

# Predation on mayfly nymph, *Baetis rhodani*, by native and introduced *Gammarus*: direct effects and the facilitation of predation by salmonids

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## SUMMARY

1. In a series of laboratory experiments, we assessed the predatory nature of the native Irish amphipod, *Gammarus duebeni celticus*, and the introduced *G. pulex*, towards the mayfly nymph *Baetis rhodani*. We also investigated alterations in microhabitat use and drift behaviour of *B. rhodani* in the presence of *Gammarus*, and indirect predatory interactions with juvenile Atlantic salmon, *Salmo salar*.
2. In trials with single predators and prey, *B. rhodani* survival was significantly lower when *Gammarus* were free to interact with nymphs as than when *Gammarus* were isolated from them. The invader *G. pulex* reduced the survival of *B. rhodani* more rapidly than did the native *G. d. celticus*. Both *Gammarus* spp. were active predators.
3. In 'patch' experiments, *B. rhodani* survival was significantly lower both when *G. pulex* and *G. d. celticus* were present, although the effect of the two *Gammarus* species did not differ. Again, active predation of nymphs by *Gammarus* was observed. Significantly more nymphs occurred on the top and sides of a tile, and *per capita* drifts were significantly higher, when *Gammarus* were present. *Baetis rhodani per capita* drift was also significantly higher in the presence of the introduced *G. pulex* than with the native *G. d. celticus*.
4. *Gammarus* facilitated predation by salmon parr of *B. rhodani* by significantly increasing fish–nymph encounters on exposed gravel and in the drift. There were no differential effects of the two *Gammarus* spp. on fish – *B. rhodani* encounters or consumption.
5. We conclude that *Gammarus* as a predator can have lethal, nonlethal, direct and indirect effects in freshwaters. We stress the need for recognition of this predatory role when assigning *Gammarus* spp. to a 'Functional Feeding Group'.

*Keywords:* drift behaviour, *Gammarus*, mayfly, predation, salmonids

## Introduction

The lethal effects of predators clearly have implications for prey individuals, populations and communities (Kitching, 1986; Murdoch & Bence, 1987; Sih, 1987; Crawley, 1992). At all these levels, however, it is increasingly recognised that predators have a range of

effects on prey that may be lethal, nonlethal, direct and indirect. These include apparent competition, trophic cascades and alterations in prey behaviour leading to fitness reductions and modifications of interspecific interactions (McIntosh & Townsend, 1996; Lima, 1998; Peckarsky & McIntosh, 1998; Englund & Evander, 1999; Sih & Ziemba, 2000). For instance, by causing a prey species to change habitat, a predator may indirectly increase the availability of that prey to another predator (Miller & Kerfoot, 1987; Wootton, 1994). Thus, when unravelling the effects of any predator, a number of interactions must be

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considered. *Gammarus* spp. (Crustacea: Amphipoda) are common in temperate freshwaters and are increasingly recognised as partially predatory (reviewed by MacNeil, Dick & Elwood, 1997). In the present study, we examine direct predation and facilitation of fish predation involving freshwater *Gammarus*.

*Gammarus* spp. are generally regarded as herbivorous 'shredders' and detritivores (Chamier, Sutcliffe & Lishman, 1989; Friberg & Jacobsen, 1994; Rong, Sridhar & Barlocher, 1995; Gayte & Fontvieille, 1997). However, this 'Functional Feeding Group' (FFG) classification (see Cummins & Klug, 1979) may be misleading, since accumulating evidence indicates that gammarids are partially predatory (MacNeil *et al.*, 1997). This is demonstrated by gut contents analyses, anecdotal accounts of prey capture and consumption, and studies of cannibalism and intraguild predation (Minshall, 1967; Dick, 1992, 1995; Summers, Delong & Thorp, 1996). This shift in perception is reflected in recent studies that consider *Gammarus* as predators affecting zooplankton populations (Wilhelm & Schindler, 1999; Wilhelm, Schindler & McNaught, 2000). Although *Gammarus* may be prey to a range of vertebrate and invertebrate predators (reviewed by MacNeil, Dick & Elwood, 1999), there have been no empirical studies of the variety of interactions that may occur between predatory *Gammarus* and potential macroinvertebrate prey species.

Furthermore, *Gammarus* and related genera are increasingly invading new regions, with damaging consequences for native communities (Conlan, 1994). For example, throughout Europe, *Gammarus pulex* (L.) has displaced *G. duebeni celticus* Stock & Pinkster, while Ponto-Caspian amphipods are currently invading and altering European and North American aquatic ecosystems (Dick, 1996; Dick & Platvoet, 2000; Ricciardi & MacIsaac, 2000; van der Velde *et al.*, 2000). Thus, we require elucidation of the comparative effects of native and invasive *Gammarus* spp. as predators in aquatic ecosystems.

In this study, we assess the effects of the predatory behaviour of *G. d. celticus* and *G. pulex*, the former native and the latter introduced to Ireland, on a potential prey species, nymphs of the mayfly *B. rhodani* (Pictet). *Baetis rhodani* was chosen for several reasons. First, we have observed predation on this mayfly, in both field and laboratory, by the two *Gammarus* spp. Secondly, ephemeropterans have been widely

recorded in the guts of *Gammarus* (Minshall, 1967; MacNeil *et al.*, 1997; D. Kelly, pers. observation). Thirdly, Crothers (1989) found a negative correlation in distribution and abundance between *G. pulex* and Baetidae in riffles, such patterns remaining consistent since the 1970s (J.H. Crothers, pers. communication). Fourthly, Waters (1964) found that, after experimentally denuding stream patches in a riffle, the density of Baetidae was higher after recolonisation than previously and after *Gammarus* had recolonised. Referring to the latter study, Hynes (1970) suggested that some unknown mechanism of interference might have occurred between the two groups. Fifthly, mayflies account for a significant proportion of the biomass and production of benthic macroinvertebrates and are a major component of fish diets (Elliot, Humpesch & Macan, 1988; Keeley & Grant, 1997).

Specifically, in the laboratory, we assess: (1) the ability of both *G. d. celticus* and *G. pulex* to kill and consume *B. rhodani* nymphs, (2) the impact of both *Gammarus* spp. on *B. rhodani* in 'patch' experiments, in terms of predation and alteration of prey behaviour and (3) any modification of predation of *B. rhodani* by fish in the presence of the two *Gammarus* spp.

## Methods

### *Experiment 1: single predators and prey*

This experiment assessed the survival of single *B. rhodani* nymphs with singles of both *G. d. celticus* and *G. pulex*, using four experimental groups: (1) *G. d. celticus* 'isolated' ( $n = 30$ ), (2) *G. d. celticus* 'free' ( $n = 30$ ), (3) *G. pulex* 'isolated' ( $n = 30$ ) and (4) *G. pulex* 'free' ( $n = 30$ ). The experimental design allows predation to be distinguished from mortality followed by scavenging (Dick & Platvoet, 2000).

In July–August 1999, male *G. d. celticus* (body length 13–18.5 mm) from the Cleen river (54°21' N 7°20' W), and male *G. pulex* (body length 12–16.5 mm) and *B. rhodani* nymphs (head-capsule width 0.7–1.2 mm) from the Swanlinbar river (54°13' N 7°38' W), were housed separately in aquaria (18 × 55 × 36 cm) with mixed water from the collection sites. Aquaria were aerated, substratum, plant material and other fauna added, and temperature maintained at 14 °C and photoperiod at 15 : 9 h (light : dark).

Single pebbles of about 2 × 1.5 cm were placed in crystallising dishes (9 cm diameter; 5 cm deep) filled

to a depth of 3 cm (200 mL) with filtered stream water which was aerated vigorously to provide a current. Plastic enclosures of 4 cm diameter and 6 cm deep, each perforated with six small holes, were placed centrally within each dish, allowing a single *Gammarus* to be physically 'isolated' in one experimental group and 'free' to roam the dishes in the other group. In each replicate, a single mayfly nymph without black wing-pads, and thus unlikely to emerge, was placed in the main body of the dish and allowed to settle for 5 min before the introduction of the *Gammarus*.

Each replicate was examined after 24, 48 and 72 h for survival of the mayfly and evidence of predation. For each *Gammarus* spp., data on frequency of *B. rhodani* survival at each time interval were analysed using  $2 \times 2$  contingency tables with the following two factors: (1) *Gammarus* status (Isolated/Free) and (2) *Baetis rhodani* survival status (surviving/not surviving). To compare predation frequencies of the two species of *Gammarus*, data from the 'free' groups were analysed with the following two factors: (1) *Gammarus* species (*G. d. celticus*/*G. pulex*) and (2) *Baetis rhodani* survival status (surviving/not surviving).

#### Experiment 2: 'Patch' experiments: predation and the alteration of prey behaviour

This experiment assessed the impact of the two *Gammarus* spp. on *B. rhodani* in patch-scale experiments, in terms of prey survival and alteration of prey behaviour, using three experimental groups: (1) 10 *B. rhodani*, with *Gammarus* absent ( $n = 15$ ), (2) 10 *B. rhodani*, plus 10 *G. d. celticus* ( $n = 15$ ) and (3) 10 *B. rhodani*, plus 10 *G. pulex* ( $n = 15$ ).

In December 1999, male *G. d. celticus* (body length 12.0–17.0 mm) and *B. rhodani* nymphs (head capsule width 0.7–1.1 mm) from Manor Farm (54°31' N 5°59' W), and *G. pulex* (body length 13.0–15.0 mm) from the Minnowburn (54°33' N 5°57' W), were housed as in experiment 1, but with temperature maintained at 8 °C and photoperiod at 8 : 16 h (light : dark).

Clear plastic aquaria (31 × 18 × 17 cm) were filled to a depth of 14 cm (8 L) with filtered stream water. A re-circulating stream flow system was adapted from Tikkanen, Muotka & Huhta (1994). A 15-cm air-stone was placed at one end of each aquarium behind a plexiglass baffle, producing a re-circulating current driven by ascending air bubbles. Water velocity

ranged from 18 to 25 cm s<sup>-1</sup> at 2 cm below the water surface and between 5 and 8 cm s<sup>-1</sup> at 2 cm above the substrate. A layer of slightly abraded clear glass beads (1.5 cm diameter) was placed on the tank bottom as substratum, plus a single clay tile (7.5 × 5 × 1.5 cm) supported by two pieces of plexiglass (2 × 1.5 cm). This allowed accurate counts of animals and their microdistributions.

In each replicate, nymphs were allowed to settle for 1 h before *Gammarus* were introduced. A black curtain was suspended across each tank to minimise operator disturbance. Counts of surviving *B. rhodani* were made after 10 min and 1, 3, 4.5, 6, 11 and 24 h from the introduction of *Gammarus*. At each of the first three time intervals, observations were made of *B. rhodani* habitat use, with instantaneous scan-sampling of the numbers of nymphs occurring on tank walls, substratum, upper tile and under tile. Drift behaviour was assessed as drift entries over 4 min, defined as departures from the substrate into the water flow recorded as either 'noncontact' or 'contact', the latter as a result of the contact of *Gammarus* with *B. rhodani*.

Mean percentage *B. rhodani* survival (arcsine transformed) was examined with respect to '*Gammarus* status' (absent/*G. d. celticus*/*G. pulex*) and 'time' (repeated measure) in a two-factor ANOVA. Mean percentage *B. rhodani* survival was then examined with respect to '*Gammarus* status' at each time period in a series of single-factor ANOVAs. Mean percentage of *B. rhodani* using the various microhabitats (arcsine transformed) was examined with respect to '*Gammarus* status', 'microhabitat type' and 'time' (the latter two factors as repeated measures) in a three-factor ANOVA. Mean *per capita* drifts of *B. rhodani* ( $\log_{10}x + 1$  transformed) were examined with respect to '*Gammarus* status', 'drift type' (contact and noncontact) and 'time' (the latter two factors as repeated measures) in a three-factor ANOVA. As multiple measures were taken within each aquarium for the factors 'microhabitat type' and 'drift type', repeated measures ANOVAs were appropriate for the analyses (see Sokal & Rohlf, 1995).

Invertebrate drift may simply be a function of density through, for example, increased interference (Peckarsky, 1979; Lancaster, Hildrew & Townsend, 1988). Thus, in the above experiment, any increase in *per capita* drifts in groups two and three, as compared with group one, might be attributed to the higher

overall density of invertebrates in groups two and three, as opposed to the influence of *Gammarus per se*. Therefore, under the same conditions as above, we assessed the influence of *B. rhodani* density on *per capita* drift using two experimental groups: (1) 10 *B. rhodani* per tank ( $n = 8$ ) and (2) 20 *B. rhodani* per tank ( $n = 8$ ). Drifts (entries over 4 min) were recorded after 10 min and 1 h. Mean *per capita* drifts of *B. rhodani* (arcsine transformed from proportional values) were examined with respect to *B. rhodani* 'density' and 'time' (repeated measure) in a two-factor ANOVA.

### Experiment 3: fish predation of *B. rhodani* in the presence and absence of *Gammarus*

This experiment assessed any modification of the predation of *B. rhodani* by fish in the presence of the two *Gammarus* spp., using three experimental groups: (1) one salmon parr (*Salmo salar* L.), 10 *B. rhodani*, with *Gammarus* absent ( $n = 12$ ), (2) one salmon parr, 10 *B. rhodani*, plus 10 *G. d. celticus* ( $n = 12$ ) and (3) one salmon parr, 10 *B. rhodani*, plus 10 *G. pulex* ( $n = 12$ ).

In May 2000, *G. d. celticus* (body length 12.5–18.8 mm) and *B. rhodani* (head capsule width 0.8–1.2 mm) from Manor Farm (54°31'N 5°59'W), and *G. pulex* (body length 13–18 mm) from the Minnowburn (54°33'N 5°57'W), were housed as in experiment one. Atlantic salmon parr (1+; fork length 7.9–10.9 cm), previously stocked as fry, were obtained by electro-fishing the Termon river (54°35'N 7°47'W). In the laboratory, fish were housed in artificial channels, temperature and day length being maintained as in experiment two and fed *ad libitum* with live *Simulium* and caddis larvae, mayfly nymphs and gammarids. Fish were starved for 48 h prior to experiments to allow gut evacuation (Elliot, 1972) and, thus, counts of experimental mayfly nymphs consumed from stomach dissections (see below).

Plastic aquaria (40 × 18 × 20 cm) with a substratum of sand and pebbles and with three sides covered by black tape to minimise disturbance to fish (see Elliot, 1972) were divided in half using a black plexiglass baffle. Flow (18–25 cm s<sup>-1</sup>) was provided using an electrical water pump and aquarium spray bar (9 cm long).

Each fish was allowed to acclimatise in one half of the tank for 24 h. Subsequently, *B. rhodani* nymphs were introduced to the other half of the tank and allowed to settle for 30 min, after which the *Gammarus* were introduced in groups two and three. Five

minutes later, the partition was removed and 30 min of observations began. We recorded fish–invertebrate encounters, attacks, captures and ingestions (see Wankowski, 1981; Stradmeyer & Thorpe, 1987) both on the substratum and in the water column (i.e. in the drift). After a further 2 h, the fish were killed with an overdose of tricaine methane sulphonate (MS 222) and their stomachs dissected and the mayflies counted. Counts of surviving *B. rhodani* and *Gammarus* were made for each aquarium.

The mean number of the two *Gammarus* species ingested per tank was compared using a *t*-test. Mean number of fish encounters with *B. rhodani* ( $\log_{10}x + 1$  transformed) was examined with respect to '*Gammarus* status' and 'location' (repeated measure) in a two-factor ANOVA. Mean number of *B. rhodani* in fish stomachs (arcsine transformed) was examined with respect to '*Gammarus* status' in a one-factor ANOVA.

## Results

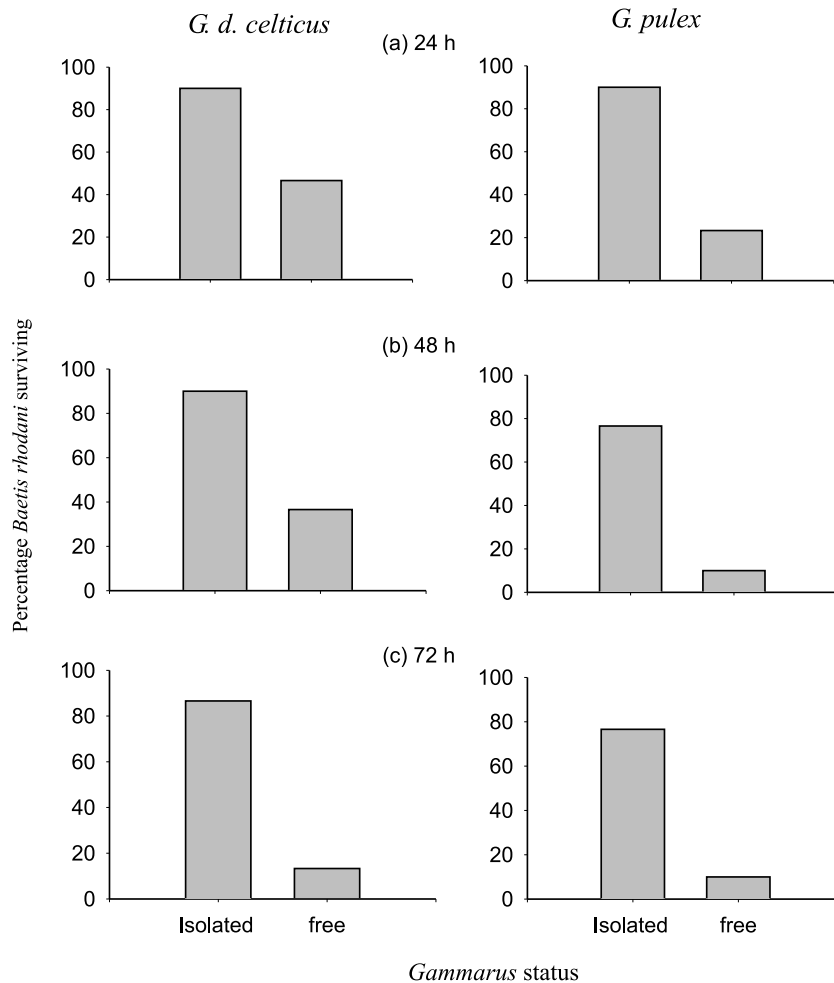
### Experiment 1: single predators and prey

*Baetis rhodani* survival at all three time intervals was significantly lower when *Gammarus* were 'free' to interact with the nymphs as opposed to 'isolated' from them (Fig. 1a–c; Table 1). Survival of *B. rhodani* was significantly lower when free to interact with *G. pulex* as compared with *G. d. celticus* after 24 and 48 h (Fig. 1a,b; Table 1). After 72 h, there were only 4/30 and 3/30 nymphs alive in the *G. d. celticus* and *G. pulex* 'free' groups, respectively (Fig. 1c).

In 'free' group replicates where nymphs did not survive, *Gammarus* were often observed attacking, capturing and actively consuming live *B. rhodani* nymphs, while nymphal body parts were always found scattered in such dishes. The data and observations thus indicate that active predation by *Gammarus* reduced the survival of *B. rhodani* in *Gammarus* 'free' as compared with 'isolated' groups.

### Experiment 2: 'Patch' experiments: predation and the alteration of prey behaviour

There was a significant '*Gammarus* status' effect on mean *B. rhodani* survival ( $F_{2,42} = 9.6$ ,  $P < 0.001$ ; Fig. 2), with Fisher's protected least significant difference (FPLSD) *posthoc* analyses showing significantly lower survival when *G. d. celticus* and *G. pulex* were present



**Fig. 1** Percentage survival of *Baetis rhodani* nymphs when 'isolated' from and 'free' to interact with both *Gammarus duebeni celticus* and *G. pulex*.

**Table 1** G-statistics and *P*-values for *Baetis rhodani* survival comparisons from  $2 \times 2$  contingency table analyses (see Fig. 1)

		Time		
Comparison		24 h	48 h	72 h
<i>Gammarus duebeni celticus</i>	'Isolated'/'free'	14.0**	24.1***	36.0***
<i>G. pulex</i>	'Isolated'/'free'	30.0***	30.0***	30.0***
<i>G. d. celticus</i> vs. <i>G. pulex</i>	'Free' groups	3.88*	5.0*	NS

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

as compared with absent (both  $P < 0.01$ ; Fig. 2). However, there was no significant difference in survival of *B. rhodani* in the presence of *G. d. celticus* versus *G. pulex*. The significant difference in survival of nymphs between the 'Gammarus present' and the 'Gammarus absent' groups occurred between the time periods of 3 and 4.5 h (Fig. 2; Table 2). There were significant 'time' and 'Gammarus status  $\times$  time' interaction effects ( $F_{6,252} = 26.8$  and  $F_{12,252} = 5.21$ ,  $P < 0.0001$ ; Fig. 2), reflecting the decreasing survival

of *B. rhodani* as time progressed in the 'Gammarus present' as compared with 'Gammarus absent' groups. As in experiment one, observations of *Gammarus* attacking, capturing and eating *B. rhodani* nymphs shows that direct predation reduced the survival of *B. rhodani* in the presence of *Gammarus*.

Microhabitat use by *B. rhodani* was influenced by the presence of *Gammarus*, as shown by the significant 'Gammarus status  $\times$  micro-habitat type' interaction effect ( $F_{6,126} = 4.6$ ,  $P < 0.001$ ; Fig. 3). This appears to

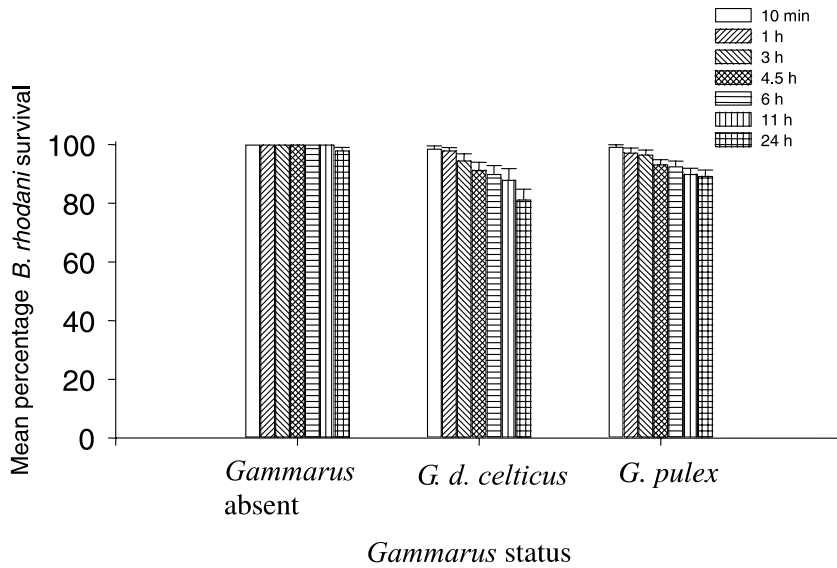


Fig. 2 Mean  $\pm$  SE percentage survival of *Baetis rhodani* nymphs over time for each *Gammarus* status group.

Table 2 Single factor ANOVAS examining the effect of *Gammarus* status on the mean percentage survival of *Baetis rhodani* nymphs (see Fig. 2)

Time	F ( d.f. 2,42)	P
10 min	1.05	0.35
1 h	1.70	0.19
3 h	3.00	0.058
4.5 h	7.30	0.002
6 h	8.20	0.001
11 h	9.92	0.001
24 h	13.70	< 0.0001

be caused by the increased use of the upper tile surface at the expense of other microhabitats in the presence of *Gammarus* (Fig. 3). There were no other significant effects.

With regards to drift behaviour, there were significant '*Gammarus* status' and '*Gammarus* status  $\times$  drift type' interaction effects ( $F_{2,42} = 28.3, P < 0.0001$  and  $F_{2,84} = 5.9, P < 0.01$ , respectively, Fig. 4). *Post-hoc* analyses (FPLSD) showed that mean *per capita* drift was higher where *Gammarus* were present as compared with absent, and higher in the presence of

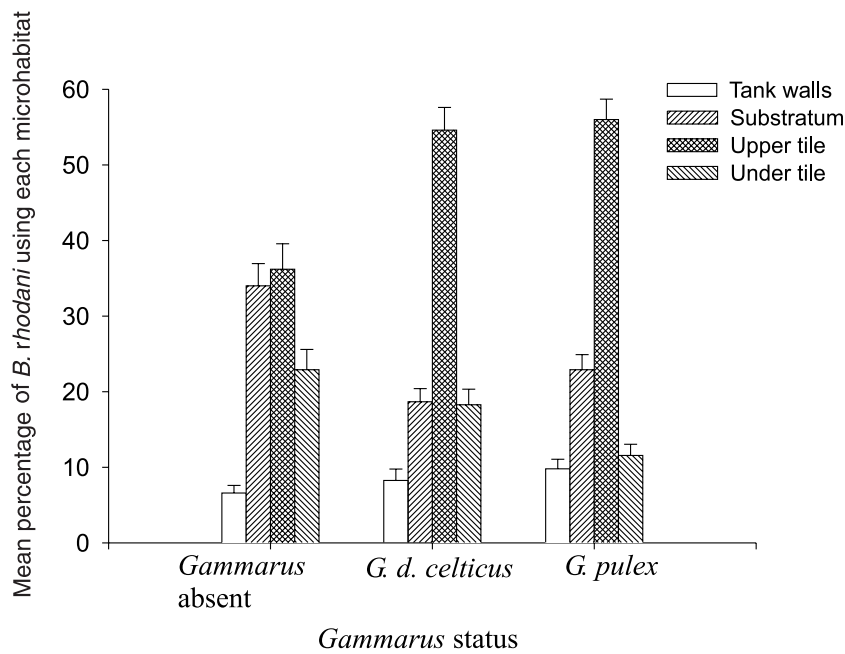


Fig. 3 Mean  $\pm$  SE percentage use of microhabitats by *Baetis rhodani* nymphs for each *Gammarus* status group.

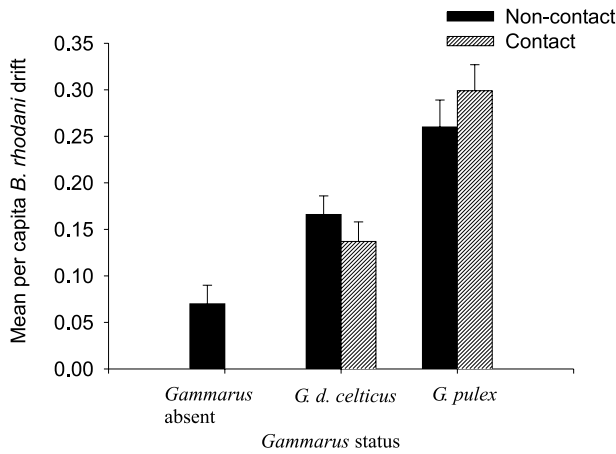


Fig. 4 Mean  $\pm$  SE per capita drift entries of *Baetis rhodani* for each *Gammarus* status group.

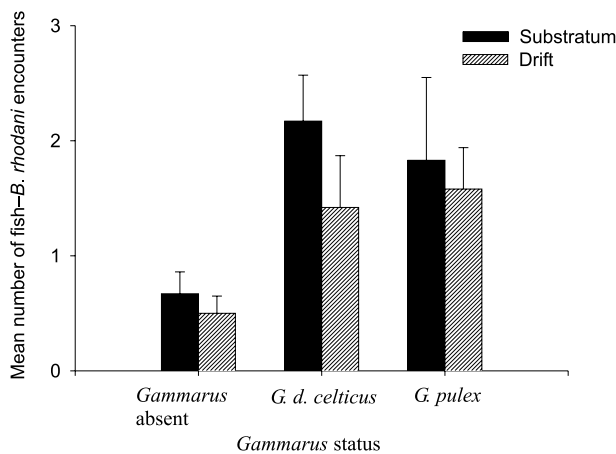


Fig. 5 Mean  $\pm$  SE number of fish-*Baetis rhodani* encounters for each *Gammarus* status group and microhabitat type.

*G. pulex* as compared with *G. d. celticus* (all  $P < 0.0001$ ; Fig. 4). There were no significant 'time' or other interaction effects.

In the mayfly only experiment, there was no significant effect of 'density' on mean per capita drift ( $F_{1,14} = 0.47$ , NS; mean  $\pm$  SE for 10 mayfly nymphs per tank =  $0.05 \pm 0.05$  and for 20 mayfly nymphs per tank =  $0.006 \pm 0.006$ ). There were no significant 'time' or 'density  $\times$  time' interaction effects.

#### Experiment 3: fish predation of *B. rhodani* in the presence and absence of *Gammarus*

While fish were observed to attack *Gammarus* in the 30 min observation period, the relatively small size of the former resulted in few ingestions, with no signi-

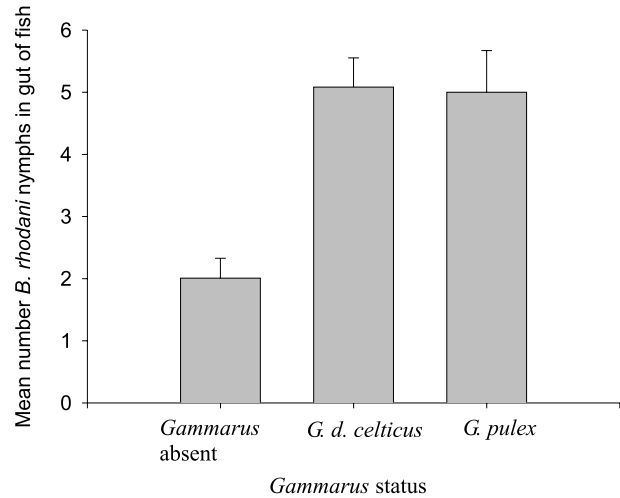


Fig. 6 Mean  $\pm$  SE number of *Baetis rhodani* nymphs consumed by salmon parr for each *Gammarus* status group.

ficant difference in the mean number of ingestions of the two *Gammarus* species per tank (mean  $\pm$  SE =  $0.6 \pm 0.2$  for *G. d. celticus* and  $1.2 \pm 0.29$  for *G. pulex*,  $t = 1.3$ , d.f. = 22, NS). On only one occasion was a live *B. rhodani* nymph observed being eaten by a *Gammarus* during the 30 min observation period.

There was a significant '*Gammarus* status' effect on overall fish-*B. rhodani* encounters ( $F_{2,33} = 5.1$ ,  $P < 0.01$ ), with *posthoc* analyses (FPLSD) showing that there were significantly more encounters between fish and *B. rhodani* when *Gammarus* were present rather than absent (both  $P < 0.01$ ; Fig. 5). *Gammarus* 'species' made no difference to the encounter rate and there were no significant 'location' or '*Gammarus* status  $\times$  location' interaction effects.

There was a significant '*Gammarus* status' effect on fish consumption of *B. rhodani* ( $F_{2,33} = 10.19$ ,  $P < 0.001$ ; Fig. 6), with *posthoc* analyses (FPLSD) showing that significantly more *B. rhodani* were ingested by fish when *Gammarus* were present as compared with absent (both  $P < 0.001$ ), but there was no significant difference in fish ingestions of *B. rhodani* between the two *Gammarus* species (Fig. 6).

#### Discussion

Cummins & Klug (1979) suggested that the occurrence of animal fragments in the guts of freshwater invertebrate 'shredders' could result from scavenging or accidental ingestion. Although gut content analyses of *Gammarus* cannot distinguish scavenging from

predation, significantly lower survival of *B. rhodani* in 'Gammarus free' as compared with 'Gammarus isolated' groups in experiment one, together with evidence of attack, capture and consumption, strongly suggest predation. Such microcosm studies may, however, fail to represent large, complex systems by exaggerating predatory effects due to increased encounters, lack of refugia, and reduced escape opportunities (Huston, 1999; Wilhelm *et al.*, 2000). In addition, in lotic systems, flow and physical heterogeneity may reduce predator foraging efficiency and thus any effects on prey abundance at larger scales (Gillinsky, 1984; Lancaster, Hildrew & Townsend, 1990; Hildrew & Giller, 1994). However, in the larger scale and heterogeneous 'patches' of experiment two, *B. rhodani* survival was still significantly lower when in the presence of *Gammarus*.

In experiment two, *Gammarus* spp. were also shown to cause alterations in the use of microhabitat by *B. rhodani*, with nymphs increasing their use of the 'upper tile surface'. Wilhelm *et al.* (2000) suggested that, by avoiding diurnal vertical migration and remaining in surface layers, *Daphnia* were separated from their main predator, *G. lacustris*, in an alpine lake. Also, Culver, Fong & Jernigan (1991) conclude that the different microdistribution of *G. minus* and the isopod *Caecidotea* spp. reduced predation. In our experiment, the upper tile surface probably represented a refuge for *B. rhodani*, since *Gammarus* occurred predominantly in the bead substratum. *Baetis rhodani* also entered the drift significantly more often in the presence of *Gammarus*, with or without *Gammarus* contact, suggesting both escape after encounter and the ability to detect *Gammarus* at a distance. This result cannot be attributed to a simple density effect, since we found no difference in *B. rhodani per capita* drift entries at densities of 10 and 20 nymphs per tank. Therefore, rather than invertebrate density *per se*, some inherent quality of *Gammarus* spp. in experiment two caused a significant increase in *B. rhodani per capita* drift.

Alterations in microhabitat use and drift by mayfly nymphs have been reported as avoidance behaviour elicited by chemical, tactile or hydrodynamic cues from predatory stonefly nymphs (Soluk & Collins, 1988a; Peckarsky, 1996; Huhta *et al.*, 1999). In addition, the fast escape response of the amphipod *Crangonyx pseudogracilis* Bousfield, when both *G. pulex* and *G. d. celticus* attempted to grasp it (see MacNeil,

Elwood & Dick, 1999), may be analogous to *B. rhodani* drift in response to contact with *Gammarus*. Although we observed *B. rhodani* drifting after *Gammarus* attempted to grasp the nymph, drift may have been caused by indirect physical disturbance caused by *Gammarus* activity. Indeed, Haden *et al.* (1999) suggested that it was simply the swimming activity of *G. lacustris* that destroyed the food capture nets of the caddis larvae *Ceratopsyche oslari* (Banks). Whatever the precise mechanisms involved, it appears that *Gammarus* species altered habitat use and drift by *B. rhodani*.

Invertebrate prey in streams generally respond differently to fish and invertebrate predators. That is, prey decrease their drift and increase refuge use in response to the former, but increase both drift and exposure on substrata in the presence of the latter (reviewed by Wooster & Sih, 1995). However, it may be erroneous to generalise prey responses to fish as benthic-feeding and drift-feeding fish can have different impacts (see Dahl & Greenberg, 1996). Nevertheless, Wooster & Sih (1995) stress the need to understand how prey species behave in the presence of several predators. In this respect, we found in experiment three that increased encounters between fish and *B. rhodani*, both in the drift and on the upper surface of pebbles, translated into greater consumption of *B. rhodani* by fish in the presence of *Gammarus*. It may be argued that the activity of *Gammarus* increased the feeding 'motivation' of fish, thus leading to greater consumption of the mayflies. Whatever the precise mechanism, *B. rhodani* are clearly more likely to be consumed by fish when *Gammarus* are present.

Soluk & Collins (1988b) showed indirect facilitation of sculpin feeding on *Ephemerella* spp. in the presence of predatory stonefly nymphs, with potential implications for prey abundance and fish energetics. Habitat complexity reduces fish foraging efficiency by providing refugia for prey (Crowder & Cooper, 1982; Power, 1992), but Soluk & Richardson (1997) showed that the presence of predatory stonefly nymphs indirectly facilitated the growth of drift feeding salmonids by increasing prey availability. Salmonids feed both on benthic occurring and drifting prey in streams (Ware, 1973; Stradmeyer & Thorpe, 1987) and, for Baetidae, exposure and intentional drift after predatory or aggressive encounters are major determinants of their importance in salmonid diets (Rader, 1997). Indeed, Richardson (1993) points out that 'bottom up' factors such as prey availability may



limit fish production, with fish feeding, biomass and growth rate often higher when prey are more available (Sagar & Glova, 1988; Keeley & McPhail, 1998; Nislow, Folt & Seandel, 1998). Our results indicate that *Gammarus* indirectly facilitate prey availability to juvenile Atlantic salmon by increasing mayfly exposure on substrata and drift entry. However, whether this leads to tangible benefits to the fish, such as increased growth rate, remains unresolved. This is because, while *Gammarus* may increase *per capita* drift of mayflies, they may also simultaneously reduce the abundance of mayfly nymphs, as shown in experiments one and two.

At small spatial scales *Baetis* spp. abundance may be influenced by mobility and habitat selection (Peckarsky, 1979; Kohler, 1992) and, thus, invoking predation to explain field patterns may be problematic. Indeed, at small spatial scales movement of prey among patches can reduce any effects of predators on prey abundance through consumption and behavioural avoidance (Cooper, Walde & Peckarsky, 1990). However, as *Gammarus* density in the field can range from <1–10 000 m<sup>2</sup> (Welton, 1979; Marchant & Hynes, 1981; Lancaster & Mole, 1999), predation, alteration of *B. rhodani* behaviour and facilitation of fish feeding may be important mechanisms explaining negatively related field abundance patterns of *Gammarus* and *Baetis* spp. both at the patch and riffle spatial scales (Waters, 1964; Crothers, 1989; D. Kelly, unpublished). Indeed, micro- and mesocosm experiments of intraguild predation have been consistent in explaining field patterns of interacting *Gammarus* spp. and other amphipods (Dick, 1996; Otto, 1998; Dick, Montgomery & Elwood, 1999).

Predation on *B. rhodani* occurred more rapidly with the introduced *G. pulex* than with the native *G. d. celticus* in experiment one, while *B. rhodani* drifted significantly more in the presence of the invader than with the native in experiment two. This may be the result of greater activity of *G. pulex*, because drift induced by contact was significantly greater with *G. pulex* than *G. d. celticus*. There was no differential predatory effect of the two *Gammarus* species in experiment two, however, perhaps due to the larger scale, lower encounter rates and greater refugia. Neither was there any difference between *Gammarus* species in facilitation of salmonid predation in experiment three, perhaps due to the inhibition of *Gammarus* activity in the presence of fish (see

Andersson *et al.*, 1986). Although these results are inconclusive, *G. pulex* is likely to have a greater impact on prey species than *G. d. celticus* for a number of reasons. First, in studies of intraguild predation between *G. pulex* and *G. d. celticus*, which explains the displacement of the latter by the former, *G. pulex* was shown to be significantly more aggressive in its predatory attack behaviour (Dick, Montgomery & Elwood, 1993, Dick, Elwood & Montgomery 1995). Secondly, *G. pulex* is generally found at higher density than *G. d. celticus*, at least in part due to its higher reproductive output and thus may have a greater overall predatory pressure on prey species (Dick, 1996; MacNeil, Elwood & Dick, 2000). Indeed, there is accumulating evidence at a range of spatial scales that *G. pulex* causes a reduced macroinvertebrate species richness, abundance and diversity when compared with *G. d. celticus* (MacNeil *et al.*, 2001; D. Kelly, unpublished).

Hildrew (1992) and Covich, Palmer & Crowl (1999) emphasised a great need for theoretical and empirical work on the function of single species in stream ecosystems and in understanding how food webs are structured. In terms of 'Functional Feeding Groups', *Gammarus* spp. have been classified as herbivorous 'shredders' (Cummins & Klug, 1979). However, others have regarded *Gammarus* as carnivore-scavengers or omnivorous opportunists (Minshall, 1967; Bjarnov, 1972; Summers *et al.*, 1996). MacNeil *et al.* (1997), reviewing such literature, urged that 'a new realism be adopted' in studies of *Gammarus* trophic ecology. This is of particular importance with increasing evidence that predators can have a variety of direct and indirect, lethal and nonlethal impacts on prey individuals, populations and communities (Kitching, 1986; Wootton, 1994; Sih, Englund & Wooster, 1998). We suggest that freshwater ecologists consider *Gammarus* species as being predatory towards other macroinvertebrates, with potentially wider impacts than previously appreciated. In addition, with the likelihood of future amphipod invasions (Conlan, 1994; Dick & Platvoet, 2000), studies should focus on the possibility of differential predation by native and introduced *Gammarus* species.

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