

The Impact of Vertebrate and Invertebrate Predators on a Stream Benthic Community

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Jonas Dahl

The impact of vertebrate and invertebrate predators on a stream benthic community

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Abstract I assessed the impact of both vertebrate and invertebrate predators on a lotic benthic community in a 1-month-long experiment, using enclosures containing cobble/gravel bottoms, with large-mesh netting that allowed invertebrates to drift freely. Brown trout (*Salmo trutta*) and leeches (*Erpobdella octoculata*) were used as predators and four treatments were tested: a predator-free control, leeches only, trout only, and leeches and trout together. A density of 26.7 leeches/m² (20 leeches/enclosure) and 1.3 trout/m² (one trout per enclosure) was stocked into the enclosures. The total biomass of invertebrate prey was significantly lower in the trout and trout plus leech treatments than in the leech and control treatments, which were due to strong negative effects of trout on *Gammarus*. On the individual prey taxon level, both trout and leeches affected the abundance of *Asellus*, *Baetis* and *Ephemerella*, whereas the abundance of *Gammarus* was only affected by trout, and the abundance of Orthocladiinae and Limnephilidae was only affected by leeches. In the treatment with trout and leeches together, the abundance of *Ephemerella* and *Baetis* was higher than when trout or leeches were alone, which was probably due to predator interactions. Leeches and trout had no effects on prey immigration but did affect per capita emigration rates. Both trout and leeches indirectly increased periphyton biomass in enclosures, probably due to their strong effects on grazers. Both trout and leeches were size-selective predators, with trout selecting large prey, and leeches selecting small prey. Size-selective predation by trout and leeches affected the size structure of five commonly consumed prey taxa. Trout produced prey populations of small sizes owing to consumption of large prey as well as increased emigration out of enclosures by these large prey. Leech predation produced prey assemblages of larger size owing to consumption and

increased emigration of small prey. These results suggest that in lotic habits, predatory invertebrates can be as strong interactors as vertebrate predators.

Keywords Predation · Interaction · Food web · Fish · Invertebrates

Introduction

The measured impact of fish on benthic communities in streams has varied greatly among studies. Several have shown weak or no effects of fish predation (Allan 1982; Flecker and Allan 1984; Culp 1986; Reice 1991), whereas others have shown strong effects (Flecker 1984; Gilliam et al. 1989; Power 1990; Bechara et al. 1992). Many factors have been implicated for explaining the variable outcome of fish manipulations in running waters. Previous studies have suggested that predation and competition are more likely to affect community structure when dispersal of invertebrates is low, and may be overwhelmed by influx/efflux dynamics when dispersal is high (Palmer et al. 1996). Recent papers have also discussed methodological differences that might affect interactions between predators and prey, including differences in enclosure size, mesh size, predator densities and sample size (Cooper et al. 1990; Sih and Wooster 1994; Englund and Olsson 1996). Further, feeding methods used by fish may explain some of the variability in fish-invertebrate studies. Benthic-feeding fish should have a greater impact on benthic communities than drift feeders, because drift feeders may include large amounts of terrestrial animals in their diet, which should reduce their impact on benthic prey (Dahl and Greenberg 1996).

Despite the fact that the impact of fish on prey densities in streams has been a subject of debate, evidence exists that fish influence prey behaviour. Previous studies have shown strong sublethal effects, where fish force prey to use different habitats, forage at different times, change their activity level or alter their foraging behaviour (Stein and Magnusson 1976; Sih 1980, 1982; Gilli-

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am and Fraser 1987; Rahel and Stein 1988; Sih and Moore 1990; Douglas et al. 1994; Forrester 1994; Scrimgeour and Culp 1994; Sih and Wooster 1994). In contrast, invertebrate predators generally reduce populations of prey in local areas (Peckarsky and Dodson 1980; Walde and Davies 1984; Peckarsky 1985, 1991; Malmquist and Sjöström 1987; Lancaster 1990; Lancaster et al. 1991; Wooster 1994; Kratz 1996). Wooster (1994) suggested that predatory invertebrates might have a larger impact on benthic prey density than predatory vertebrates, because invertebrate predators induce prey to drift relatively more than vertebrate predators (Wooster and Sih 1995). Further, the fact that streams usually contain both vertebrate and invertebrate predators may confound the effects of fish predation. Predatory invertebrates compete with fish for smaller non-predatory invertebrates, but are at the same time preferred prey of fish (e.g. Crowder and Cooper 1982; Hambrighth et al. 1986; Power 1992). So even if fish are excluded from enclosures, the enclosures are not predator free, and consumption by predatory invertebrates may compensate for the absence of fish. The impact of invertebrate predators relative to vertebrate predators may be affected by habitat complexity (Bowlby and Roff 1986; Power 1992). The relative importance of predatory invertebrates is probably greater in complex habitats than in habitats with lower complexity (Dahl and Greenberg 1997), as predatory invertebrates are protected from fish predation in habitats with high complexity, whereas in habitats with low complexity, fish are able to depress their densities (McAuliffe 1984).

Even if many studies have assessed the impact of vertebrate or invertebrate predators, few have attempted to measure the impact of both predator types together (exceptions include the studies by Soluk and Collins 1988a,b; Soluk 1993; Dahl and Greenberg 1997). However, none of these studies has compared the impact of vertebrate and invertebrate predators in streams under field conditions, where dispersal of invertebrate prey is allowed. In this study, I assessed the impact of invertebrate and vertebrate predators on a natural benthic community, measuring both immigration and emigration of prey as well as predator diet.

Based on a previous experiment (Dahl and Greenberg 1997), I chose leeches (*Erpobdella octoculata*), an opportunistic feeder (Sawyer 1986), as the main invertebrate predator. I used brown trout (*Salmo trutta*) as the vertebrate predator. Here, I assessed experimentally the impact of leeches and trout alone and together on densities, drift rates and the size distribution of prey.

Materials and methods

Study site and experimental units

The study was conducted in an old mill channel that leads the water from Snällersödsån Creek to a small cattle pond and back into the creek. Snällersödsån Creek, a tributary of the Rönneå River, is

situated in southern Sweden. Sixteen flow-through plexiglas enclosures, measuring $1.5 \times 0.5 \times 0.5$ m, were used as experimental units. Plastic netting (mesh size 6 mm) was attached to both ends of the enclosures, with the netting ends facing upstream and downstream. The enclosures were placed in the channel in 25–35 cm water depth, at least 3 m apart from each other. The bottom of all enclosures was covered by a 1- to 2-cm-thick layer of gravel (2.1–8 mm diameter). I also placed 12 cobbles (≈ 20 cm diameter), evenly dispersed, in each enclosure.

Vertebrate and invertebrate predators

Brown trout were collected in Snällersödsån Creek by electrofishing. Fish used were 125 ± 3.7 mm in total length (mean ± 1 SD) and 22.3 ± 1.9 g wet weight ($n = 8$). One trout, which corresponds to a density of 1.33 trout/m², was stocked into each fish enclosure. The natural densities of trout in south Swedish streams often range from one to three individuals/m² (Eklöv 1996), so the density used in this study was well within natural densities.

Leeches were collected in Snällersödsån Creek. They were 31.6 ± 5.7 mm in total length and weighed 7.6 ± 1.9 mg wet weight ($n = 160$). Twenty leeches, which corresponds to a density of 26.7 leeches/m², were stocked into each leech enclosure at the beginning of the experiment. The density of *E. octoculata* in Snällersödsån Creek in cobble habitats usually ranges from 3 to 40 individuals/m², so leech densities used in this study were within natural densities (Dahl and Greenberg 1998). Trout and leech diets were estimated only at the end of the experiment.

Experimental design

Four treatments, each replicated four times, were randomly assigned to the enclosures: (1) a predator-free control; (2) leeches only (20 per enclosure); (3) trout only (one per enclosure), or (4) leeches (20 per enclosure) and trout (one per enclosure) together. All enclosures were placed in the mill channel on 5 June 1995, 1 month before the experiment started, which allowed invertebrates to colonise the enclosures. The experiment began on 5 July 1995 when predators were introduced. Before introduction, trout were anaesthetised with MS-222, weighed to the nearest 0.1 g on an electronic balance and measured to the nearest millimetre (total length).

The experiment was terminated on 6 August. At this time, trout and leeches were collected and weighed and trout were stomach flushed. The surfaces of all cobbles in the enclosures were brushed into a sieve, and all the material in the enclosures was emptied into a large net (234- μ m mesh netting). Samples were frozen for later processing.

Invertebrate drift was sampled on three occasions during the experiment (10–12 July, 20–22 July and 3–5 August). Drift samplers, which sampled a 0.22×0.46 m area, sampled the entire water column. They consisted of 234- μ m mesh netting. On one day, drift nets were placed just downstream of enclosures to collect invertebrates that emigrated from enclosures. The following day, drift nets were placed inside the enclosures at the upstream end to collect animals that entered the enclosure. The nets operated for 24 h, whereupon the contents were removed. Samples were frozen for later processing.

Ceramic tiles, measuring 2×2 cm, were placed in Snällersödsån Creek for colonisation 1 month before the experiment started (5 June). On 5 July, eight tiles were evenly dispersed on the bottom of each enclosure. An additional eight tiles were frozen for determination of initial biomass of chlorophyll a in periphyton. At the end of the experiment, all ceramic tiles were collected and placed in aluminium foil and frozen for later measurements of chlorophyll a concentrations using ethanol as the extraction solvent (Jespersen and Christoffersen 1987).

In the laboratory, benthic invertebrate samples were sorted. Animals from enclosures, drift and stomach samples were identified and lengths were measured using a Nikon light microscope. The diet of the leeches was ascertained by slicing the leech into three

pieces, whereupon the gut contents could easily be separated from the leech itself.

Temperature varied between 10.9°C and 14.4°C during the experiment, and water velocities in enclosures were relatively low throughout the experiment, varying between 2–12 cm/s. To avoid clogging, the enclosures were cleaned every day, during both the incubation and experimental periods.

Statistics

Statistical analyses were conducted on the abundance, body lengths and drift rates of invertebrates. All statistical tests were conducted on log-transformed data using SYSTAT (Wilkinson 1992). Separate one-way ANOVAs were conducted on each taxon in both benthic and drift samples followed by Tukey's tests if necessary. Per capita drift rate of prey taxa was calculated by dividing the number of emigrating prey at the last drift sampling by the total number of prey within enclosures for each prey taxon.

To test if predators were size selective, I calculated prey size selectivity of trout and leeches using the Manly/Chesson 'α' index (Chesson 1983; see also Bechara et al. 1993). The index varies from 0 to 1, and random selection is indicated by $\alpha_i = 1/m$ (m is the number of prey size classes). To calculate the index, I estimated the density of prey in 1–2 mm size classes in both the enclosures and in predator diets.

To distinguish whether direct predation or avoidance behaviour of prey most likely produced the density patterns in enclosures, I calculated the daily consumption rate of predators, migration of prey per day and benthic abundances using data on predator diet, drift rates and number of prey in cages. To determine daily per capita mortality imposed by predator, I estimated the number of prey eaten per 24 h for each prey taxon. In trout, I used an evacuation rate of 15 h according to Elliott (1972), and in leeches the corresponding figure was 24 h (Sawyer 1986). Invertebrate mortality from predators was divided by the final densities of potential prey in the enclosures. To estimate the avoidance response of prey per day, I first calculated the net drift out of predator enclosures per day by subtracting the number of prey emigrating in predator treatments from the number of prey emigrating from control enclosures. This difference is a measure of the predators effect on emigration, i.e. an avoidance response. This number was then divided by the number of prey in predator enclosures at the end of the experiment. Both direct predation and avoidance behaviour are expressed in percentages (cf. Kratz 1996).

Results

Invertebrate predator biomass

Twenty *E. octoculata* were stocked in enclosures assigned to predatory invertebrate treatments. However, numbers of predatory invertebrates increased in enclosures over the course of the experiment because of colonisation. Other predatory invertebrates identified in enclosures at the end of the experiment included *Glossiphonia* spp. leeches, dytiscids, ceratopogonid larvae, *Rhyachophila* caddis larvae, *Sialis* spp. alderfly larvae and zygopteran larvae. Nevertheless, *E. octoculata* made up 75–80% of the total biomass of predatory invertebrates. Potentially, *E. octoculata* had the opportunity to leave enclosures but they were, at least in the leech treatment, stationary, as approximately the same number of leeches was found at the end of the experiment as that implanted at the start. The total biomass of predatory invertebrates differed between treatments at

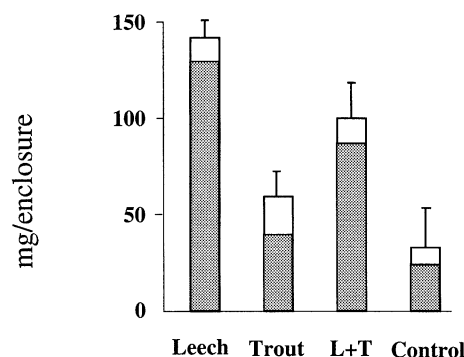


Fig. 1 Biomass of *Erpobdella octoculata* (dark bars) and other predatory invertebrates (open part of bars) in enclosures with leech and trout predator treatments at the end of the experiment. Error bars denote 1 SD, and refer to total biomass of invertebrate predators

the end of the experiment (ANOVA: $F_{3,12} = 4.91$, $P = 0.019$) (Fig. 1). Tukey's tests showed that both the leech and the leech-plus-trout treatment had a higher biomass of predatory invertebrates than trout and control treatments (Tukey's test: $P < 0.02$ for all comparisons), but there was no difference in predatory invertebrate biomass between leeches and leeches plus trout (Tukey: $P = 0.10$). The number of leeches found after the experiment followed that of biomass (ANOVA: $F_{3,12} = 5.55$, $P = 0.013$; leech treatment: 18.0 ± 2.9 ; trout treatment: 4.5 ± 2.9 ; leech-plus-trout treatment: 10.25 ± 2.9 ; control treatment: 2.75 ± 2.5 , mean \pm 1 SD).

Fish growth

The fish in each enclosure grew on average 1.05 ± 0.25 g (1 SD) during 1 month-long experiment. I found no difference in trout growth between treatments (Mann-Whitney U -test, $n = 8$, $P > 0.05$).

Invertebrate prey biomass and abundance

ANOVA of the total biomass of potential prey found in enclosures showed a significant effect of predator treatment (one-way ANOVA: $F_{3,12} = 9.82$, $P = 0.001$). Tukey tests showed that prey biomass in trout and trout-plus-leech treatments was significantly lower than in the controls, whereas prey biomass when leeches were alone was similar to the control (Tukey's test: trout and trout plus leeches vs controls: $P < 0.002$ for both comparisons; leeches vs. controls: $P = 0.2$). The reason for this difference was that *Gammarus pulex* was the dominant prey taxon in terms of biomass in the enclosures, and only trout had a negative impact on the density of *Gammarus*.

ANOVA of the abundance of 13 potential prey taxa (Table 1, Fig. 2) revealed significant effects of both trout, leeches and trout plus leeches, but the effects

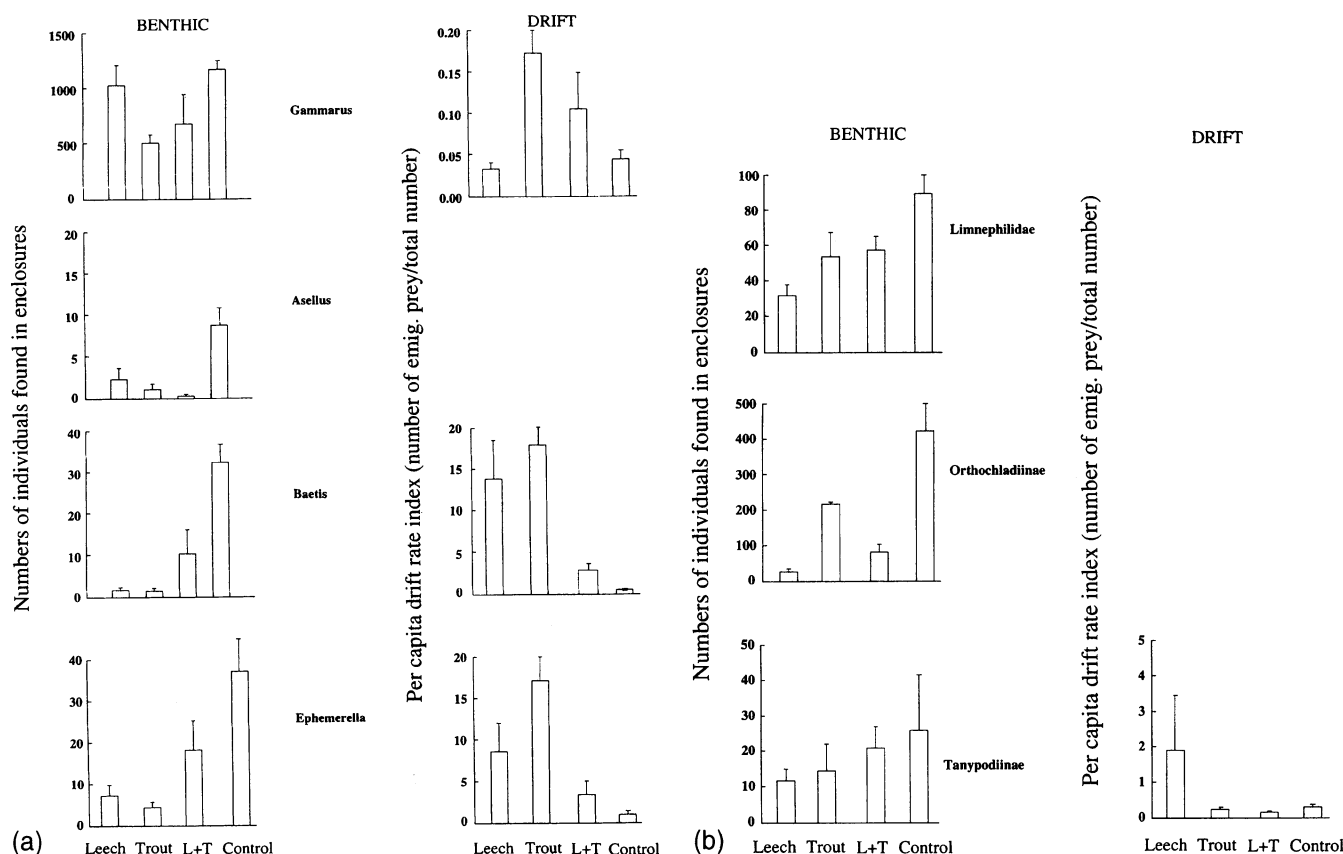


Fig. 2 Average abundance of invertebrate prey taxa in benthic samples (left panels) and the per capita drift rate index (right panels) at the end of the experiment. Units for benthic samples are individuals/enclosure and for per capita drift, number of individuals emigrating per 24 h at the last sampling occasion/total number of individuals found in the enclosures. Error bars denote 1 SD

varied with predator treatment. Leeches affected *Asellus*, *Baetis*, *Ephemerella*, Limnephilidae and Orthocladiinae, while trout affected *Gammarus*, *Asellus*, *Baetis* and *Ephemerella* and leeches plus trout affected *Gammarus*, Orthocladiinae, *Baetis* and *Asellus*. The effects of trout, leeches and trout plus leeches on prey abundance were negative for all taxa.

Table 1 ANOVA results for the effects of leech, trout and leech-plus-trout predators on the abundance of invertebrate prey taxa in benthic samples. $F_{3,12}$ and P -values refer to ANOVA results for log-transformed data (< indicates a P -value smaller than 0.05)

| Prey taxon | Predator treatment F | P | Tukey's test |
|---------------------------|------------------------|---------|--|
| <i>Gammarus</i> | 2.89 | 0.05 | Trout, leech + trout < leech, control |
| <i>Asellus</i> | 6.74 | 0.006 | Leech, trout, leech + trout < control |
| <i>Baetis</i> | 7.34 | 0.005 | Leech, trout < leech + trout < control |
| <i>Ephemerella</i> | 4.79 | 0.02 | Leech, trout < leech + trout, control |
| <i>Heptagenia</i> | 0.43 | 0.73 | |
| <i>Ephemerella danica</i> | 1.15 | 0.37 | |
| Limnephilidae | 3.33 | 0.056 | Leech < trout, leech + trout, control |
| Trichoptera pupae | 0.67 | 0.59 | |
| <i>polycentropus</i> | 0.34 | 0.08 | |
| Chironomids total | 12.45 | 0.001 | Leech, leech + trout < trout, control |
| Orthocladiinae | 15.96 | < 0.001 | Leech, leech + trout < trout, control |
| Tanypodiinae | 0.46 | 0.72 | |
| Tipulidae | 0.78 | 0.53 | |
| <i>Leuctra</i> | 0.21 | 0.89 | |

Invertebrate drift

ANOVA revealed that predator treatment had a significant effect on total biomass of emigrating prey ($F_{3,12} = 3.58$, $P = 0.047$). The effect was due to prey in the leech and control treatments having lower emigration rates than prey in the trout and trout-plus-leech treatments (Tukey's test: $P < 0.04$ for all comparisons). There was no effect on total prey biomass immigrating into enclosures (ANOVA: $F_{3,12} = 0.58$, $P > 0.05$).

Analysis of absolute numbers of immigrating/emigrating prey for each taxon revealed no significant differences between treatments (ANOVA: $F_{3,12} < 3.14$, $P > 0.065$ for all comparisons). Analysis of per capita emigration rates from enclosures revealed several significant effects. The per capita emigration rate index for *Gammarus*, *Ephemerella* and *Baetis* increased when trout was present, whereas the per capita emigration rate index for *Ephemerella*, *Baetis* and Tanypodiinae increased in the presence of leeches. (Table 2, Fig. 2).

Predator diets and size distribution of prey

The dominant prey taxa consumed by trout were *G. pulex*, *Baetis rhodani* and *Ephemerella ignita*. Chironomids, particularly Orthoclaadiinae were the dominant prey of leeches (Table 3). Analyses comparing dietary and enclosure prey size showed that trout and leeches preyed selectively on different sizes. For those taxa that dominated the diets of trout, trout consumed large individuals, whereas for those taxa that dominated the diets of leeches, leeches consumed small-sized individuals (Fig. 3).

Analyses of the impact of predators on the size distribution of prey (Table 4) revealed significant effects of both trout and leeches. Trout reduced the mean size of *Gammarus* and *Baetis* within enclosures compared to the control (Table 4, Fig. 4). Leeches reduced the mean size of *Baetis* (Table 4, Fig. 4) and increased the mean size of Orthoclaadiinae (Table 4, Fig. 4) relative to controls. Predation of trout and leeches had no effect on the size

Table 3 Average number of prey eaten by leeches (*Erpobdella octoculata*) and trout (*Salmo trutta*). Predator diets were analysed at the end of the experiment

| Prey taxon | Average number of prey in guts of individual predators | |
|--------------------|--|------------------------------------|
| | <i>Erpobdella</i> ($n = 140$) | <i>Salmo trutta</i> ($n = 8$) |
| <i>Gammarus</i> | 0.18 ± 0.18 | 3.75 ± 2.1 |
| <i>Asellus</i> | 0.06 ± 0.04 | 0.5 ± 0.5 |
| <i>Baetis</i> | 0.21 ± 0.31 | 2.8 ± 2.1 |
| <i>Ephemerella</i> | 0.03 ± 0.06 | 1.95 ± 1.15 |
| <i>Heptagenia</i> | 0.11 ± 0.16 | 0.12 ± 0.33 |
| Limnephilidae | 0.14 ± 0.17 | 0.12 ± 0.33 |
| Orthoclaadiinae | 3.02 ± 2.25 | 0.25 ± 0.43 |
| Tanypodiinae | 0.28 ± 0.23 | 0 ± 0 |
| <i>Leuctra</i> | 0.23 ± 0.28 | 0.12 ± 0.33 |
| <i>Erpobdella</i> | 0 ± 0 | 0.25 ± 0.5 |

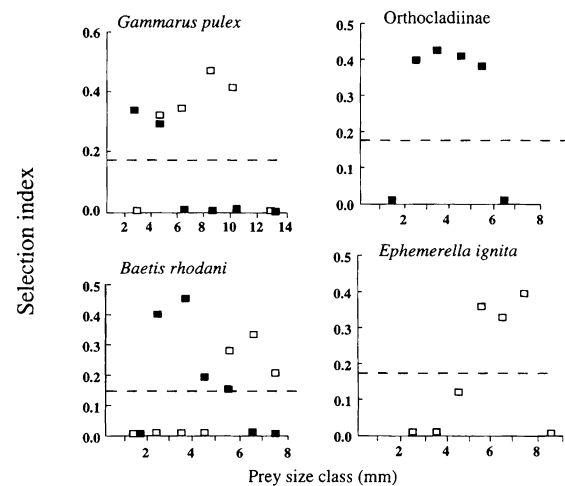


Fig. 3 Manly/Chesson prey size selectivity index of trout (open squares) and leeches (filled squares) consuming *Gammarus pulex*, *Baetis rhodani*, Orthoclaadiinae and *Ephemerella ignita*. The horizontal dashed lines indicate random selection

distribution of either *Ephemerella* or Tanypodiinae (Table 4, Fig. 4).

The size distributions of immigrating prey were not significantly different among treatments for *Gammarus*, *Baetis*, *Ephemerella* and Tanypodiinae (ANOVA: $F_{3,12} < 0.8$, $P > 0.5$, for all comparisons). Orthoclaadiinae were in drift samples so no measures of their drift were calculated. Analyses of prey size at emigration revealed significant effects of trout and/or leeches for *Gammarus*, *Baetis*, *Ephemerella* and Tanypodiinae (Table 4). The presence of trout caused larger *Gammarus*, *Baetis* and *Ephemerella* to drift relative to the control, whereas leeches increased the drift of smaller individuals of *Gammarus*, *Baetis* and Tanypodiinae relative to the control (Table 4, Fig. 4).

I also tested whether per capita emigration of each size class of *Gammarus*, *Baetis* and *Ephemerella* was correlated with size selectivity of trout and leeches (selection index of these size classes). I found a positive

Table 2 ANOVA testing the effect of the different predator treatments on the per capita drift rate index (number of individuals emigrating per 24 h at the last sampling occasion/total number of individuals found in enclosures). $F_{3,12}$ and P -values refer to ANOVA of log-transformed data

| Taxon | Treatment F | P | Tukey's test |
|--------------------|------------------|-------|---|
| <i>Gammarus</i> | 3.68 | 0.044 | Trout > leech, trout + leech, control |
| <i>Baetis</i> | 6.67 | 0.007 | Trout, leeches > trout + leeches, control |
| <i>Ephemerella</i> | 7.8 | 0.004 | Trout, leeches > trout + leeches, control |
| Tanypodiinae | 9.92 | 0.001 | Leech > trout, trout + leeches, control |
| <i>Leuctra</i> | 0.65 | n.s. | |

Table 4 ANOVA results for the effects of different predator treatments on prey size in enclosures and at emigration. $F_{3,12}$ - and P -values refer to ANOVAs on log-transformed data (L leeches

only, T trout only, $T+L$ trout and leeches together, C predator-free control, *orthoclaadiinae larvae were rare in drift samples, precluding analysis)

| Taxon | Size within enclosures | | | Size at emigration | | |
|------------------------|------------------------|-------|---------------|--------------------|-------|----------------|
| | Treatment F | P | Tukey's test | Treatment F | P | Tukey's test |
| <i>Gammarus pulex</i> | 3.6 | 0.05 | T, T+L < C, L | 5.14 | 0.004 | T > C, T+L > L |
| <i>Baetis rhodani</i> | 3.64 | 0.045 | T, T+L, L < C | 4.71 | 0.02 | T, T+L > C > L |
| <i>Ephemera ignita</i> | 1.53 | n.s. | | 3.06 | 0.08 | T, T+L > C, L |
| Orthoclaadiinae | 5.52 | 0.013 | L > T, T+L, C | * | | |
| Tanyptodiinae | 0.59 | n.s. | | 3.67 | 0.03 | T, C > L, L+T |

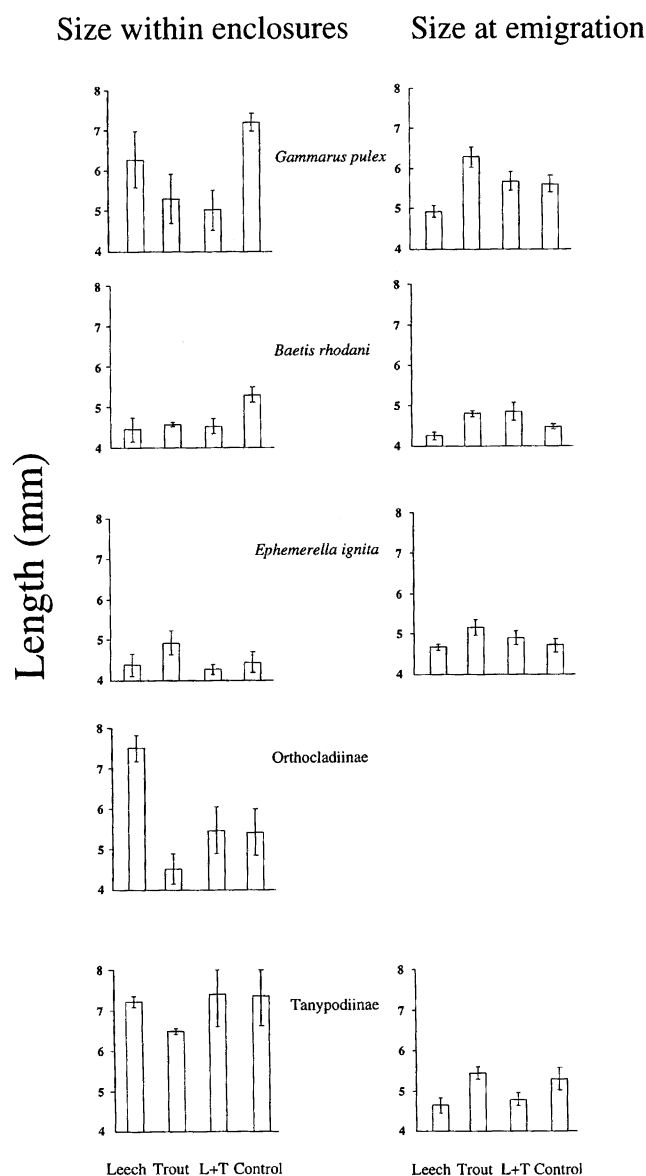


Fig. 4 Average length of benthic invertebrates (left panels) and average length of emigrating prey (right panels) for different predator treatments. Error bars denote ± 1 SD

correlation for *Gammarus*, *Baetis* (Fig. 5) (Spearman rank correlation. *Gammarus*: trout $r_s = 0.790$, $P < 0.05$, $n = 6$; leeches $r_s = 0.850$, $P < 0.05$, $n = 6$;

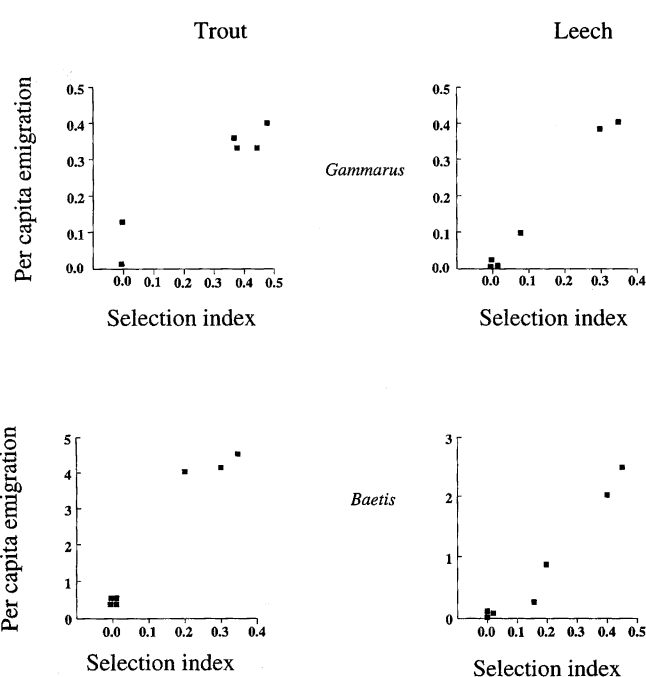


Fig. 5 Relationships between the per capita emigration rates found in the predator enclosures and predator prey size selectivity. Data are only shown for taxa with statistically significant relationships. Each square represents a single prey size class

Baetis: trout $r_s = 0.82$, $P < 0.05$, $n = 7$; leeches: $r_s = 0.97$, $P < 0.05$, $n = 7$), whereas no correlation existed between trout selection and emigration of different size classes of *Ephemera* (Spearman rank correlation: $r_s = 0.66$, $P < 0.05$, $n = 7$).

Direct predation versus avoidance behaviour

The analyses of whether selective predation or avoidance behaviour produced size distribution patterns in enclosures indicated that avoidance behaviour and direct predation by predators were equally important for those taxa that were both consumed by predators and drifted [Trout: *Gammarus* direct consumption $2.1 \pm 0.82\%$ (± 1 SD), avoidance behaviour $1.2 \pm 0.86\%$; *Baetis* direct consumption $89 \pm 36.8\%$, avoidance behaviour $120 \pm 32.6\%$; *Ephemera* direct consumption

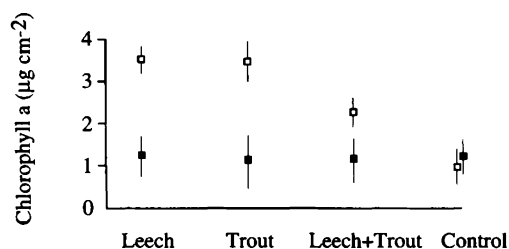


Fig. 6 Changes in total chlorophyll a ($\mu\text{g cm}^{-2}$) in the four different treatments. The open squares show chlorophyll a concentrations after 1 month. The filled squares show the initial concentration of chlorophyll a. Error bars are 1 SD

$50 \pm 40.5\%$, avoidance behaviour $80 \pm 52\%$; *Erpobdella*: *Baetis* direct consumption $80 \pm 24.5\%$, avoidance behaviour $50 \pm 32.6\%$; Mann-Whitney *U*-test: $P > 0.50$ for all comparisons].

Cascading effects

One-way ANOVA showed that periphyton biomass as measured by chlorophyll a was significantly affected by predator treatment ($F_{3,12} = 135.8$, $P < 0.001$) (Fig. 6). Trout alone and leeches alone had stronger effects on periphyton biomass than trout plus leeches (Tukey's test: $P < 0.001$ for all comparisons), which in turn had a stronger effect than controls (Tukey's test: $P < 0.001$).

Discussion

Invertebrate predators have been suggested to have a stronger effect on benthic prey in streams than vertebrate predators (Wooster 1994). In contrast, my study shows that trout had stronger effects on total invertebrate biomass than the control and the leech treatment. The effect on total invertebrate biomass was probably due to strong trout effects on density of the *Gammarus*, which was the dominant invertebrate prey taxon in the stream. On the individual prey taxon level, trout and leeches affected about the same number of prey taxa, but their impact varied to some extent with prey type. There were tendencies for trout to have its strongest effects on actively drifting prey (i.e. three of four prey taxa with high drift rates, except *Asellus*), whereas leeches had stronger effects on prey with low drift rates (i.e. three of five prey taxa with low drift rates, except *Baetis* and *Ephemerella*).

A reduction of prey density in the presence of a predator does not necessarily mean that a predator's direct consumption of prey is the cause for the decline. The decline may also be related to avoidance behaviour of prey, and prey may be more prone to emigrate out of enclosures when predators are present (Peckarsky and Dodson 1980; Peckarsky 1985; Forrester 1994; Sih and Wooster 1994; Wooster 1994). Wooster and Sih (1995) reviewed 22 studies measuring predator impacts on prey behaviour and found that on average, predatory inver-

tebrates increased prey emigration more than predatory vertebrates. My results did not support their generalisation, as *Gammarus* had a higher per capita drift in the presence of trout than in the presence of leeches and *Baetis* and *Ephemerella* had similar per capita drift rates regardless of predator type. Only Tanypodiinae showed a pattern consistent with the Wooster and Sih (1995) findings as the per capita drift rate index was higher in the leech treatment than in the other treatments. Distinguishing whether direct predation or avoidance behaviour produced the density patterns of prey may be easy to determine in some cases. The effects of trout on *Asellus* and leeches on Orthocladinae, Limnephilidae and *Asellus* are probably mostly related to direct predation, as *Asellus*, Orthocladinae and Limnephilidae rarely occurred in drift samples. In other cases it may be more difficult to determine which of the mechanisms is most important. Because I estimated invertebrate densities, drift input, drift outputs and predator consumption rates, I was able to construct a budget for each enclosure. These budgets showed that direct consumption by predators and avoidance behaviour of prey in the form of drift were equally important in explaining the reduced densities of prey. A review of the literature also indicates that the relative importance of prey emigration and direct predator consumption to prey population decline will vary widely across systems, taxa and scales (Feltmate and Williams 1989; Lancaster 1990; Sih et al. 1992; Forrester 1994; Sih and Wooster 1994; Wooster and Sih 1995; Englund and Olsson 1996; Kratz 1996).

Interaction modifications occur when one species modifies the interaction between two other species, often through changes in behaviour. Thus, interpredator aggression may reduce or increase consumption of prey species (Soluk and Collins 1988a,b; Soluk 1993; Brönmark et al. 1997; Soluk and Richardson 1997). In my study, leeches or trout alone had strong effects on *Ephemerella* and *Baetis* densities, whereas leeches and trout together had a lower impact on these prey, although the effects were still stronger than controls. The mechanisms producing this interaction modification are not clear, but per capita emigration rates of *Baetis* and *Ephemerella* were lower in the treatment with trout and leeches together than in treatments with trout and leeches alone. However, the mechanism producing this lower per capita emigration of *Baetis* and *Ephemerella* is unclear (see below). The interaction was presumably also due to reduced consumption of *Baetis* and *Ephemerella* by leeches in the presence of trout. In a previous experimental study, Dahl and Greenberg (1997) found that leeches decreased their consumption of *Baetis* in the presence of trout. Another potential effect could have been that trout consumed leeches. Only two leeches were actually found in trout stomachs in the trout-plus-leech treatment, but I only measured diet at the end of the experiment. There was no significant difference in number or biomass of *Erpobdella* between leech or trout-plus-leech treatments, but there was a

tendency for higher leech number and biomass in the leech treatment. It is also known from other studies that trout usually consume leeches and affect their densities (Dahl and Greenberg 1998; J. Dahl and L. Greenberg, unpublished data).

Previous studies in streams have found that fish predators may have differential effects on the behaviour and abundance of differently sized prey (Bechara et al. 1993; Culp and Scrimgeour 1993; Tikkanen et al. 1994; Scrimgeour et al. 1997), whereas the impact of invertebrate predators on differently sized prey has received less attention. This study demonstrated that both trout and leeches were size-selective predators. Trout fed primarily on large prey items, whereas *Erpobdella* fed on small prey items. This size-selective predation by trout and leeches affected the size distribution of prey in enclosures and interestingly it was also linked to the size of prey at emigration. Thus, trout seemed to cause large prey to emigrate whereas leeches forced small prey to emigrate. There was a significant correlation between emigration rates of the different size classes and trout and leech size selectivity for *Gammarus* and *Baetis*, supporting the idea that *Gammarus* and *Baetis* emigration were driven by feeding selectively of the predators.

The results of this research also raise questions about how the avoidance behaviour of different prey and prey size classes in response to different predators is initiated. Avoidance behaviour of prey may be elicited by a direct attempt of predators to consume prey, or as prey responses to the close proximity of a predator (Peckarsky 1980; Malmqvist and Sjöström 1987; Lancaster 1990; Culp et al. 1991). Tikkanen et al. (1994) found a nocturnal peak in *Baetis* drift in aquaria containing minnows of constant overall activity across time, suggesting that drift responses depended not only on encounters between predators and prey. Long-distance cues may also inform prey whether or not predators are present. Chemical cues released by predators are known to affect prey behaviour (Holomuzki and Short 1988). However, Tikkanen et al. (1996) found that chemical cues alone did not cause any avoidance responses. They used *Baetis* nymphs and found that drift rates of *Baetis* were strongest when fish were uncaged, which suggests that visual or hydrodynamic cues are needed in addition to chemical cues for an assessment of predation risk.

Cascading effects were found in all predator treatments, and interestingly, leeches were found to have the same impact on periphyton biomass as trout. The effect was probably due to both direct consumption of grazers by trout and leeches and indirect behavioural responses, e.g. drift, by potential grazers. Trophic cascades through direct predation have been reported previously in streams (Power 1990; Bechara et al. 1992), but trophic cascades through behavioural alterations of grazers seem to be rare (but see McIntosh and Townsens 1996). Cascading effects were stronger in leech or trout treatments than in the leech-plus-trout treatment, but the leech-plus-trout treatment still had a significant positive

effect on the periphyton compared with the control. Both leeches and trout had strong negative effects on the *Baetis* and *Ephemerella* grazers, and leeches also on limnephilid caddis larvae that could be related to the effects on periphyton. The interaction strength was probably lower in the leech-plus-trout treatment due to interaction modifications (discussed above).

This study suggests that invertebrate predators can have similar impacts on benthic prey as fish predators, but that their impact depends to some extent on prey taxon and prey size. This study also suggests that interactions in streams are very complex and that behavioural interactions may potentially play a larger role than previously thought (Soluk and Richardson 1997). The presence of different predators may actually lower the risk of being consumed by some invertebrates and may potentially explain some of the variable outcomes of fish-invertebrate studies in previous studies, i.e. compensatory impact of different predators and interaction modifications may alter the impact of predators (sensu Wootton 1994). The results of this study also suggest that prey exposed to different predators during their development may have life history strategies adopted to a variable predation pressure. Life history theory predicts that reduced adult survival will select for earlier maturation and increased reproductive effort; conversely, reduced juvenile survival will select for the opposite strategy (Roff 1992; Stearns 1992; Wellborn 1994; Sparkes 1996).

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