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Stenroth, Patrik; Nyström, Per

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*Total number of authors:*
2

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

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# Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae

PATRIK STENROTH AND PER NYSTRÖM
*Lund University, Department of Ecology, Limnology, Ecology Building, Lund, Sweden*

## SUMMARY

1. The impact of the introduced omnivorous signal crayfish (*Pacifastacus leniusculus*) on trout fry, macroinvertebrates and algae was evaluated in a brown water stream in southern Sweden using *in situ* enclosures. We also examined the gut content of all surviving crayfish in the enclosures. Two crayfish densities in addition to a control without crayfish were used in replicate enclosures (1.26 $m^2$) in a 1-month experiment. Additionally, 20 trout fry (*Salmo trutta*) were stocked in each enclosure to assess the effects of crayfish on trout survival and growth.
2. Detritus was the most common food item in crayfish guts. Animal fragments were also frequent while algae and macrophytes were scarcer. Crayfish exuviae were found in crayfish guts, but the frequency of cannibalism was low.
3. Trout survival in enclosures was positively related to water velocity but was unaffected by crayfish.
4. Total invertebrate biomass and taxon richness were lower in crayfish treatments. The biomass of all predatory invertebrate taxa was reduced but only three of six non-predatory taxa were reduced in the crayfish treatments.
5. Epiphytic algal biomass (measured as chlorophyll *a*, on plastic strips) was not related to crayfish density, whereas the biomass of epilithic algae (measured as chlorophyll *a*) was enhanced by high water velocity and high crayfish density. The latter was possibly mediated via improved light and nutrient conditions, as active crayfish re-suspend and/or remove detritus and senescent algal cells during periods of low water velocity.
6. We conclude that the introduced signal crayfish may affect stream communities directly and indirectly. Invaded communities will have reduced macroinvertebrate taxon richness and the signal crayfish will replace vulnerable invertebrate predators such as leeches. In streams that transport large amounts of sediment or organic matter, a high density of crayfish is likely to enhance benthic algal production through physical activity rather than via trophic effects.

*Keywords*: crayfish, indirect effects, invertebrates, omnivory, stream

## Introduction

An increasing number of empirical and theoretical studies suggest that omnivory is prevalent in aquatic communities where it can have complex effects on trophic interactions (e.g. Menge & Sutherland, 1987; Diehl, 1993; Pringle & Hamazaki, 1998). For example, indirect effects such as trophic cascades may be prevented if omnivores feed on both primary consumers and primary producers (Polis & Strong, 1996). Even though the number of studies involving the role of omnivorous predators in freshwater communities is increasing, most of our knowledge is based on work from lakes and ponds (e.g. Diehl, 1992, 1993, 1995; Lodge *et al*., 1994). Few studies have examined the role of omnivores in streams, even though a high

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Correspondence: Patrik Stenroth, Department of Ecology, Limnology, Ecology Building, S-223 62 Lund, Sweden.
E-mail: patrik.stenroth@limnol.lu.se

degree of omnivory may characterise many stream food webs (e.g. Hildrew, Townsend & Hasham, 1985; Pringle & Hamazaki, 1998; Woodward & Hildrew, 2001; Schmid-Araya *et al.*, 2002).

Crayfish dominate the invertebrate biomass of many streams where they feed omnivorously on detritus, algae, plants, invertebrates (including other crayfish) and vertebrates (e.g. Momot, 1995). Stable isotope ratios of crayfish from both lentic (Nyström, Brönmark & Granéli, 1999) and lotic (Whitledge & Rabeni, 1996; Parkyn, Collier & Hicks, 2001) systems suggest, however, that crayfish depend primarily on animal protein for their growth. They might thus be expected to feed predominantly on macroinvertebrates when these are available. Low-protein resources such as plants, detritus and algae may be an important energy source for maintenance (e.g. Nyström *et al.*, 1999).

Crayfish can have negative effects on the biomass and species richness of invertebrates in lentic (Lodge *et al.*, 1994; Nyström, Brönmark & Granéli, 1996) and lotic (Charlebois & Lamberti, 1996; Parkyn, Rabeni & Collier, 1997) systems. When crayfish become abundant in lentic systems, species composition of invertebrates may change towards less vulnerable prey species. For example the relative abundance of mobile predatory invertebrates such as heteropterans, adult beetles and insect grazers may increase at the expense of slow moving invertebrates such as molluscs, which are significantly reduced by crayfish (e.g. Lodge *et al.*, 1994; Nyström *et al.*, 1996; Nyström *et al.*, 1999). In streams, crayfish have less predictable effects on invertebrate communities. Some studies indicate negative effects on most invertebrates (e.g. Charlebois & Lamberti, 1996; Stelzer & Lamberti, 1999; Usio, 2000), whereas others indicate minor effects or effects only on a few preferred taxa (Parkyn *et al.*, 1997; Perry, Lodge & Lamberti, 1997; Keller & Ruman, 1998). Similarly, the response of algae to crayfish in streams seems to be more variable than in lentic systems and algal biomass may increase (Charlebois & Lamberti, 1996), decrease (Creed, 1994; Keller & Ruman, 1998) or be unaffected by lotic crayfish (Stelzer & Lamberti, 1999).

The exotic signal crayfish (*Pacifastacus leniusculus* Dana) is found in lakes, ponds and streams in most European countries (e.g. Gherardi & Holdich, 1999). It can have strong effects on species richness and the structure of food webs in lakes and ponds by feeding at several trophic levels (e.g. Nyström *et al.*, 1996), but its impact on stream communities is less well known (but see Guan & Wiles, 1997). The present study was undertaken in a stream that is qualitatively and functionally different from previously studied lentic systems invaded by the signal crayfish. In permanent ponds in southern Sweden, where predatory fish and crayfish are absent, thin-shelled pulmonate snails dominate the grazer community. The snails regulate algal biomass efficiently, because predatory invertebrates (i.e. heteropterans, beetles and leeches) typically have weak effects on their biomass (Brönmark, 1992, 1994). In contrast, leeches dominate predatory invertebrate biomass in southern Swedish streams, whereas insects dominate the grazer guild. When leeches are abundant, algae increase in abundance because of consumption and predator-induced emigration of small insect grazers (Dahl, 1998). Brown trout (*Salmo trutta* L) are also widespread in Swedish streams and are potential predators of juvenile crayfish, although experimental studies have shown that eggs and juveniles of trout are also potential prey of adult crayfish (Rubin & Svensson, 1993).

We propose that invertebrate community composition and algal community structure should determine the ability of crayfish to control lower trophic levels via direct and indirect effects. This is because invertebrates are not equally vulnerable to consumption by crayfish. Furthermore, depending on the composition of the algal community, grazers (including crayfish) do not always effect standing stocks of algae. Thus, it is reasonable to find variable effects of crayfish in stream communities depending on the strength of the direct and indirect feeding links.

The purpose of our study was to determine experimentally the direct and indirect effects of omnivory in a lotic system with three trophic levels. In order to determine the mechanisms affecting the impact of omnivores in streams, we manipulated the density of signal crayfish in enclosures and simultaneously assessed their impact on algae, invertebrate grazers, predatory invertebrates and juvenile brown trout.

## Methods

### Study site

An enclosure experiment was conducted in a stream (Bräkneån) in southern Sweden (56°16′N, 15°6′E), in May and June 1999. The catchment (460 km$^2$) is dominated by coniferous forest, which strongly

**Table 1** Water quality data for the study stream (Bräkneån), from a sample taken 4 km downstream of the study site, 15 June 1999. Data from KM Laboratory in Sweden who are responsible for the municipal control of water quality in the stream

| | |
|---|---|
| Temperature (°C) | 16.9 |
| Discharge ($m^3 s^{-1}$) | 2.4 |
| Conductivity ($mS m^{-1}$) | 10.8 |
| pH | 6.9 |
| Alkalinity ($mEqv L^{-1}$) | 0.20 |
| Oxygen concentration ($mg L^{-1}$) | 8.7 |
| Turbidity (Jackson turbidity units) | 1.9 |
| TOC ($mg L^{-1}$) | 22 |
| Colour ($mg Pt L^{-1}$) | 180 |
| Total phosphorus ($\mu g L^{-1}$) | 23 |
| Total nitrogen ($\mu g L^{-1}$) | 1200 |

influences water chemistry. Thus, the stream has low alkalinity and a high concentration of dissolved organic carbon (DOC) (Table 1). The catchment is also subject to liming because of the presence of the endangered freshwater pearl mussel (*Margaritifera margaritifera* L) that is vulnerable to acidification. The study site is located about 250 m below Tararp village, where the western bank is pasture grazed by cattle and the eastern bank is lined by deciduous forest, mainly alder (*Alnus glutinosa* L). Emergent species dominated the macrophyte assemblage at the study site (*Scirpus lacustris* L., *Menyanthes trifoliata* L. and *Glyceria fluitans* L). In five Surber samples (total area 0.25 $m^{-2}$) the catch of invertebrates could be up to 45 species in some areas of the stream. A natural population of anadromous brown trout is present. Other common fishes in the stream are burbot (*Lota lota* L), minnow (*Phoxinus phoxinus* L) and roach (*Rutilus rutilus* L). Before 1986, the stream had a dense population of the native noble crayfish (*Astacus astacus* L), but it was eliminated by the crayfish plague in the years after 1986. Subsequently, signal crayfish were introduced both up- and downstream of our study site. We never observed any naturally occurring signal crayfish at our study site.

### *General design*

Fifteen enclosures were installed along a 50-m reach that is exposed to full sunlight from noon until sundown. Five replicates of three treatments were randomly assigned to 15 in-stream enclosures: three crayfish densities, low (L) (5 individuals per enclosure), high (H) (10 individuals per enclosure) and a no-crayfish control (C). Enclosures had a steel frame, a solid steel base and a 2-mm steel mesh on the sides. Their bottom area was 1.26 $m^2$ and their height was 0.6 m. To increase water flow through the enclosures, each had an approximately 4 m long pipe (diameter 110 mm) attached to the upper front part of the frame and directed into the main current of the stream. The pipe inlet was covered by a cone shaped steel net (mesh size 5 mm). Enclosures were covered by a removable 2 mm mesh lid to prevent fish and crayfish from escaping. The bottom of each enclosure was covered with sediment (15 L of 0–15 mm sand/gravel and 60 L of 60–250 mm cobbles) from a nearby gravel pit. Two aluminium trays (17 by 21 cm wide, 5 cm deep), filled with the same sediment mixture, were also added to each enclosure. An artificial macrophyte stand consisting of polypropylene rope was added to each enclosure to increase habitat complexity, and stands of *M. trifoliata* and *G. fluitans* were planted in the sediment. Coarse detritus (of macrophyte origin) was added as a food source for crayfish and invertebrates (10 ± 0.5 g dry-weight per enclosure). Each enclosure also contained two refuges for invertebrates, which crayfish could not enter. These consisted of eight hard-board squares (20 by 20 cm) separated by 5 mm high spaces, piled on top of each other. Ten clay pipes (5 cm in diameter) were provided as crayfish shelters.

On 3–7 May, enclosures were placed in the stream and sediment, aluminium trays, invertebrate refuges, clay pipes and artificial macrophytes were added. Macrophytes, coarse detritus and invertebrates (see below) from the stream were introduced on 17–18 May. Crayfish and trout were introduced on 20 May. The experiment ended on 21–22 June when enclosures were destructively sampled. The steel mesh sides of the enclosures were cleaned at least biweekly to enhance water exchange. One enclosure (L) was damaged a week before the experiment was intended to end, and was excluded from all subsequent analyses except for the analysis of algae. Water velocity inside enclosures was measured before the introduction of crayfish and averaged 0.11 m $s^{-1}$ ± 0.03 SD. No differences in flow were found among treatments (ANOVA $F_{2,12} = 1.22, P = 0.33$).

### *Crayfish*

The size distribution of crayfish used in the experiment reflected that of native noble crayfish in the littoral zone of Swedish lakes (Appelberg & Odelström, 1986). Thus, signal crayfish were stocked in the ratio of one adult (males only): one 2-year-old (mixed sexes): three 1-year-olds (mixed sexes). The three groups had carapace lengths of 45.9 ± 1.9, 23.0 ± 2.1 and 15.8 ± 1.0 mm (mean ± 1 SD) in the low-density treatment and 46.5 ± 1.6, 23.7 ± 1.3 and 16.3 ± 0.7 mm in the high-density treatment, and did not differ significantly between crayfish treatments (ANOVA, $F_{1,8} = 0.27$, $P = 0.61$; $F_{1,8} = 0.33$, $P = 0.58$; $F_{1,8} = 0.93$, $P = 0.36$, respectively). Both the high (10 crayfish per enclosure) and low (five per enclosure) density treatments were well within the range of natural densities of signal crayfish found in streams (Shimizu & Goldman, 1983; Guan & Wiles, 1996). Crayfish mortality was low during the experiment, with only two 1-year-old individuals in the high-density treatment being lost. At the end of the experiment crayfish were frozen within 12 h of their enclosure being sampled. After thawing, crayfish gut contents were examined under a binocular microscope.

### *Fish*

Brown trout fry belonging to the anadromous stock native to the stream were obtained from a nearby hatchery. Twenty fish (approximately 14 days after emergence) were introduced to each enclosure so their density was within that reported for streams in southern Sweden (Eklöv *et al.*, 1999). A sample of 20 trout was taken to describe the initial condition of the fish. The mean (±1 SD) total length, wet weight and dry weight of a sample of 20 fish were 31.6 ± 1.4 mm, 0.228 ± 0.045 g and 0.039 ± 0.008 g, respectively. At the end of the experiment surviving trout were counted, scanned for injuries and weighed when wet and after drying (24 h) at 65 °C.

### *Invertebrates*

To ensure enclosures had a fauna similar to that of the stream, kick samples from approximately 1.25 $m^2$ of stream bottom were randomly added to each enclosure. The two aluminium trays and the sediment they contained were used as subsampling units for estimating total biomass of chironomids. At the end of the experiment, each tray and its contents were frozen for later processing. When the experiment ended, the enclosures were lifted onto land. The walls, base and all cobbles in the enclosures were searched for invertebrates, and the invertebrates were preserved in 70% ethanol. The remaining fine sediment was frozen for later processing. The frozen samples were searched for invertebrates in the laboratory. All invertebrates were identified to the lowest possible level using the guides of Nilsson (1996, 1997) dried (24 h, 65 °C) and weighed to 0.1 mg. Taxa were classified as predators or primary consumers based on the information provided by Nilsson (1996, 1997). One macroinvertebrate sample (L) was accidentally destroyed and could not be included in analyses.

### *Algae*

We used ceramic tiles and plastic strips as substrata to monitor treatment effects on periphyton. Five ceramic tiles were placed (glazed side up) on the bottom of each enclosure and were thus susceptible to crayfish grazing and disturbance. Plastic strips (length 0.6 m, width 20 mm; five per enclosure) with a lead sinker at one end and a float at the other were used as substrata not disturbed by crayfish (Nyström *et al.*, 1999). At the end of the experiment, each ceramic tile was wiped with a piece of tissue paper to remove periphyton and the paper placed in a glass jar and frozen. The upper 15 cm of each plastic strip was also frozen. Samples were then freeze dried, chlorophyll *a* content of all periphyton samples was later determined following ethanol extraction as described by Jespersen & Christoffersen (1987).

### *Statistical analysis*

Sample means per enclosure were used in all statistical analyses. Data were transformed, when necessary (judged by Lilliefors test of normality and plotting of residuals). One-way ANOVAS and Tukey's *post hoc* test were used to examine treatment effects but, when variables were affected by water velocity as indicated by linear regression, water velocity was introduced as a covariate. ANCOVAS were run initially to check whether there were water velocity by treatment interactions but, as none were significant ($P > 0.3$ in all cases), the interaction terms were omitted from subsequent analyses.

## Results

### *Crayfish diet*

Crayfish consumed a broad diversity of food items, the most common being detritus which was found in 90% of crayfish guts examined (Fig. 1). Fragments of non-predatory invertebrates were also common. Fragments of predatory invertebrates (including pieces of crayfish exoskeleton) and fresh algal cells and vascular plant material were also present. Fish and mollusc tissue was never found, despite their being present in the enclosures.

### *Fish*

On average, 17% of the juvenile trout survived the experiment, but percentage survival was highly variable among enclosures, ranging between 0 and 45%. Trout increased in size during the experiment, but crayfish had no detectable effect on any of the fish parameters measured (survival, length or weight, Table 2). No trout injuries attributable to attack by crayfish were found. Trout survival was positively related to water velocity (Fig. 2). An ANCOVA showed no effect of treatment on fish survival even when water velocity was controlled for (treatment: $F_{2,10} = 2.03$, $P = 0.18$; water velocity: $F_{1,10} = 17.91$, $P = 0.0017$).

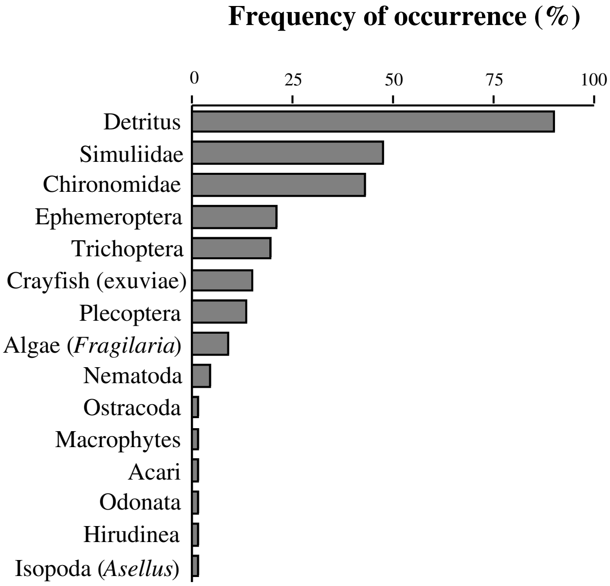

**Fig. 1** Frequency of different food items identified in stomachs of signal crayfish ($n = 68$) at the end of the experiment.

### *Invertebrates*

Predatory leeches (53.3%) and dragonflies (14.0%) dominated the biomass of invertebrates in control cages. Among the non-predatory invertebrates, caddisflies and mayflies had the highest biomass, constituting 10.6 and 7.1% of the total, respectively. Invertebrate taxon richness differed significantly among treatments (ANOVA, $F_{2,10} = 11.06$, $P = 0.0029$). The mean number of taxa in control cages was 27.8 (range 25–30), whereas the numbers in low and high crayfish density cages were 23.0 (range 22–24) and 21.2 (range 16–23), respectively. Invertebrate taxon richness in controls was significantly higher than in the two crayfish treatments (Tukey's *post hoc* test, $P = 0.0391$ and $P = 0.0027$, respectively) but there was no difference between the crayfish treatments (Tukey's *post hoc* test, $P = 0.54$). Significant differences were found among the three treatments with respect to total biomass of invertebrates (ANOVA, $F_{2,10} = 11.74$, $P = 0.0024$), biomass of predatory invertebrates (ANOVA, $F_{2,10} = 9.79$, $P = 0.0044$) and biomass of non-predatory invertebrates (ANOVA, $F_{2,10} = 5.50$, $P = 0.0245$). Crayfish reduced total invertebrate biomass and the biomass of predatory and non-predatory invertebrates, but the reduction was proportionally larger for predatory invertebrates (Fig. 3). The effect of crayfish on the total biomass of

**Table 2** Number (means ± 1 SD) of surviving trout, their weight and total length in different treatments at the end of the experiment. Treatments are controls without crayfish (C), low density of crayfish (L), and high density of crayfish (H). $F_{2,8}$ and *P*-values refer to ANOVAS testing differences between treatments

| Source | C ($n = 5$) | L ($n = 4$) | H ($n = 5$) | F | *P*–value |
|---|---|---|---|---|---|
| Survivors | 4.2 ± 3.0 | 4.0 ± 1.4 | 2.6 ± 3.7 | 0.2479 | 0.7862 |
| Wet weight (g) | 0.504 ± 0.061 | 0.411 ± 0.051 | 0.542 ± 0.139 | 2.2986 | 0.1627 |
| Dry weight (g) | 0.083 ± 0.010 | 0.066 ± 0.011 | 0.090 ± 0.036 | 0.3956 | 0.6857 |
| Total length (mm) | 39.9 ± 1.9 | 37.7 ± 1.4 | 40.4 ± 2.6 | 1.9404 | 0.2056 |

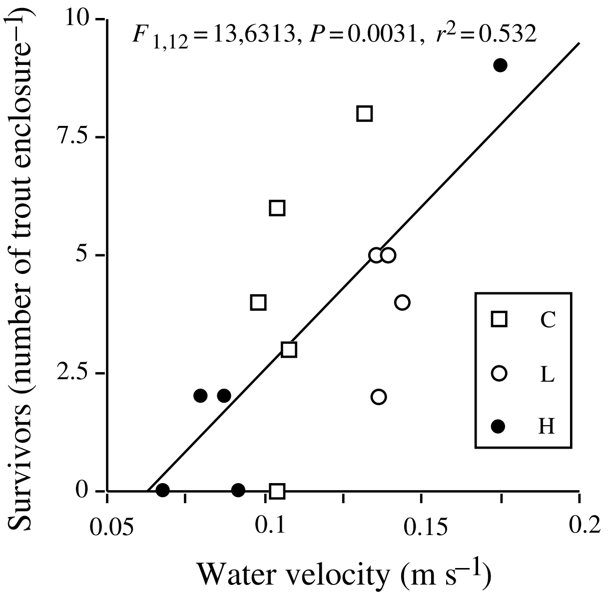

**Fig. 2** Relationship between number of surviving juvenile trout per enclosure and water velocity inside enclosures (m s$^{-1}$) ($n$ = 14). Different symbols indicate the three treatments. Treatments are controls without crayfish (C), low density of crayfish (L), and high density of crayfish (H).

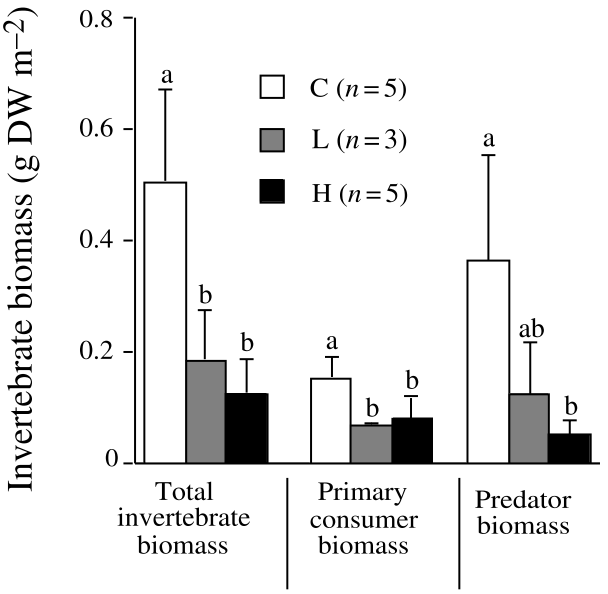

**Fig. 3** Total invertebrate biomass, primary consumer biomass and predator invertebrate biomass in enclosures (mean ± 1 SD). Treatments are controls without crayfish (C), low density of crayfish (L), and high density of crayfish (H). Different letters above error bars denote significant effects of treatment at the 0.05 level using Tukey's *post hoc* test (statistics in Table 3).

**Table 3** Results of ANOVAs and Tukey's *post hoc* tests (< indicates a $P$-value smaller than 0.05) on mean invertebrate biomass of the eight most common invertebrate taxa sampled in enclosures at the end of the experiment. Treatments are controls without crayfish (C), low density of crayfish (L) and high density of crayfish (H). Data were log-transformed for Hirudinea, Trichoptera and Plecoptera and square-root transformed for Odonata and Bivalvia

| Taxon | $F_{2,10}$ | $P$ | Tukey's *post hoc* test |
|---|---|---|---|
| Hirudinea | 9.1157 | 0.0056 | H < C; C = L; L = H |
| Odonata | 6.6425 | 0.0146 | H = L < C |
| Bivalvia | 12.7449 | 0.0018 | H = L < C |
| Ephemeroptera | 17.0147 | 0.0006 | H = L < C |
| Isopoda | 4.8683 | 0.0334 | H = L = C |
| Trichoptera | 5.0835 | 0.0300 | L < C; L = H; C = H |
| Diptera | 0.0253 | 0.8177 | – |
| Plecoptera | 0.0946 | 0.9106 | – |

invertebrates was mainly due to reductions in the biomass of Hirudinea, Odonata, Bivalvia, Ephemeroptera and Trichoptera. Diptera and Plecoptera were unaffected by crayfish (Table 3, Fig. 4).

### *Algae*

Crayfish had no effect on algal biomass measured as chlorophyll *a* on plastic strips (ANOVA $F_{2,12} = 0.58$, $P = 0.57$). However, analysis of algal biomass on tiles was complicated by the effect of water velocity. In an ANCOVA between treatments with water velocity as covariate, water velocity had a positive effect on algal biomass ($F_{2,11} = 49.91$, $P < 0.0001$), and there was a difference between treatments ($F_{2,11} = 27.86$, $P < 0.0001$). Thus, algal biomass was higher on tiles in the high density crayfish treatment compared with the low density or no crayfish treatments (Tukey's *post hoc* test, $P < 0.0001$ in both cases). However, no difference in algal biomass was found between enclosures with low crayfish densities and no crayfish (Tukey's *post hoc* test, $P = 0.41$, Fig. 5).

## Discussion

### *Community responses to omnivorous crayfish*

Stomach content analysis indicated a high degree of omnivory in signal crayfish, as found in earlier studies of stream-dwelling crayfish (e.g. Whitledge & Rabeni, 1997; Guan & Wiles, 1998; Parkyn *et al.*, 2001). As observed elsewhere, crayfish reduced the biomass of

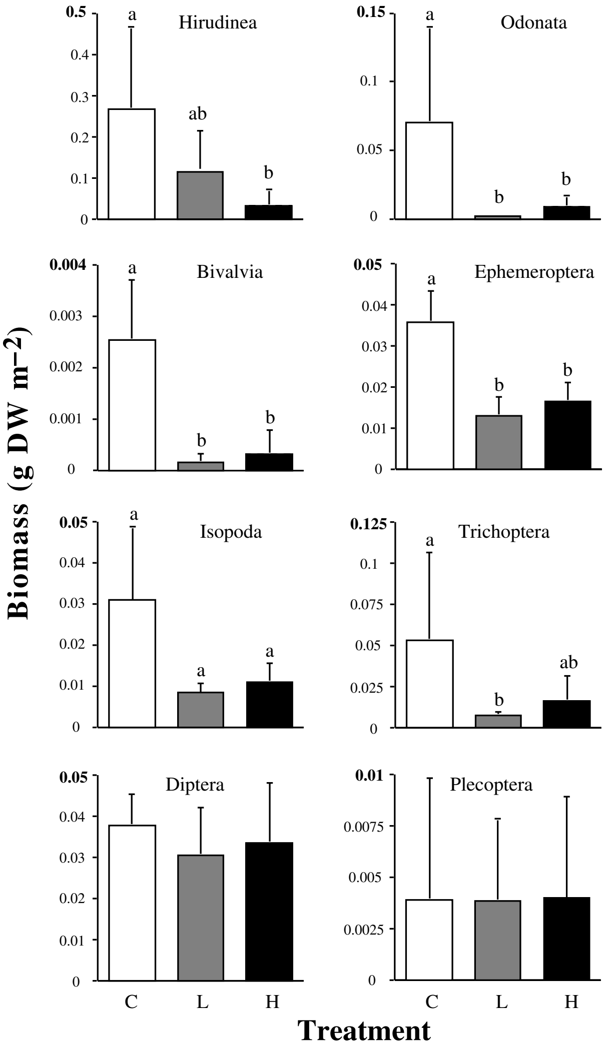

**Fig. 4** Invertebrate biomass (mean ± 1 SD) for the eight most common taxa in enclosures. Treatments are controls without crayfish (C), low density of crayfish (L), and high density of crayfish (H). In the L-treatment $n = 3$ for all taxa but Diptera where $n = 4$. ANOVAs were non-significant for Diptera and Plecoptera. Different letters above error bars denote significant effects of treatment at the 0.05 level using Tukey's *post hoc* test (statistics in Table 3).

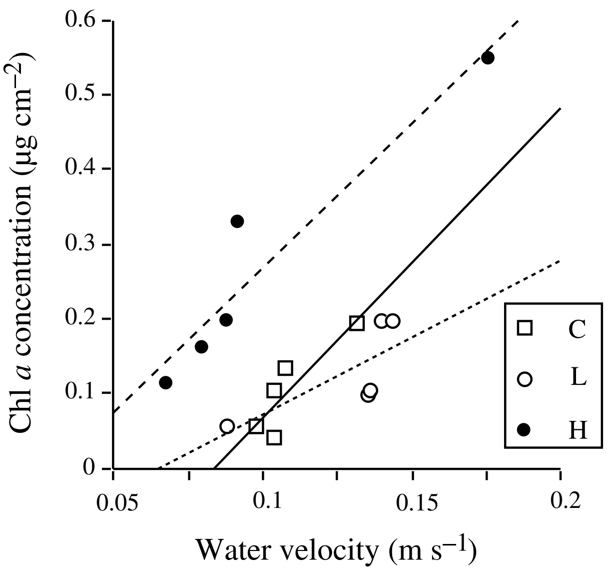

**Fig. 5** Algal biomass (as chlorophyll *a*) on ceramic tiles. Each data point represents a mean for the five tiles in an enclosure. Treatments are controls without crayfish (C), low density of crayfish (L), and high density of crayfish (H). Results of ANCOVA in text.

several invertebrate taxa in the stream (e.g. Charlebois & Lamberti, 1996), whereas fish were not affected by crayfish predation (Dean, 1969; Ilhéu & Bernardo, 1993; Xinya, 1995). The mechanism behind the reduction of prey in our enclosures is likely to be related to the relative size difference between crayfish and their prey. This is a common situation found in food webs with omnivorous predators (Diehl, 1993). However, prey behaviour and mobility probably also play a crucial role in determining crayfish effects on specific prey species (Lodge *et al.*, 1994; Parkyn *et al.*, 1997; Perry *et al.*, 1997). In Swedish lentic habitats, primary consumers, especially snails can be reduced by signal crayfish (Nyström *et al.*, 1999), not because they are grazers but because of their low mobility and large size. Thus, they are easily caught by crayfish and are profitable prey. On the other hand, the dominant predatory invertebrates are often mobile taxa among Coleoptera and Heteroptera, which are less easily captured and less affected by crayfish predation (Nyström *et al.*, 1999). In contrast to lentic habitats, invertebrate biomass in streams is often dominated by slow moving predators, e.g. Hirudinea and Odonata (Dahl, 1998), whereas the smaller herbivores (e.g. Ephemeroptera and Plecoptera) are more mobile and less likely to be captured by crayfish (Moore & Williams, 1990). In this study, slow-moving organisms declined in enclosures with crayfish (i.e. leeches, dragonflies, caddisflies, isopods and molluscs) whereas more mobile prey, or prey living in sediments, were less affected by crayfish (i.e. trout fry, chironomids and stoneflies).

Based on our results, and previous studies of interactions between crayfish and invertebrates, we would expect crayfish to affect primary consumers proportionally more in ponds and lakes than they affect predators, whereas in streams the opposite should be the case.

As leeches, the dominant predatory invertebrate in our study, reduce the abundance of primary consumers such as mayflies, caddisflies and isopods in Swedish streams (Dahl, 1998), we might expect a simultaneous release of these primary consumers from predation if the biomass of leeches declines. However, no taxon increased in biomass in enclosures with crayfish, and in fact most declined, suggesting that crayfish affect both leeches and their prey species simultaneously. These results indicate that indirect effects such as trophic cascades can be decoupled by a predator feeding at several trophic levels, and consuming other predators as well as their prey (Diehl, 1993; Polis & Strong, 1996).

Epilithic algae (chl *a*) increased in the presence of high crayfish density and high water velocitiy. No crayfish effect was found for algae growing on plastic strips. If the alterations in the grazer community alone were responsible for the increase in algal biomass, the increase would have been expected on both substratum types and at both crayfish densities. As this was not the case, the increase in epilithic biomass was probably because of the physical impact of crayfish, which had no access to the plastic strips. Charlebois & Lamberti (1996) suggested that the removal of detritus and senescent algal cells by crayfish could result in increased chlorophyll *a* concentration. Furthermore, Whitmore (1997) found that the presence of *Paranephrops zealandicus* (White) prevented the accumulation of silt in stream enclosures and hypothesised that by keeping stone surfaces free of surface deposits, bioturbation by crayfish might stimulate epilithic primary production. Our finding that water velocity also affected algal biomass supports such an explanation. The effects of crayfish bioturbation on algal communities may also depend on substratum type as shown by Statzner *et al.* (2000).

### *Effects of crayfish on prey in streams*

Except for the reduction in biomass of leeches in cages with high crayfish density, there were only minor differences in invertebrate biomass between high and low crayfish densitiy. Because crayfish are cannibalistic (e.g. Abrahamsson, 1966; Whitledge & Rabeni, 1996) aggressive interactions among them could potentially reduce their impact on lower trophic levels. Cannibalistic behaviour is often judged by gut content analysis. We found pieces of exoskeleton in 10 of 68 crayfish stomachs, but only two crayfish were missing from the enclosures. Thus, the stomach contents were probably consumed exuviae because pieces of exoskeleton were often found in crayfish from cages where all crayfish survived. Cannibalism is therefore an unlikely explanation for the similar biomass of most invertebrates in the two crayfish treatments. Potentially, the major reduction in biomass of predatory invertebrates in cages with a high density of crayfish may have released some primary consumers from predation.

Small mesh size has been shown to reduce the number of drifting invertebrates entering cages and therefore enhance the possibility of detecting predator effects (Cooper, Walde & Peckarsky, 1990). In this experiment, the density of Hirudinea was higher in all treatments at the termination of the experiment than when it started. Thus, even if drift dynamics were affected, there was a substantial flux of invertebrates into, and probably also out of, enclosures. It is not clear whether the reduced biomass of invertebrates found in crayfish treatments was because of altered drift dynamics induced by the presence of predators, or from predation. However, the biomass of leeches, isopods and cased caddisflies in cages was reduced in the presence of crayfish in this study and these taxa rarely enter the drift (Dahl, 1998; Dahl & Greenberg, 1999). Thus, crayfish predation rather than predator-induced emigration out of cages is probably the most important mechanism behind the reduction in biomass of these taxa in crayfish enclosures. Moreover, stomach contents of crayfish indicated that these taxa were consumed by crayfish. Regardless, our results reflect the risk of predation and as crayfish density increases in a stream, predation is likely to become more important.

### *The invading signal crayfish*

The signal crayfish is an invading species whose range is rapidly expanding in Europe at the expense of native crayfish (Gherardi & Holdich, 1999). Even though signal crayfish may reach a density exceeding 20 $m^{-2}$ in some European streams, their effect on stream food webs is poorly known. At these high densities it may frequently encounter small benthic fishes, potentially affecting their distribution (Guan & Wiles, 1997). Our results suggest that, even at moderate density, the signal crayfish can have strong effects on the stream invertebrate community structure. Its effects on juvenile trout were non-significant, however. The main effects of the signal crayfish in our study were the replacement of leeches as the dominant invertebrate predator, and an increase in benthic algae biomass. Thus, crayfish may alter the structure of the food webs in two ways: they increase connectance by feeding at several trophic levels in contrast with the strictly predatory leeches, and they increase the availability of autochthonous carbon as a food source for other stream invertebrates. Based on this and previous studies (summarised in Nyström, 1999), we hypothesise that the invasion of signal crayfish in streams will lead to increased predator control of benthic communities, as signal crayfish are more voracious, more tolerant to changeable environmental conditions, and less susceptible to predation than the crayfish species native to Europe.

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