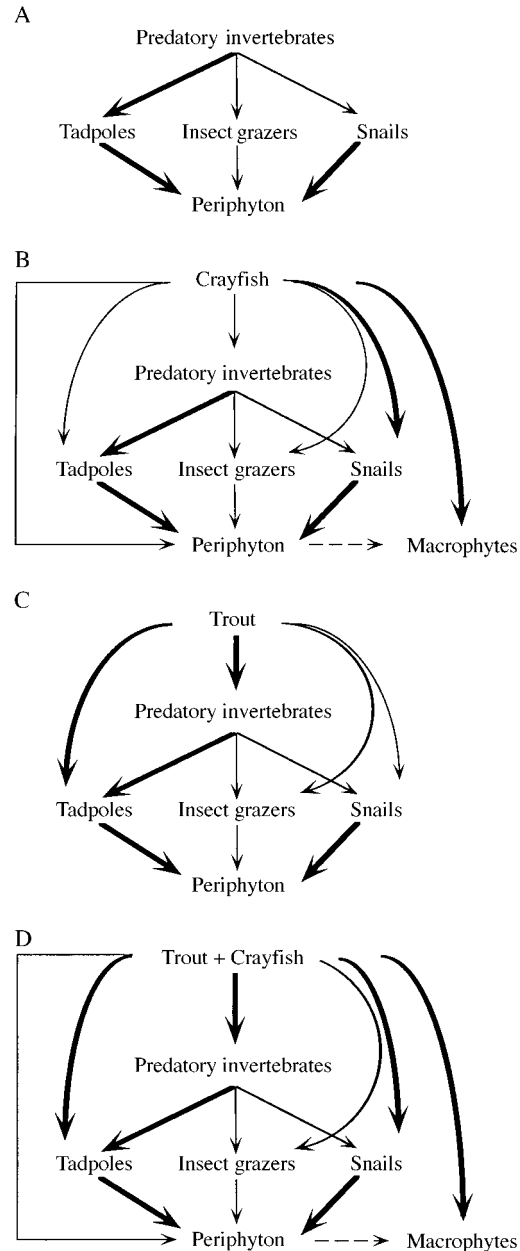


FIG. 1. Hypothesized food-web links, in the littoral pond (A) without introduced predators, (B) with signal crayfish, (C) with rainbow trout, and (D) with both crayfish and trout assuming these predators have independent effects. Arrow thickness indicates expected interaction strengths. Solid lines indicate consumption, and dashed lines indicate competition.

1989, Fauth 1990, Lefcort 1996). Periphytic algae are also consumed by signal crayfish (Flint and Goldman 1975), but crayfish are less efficient grazers on microalgae than are snails (Luttenton et al. 1998, Nyström et al. 1999, Fig. 1B). In fact macrophytes may indirectly benefit from snail removal of shading periphyton (Brönmark 1989, 1994, Brönmark and Vermaat 1998, Fig. 1B).

In its native habitats, predation by the visually hunting rainbow trout has been shown to affect large active prey such as predatory invertebrates, herbivorous tadpoles, stoneflies, and amphipods (Ware 1973, Cooper 1988, Feltmate and Williams 1989). Moreover, introduced trout species usually have strong negative impacts on amphibian larvae (e.g., Macan 1966, Bradford et al. 1998) and weak effects on snails (Macan 1966, Fig. 1C).

In a field enclosure experiment, we tested the single and combined effects of the introduced signal crayfish and rainbow trout on the interactions in a littoral pond community. Our design enabled us to test whether crayfish and trout had interactive or noninteractive effects on pond communities (Fig. 1D). Interactive effects were expected if; (1) trout reduce crayfish effects by predation or by altering crayfish foraging behavior (e.g., Stein and Magnuson 1976, Hill and Lodge 1995); (2) a change in behavior of tadpoles to one predator affects predation risk to the other predator (e.g., Morin 1995, Peacor and Werner 1997, Kiesecker and Blaustein 1998); or (3) crayfish reduce the biomass of macrophytes, facilitating fish effects on predatory invertebrates, tadpoles, and insect grazers (Crowder and Cooper 1982, Diehl 1992). Finally, reduction of large grazers (i.e., snails or tadpoles) was expected to have strong positive effects on the biomass of periphyton (i.e., a trophic cascade).

METHODS

Field experiment

A field experiment was carried out in a shallow eutrophic pond in southern Sweden (13°50' E, 55°50' N), with no fish or crayfish (area, 2500 m²; maximum depth, 2 m) from 9 May to 14 July 1997. During summer, water is alkaline (pH ~8, alkalinity = 2 mmol/L, total phosphorus of 34 µg/L and total nitrogen of 0.9 mg/l). Pond sediment was covered by submerged macrophytes, especially *Elodea canadensis*. Emergent vegetation was dominated by *Carex rostrata* and *Glyceria fluitans*.

We set up 20 cages (6 m², 2 × 3 m) in the pond in early April, each including natural emergent vegetation and a terrestrial zone of the shoreline. Cobbles and stones were abundant in the shallow part of enclosures, providing a suitable habitat for crayfish (Lodge and Hill 1994). Maximum cage depth was ~1.5 m. Each cage was constructed with nylon-reinforced plastic walls attached to wooden frames. At the sediment surface, 20 cm of the plastic was folded into the cage, and covered with gravel and sediments to create a tight seal against the sediment. Two triangular mesh windows (0.5 × 1.3 m, mesh size: 1.8 × 3.2 mm) in each of the longer walls allowed water circulation and immigration/emigration of smaller invertebrates (but not tadpoles). To prevent disturbance from birds but not insects, cages were covered with a net (mesh-size 20 mm)

(Nyström et al. 1999). Four treatments were randomly assigned to the 20 cages, each replicated five times: control (no crayfish and no trout, C), crayfish (CR), trout (T), and crayfish + trout (CR + T). When the experiment was terminated, cages were removed and predators released into the pond.

Crayfish were collected from nearby ponds and added to cages on 16 May 1997, except for young-of-the-year crayfish that were stocked on 6 June, when hatching normally occurs in south Swedish ponds. Natural densities of signal crayfish are similar to those of the native noble crayfish (Anonymous 1993), and densities (12 crayfish/m²) and size distributions of crayfish used in this experiment mimicked those found for noble crayfish in the littoral zone of Swedish lakes (Appelberg and Odelström 1986). In each crayfish cage, we stocked ten 3-yr-old crayfish (carapace length, 48.8 ± 0.4 mm [mean ± 1 SE]; $n = 100$), eight 2-yr-old crayfish (40.4 ± 0.6 mm, $n = 80$), 17 1-yr-old crayfish (18.8 ± 0.3 mm, $n = 170$) and 37 hatchlings. Five dead adult crayfish were found during the experiment and were replaced by crayfish of similar sizes. On 24 July, we placed one cylindrical trap (mesh 15 mm) baited with roach (*Rutilus rutilus*) in each cage overnight to estimate the relative abundance of adult crayfish at the end of the experiment. On average, 5.0 ± 0.9 adult crayfish were caught in each cage, and the number of crayfish caught did not differ between crayfish and crayfish + trout cages (ANOVA, $F_{1,8} = 0.57$, $P = 0.47$).

Rainbow trout with an average wet mass of 90 ± 7 g (mean ± 1 SE, ~18 cm, estimated from five randomly chosen fish) were also introduced into cages on 16 May. According to Swedish legislation, trout had to originate from an approved hatchery in order not to spread diseases. Because no data exist on densities of rainbow trout in Swedish ponds and lakes, we placed two fish in each cage, a density corresponding to that of predatory perch (*Perca fluviatilis*), in nearby lakes (Persson 1986). This density is also well within the ranges of rainbow trout in southern Ontario streams (Feltmate and Williams 1989), and brown trout in southern Swedish streams (Eklöv 1996). Three trout were replaced during the experiment, since they were caught in the nets covering the enclosures. When the experiment was terminated, all fish were alive.

In Europe, the common frog (*Rana temporaria*) breeds in a wide range of habitats from temporary to permanent ponds and lakes with predatory fish (Beebee 1985, Marnell 1998). Although the common frog does not avoid ovipositing in habitats with fish, fish introduction may cause local population declines (Meyer et al. 1998). In Sweden the common frog breeds in ponds with dense populations of signal crayfish as well as in ponds with both rainbow trout and signal crayfish (Nilsson 1999; P. Nyström, *personal observations*). Fifteen *Rana* egg masses were collected from a nearby pond and placed in a plastic wading pool (4.5 m²) near the experimental pond on 10 April. Hatching occurred on

29 April and on 12 May; 600 tadpoles (100 tadpoles/m², stages: 26–27 according to Gosner 1960) were randomly chosen from the pool and stocked in each cage. This initial density is within the range of natural tadpole densities of common frogs found in most ponds, including those with signal crayfish and rainbow trout (B. Lardner, *unpublished data*).

Sampling

Macroinvertebrates.—We destructively sampled macroinvertebrates inside cages on three occasions: once before predator stocking (9–14 May) and twice after predator stocking (16–18 June and 1–7 July). To ensure efficient sampling of macroinvertebrates with different behaviors and activity periods we combined three sampling methods. Macroinvertebrates on cage walls were sampled by scraping a 0.6-m² area on each of the longer walls with a small hand net (Lodge et al. 1994; size, 20 × 10 cm; mesh, 300 μm). Macroinvertebrates associated with macrophytes or appearing in the water column were sampled by placing a metal frame (1 × 1.4 m) in the center of the cage. Using the same hand net we collected invertebrates by seven standard sweeps (during 1 min) through the whole water column within the frame area. In order to collect invertebrates living in or on the sediment surface as well as invertebrates active during hours of darkness, we used active-fauna traps. The trap is a modified plastic beaker with a cone-shaped net funnel (1.0-mm mesh size) welded onto the opened bottom end. At the top end, a removable lid is furnished with an identical plastic net (Wagner 1997). These traps are particularly useful for collecting invertebrates such as bugs and beetles that otherwise may be missed using conventional sampling methods (e.g., nets and corers). Traps were placed at the sediment surface at five locations within each cage. Trapped invertebrates were collected after 48 h. All collected invertebrates were frozen for later identification. After thawing, invertebrates were counted and their total length measured to the nearest 0.1 mm. Dry mass (shell-free dry mass for snails) was determined for all invertebrates using length–mass regressions (P. Nyström, *unpublished data*). Macroinvertebrate biomass from the three sampling methods was pooled, giving invertebrate biomass per cage (Lodge et al. 1994).

Tadpoles.—Relative abundance and tadpole activity were estimated nondestructively using the same active-fauna traps as for invertebrates. Five traps were placed at the sediment surface of each cage on three occasions: once before predator stocking (14 May, 2 d after tadpoles were stocked) and twice after predators had been stocked (27 May and 16 June). After 48 h we counted the number of tadpoles in each trap, recorded tail injuries and then released the tadpoles in the shallow part of the cages.

Froglets.—Starting in mid-June we checked cages daily for metamorphs when tadpoles had reached larval

stage 40 (according to Gosner 1960) after which forelimbs appear (froglets). We counted and collected froglets daily (above the water line, or swimming without using their tail), recorded date of collection, and determined their size at metamorphosis (snout–vent length) to the nearest 0.1 mm. Froglets were then released in a nearby pond. Response variables for each enclosure included percentage of stocked individuals that metamorphosed, mean size at metamorphosis, mean duration of the larval period (number of days between stocking and metamorphosis), and mean growth rate (froglet size divided by larval period). After 14 July we observed no froglets in any of the cages, and thus assumed metamorphosis to be completed.

Macrophytes.—Macrophyte coverage was estimated within the metal frame where invertebrates were swept netted. Coverage was expressed as percentage total area (large stones excluded). The nonconsumptive destruction of macrophytes by crayfish was assessed weekly by netting live macrophyte fragments floating on the water surface within each cage (Lodge et al. 1994). Collected plants were dried (65°C, until constant mass) and weighed.

Periphytic algae.—We used two different substrates to evaluate the effects of treatments on algae. In each cage we put nine glazed ceramic tiles (10 × 10 cm) on the sediment surface (0.5 m depth), and nine polyethylene strips (1.6 × 50 cm), which were anchored to the sediment at one end and kept floating by a piece of cork nailed to the other end. Tiles may be grazed by all grazers, whereas strips were inaccessible to signal crayfish (Nyström et al. 1999). To allow algal colonization of substrates before the experiment, substrates were placed in the pond on 13 March and then transferred to the cages in early April. On the same dates as macrophytes and invertebrates were sampled, three tiles and three strips were randomly collected from each cage and frozen. Plastic strips were preserved in vials, whereas periphyton on tiles was scraped off with a razor blade and then transferred to vials. Chlorophyll *a* per unit surface area was then measured spectrophotometrically after extraction with ethanol (Jespersen and Christoffersen 1987).

Statistical analyses

Statistical analyses of response variables were performed on the means from each cage. In most cases a two-way factorial design with repeated measures was used to examine effects of crayfish, trout, and the interactions between these two groups (e.g., Fauth 1990, Pringle and Hamazaki 1998). Prior to analysis, all data used in two-way MANOVAs or ANOVAs were natural log- or log($x + 1$)-transformed to normalize distributions and stabilize variances. The use of log-transformed data also changes the underlying model of multiple predator effects from an additive model to a multiplicative risk model. The multiplicative model is more appropriate to apply to experimental data on prey bio-

TABLE 1. Two-way, repeated-measures MANOVA for effects of crayfish, trout, and their interactive effects on communities in cages (predatory invertebrates, snails, insect grazers, tadpoles, periphyton on tiles and strips, and macrophyte coverage) after predator introduction in June and July (Time).

Source	df	Wilks' lambda	F	P
Between cages				
Crayfish	7, 10	0.1566	7.6907	0.0023
Trout	7, 10	0.0456	29.8749	<0.0001
Crayfish × Trout	7, 10	0.4792	1.5521	0.2548
Within cages				
Time	7, 10	0.0057	247.5448	<0.0001
Time × Crayfish	7, 10	0.1143	11.0656	0.0005
Time × Trout	7, 10	0.0226	61.8320	<0.0001
Time × Crayfish × Trout	7, 10	0.4829	1.5299	0.2614

Note: We assessed tadpoles by using the number caught in traps after predator introduction on 27 May and 16 June 1997.

mass and survivorship measured over time, particularly when predators have strong effects on prey survival (Wootton 1994, Sih et al. 1998). Percentage data used in one-way ANOVAs were arcsine-transformed prior to analysis.

The analysis of predator effects on community structure was complicated by the occurrence of several response variables, which most likely were correlated, and which were sampled repeatedly over time. Multiple univariate analyses for a large number of species made in the same community increase the risk of type I error (e.g., Morin 1987). Therefore, we first performed a two-way MANOVA with time as a repeated measure to test for overall effects of crayfish, trout, and both predators on multiple response variables in enclosures (the dependent variables in the MANOVA were the biomass of predatory invertebrates, snails, insect grazers, number of trapped tadpoles, macrophyte coverage, and periphyton biomass on strips and tiles). Finally, to clarify the interpretation of the MANOVA, two-way, repeated-measures ANOVAs for each dependent variable tested the effects of crayfish, trout, and their combined effect over time.

Because very few froglets survived in cages with crayfish + trout, this treatment was omitted from calculations of tadpole size at metamorphosis, growth rate, and length of the larval period. Instead, the effect of each predator on the performance of froglets was tested by a one-way MANOVA. Individual ANOVAs of each variable then clarified the interpretation of the MANOVA, and Tukey's post hoc test revealed differences between control, crayfish, and trout cages. Because growth rate among tadpoles may be density dependent, we compared growth rate in control, crayfish, and trout cages including froglet survival as a covariate (ANCOVA).

RESULTS

Because enclosures were installed in a natural pond community, we tested if initial conditions in May were significantly different between cages assigned to dif-

ferent treatments, using a one-way MANOVA. Because neither MANOVA ($F_{21,29} = 0.56$, $P = 0.91$) nor any individual ANOVAs showed significant differences between cages assigned to different treatments ($P > 0.09$ in all cases), differences between response variables on the subsequent sampling dates (June and July for invertebrates and primary producers and May and June for tadpoles) were assumed to reflect effects of the introduced predators. Therefore, only the samplings in June and July (May and June for tadpoles) were included in the analysis of treatment effects over time. MANOVA indicated that both crayfish and trout had significant effects on enclosed communities over time (Table 1). Furthermore, crayfish and trout effects on caged communities were independent indicated by non-significant crayfish-by-trout interactions (Table 1). Below we interpret these results using two-way, repeated-measures ANOVAs by examining the effects of crayfish, trout, and their combined effect on each of the dependent variables when samples taken after predator stocking in June and July are included.

Macroinvertebrates

Before predators were added, macroinvertebrate biomass in the pond (results from all 20 cages pooled) was dominated by predatory heteropterans such as Notonectidae (29%), Naucoridae (21%), and Corixidae (2%). Dystiscidae constituted 28% of the total biomass. Macroinvertebrate grazers made up 16% of the total biomass, and were dominated by thin-shelled pulmonate snails (*Lymnaea* spp., 60%) and the mayfly *Cloeon* sp. (28%).

Trout dramatically reduced the biomass of predatory macroinvertebrates, whereas crayfish had a less strong yet significant effect (Table 2, Fig. 2A). Predatory macroinvertebrates were almost eliminated in cages with trout present, and in two of the crayfish + trout cages no predatory macroinvertebrates were collected on the last sampling date. However, the effects of crayfish and trout on the biomass of predatory invertebrates were independent of each other (no significant interaction,

TABLE 2. Two-way, repeated-measures ANOVAs for effects of crayfish, trout, and their interactive effects on the biomass of (A) predatory invertebrates (B) snails, and (C) insect grazers after predator introduction in June and July 1997 (Time).

Source	df	MS	F	P
A) Predatory invertebrates				
Between cages				
Crayfish	1	23.9085	10.9705	0.0044
Trout	1	63.4731	29.1249	<0.0001
Crayfish × Trout	1	6.1686	2.8305	0.1119
Error	16	2.1793		
Within cages				
Time	1	5.4870	5.3143	0.0349
Time × Crayfish	1	0.7813	0.7567	0.3972
Time × Trout	1	14.2803	13.8307	0.0019
Time × Crayfish × Trout	1	0.0026	0.0025	0.9604
Error	16	1.0325		
B) Snails				
Between cages				
Crayfish	1	155.5614	68.1280	<0.0001
Trout	1	11.5948	5.0779	0.0386
Crayfish × Trout	1	0.0750	0.0329	0.8584
Error	16			
Within cages				
Time	1	0.0039	0.0152	0.9034
Time × Crayfish	1	0.1043	0.4096	0.5312
Time × Trout	1	0.0001	0.0004	0.9837
Time × Crayfish × Trout	1	0.4329	1.7002	0.2107
Error	16	0.2546		
C) Insect grazers				
Between cages				
Crayfish	1	0.1090	0.2354	0.6341
Trout	1	25.0506	54.0991	<0.0001
Crayfish × Trout	1	0.3951	0.8532	0.3694
Error	16	0.4630		
Within cages				
Time	1	3.2877	6.6504	0.0202
Time × Crayfish	1	0.1866	0.3774	0.5476
Time × Trout	1	1.9334	3.9109	0.0655
Time × Crayfish × Trout	1	0.0155	0.0314	0.8615
Error	16	0.4944		

Table 2). The biomass of snails was greatly reduced by crayfish (Table 2, Fig. 2B), whereas crayfish did not significantly reduce insect grazers (mainly the summer generation of *Cloeon* sp., Fig. 2C). In contrast to crayfish, trout had a much weaker, though significant effect on the biomass of snails, but had strong effects on insect grazers (Table 2, Fig. 2B, C). Similarly, there were no significant crayfish-by-trout interactions (Table 2) indicating that effects of each predator were independent. Generally, the effect of combined predators (crayfish + trout) reflected the most dangerous predator in each case (trout for predatory invertebrates and insect grazers, crayfish for snails).

Tadpoles and froglets

The number of tadpoles caught in active-fauna traps was significantly reduced by trout (Table 3, Fig. 3). In crayfish cages, more tadpoles tended to be caught compared to controls, but the lowest number of tadpoles was caught in crayfish + trout cages. Thus there was a significant crayfish-by-trout interaction. Nonetheless,

the effect of combined predators was similar to the trout effects (Fig. 3). In trout, and crayfish + trout cages, so few tadpoles were collected that we could not include them in the analysis of tadpole tail injury. On the last sampling date, however, the proportion of tadpoles with tail injuries was significantly higher in the crayfish cages ($18 \pm 3.3\%$, mean ± 1 SE) compared to control cages ($0.9 \pm 0.1\%$, one-way ANOVA, $F_{1,8} = 25.80$, $P = 0.0010$).

In total 725 froglets survived through metamorphosis that occurred from 22 June to 14 July. A two-way ANOVA indicated that the proportion of froglets metamorphosing in control cages ($15.5 \pm 2.9\%$) was significantly higher than in crayfish ($5.4 \pm 1.6\%$, $F_{1,16} = 14.47$, $P = 0.0016$) and trout cages ($3.1 \pm 1.2\%$, $F_{1,16} = 27.39$, $P < 0.0001$). The lowest number of surviving froglets was found in crayfish + trout cages ($0.2 \pm 0.1\%$). In two of the crayfish + trout cages no individuals metamorphosed. Even though the effects of crayfish and trout individually on froglet survival were strong, a marginally nonsignificant crayfish-by-trout

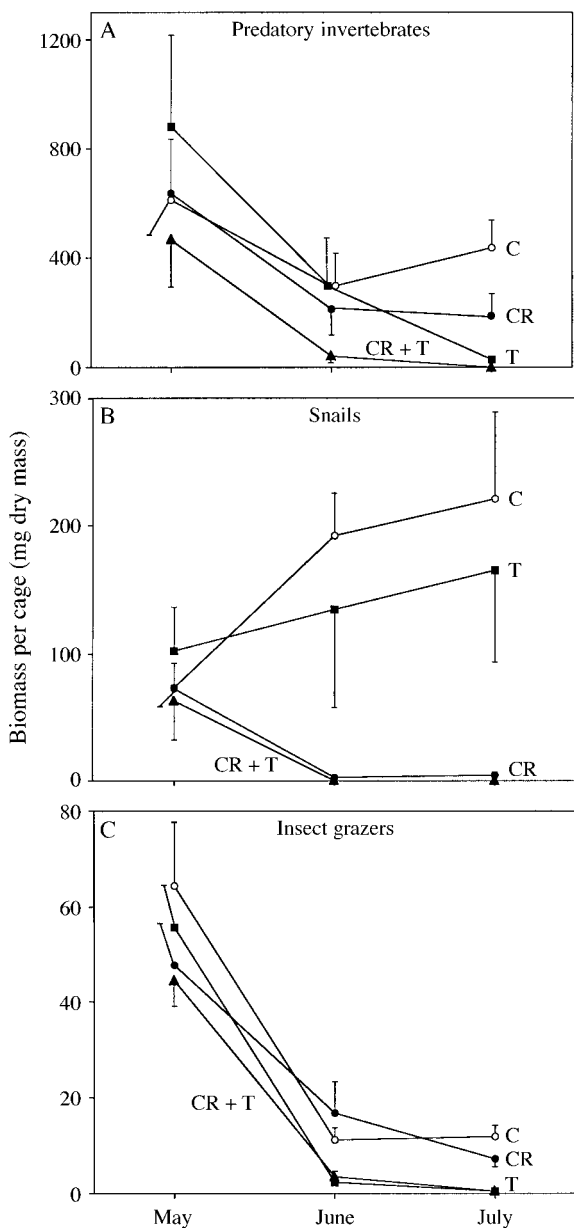


FIG. 2. Total biomass of (A) predatory invertebrates, (B) snails, and (C) insect grazers (means \pm 1 SE) over time sampled in control cages (C), crayfish cages (CR), trout cages (T), and in crayfish + trout cages (CR + T). Note the different scales on the y-axes (statistics in Table 2).

interaction indicated that these predator effects were independent (two-way ANOVA, crayfish-by-trout interaction; $F_{1,16} = 4.11$, $P = 0.0596$).

Due to low survival in crayfish + trout cages (six froglets in total), this treatment was omitted from analyses of size at metamorphosis, growth rate, and length of the larval period. A one-way MANOVA showed that overall froglet performance differed among control, crayfish, and trout cages (Table 4). Individual ANOVAs showed that mean length of the larval period did not

contribute to the significance of the MANOVA (54 ± 0.5 d in control cages, 52 ± 1.1 d in crayfish cages, and 53 ± 1.0 d in trout cages [all mean \pm 1 SE]). However, both size at metamorphosis and growth rate differed between treatments (Table 4). Mean size of froglets in control cages was similar to that in crayfish cages, but froglets in trout cages were significantly smaller than in both control and crayfish cages (Table 4, Fig. 4). To test if differences in growth rate of tadpoles persisted after controlling for variation in final froglet density, we analyzed growth rates using ANCOVA, with number of surviving froglets as covariate in the analysis. The ANCOVA showed that growth rates had statistically indistinguishable slopes (treatment-by-survivor interaction: $F_{2,9} = 1.36$, $P = 0.30$); therefore, we tested if population growth rates differed between treatments by omitting the interaction term in the next analysis. With increasing number of survivors, growth rate declined linearly (ANCOVA, $F_{1,9} = 8.58$, $P = 0.0168$, Fig. 5), but the intercepts differed between treatments (ANCOVA, $F_{2,11} = 23.04$, $P = 0.0001$, Fig. 5). Growth rate was significantly lower in trout cages in comparison with control (Tukey's post hoc test, $P = 0.0017$) and crayfish cages (Tukey's post hoc test, $P = 0.0003$), but there was no difference between crayfish and control cages (Tukey's post hoc test, $P = 0.80$).

Macrophytes

Crayfish significantly reduced macrophyte coverage, whereas trout had no impact on macrophytes (Table 5, Fig. 6A). Due to crayfish feeding activity, floating macrophyte parts (mainly live stems of *Glyceria fluitans*) accumulated in cages with crayfish and in crayfish + trout cages (Fig. 6B). The variation in macrophyte coverage and the biomass of floating macrophytes reflected the effect of crayfish, as indicated by the nonsignificant crayfish-by-trout interactions (Table 5, Fig. 6).

Periphyton

The biomass of periphyton on strips was strongly dependent on treatment. Chlorophyll *a* increased in both crayfish and trout cages. Again, there was no significant crayfish-by-trout interaction, but the combined effect of crayfish + trout was higher than each predator separately (Table 6, Fig. 7A). On the June sampling date the periphyton biomass on tiles followed the same pattern as biomass on strips. However, the chlorophyll *a* levels in all predator treatments conveyed by the end of the experiment, resulting in a significant crayfish-by-trout interaction (Table 6, Fig. 7B).

DISCUSSION

This study shows that both rainbow trout and signal crayfish have strong multitrophic level effects on benthic communities, through direct consumption and indirect effects on lower trophic levels. In most cases, predators had independent effects on prey (e.g., Fig. 1D). Signal crayfish had a strong impact on snails and

TABLE 3. Two-way repeated-measures ANOVAs for effects of crayfish, trout, and their interactive effects on the abundance of tadpoles caught in active-fauna traps after predator introduction in May and June 1997 (Time).

Source	df	MS	F	P
Between cages				
Crayfish	1	0.4738	3.1885	0.0931
Trout	1	7.1030	47.8030	<0.0001
Crayfish × Trout	1	1.2896	8.6787	0.0095
Error	16	0.1486		
Within cages				
Time	1	0.0288	0.5751	0.4593
Time × Crayfish	1	0.2017	4.0271	0.0620
Time × Trout	1	0.0141	0.2810	0.6033
Time × Crayfish × Trout	1	0.1675	3.3452	0.0861
Error	16	0.0501		

macrophytes as predicted (Fig. 1B), but had less of an impact on predatory invertebrates, tadpoles, and insect grazers. Signal crayfish have weak direct effects on actively moving prey such as those predatory invertebrates and insect grazers that dominated the invertebrate biomass in this pond (Nyström et al. 1999). Several crayfish species have been found to have a negative impact on snails and aquatic macrophytes, introduced species in particular (e.g., Nyström 1999). Correlative studies also suggest that signal crayfish have a strong negative impact on aquatic macrophytes and snails in Swedish ponds (Nyström et al. 1996).

In contrast, trout had a strong negative impact on the biomass of large active predatory invertebrates. Moreover, trout also reduced biomass of invertebrate grazers, such as insect grazers, but had less of an impact on snail biomass. The number of tadpoles caught in traps and the number of surviving froglets were also low in cages with trout; froglets had a reduced growth rate compared to control and crayfish cages. The effect of trout in our experiment is consistent with the results

from previous studies showing that native (e.g., Ware 1973, Cooper 1988, Wiseman et al. 1993) and introduced rainbow trout (Bradford et al. 1998) have strong effects on large active prey. Similarly, snails were relatively unaffected by trout in other studies (cf. Macan 1966, Hemphill and Cooper 1984).

Overall, our results suggest that when two noninteracting predators have strong but different effects on prey survival or behavior, their combined effects on intermediate trophic levels reflect responses to the more dangerous predator (e.g., Kurzava and Morin 1998). Our data suggest several different mechanisms that explain the direct and indirect predator effects on these pond communities.

Trophic cascades and effects of predators on algae

In food chains, trophic cascades occur if primary consumers that regulate primary producers are significantly reduced by predators, or if these primary consumers respond to predators by reduced feeding activity (McIntosh and Townsend 1996, Turner 1997, Peckarsky and McIntosh 1998). However, trophic cascades may not be readily observed if top predators are omnivorous, having direct effects on primary producers (Nyström et al. 1996, Pringle and Hamazaki 1998).

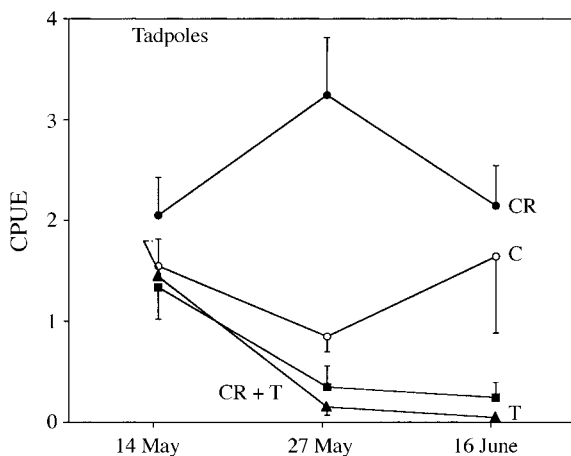


FIG. 3. The number of tadpoles (means \pm 1 SE) caught per active-fauna trap over time (CPUE = catch per unit effort) in control cages (C), crayfish cages (CR), trout cages (T), and in crayfish + trout cages (CR + T) (statistics in Table 3).

TABLE 4. One-way MANOVA, univariate one-way ANOVAs and Tukey's post hoc tests for effects of treatment (control, crayfish, and trout) on length of the larval period of *Rana temporaria*, size at metamorphosis, and growth rate.

Response variable	df	MS	F	P
Multivariate analysis	6, 20	0.1234†	6.1540	0.0009
Larval period	2, 12	0.0025	1.6577	0.2314
Size at metamorphosis	2, 12	0.0455	27.8297	<0.0001
Control vs. Crayfish				0.7683
Control vs. Trout				0.0003
Crayfish vs. Trout				0.0002
Growth rate	2, 12	0.0026	14.4142	0.0006
Control vs. Crayfish				0.4859
Control vs. Trout				0.0052
Crayfish vs. Trout				0.0008

†Wilks' lambda.

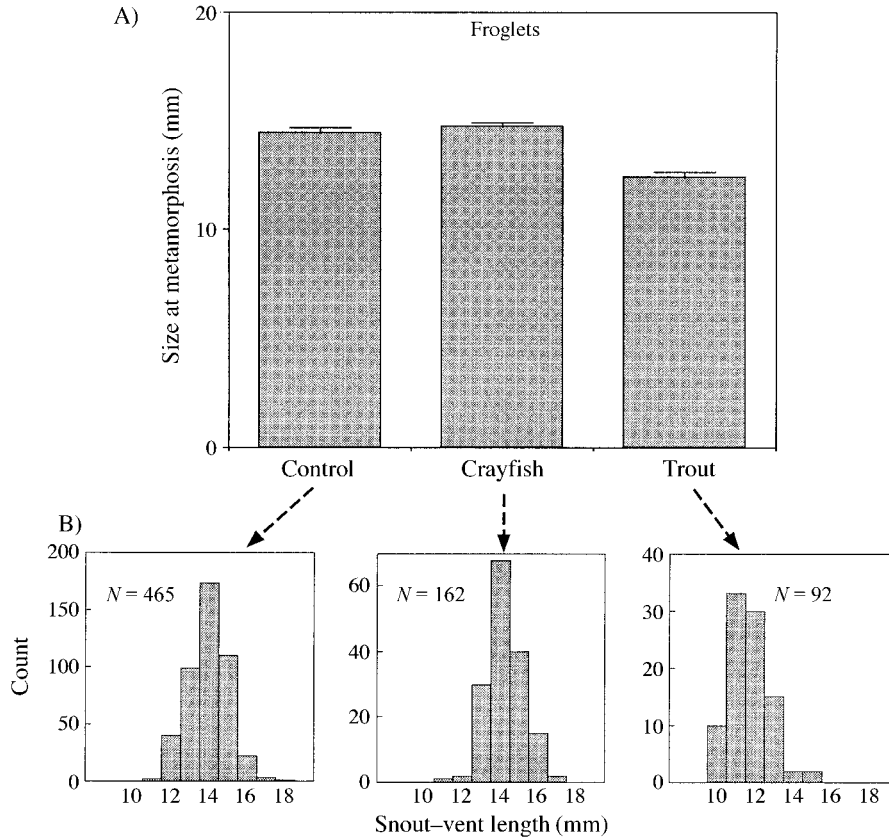


FIG. 4. Size at metamorphosis of surviving froglets (means + 1 SE) in (A) different treatments, and (B) the number of froglets surviving from different size classes (all froglets pooled from five replicates) (statistics in Table 4).

Since both *Lymnaea* snails and *R. temporaria* tadpoles reduce the biomass of periphytic algae (Brönmark et al. 1991), we expected strong indirect effects of predators on periphyton if those predators significantly reduced grazer biomass or activity. In crayfish cages,

snail densities decreased dramatically and periphyton increased on both tiles and strips. Interestingly, signal crayfish is an omnivore that also consumes periphyton in Swedish ponds (Lirås et al. 1998), which may have been expected to conceal any cascading effects. How-

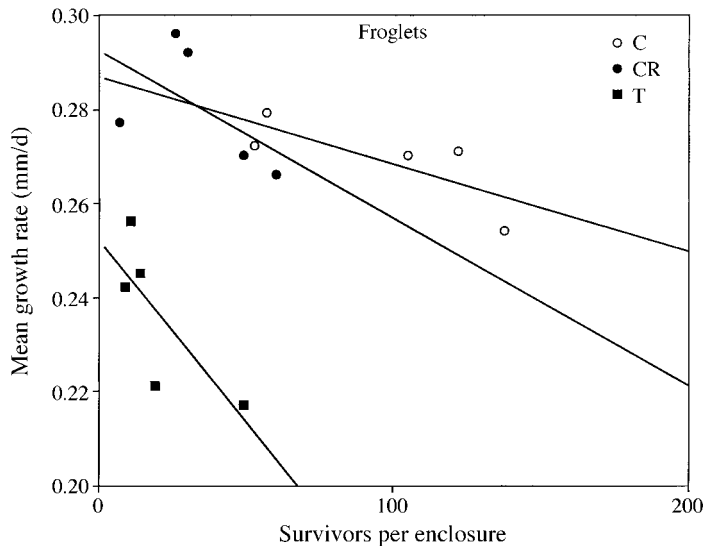


FIG. 5. Growth rate of froglets (mm/d) from stocking until metamorphosis in relation to the final number of surviving froglets in control cages (C), crayfish cages (CR), and trout cages (T) (ANCOVA, see Results: Tadpoles and froglets).

TABLE 5. Two-way repeated-measures ANOVAs for effects of crayfish, trout, and their interactive effects on (A) macrophyte coverage after predator introduction in June and July 1997 (Time) and (B) the cumulative biomass of floating live macrophyte parts in cages.

Source	df	MS	F	P
A) Macrophyte coverage				
Between cages				
Crayfish	1	1.0582	28.9446	<0.0001
Trout	1	0.0068	0.1852	0.6727
Crayfish × Trout	1	0.0014	0.0378	0.8484
Error	16	0.0366		
Within cages				
Time	1	0.0020	1.1078	0.3082
Time × Crayfish	1	0.0225	12.7970	0.0025
Time × Trout	1	0.0027	1.5230	0.2350
Time × Crayfish × Trout	1	0.0043	2.4677	0.1358
Error	16	0.0018		
B) Floating macrophytes				
Between cages				
Crayfish	1	70.8141	88.5051	<0.0001
Trout	1	1.6065	2.0078	0.1757
Crayfish × Trout	1	1.0025	1.2530	0.2795
Error	16			
Within cages				
Time	5	0.6413	9.1735	0.0036
Time × Crayfish	5	0.1266	1.8116	0.1933
Time × Trout	5	0.1466	2.0964	0.1589
Time × Crayfish × Trout	5	0.0508	0.7269	0.4409
Error	80	0.0699		

Note: ANOVA for effects on the cumulative biomass of floating live macrophyte parts (B) includes data from six weekly samplings after predator introduction (Time).

ever, in this and other studies, crayfish grazing on periphyton did not outweigh the positive indirect effect of a reduction in snail densities (Weber and Lodge 1990, Lodge et al. 1994, Nyström et al. 1999). Due to a mismatch of their feeding morphology, crayfish are not as efficient grazers on microalgae as are snails (Luttenton et al. 1998); and therefore indirect effects of omnivorous crayfish on algae may be strong. In contrast, in systems with algal communities having filamentous forms, crayfish grazing may be significant (Hart 1992, Creed 1994) and may outweigh reduced grazing from snails (Nyström et al. 1996).

Furthermore, presence of refuges in heterogenous habitats (e.g., Power 1992b) and effective prey defenses (e.g., snails with thick shells) may also prevent cascading effects of top predators (Brönmark 1994, Brönmark and Weisner 1996). Here, crayfish reduced snail abundance and habitat complexity simultaneously by reducing macrophytes, but even in complex habitats signal crayfish have strong effects on *Lymnaea* snails (Nyström and Pérez 1998). As opposed to molluscivorous fish, crayfish are not gape-limited and may reduce the abundance of even large thick-shelled snail species (Lodge et al. 1998). Therefore, cascading effects of crayfish were observed even though crayfish are omnivorous, habitats were heterogenous, and prey were apparently defended.

The trophic cascade observed in cages with trout was due to a different mechanism. The high periphyton biomass in cages with trout in this study may be a com-

ination of both density and trait-mediated trout effects on tadpole grazing. In cages with trout, both tadpole survival to metamorphosis and the number of trapped tadpoles (activity) were reduced, even though habitats were complex. In streams, trout may have positive indirect effects on periphyton by consuming large important invertebrate grazers (Bechara et al. 1992), or by forcing grazers to reduce their feeding activity (e.g., McIntosh and Townsend 1996). In another system, predatory newts in pond communities indirectly affect phytoplankton (Morin 1995) and periphyton (Leibold and Wilbur 1992, Wilbur 1997) by consuming tadpoles. Peacor and Werner (1997) found that the nonlethal presence of a caged dragonfly led to increased periphyton levels by changing tadpole activity. In addition, *Rana* tadpoles from the same population we used in our experiment increased their time spent in refuges in the presence of chemical cues released by rainbow trout. This change in behavior was sufficient to allow periphyton to increase (Nyström and Åbjörnsson 2000).

Our results suggest that trophic cascades may develop in aquatic food webs even with omnivores such as crayfish, and in complex habitats with trout. These strong indirect effects are mediated through both predation on important grazers (i.e., the crayfish–snail–periphyton link) and a combination of density and behavioral responses of grazers to predators (i.e., the trout–tadpole–periphyton link).

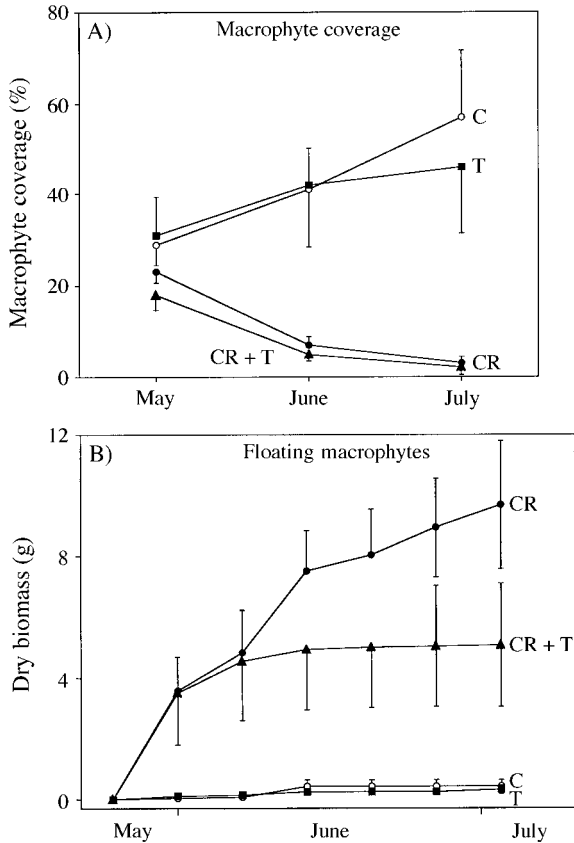


FIG. 6. (A) Percentage macrophyte coverage and (B) accumulated macrophyte dry biomass (means \pm 1 SE) floating in control cages (C), crayfish cages (CR), trout cages (T), and in crayfish + trout cages (CR + T) (statistics in Table 5).

Effects of predators on tadpoles and froglets

Predator avoidance behaviors are very common in nature (Lima and Dill 1990) and may reduce direct effects on prey mortality (Scheffer 1997). However, predator avoidance often has associated fitness costs (Lima 1998, McPeck and Peckarsky 1998). In our study, tadpoles associated with crayfish suffered more tail injuries than in controls, in agreement with experimental studies (Figiel and Semlitsch 1991, Axelsson et al. 1997). Tail length affects tadpole swimming speed (Wassersug and Sperry 1977) and, thus, the risk of being caught by crayfish (Figiel and Semlitsch 1991). Moreover, the swimming ability of tadpoles is greatly reduced during metamorphosis and froglets are more sensitive to predation than pre-metamorphic stages (Wassersug and Sperry 1977, Huey 1980, Brown and Taylor 1995). The sublethal effect of crayfish may explain why fewer tadpoles metamorphosed in crayfish cages than control cages.

In trout cages, however, survivorship, growth rate, and size at metamorphosis were lower than in control and crayfish cages. Size at metamorphosis is positively correlated to juvenile survivorship and fitness in the adult

state (Berven and Gill 1983, Smith 1987). In the common frog, large females produce more eggs than small females, and egg fertility is also positively correlated to the length of the male (Gibbons and McCarthy 1986). Thus, although the direct mortality effects of trout and crayfish on froglets were significant in this study, the negative effect of trout on *Rana* populations is probably stronger than for crayfish since surviving froglets were smaller in trout cages. The size distribution of surviving froglets in trout cages indicates that selective predation was unlikely since the mean size of the entire population of froglets had shifted toward smaller sizes, rather than being truncated due to selective removal of larger tadpoles (Fig. 4B, see also Fauth 1990). Furthermore, predator-induced reduction in the density of tadpoles could have reduced intraspecific competition, resulting in higher growth rates of surviving tadpoles in cages with low survivorship (Fig. 5, see also Morin 1983). However, if tadpoles alter their microhabitat to avoid predators, reduced feeding rate may decrease tadpole growth rate and size at metamorphosis (Skelly 1992). *Rana* tadpoles reduce their activity when exposed to waterborne

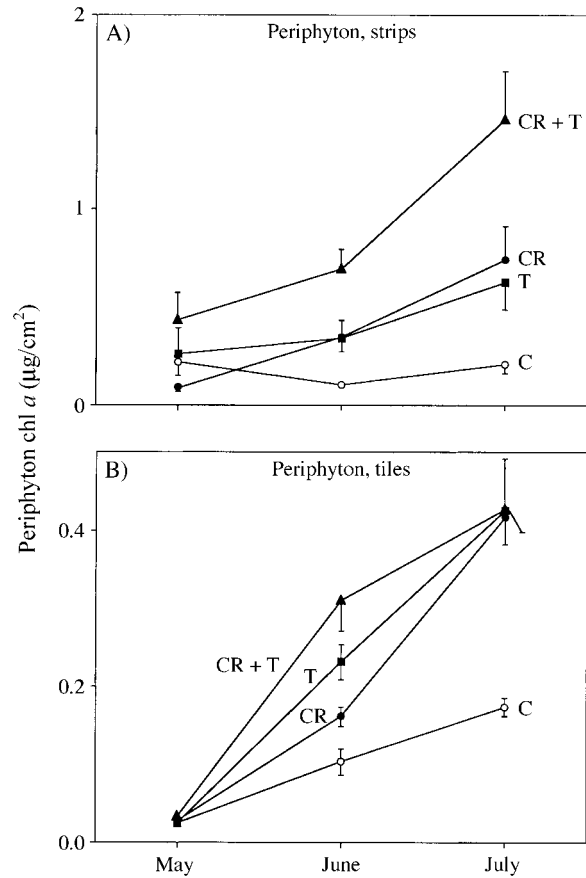


FIG. 7. Areal periphyton on (A) strips and on (B) tiles measured as chlorophyll *a* (means \pm 1 SE) over time in control cages (C), crayfish cages (CR), trout cages (T), and in crayfish + trout cages (CR + T). Note the different scales on the y-axes (statistics in Table 6).

TABLE 6. Two-way repeated-measures ANOVAs for effects of crayfish, trout and their interactive effects on periphyton measured as chlorophyll *a* (A) strips and (B) tiles after predator introduction in June and July 1997 (Time).

Source	df	MS	<i>F</i>	<i>P</i>
A) Periphyton (strips)				
Between cages				
Crayfish	1	10.2707	34.2906	<0.0001
Trout	1	8.3586	27.9067	<0.0001
Crayfish × Trout	1	0.3773	1.2596	0.2783
Error	16	0.2995		
Within cages				
Time	1	4.3926	46.9326	<0.0001
Time × Crayfish	1	0.0238	0.2542	0.6210
Time × Trout	1	0.0084	0.0901	0.7679
Time × Crayfish × Trout	1	0.0024	0.0253	0.8757
Error	16	0.0936		
B) Periphyton (tiles)				
Between cages				
Crayfish	1	1.5632	12.3666	0.0029
Trout	1	3.4244	27.0907	<0.0001
Crayfish × Trout	1	0.7848	6.2086	0.0241
Error	16	0.1246		
Within cages				
Time	5	3.6895	241.3404	<0.0001
Time × Crayfish	5	0.0052	0.3386	0.5688
Time × Trout	5	0.2089	13.6622	0.0020
Time × Crayfish × Trout	5	0.3044	19.9094	0.0004
Error	80	0.0153		

chemical cues from rainbow trout (Nyström and Åbjörnsson 2000).

Effects of multiple predators

Several studies have revealed that multiple predators often have interactive effects on prey due to risk reduction or risk enhancement (Sih et al. 1998). Here, the overall impact of crayfish and trout on components of the pond community reflected different responses by intermediate consumers to the most dangerous predator. Predators primarily had independent effects on the community, because predator–predator interactions were weak and neither risk reduction nor enhancement occurred. Similar multiple predator effects have been observed in systems where the two predators differ in their effects on prey, so that one predator has weak effects on a certain prey species, and the other has strong effects (Sih et al. 1998). Based on their studies of stream-living mayflies, McIntosh and Peckarsky (1999) predict that predator avoidance should take place in the form of a hierarchy when one predator presents a substantially higher predation risk than the other. In this study, the effects on snails and macrophytes were due to crayfish, whereas the effects on insect grazers and predatory invertebrates were mostly due to trout. Rainbow trout consume signal crayfish (Frantz and Cordone 1970; P. Nyström, unpublished data), and juvenile crayfish often reduce their activity levels and increase the use of refuges in the presence of fish (Stein and Magnuson 1976, Butler and Stein 1985, Blake and Hart 1993). Predatory fish could, therefore, reduce crayfish impact on lower trophic levels (Stein and Magnuson 1976, Hill and Lodge 1995).

However, adult crayfish have a size refuge from most fish predators and do not respond to predatory fish (Stein and Magnuson 1976, Butler and Stein 1985). In this study, catches of adult crayfish did not differ between crayfish and crayfish + trout cages, suggesting that the abundance of adult signal crayfish was unaffected by trout. Two years after the experiment, 12 of the rainbow trout used in the experiment were recaptured in the pond and their stomach contents analyzed. None of the trout had consumed crayfish (P. Nyström, unpublished data) indicating weak direct effects of trout on crayfish.

Behavioral differences between prey species may affect their vulnerability to predators with different foraging strategies (Rahel and Stein 1988, Blois-Heulin et al. 1990, McPeck 1990, Kurzava and Morin 1998). Hence, presence of multiple predators may alter an animal's mortality risk, if avoiding one predator affects the predation risk from another predator (Soluk and Collins 1988, Kiesecker and Blaustein 1998, Losey and Denno 1998). Here, decreased tadpole activity in the presence of rainbow trout did not increase predation risk from signal crayfish, similar to results in Nyström and Åbjörnsson (2000). Tadpoles in this study responded to trout by reducing their activity, but tended to be more active in crayfish cages. The number of trapped tadpoles in the combined treatment was similar to the numbers active in trout cages, suggesting that tadpoles responded to the more dangerous predator.

Depending on substrate type, the indirect effects on periphyton by crayfish and trout differed on the last sampling date. Periphyton on strips in cages with both predators was higher than when crayfish or trout were

alone, due to reduced grazing from snails in crayfish cages and reduced grazing from tadpoles in trout cages. Since tadpoles responded to the more dangerous trout by reduced feeding, trait-mediated indirect effects on periphyton persisted in the combined predator treatment. There are presently few demonstrations of indirect effects on primary producers in food webs influenced by multiple predators. Morin (1995) showed that two species of salamanders had noninteractive effects on phytoplankton biomass by predation on tadpoles. Nyström and Åbjörnsson (2000) found that direct lethal effects of signal crayfish on common frog tadpoles had positive indirect effects on periphyton, and nonlethal presence of trout had similar effects on periphyton by trait-mediated effects on tadpole behavior. These predator effects were independent and in the combined predator treatment periphyton biomass was the product of single predator effects. Trait-mediated indirect effects on periphyton have also been shown in other systems with multiple predators (Peacor and Werner 1997, Peckarsky and McIntosh 1998). Periphyton on tiles conveyed at the last sampling date resulting in a significant crayfish-by-trout interaction. It is possible that periphyton on tiles (sampled at a water depth of 0.5 m) became more light limited than periphyton growing on strips (sampled just below the water surface) in cages with predators. At the end of the experiment we observed an increase in turbidity in predator cages that might have prevented thick algal mats from building up on tiles.

Effects of multiple introduced predators

Predictions about the impact of exotic species are hard to make, since the characteristics of the target community are as important as the characteristics of the introduced species, each of which is rarely known in detail (e.g., Lodge 1993, but see Holway 1999 for an exception). Theoretical and empirical studies suggest that the impact of an introduced predator will most likely be severe in species-poor systems where native predators and competitors are absent (Diamond and Case 1986, Pimm 1989, Lodge 1993). Native prey may also be vulnerable to new predators if they have no prior experience with functionally similar predators. Prey that have not been exposed to predators or to native predators only, may not have evolved efficient defense systems against nonnative predators. Thus, to predict the effects of multiple introduced predators on community structure we first need to determine interaction strength between species in the native food web; we also need to determine if the exotic predators interact with each other and with lower trophic levels. Finally it is important to know if native prey have any experience with the introduced predator type and show appropriate avoidance behaviors or other defense adaptations.

In this and other systems, introduced crayfish species may have stronger effects on snails and macrophytes than native crayfish due to higher consumption rates (Olsen et al. 1991, Nyström and Strand 1996, Lodge

et al. 1998, Nyström et al. 1999). The strong impact of crayfish on snails observed in this study suggests that snails lack or have inefficient antipredator defenses against crayfish, possibly even less efficient to an introduced species. In this study, the coevolutionary history of crayfish and snails in Sweden may not have been sufficiently long to allow the development of efficient antipredator behaviors in snails. Similarly, the predatory invertebrates in these ponds may have little experience with the "trout type predator" because native brown trout in southern Sweden are mostly found in streams. For example, introduced trout in fishless California alpine lakes has eliminated or greatly reduced the numbers of large, mobile, and epibenthic limnetic taxa including invertebrates and amphibians (Bradford et al. 1998).

Predictions and future investigations

Based on the results from this study, we predict that effects of multiple introduced predators on community structure can be strong when the introduced predators: (1) experience little predation or competition from native predators, (2) do not affect each other's biomass or foraging efficiency, and (3) have prey that lack efficient defense adaptations to the introduced predators. Our data further suggest that lethal predator effects should be most important for naive prey (e.g., snails in this study), but trait-mediated effects on prey should be more important if prey show significant antipredator responses to the predators (e.g., the common frog tadpoles in this study). Trophic cascades may develop if vulnerable prey are strong interactors in the native food web, and the introduced predators, though omnivorous, are less efficient consumers on prey resources. These cascades may be strong if the multiple introduced predators affect different grazers in the native food web, each of which has the potential to control plant resource levels.

To understand the mechanisms that structure more complex food webs we have to consider both direct and indirect effects of multiple predators, and the relative importance of density and trait-mediated effects of multiple predators on prey populations. Also as a result of antipredator behavior, prey mortality rate may not increase linearly with increasing predator density (Abrams 1993). Future studies, should, therefore address interactive effects of predators by including variations in predator and prey density (e.g., Diehl 1995). Further, in an era of faunal homogenization due to anthropogenic effects on dispersal rates, the role of exotic species, and especially exotic predators, will become more and more important to understanding the structure of communities.

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