

Predator–prey interactions between brown trout *Salmo trutta* and native and introduced amphipods; their implications for fish diets

Calum MacNeil, Robert W. Elwood and Jaimie T. A. Dick

MacNeil, C., Elwood, R. W. and Dick, J. T. A. 1999. Predator–prey interactions between brown trout *Salmo trutta* and native and introduced amphipods: their implications for fish diets. – Ecography 22: 686–696.

An attempt to improve the food base for brown trout *Salmo trutta* in Northern Ireland was made in 1958/59 by deliberately introducing English *Gammarus pulex* into several Irish rivers. In addition, another amphipod *Crangonyx pseudogracilis*, was later accidentally introduced into Irish waters. Our study represents the first attempt to examine the trophic interactions between a native fish predator (*S. trutta*) and an array of these native (*Gammarus duebeni celticus*) and introduced (*G. pulex* and *C. pseudogracilis*) amphipods. Feeding experiments, involving young brown trout predators and amphipod prey, revealed that the fish actively selected *C. pseudogracilis* relative to two alternative *Gammarus* prey species. Although the trout encountered the *Gammarus* species more than *C. pseudogracilis*, they were eaten less than *Crangonyx*. Difficulties in handling and ingestion of *Gammarus* by trout may be a key component of the preference for the smaller, more easily handled *Crangonyx*. The microdistribution of the species was altered by the fish, due to predation being greater in particular microhabitats. Our study showed that the introduction of the herbivorous *C. pseudogracilis* into Irish freshwaters may represent a useful addition to fish diets, particularly for small and/or juvenile fish. The repercussions of the deliberate introduction of *G. pulex* are less clear. It may improve feeding for fish, but only if it can coexist with indigenous macroinvertebrates and thus ultimately improve the range and quantity of possible food items in predator diets. Alternatively, being highly predatory towards other macroinvertebrates including *G. d. celticus* and *C. pseudogracilis*, *G. pulex* may be deleterious to the diversity of the resident benthic community and hence reduce the diversity of prey available to fish predators.

C. MacNeil, R. W. Elwood and J. T. A. Dick, School of Biology and Biochemistry, The Queen's Univ. of Belfast, Belfast, N. Ireland, U.K. BT7 7BL (present address of C.M.: 24 The Wynd, Pelton, Chester-le-st, Co. Durham, U.K. DH2 1EH).

An understanding of the different motivational causes underlying variations in food intake by fish is vital, should the manipulation of fish diets be attempted (Metcalfe et al. 1987). One such attempt was made with respect to brown trout *Salmo trutta* in Northern Ireland. In 1958 and 1959, 115000 and 19000 non-native *Gammarus pulex*, respectively, were transplanted from North Yorkshire, England into Northern Irish rivers (Strange and Glass 1979). This introduction, however, has not necessarily led to an enhancement of diets due to the introduced species replacing the native species *Gam-*

marus duebeni celticus, rather than coexisting. Furthermore, the extent that amphipods are eaten by trout in different rivers is highly variable (MacNeil 1997). In addition, the rapid spread of another recent (albeit accidental) amphipod (*Crangonyx pseudogracilis*) introduction into Irish, British and European waters may have further implications for fish feeding in the future (Dick 1996a, b, MacNeil 1997). Thus the array of amphipods has changed dramatically in recent times and it is the relative susceptibility of these species to predation by young trout that is assessed in the present study.

Accepted 26 March 1999

Copyright © ECOGRAPHY 1999

ISSN 0906-7590

Printed in Ireland – all rights reserved

Prey selection is ultimately determined by the encounter rate between predators and prey, the probability that the encounter results in an attack, the probability that the attack results in capture and finally the probability that the capture results in ingestion (Osenberg and Mittelbach 1989). Each sequence or stage in this interaction involves behavioural decisions made by the predator or prey, or both (Tikkanen et al. 1997). Therefore, prey preference is determined by both active predator choice and by the relative vulnerability of the prey taxa (Jeffries 1988, Tikkanen et al. 1997). Insights into the actual mechanisms underlying prey selection (i.e. how and why a predator selects a specific prey) can be achieved by quantifying all of the components of the predator-prey interaction via direct behavioural observations (Cooper et al. 1985, Allan and Flecker 1988, Osenberg and Mittelbach 1989, Sih and Moore 1990, Tikkanen et al. 1997). Juvenile salmonids provide ideal subjects for such studies of feeding behaviour and previous studies have noted the typical sequence described above (Ware 1972, Metcalfe et al. 1987).

Trout are visual predators (Ware 1972) and environmental complexity reduces their ability to prey on amphipods (e.g. Nelson 1979, Stoner 1982, Holomuzki and Hoyle 1990, Power 1992, Drake et al. 1995). The presence of a predator can influence the habitat use, activity patterns and microdistribution of amphipods and other macroinvertebrates, in a way that reduces susceptibility to predation (i.e. Goss-Custard 1970, Stein and Magnuson 1976, Holomuzki and Hoyle 1990, Bechara et al. 1993, Sih and Wooster 1994, Dahl and Greenberg 1996). Therefore, a further aim of our experiment was to investigate the microdistribution of introduced and native amphipod prey species to assess if their respective microdistributions were influenced by the presence of trout. Our findings on predation, microdistribution and response to predators by prey species, are discussed with respect to both the distribution of these amphipods in the rivers and loughs of N. Ireland and the possible impacts of amphipod introductions on native fish diets.

Materials and methods

Preparation of habitat simulations

During late September 1996, we collected animals by kick-sampling, *G. d. celticus* from Manor Farm, Lagan River (ordnance survey grid ref J 308646), *G. pulex* from Shaws Bridge, Lagan River (grid ref D335685) and *C. pseudogracilis* from Kiltonga Lake, Newtowndards (grid ref J477746), all in N. Ireland. Only healthy, parasite-free, non-gravid, adult *G. d. celticus* (ca 12.0–16.5 mm body length), *G. pulex* (10.0–14.0 mm) and *C. pseudogracilis* (4.0–7.0 mm) were selected for the simu-

lation. Each species was maintained in separate (36 × 60 × 20 cm deep), well aerated tanks, filled with ca 50% of their respective source waters and 50% of filtered Lough Neagh water. They were also supplied with substratum and habitat in the form of cobbles, pebbles and gravel, together with flora (i.e. Canadian pondweed, *Elodea canadensis*) and fauna, from their sites of origin. Food, in the form of leaves and pelleted catfish food, which the animals have been previously observed to grab and devour (Dick et al. 1993, Dick and MacNeil unpubl.), was supplied as additional nutrition to these trophically versatile animals (MacNeil et al. 1997). In the absence of predators, all of these species can be maintained for several months under such conditions (Dick et al. 1993, Dick 1995, MacNeil 1997).

The light:dark cycle was kept constant at 12:12 h and the water temperature at 9.5°C, both regimes being appropriate for the time of year (Dick 1992, 1995, Dick et al. 1993). A total of 28 observation tanks, measuring ca 40 × 18 × 20 cm deep, were set up with (a) a complex habitat simulation (14 replicates) and (b) a simple habitat simulation (14 replicates). The complex habitat consisted of a washed Lough Neagh sand substrate, upon which was placed a piece of slate (5 × 5 cm) held off the sand via a glued piece of filter tube (1 × 1 cm). This permitted access for amphipods under the slate, while still allowing us an unrestricted view beneath the slate. *Elodea canadensis* pondweed was common to all of the sites where amphipods were collected. Therefore, four 5 cm length strands of pondweed were weighted down and placed in the sand next to the slate in each tank. The simple habitat consisted merely of a bare sand substrate. All observation tanks contained 50% filtered Lough Neagh water and 50% piped water and were covered on three sides with black plastic, leaving one side clear. The mixture of Lough and piped water meant all these species would be equally favoured or disadvantaged by the water's chemical properties and quality, as it differed from their source waters. Each tank was well lit via overhead neon tube lights and the black background permitted our clear observation of amphipods. A partition separated each observation tank into two halves, of which one contained the habitat simulation and the other contained a single fish predator and a bare sand substrate. Thirty adult gammarids, ten individuals each of *G. d. celticus*, *G. pulex* and *C. pseudogracilis* were placed in the habitat simulation section of each tank. Air stones were used to supply oxygen to each tank but were removed immediately prior to the beginning of each observation period, as otherwise trout tended to congregate around water currents generated by air stones (MacNeil unpubl.).

The fish used in experiments were farmed brown trout from a Dept of Agriculture fish farm. These were < 1 yr old, with a mean fork length of 70 mm (range 59–74 mm). The trout were acclimated to laboratory

conditions (including light regime) and observation tank water, for at least 4 wk prior to observations. Fish were sustained during this period, on a diet of mackerel strips in brine and live mayflies. In order to standardize the feeding motivation of the fish, all were deprived of food for 48 h prior to the start of the experiment (a similar time period used in other feeding trials – Ware 1972, Bakker et al. 1997). The work was conducted under a U.K. Home Office licence.

Trout were placed into the observation tanks ca 24 h prior to the commencement of the experiment (Caine 1989, Kaiser et al. 1992). The amphipods, however, were introduced only 30 min prior to the experiment. This was because intraguild predation (IGP) on *C. pseudogracilis* by both *Gammarus* species was found to be rife during time periods any longer than this in mixed amphipod species assemblages (MacNeil 1997). This period, however, was still adequate for the prey to disperse and find cover in the complex habitat simulation. Immediately before the start of each experiment, any dead amphipods were carefully replaced where possible. Despite such precautions, in some tanks even a time period of only 30 min was evidently sufficient, for a large number of gammarid (principally *Cranogonix*) deaths to occur and we replaced such tanks for the purposes of the current study. Each fish predator and each potential prey were used once.

Predation events

After the acclimatization period, the partition was removed carefully to minimize disturbance to both fish predator and prey. We began observations at the moment of the first predator attack on prey and all subsequent predation events were recorded by direct observation for the next hour (Cooper et al. 1985, Brown and Thompson 1986, Metcalfe et al. 1987). The parameters recorded for the fish's response to each prey item were: encounters (E), attacks (A), captures (C) and ingestions (I) (see Cooper et al. 1985, Allan and Flecker 1988, Tikkanen et al. 1997). An encounter (E) between predator and prey was recorded when the fish first displayed the characteristic 'orientation' movement towards an individual amphipod (defined as a sudden twitch of the head towards a particular prey item – Metcalfe et al. 1987). An attack (A) was defined as when the fish made a sudden lunge or 'start' from a resting position towards the prey item (Ware 1972). Such attacks were then defined as being either unsuccessful or successful, depending on their outcomes. An unsuccessful attack led to a miss/reject outcome (Metcalfe et al. 1987), with the fish either merely lunging at the prey but not snapping at it, or alternatively appearing to snap at the prey and miss (a 'snap' being defined as a rapid opening and closing of the jaw in the immediate vicinity of the prey item). In contrast, a

successful attack resulted from the fish snapping at and gaining hold of the amphipod in its mouth. This then constituted a prey capture (C). The prey item was held in the mouth of the fish and then either spat out (expulsion of the prey item from the mouth during handling) and rejected, or successfully ingested (I). This last component of the predation event occurred when the amphipod was no longer visible at or in the mouth, and the fish appeared to have successfully swallowed the prey item (this was usually accompanied by characteristic 'gulping' motions). Only four components of each predation event were defined in order to minimise ambiguity between analyses (Gill and Hart 1994). This allowed calculation of attack probability (proportion of encounters resulting in attack = A/E), capture success (proportion of attacks resulting in capture = C/A) and ingestion efficiency (proportion of captures resulting in ingestion = I/C) for each predator. Pilot studies showed that sometimes trout required multiple attacks in order to successfully capture a single amphipod prey item. Therefore, the proportion of total successful captures resulting from only multiple attacks (C_m) was also calculated (C_m/C), in order to examine if fish found some amphipod species more difficult to successfully capture than others.

Effects of fish presence on amphipod microdistribution in complex habitat simulations

After 1 h of predation, we recorded the instantaneous locations of any surviving amphipods in the complex habitat simulation, i.e. on the sand, in the pondweed, on or under the slate, on the tank wall or in the water column. These were then compared with the locations of amphipods after 1.5 h in identical complex habitat simulations, but without a fish predator (10 replicates). Percentage abundance data only was used in such comparisons, because of the relatively high mortalities of amphipods with fish predation. All of the surviving amphipods were removed from the tank and counted and all of slate and pondweed was removed from the complex habitat simulations and examined for amphipods.

The influence of fish size (fork length) on predator–prey interactions

When the observation period ceased, each trout was removed from the tank and killed with an overdose of the anaesthetic MS-222 (Sandoz – tricain methan sulphonate) and the fork length recorded. This method of dispatch was considered at least as humane as a sharp blow to the head or severing of the spinal column and conforms to published guidelines for the use of fish in scientific research (see Kelsch and Shields 1996). Fish

body length has been shown to be a major determinant of the outcomes of predator-prey interactions between fish predators and macroinvertebrate prey (Osenberg and Mittelbach 1989).

Each trout's stomach was dissected out and the contents extracted to provide a final check on the number of amphipods successfully ingested. Our preliminary observations had ascertained that even trout of the shortest fork length used in the experiment were capable of ingesting all three species of amphipod.

Data analysis

A series of univariate ANOVA's was carried out using the SuperANOVA statistical package (Anon. 1989), to assess the effects of amphipod species and habitat complexity on the components of predation events witnessed in each tank ('species' and 'habitat', the former factor as a repeated measure). Because the different components of predatory events were highly dependent on each other, presenting the dangers of escalating type one errors, statistical significance was evaluated at $p < 0.01$. Data relating to numbers of encounters, attacks, captures and ingestions were normalized via the $\log(x+1)$ transformation. Proportional data relating to attack probability, capture success, ingestion efficiency and proportion of total captures due to multiple attacks, and percentage data relating to amphipod relative abundance in specific habitat types, were normalized via the arcsine transformation (Fowler and Cohen 1990, Sokal and Rohlf 1995). We examined the effects of trout presence or absence (1 h with the fish either absent or present), microhabitat type and species on amphipod microdistribution in a three factor ANOVA ('trout presence/absence', 'species' and 'micro-habitat', the latter two factors as repeated measures). Although post-hoc analyses such as Fisher's Protected Least Significant Differences (FPLSD) are not available for within-subject factors in repeated measures ANOVA designs, least square means tests were used as an alternative (Anon. 1989). The relationships between trout fork length and components of predation events were assessed by Spearman rank correlation analysis.

Results

Predation events

Most trout appeared to orientate towards amphipod prey within 30 s of the partition being removed and launch an attack within 60 s of partition removal. The longest period before a recognizable attack occurred, was only 2 min after removal of the partition. All of the 28 fish ate at least one amphipod during the hour long observation period, so no fish were disregarded from

the study. No amphipod species was completely eliminated in any of the 28 feeding trials.

Species had a significant effect on the number of encounters, captures and ingestions ($F_{2,52} = 14.122$, 43.591 and 49.752, respectively, all at $p < 0.0001$) (Fig. 1a-c). However, there was no significant difference in the number of attacks experienced by the three amphipod species (Fig. 1d). Least square means tests showed that *C. pseudogracilis* was encountered significantly less than both *G. d. celticus* and *G. pulex* ($t = 4.518$ and $t = 4.682$, respectively, both $p < 0.0001$) but captured significantly more than either *G. d. celticus* and *G. pulex* ($t = 8.553$ and $t = 7.520$ respectively, both $p < 0.0001$). In addition, more *C. pseudogracilis* individuals were ingested than either *G. d. celticus* or *G. pulex* ($t = 8.641$ and $t = 8.637$, respectively, both $p < 0.0001$). There was no significant difference in the number of encounters, captures or ingestions involving the two *Gammarus* species. Habitat complexity had no

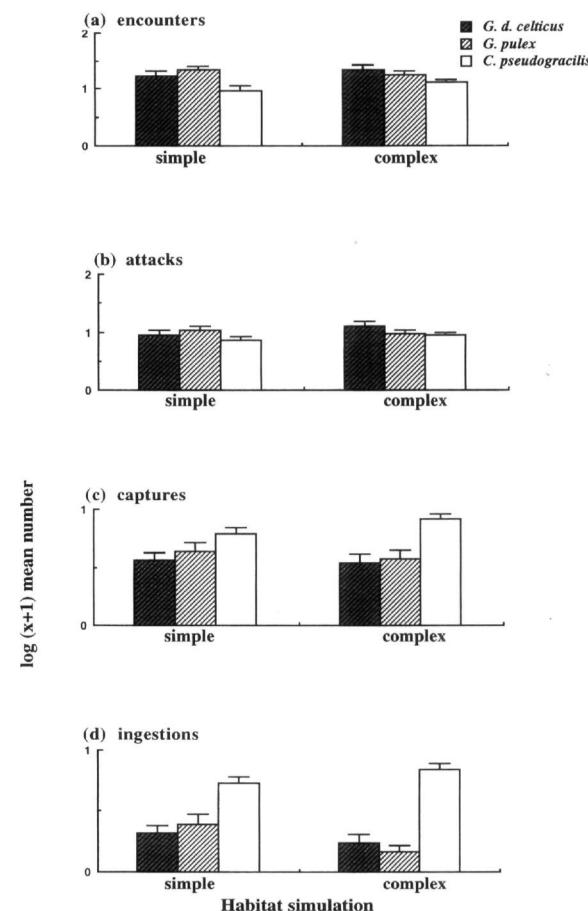


Fig. 1. Mean number (\pm SE) of: (a) encounters between 0 + brown trout and amphipods, (b) trout attacks upon amphipods, (c) amphipods captured by trout, (d) amphipods ingested by trout, in simple and complex habitat simulations.

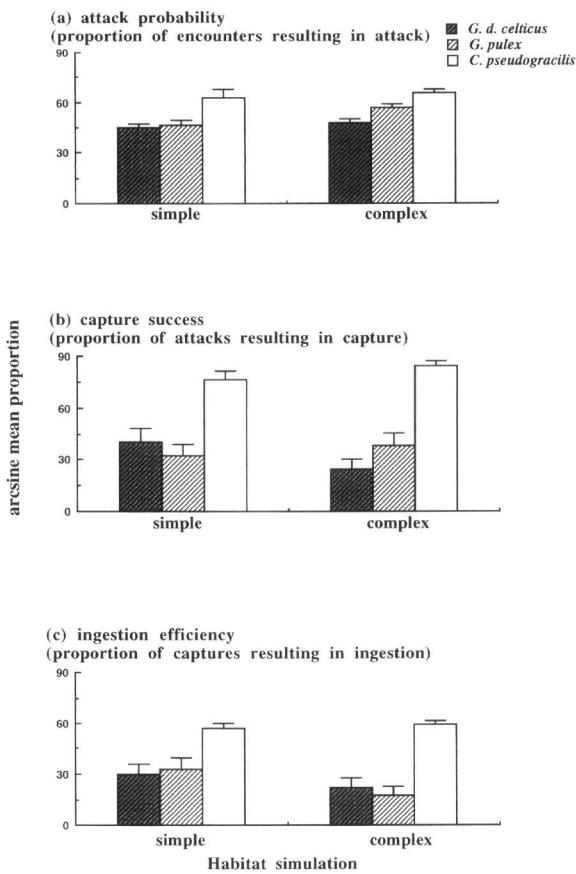


Fig. 2. Predation events between 0+ brown trout and amphipods in simple and complex habitat simulations, subdivided into (a) attack probability, (b) capture success, (c) ingestion efficiency. (All mean proportions (\pm SE) arcsine transformed).

significant effect on the number of encounters, attacks, captures and ingestions amphipods experienced. There were no significant habitat effect and no species and habitat interaction effect on the number of encounters, attacks, captures and ingestions amphipods experienced, although there was almost a significant species and habitat complexity interaction effect in terms of amphipod ingestion, with a trend for more ingestions of *Crangonyx* and less ingestions of *Gammarus* spp. in complex habitats as opposed to simple ones.

There was a significant species effect in attack probability (A/E), capture success (C/A) and ingestion efficiency (I/C) ($F_{2,52} = 24.990$, 49.118 and 11.765 respectively, all at $p < 0.0001$) (Fig. 2a–c). Least square means tests showed the attack probability of *C. pseudogracilis* was significantly higher than that associated with either *G. d. celticus* or *G. pulex* ($t = 4.968$ and $t = 6.840$ respectively, both $p < 0.0001$), significantly more *C. pseudogracilis* were successfully captured when attacked than either *G. d. celticus* or *G. pulex* ($t = 8.875$ and $t = 8.259$ respectively, both $p < 0.0001$) and there

was a significantly higher proportion of captures resulting in ingestion for *C. pseudogracilis* than either *G. d. celticus* or *G. pulex* ($t = 4.207$ and $t = 4.195$ respectively, both $p < 0.0001$). There was no significant difference in the proportion of prey captures due to multiple attacks required to capture each species. Although, there were no significant habitat effects or species and habitat interaction effects for attack probability, capture success, ingestion efficiency or proportion of prey captures due to multiple attacks, least square means tests revealed a trend for *G. pulex* to be more efficiently ingested than *G. d. celticus* in the simple habitat ($t = 2.304$, $p < 0.05$), with the reverse true in the complex habitat ($t = 2.230$, $p < 0.05$) (Fig. 2c). In addition, there was also a trend for the ingestion efficiency of *C. pseudogracilis* to be higher in the complex as opposed to the simple habitat ($t = 2.073$, $p < 0.05$) (Fig. 2a–c).

Effects of fish presence on amphipod microdistribution in complex habitat simulations

There was no significant trout presence/absence effect or species effect on the percentage abundance of amphipods in tanks (this being due to each tank population of each species being regarded as 100% for the purposes of the microdistribution analysis, despite obvious differences in mortality). There was a highly significant habitat effect ($F_{5,110} = 28.139$, $p < 0.0001$) but this cannot be attributed to choice because the sizes of the microhabitats varied. The key analysis concerns the interaction effects. There was a significant trout presence/absence and habitat interaction effect ($F_{5,110} = 3.924$, $p < 0.01$) (Fig. 3). In tanks with trout present, there was a lower mean percentage of total amphipods present on or in the sand or in the water column but a higher mean percentage of amphipods present in the pondweed than in tanks without trout. There was also a significant species and habitat interaction effect

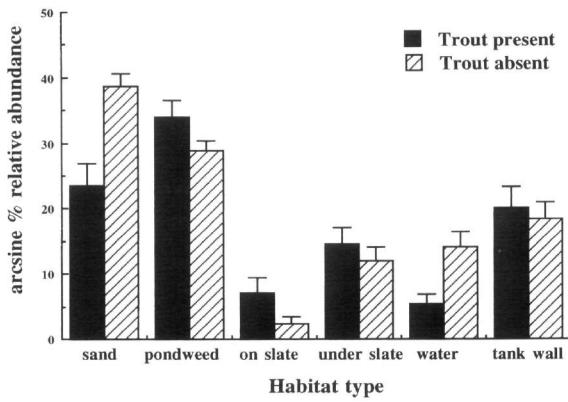


Fig. 3. The effects of 0+ brown trout presence on the mean relative abundance (\pm SE) of all amphipods in microhabitats, after 1 h, in a complex habitat simulation.

($F_{10,220} = 1.937$, $p < 0.05$) with different amphipod species exhibiting different overall microdistribution patterns with respect to the 'available' habitat types. Least square means tests showed there was no significant difference between *G. d. celticus* and *G. pulex* percentage relative abundance on/in any of the habitat types. There were, however, significant differences in the relative distributions of both *G. d. celticus* and *G. pulex* in respect of *C. pseudogracilis* (i.e. a significantly lower percentage of both *G. d. celticus*, $t = 2.234$; and *G. pulex*, $t = 2.238$; than *C. pseudogracilis* in the pondweed, both at $p < 0.05$; but conversely, a significantly higher percentage of both *G. d. celticus*, $t = 2.275$; and *G. pulex*, $t = 1.989$; than *C. pseudogracilis* under the slate, both at $p < 0.05$). There was also a significant overall trout presence/absence, species and habitat interaction effect ($F_{10,220} = 2.542$, $p < 0.01$), indicating different amphipod species distributed themselves (or were left distributed by the onslaughts of the predator) differently amongst the microhabitat types, when fish predators were present or absent. For instance, there was a reduction in the percentage of both *Gammarus* species on the sand when the trout was present, but the percentage of *Crangonyx* on the sand did not change in the presence of the predator. Conversely, there was a reduction of *Crangonyx* in the water column when trout were present but the percentage of both *Gammarus* species in the water column did not change in the presence of the trout. There was no significant trout presence/absence and species interaction effect on amphipod relative abundance.

The influence of fish size (fork length) on predator-prey interactions

Spearman rank correlation coefficients revealed that there were no significant correlations between fish predator fork length and the attack probability (A/E), capture success (C/A), ingestion efficiency (I/C) or proportion of total captures resulting from multiple attacks (Cm/C), for any of the three prey species.

Discussion

Preference that is exclusively reliant on differential encounter and capture rates is regarded as passive, whereas active selection requires that predators differentiate among prey in attacks per encounter (Pastorok 1981, Allan and Flecker 1988). The significantly higher attack probabilities (A/E) associated with *C. pseudogracilis* prey, as opposed to either of the two *Gammarus* species, indicated prey preference by the trout was indeed based on active selection. In other words, in the majority of cases trout attacked nearly all *Crangonyx* prey that were encountered. This was in contrast to

encounters with *G. d. celticus* and *G. pulex* which were often limited merely to the 'orientation' movement of the fish, as the predator simply registered the presence of the prey item (Metcalfe et al. 1987). Therefore, despite the two *Gammarus* species being encountered more than *C. pseudogracilis*, and no significant difference in the absolute number of attacks experienced by the three species, nevertheless *C. pseudogracilis* was the most ingested of the three species. This higher rate of ingestion, however, was not due simply to the higher attack probability if encountered. There was also a higher capture success and a higher ingestion efficiency associated with *Crangonyx* than with either of the two *Gammarus* species. It should be noted that the native *G. d. celticus* and the introduced *G. pulex* were 'equivalents' in terms of the outcomes of each component of the trout predation event, with no significant differences in the attack probability, capture success or ingestion efficiency between these two species.

Large amphipods with prominent appendages are difficult for small fish such as stickleback to swallow and can lead to periods of repeated chewing and spitting (Croy and Hughes 1991, Kaiser et al. 1992). Similar behaviour was observed during interactions involving young brown trout and *G. d. celticus* and *G. pulex*, but rarely occurred with interactions involving trout and the smaller *Crangonyx* prey. *Crangonyx pseudogracilis* represented a far easier prey to handle than either of the *Gammarus* species, hence the significantly higher ingestion efficiencies associated with this latter prey type. However, it is interesting to note that gastric evacuation rates do not significantly differ between the larger *Gammarus* species and the smaller *Crangonyx* (MacNeil 1997). Future studies should measure respective handling times for *Crangonyx* and *Gammarus* to assess if energy per handling time is higher for *Crangonyx* relative to *Gammarus*.

In the short term, less vulnerable species such as *G. d. celticus* and *G. pulex* probably both fared better in the presence of the more vulnerable *Crangonyx* than either would if placed in a monoculture situation, where all of the predation pressure would be focussed solely on them (Jeffries 1988). Size selective predation can have potentially wide ranging effects on the population dynamics of amphipods. For example, Drake et al. (1995) found that as striped killifish *Fundulus majalis* grew, their food preferences changed from small to large *G. mucronatus* and thus different parts of benthic populations experienced different intensities of predation from the same predator.

Handling time of a prey item by a predator, depends substantially on the prey size/predator size ratio (Allan and Flecker 1988). Any increase in fish size or alternatively decrease in prey size (i.e. *Crangonyx* as opposed to *Gammarus* in this study), would mean that prey could be eaten without having to deal with correct alignment of the prey body, in order to permit swallow-

ing (Gill and Hart 1994). Fish size (as gauged by fork length) in the present study appeared to have little influence on the attack probability, capture success or ingestion efficiency of each species in the present study. However, the trout used were all of a very similar size in terms of fork length, with negligible differences in mouth or gape width.

As has been previously found in other fish predator amphipod prey interactions (Caine 1989), amphipod movement appeared to be an important feeding stimulus for the trout. If the amphipods remained motionless, the trout tended to move elsewhere. Similar observations were made by Delbeek and Williams (1988), investigating stickleback predation on *Gammarus*. In the current study, the most common escape response employed by both *G. d. celticus* and *G. pulex* was observed to be swimming. However, if the same individual was subjected to repeated attacks, it usually adopted a 'C-shaped' posture. This response would have increased the height:length ratio of the victimized *Gammarus*, making handling by the small fish predators difficult (Kaiser et al. 1992). As in the case of the *Gammarus* species, the most common escape response observed for *C. pseudogracilis* was also to simply swim away. However, if a stationary or slowly crawling *C. pseudogracilis* was attacked, it did not adopt the characteristic or stationary 'C' shape of the *Gammarus* species but rather performed an extremely rapid 'jumping' movement. This had the effect of rapidly distancing the individual *Crangonyx* from the oncoming fish by several centimetres, before the amphipod once again resumed its stationary position or its characteristically slow upright gait (MacNeil 1997). However, such a 'fright' or 'escape' response was, evidently, seldom effective.

Increased habitat structural complexity should provide more spatial refuges for prey and thus lower predator efficiency, due to the reduction of prey detection, pursuit and final capture (Crowder and Cooper 1982). The relative degree of habitat complexity in the current study (i.e. bare sand vs sand combined with slate and pondweed), however, seemed of little consequence as regards attack probability, capture success and ingestion efficiency in relation to *Crangonyx* or, indeed, the two *Gammarus* species. Despite their small size and the refuges provided, individual *Crangonyx* were still caught and killed in high numbers by the trout, the pondweed and slate apparently offering minimal protection. Indeed, there was a trend for *C. pseudogracilis* to suffer a greater degree of fish predation in the complex as opposed to the simple habitat. The complex habitat simulation may have been insufficient to provide effective refuges from these small highly manoeuvrable fish predators. It must also be noted that the two amphipod 'prey' species present *G. d. celticus* and *G. pulex*, also constituted potential predators of *Crangonyx* (MacNeil et al. 1997) and their presence in

the tanks may have had some influence on *Crangonyx* distribution. For instance, as the two *Gammarus* species sought refuge, *C. pseudogracilis* may have become relatively more susceptible to predation. Even in the absence of a fish predator there were differences between *Crangonyx* and the two *Gammarus* species in their respective microdistributions in the complex habitat simulation, with more *C. pseudogracilis* in the water column and on the tank walls than either of the two *Gammarus* species, both of which tended to congregate on the sand (MacNeil 1997). Given the greater heterogeneity in natural habitats, field studies are needed to ascertain differences in microdistribution patterns of these three amphipod species in the field. However, previous studies have shown that in both lentic and lotic systems, *C. pseudogracilis* tends to occur in those shoreline habitats where *Gammarus* species are at their most scarce (Dick 1996a, MacNeil 1997).

There was a significant trout presence/absence, species and habitat interaction effect, implying the microdistribution of different species altered when a fish predator was introduced and these changes in microdistribution patterns differed depending on the species involved. After one hour in the presence of trout there was a significantly lower percentage relative abundance of 'survivors' located in the water column, than was the case in the absence of the predator. This may indicate that, in the presence of fish, amphipods distributed themselves amongst those microhabitats offering the most protection, as has been shown in crayfish prey in the presence of fish predators (Stein and Magnuson 1976). Dahl and Greenberg (1996) also found that *G. pulex* changed activity patterns when fish were introduced, tending to remain within the benthos, but swimming freely in the water column when fish were absent. In the present study, however, the reduced number of amphipods in the water column may simply be due to predation in that location rather than active avoidance by the amphipods, particularly as a high percentage of the *C. pseudogracilis* tank populations were eliminated from this position. There is some debate as to the extent to which amphipods can detect fish predators. Various studies have suggested that *Gammarus* can use chemical cues to detect fish (Williams and Moore 1982, 1985, Holomuzki and Hoyle 1990, Bechara et al. 1993, Dahl et al. 1998). However, Kaiser et al. (1992) found that *Gammarus locusta* detected approaching stickleback predators very inefficiently and seldom produced an appropriate escape response. In common with previous studies (e.g. Gee 1982) the current study was conducted entirely in the light and thus conclusions about fish predation on amphipods must be treated with caution, as *Gammarus* activity and habitat linkages may change during the night. Predation on *Gammarus* by visual predators such as trout is also strongly influenced by the light/dark cycle, as in riverine habitats *Gammarus* species exhibit behavioural

'night active' drift, rising out of the benthos to drift downstream in the current and becoming highly vulnerable to fish predation during dusk and dawn (Allan 1978). No such studies have examined the influence of the light/dark cycle on *Crangonyx* activity.

If refuge habitats are limiting and prey capture rates are even slightly reduced in these few refuges, there could be strong selection pressure for prey to occupy these 'safer' regions preferentially (Crowder and Cooper 1982). Therefore, if prey species differ in aggressiveness, such as *Gammarus* in respect of *Crangonyx* (Dick 1996a, MacNeil et al. 1997), subordinate species (i.e. *C. pseudogracilis*) may be forced to use suboptimal habitats, with higher risks of encountering the predator. Thus, the physical capacity of the tank refuges to contain amphipods, coupled with the behaviour of the prey, could have determined which prey items were easily available to the fish predator (Greenberg 1994). When trout were added, *Crangonyx* were in effect suffering predation pressure from three species of potential predator and perhaps presented the interesting effect of interguild predation and intraguild predation (IGP) and hence interspecific exclusions operating within the same (albeit artificial) system. However, there appeared to be a reduction in IGP by *Gammarus* on *Crangonyx* when a fish predator was present, as opposed to when it was absent. While this may have been the trout's presence inhibiting *Gammarus* attacking *Crangonyx*, it may simply have been due to the extremely high numbers of *Crangonyx* already being harvested by the trout, resulting in a greatly reduced chance of *Gammarus* encountering *Crangonyx*. This latter explanation seems more likely, as previous studies have shown that the microdistribution of tank populations of *C. pseudogracilis* in complex habitats, does not differ in the presence of *Gammarus* to that observed in *Crangonyx* monocultures (MacNeil 1997).

Ireland was to enhance fish feeding in angling waters and it has recently been found to constitute $87\% \pm 6\%$ (mean \pm SE, n = 22) of the total abundance of macroinvertebrate fauna in the stomachs of 1+ / 2+ brown trout in a tributary of the Ballinderry river, the site of *G. pulex*'s original introduction (MacNeil 1997). Therefore, although our laboratory study has shown that small fish predators may have difficulties in handling *Gammarus*, larger fish seem to have little problem incorporating the introduced species into their diet. However, whether the introduction of *G. pulex* has provided more food for brown trout or merely replaced one *Gammarus* sp. with another remains open to debate, as no studies have so far examined whether the introduced species has improved trout growth in rivers where it now dominates.

In contrast to the *Gammarus* species, *C. pseudogracilis* appeared much more amenable as a prey item to small trout predators. Although *C. pseudogracilis* can occasionally be found co-occurring with the two *Gammarus* species in patches of lake and river systems (MacNeil 1997), it is more pollution tolerant than the *Gammarus* species (Hynes 1956, Pinkster et al. 1977, Fitter and Manuel 1994, MacNeil 1997, Dick et al. 1998) and consequently can be found in areas of rivers and lakes associated with low biological water quality, which may be devoid of *Gammarus* (MacNeil 1997). In these areas, more physicochemically tolerant fish species than salmonids, such as roach and stickleback, may be present and their potential food base may have benefited from this introduction. In addition, *C. pseudogracilis* can also be found in areas of higher water quality if *Gammarus* are scarce or in different microhabitats than *Gammarus* (MacNeil 1997). Thus our laboratory simulation of fish feeding indicates how the introduction of *C. pseudogracilis* may represent a useful supplement to the diets of native fish, especially juvenile salmonids and probably small fish species such as stickleback, stone loach and minnow, as all of these latter species have been shown to feed on *C. pseudogracilis* (MacNeil 1997).

Given that *C. pseudogracilis* is mainly herbivorous as opposed to *G. pulex* which is highly predatory to other macroinvertebrate taxa (MacNeil et al. 1997), these two introductions may have had differing positive and negative impacts on indigenous macroinvertebrate communities and their dependant fish predators (Gledhill et al. 1993, Dick 1996b). Ireland's isolation has resulted in a pauperate macroinvertebrate fauna compared to Britain and mainland Europe (Mitchell 1986) and the resident native macroinvertebrate communities may be capable of integrating *G. pulex* with minimal community disturbance (Dick 1996a). Alternatively, many animal invasions impact negatively on host communities (Diamond and Case 1986). In particular, the predatory nature of *G. pulex* towards other macroinvertebrates may be deleterious (Conlan 1994, MacNeil et al. 1997).

Conclusions and implications of amphipod introductions for fish diets

All three of the amphipod species in our study have been reported as being found in the stomachs of several native and introduced fish species, including brown trout (Fitzsimons and Andrews 1993, Kennedy and Vickers 1993, Dick 1996a, MacNeil 1997). Hynes (1956) noted that "when *G. pulex* has been present in any land mass for a considerable time *G. duebeni* is completely absent from fresh water" and *G. d. celticus* is being gradually ousted by the more aggressive *G. pulex* from many Irish rivers (Dick et al. 1990a, b, 1994, 1996a, MacNeil 1997, MacNeil et al. 1997). In terms of the response of small trout to these two amphipod species, the introduced species appeared equivalent to the native. The reason behind *G. pulex*'s introduction into N.

and Ireland's isolation with its limited range of native fauna and possibly unique races and gene pools means such an introduction could be highly damaging if the few native species are detrimentally affected (Dick 1996a). Loss of biodiversity is a worldwide problem, with a tendency for the world's fauna to become increasingly homogenous (Kinzelbach 1995) and invasions pose a major threat to freshwater biodiversity (Allan and Flecker 1993). The environmental impacts of amphipod introductions have been reviewed by Conlan (1994), who showed that amphipods can be creators of major disturbance through predation on commercial fish harvests, destruction of macroalgae and interference competition among indigenous and invasive species. Indeed, introduced populations of *G. tigrinus*, in German rivers, have been blamed for destroying fishing gear and injuring fish caught in nets (Pinkster et al. 1977) and, in the Netherlands it has virtually eliminated several amphipod species (Pinkster et al. 1992).

The impact of *G. pulex* as predator and/or competitor on native species is made more difficult to quantify, because in common with many other aquatic macroinvertebrate invaders, *G. pulex* is a generalist consumer (MacNeil et al. 1997). Brönmark (1994) emphasized the importance of cascading trophic interactions in a freshwater benthic food chain, where one or a few strong interactants termed 'keystone' species could have major direct and indirect impacts on numerous species throughout the food chain. For example, the introduction of opossum shrimps *Mysis relicta* as fish food in Flathead lake, Montana caused the collapse of kokanee salmon by consuming the salmon's zooplankton food, which in turn negatively impacted on predators of the salmon such as eagles and bears (Spencer et al. 1991). It is possible that *G. pulex* represents such a 'keystone' species in Northern Irish waters (MacNeil 1997).

Because the amphipod prey in this study differ in behavioural, foraging, and life-history strategies, the selectivity for specific prey in trout could potentially affect trophic interactions and community dynamics. Selective feeding preferences by fish on individual species within amphipod communities have not been reported (Jenio 1979, MacNeil 1997) and N. Ireland would be an ideal setting for such an investigation, where up to four amphipod species can co-occur in patches of rivers and lakes (Dick 1996a, MacNeil 1997).

Gammarus pulex has now been present in Irish waters for four decades and *C. pseudogracilis* nearly two, and both species continue to spread rapidly (Strange and Glass 1979). Our study represents the first attempt to assess how native predators have interacted with introduced prey species and how the morphology and behaviours of different prey species influence their respective probabilities of being incorporated into native fish diets. Such findings have implications for future studies investigating the impacts of introduced prey species on indigenous predators in freshwater communities.

Acknowledgements – This study was undertaken during a Dept of Education for Northern Ireland (D.E.N.I.) Research Studentship awarded to C. MacNeil. We are grateful to Gary O'Neill and all the staff at Movaganer fish farm, Allan Keys and Orton fish hatchery, Newel McCreight and the Fisheries Development Office and Tommy McGrath and the River Moyola angling club. Thanks also to Gillian Bell, Andy Bridge, John Prenter, John McCotter, Mark Briffa, Katie Wood and Simon Hookham. Thanks to Anders Nilsson and Thomas Bohn, whose comments greatly improved this manuscript. We reserve special thanks to Chris Nelson, whose excellent aquarium set-up made this work possible.

References

- Allan, J. D. 1978. Trout predation and the size composition of stream drift. – Limnol. Oceanogr. 23: 1231–1237.
- Allan, J. D. and Flecker, A. S. 1988. Prey preference in stoneflies: a comparative analysis of prey vulnerability. – Oecologia 76: 496–503.
- Allan, J. D. and Flecker, A. S. 1993. Biodiversity conservation in running waters. – Bioscience 43: 32–43.
- Anonymous. 1989. SuperANOVA. – Abacus Concepts, Berkeley.
- Bakker, T. C. M., Mazzi, D. and Zala, S. 1997. Parasite-induced changes in behaviour and color make *Gammarus pulex* more prone to fish predation. – Ecology 78: 1098–1104.
- Bechara, J. A., Moreau, G. and Hare, L. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. – J. Anim. Ecol. 62: 451–464.
- Brönmark, C. 1994. Effects of tench and perch on interactions in a freshwater, benthic food chain. – Ecology 75: 1818–1828.
- Brown, A. F. and Thompson, D. B. A. 1986. Parasite manipulation of host behaviour: acanthocephalans and shrimps in the laboratory. – J. Biol. Ed. 20: 121–127.
- Caine, E. A. 1989. Caprellid amphipod behaviour and predatory strikes by fish. – J. Exp. Mar. Biol. Ecol. 126: 173–180.
- Conlan, K. E. 1994. Amphipod crustaceans and environmental disturbance: a review. – J. Nat. Hist. 28: 519–554.
- Cooper, S. D., Smith, D. W. and Bence, J. R. 1985. Prey selection by freshwater predators with different foraging strategies. – Can. J. Fish. Aq. Sci. 42: 1720–1732.
- Crowder, L. B. and Cooper, W. E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. – Ecology 63: 1802–1813.
- Croy, M. I. and Hughes, R. N. 1991. Hierarchical response to prey stimuli and associated effects of hunger and foraging experience in the fifteen-spined stickleback, *Spinachia spinachia* (L.). – J. Fish Biol. 38: 599–607.
- Dahl, J. and Greenberg, L. 1996. Effects of habitat structure on habitat use by *Gammarus pulex* in artificial streams. – Freshwat. Biol. 36: 487–495.
- Dahl, J., Nilsson, P. A. and Pettersson, L. B. 1998. Against the flow: chemical detection of downstream predators in running waters. – Proc. R. Soc. Lond. B. 265: 1339–1344.
- Delbeek, J. C. and Williams, D. D. 1988. Feeding selectivity of four species of sympatric stickleback in brackish-water habitats in eastern Canada. – J. Fish Biol. 32: 41–62.
- Diamond, J. M. and Case, T. J. 1986. Overview: introductions, extinctions, extirpations and invasions. – In: Diamond, J. M. and Case, T. J. (eds), Community ecology. Harper and Row, pp. 65–79.
- Dick, J. T. A. 1992. The nature and implications of differential predation between *Gammarus pulex* and *G. duebeni celticus*. – J. Zool. Lond. 227: 171–183.
- Dick, J. T. A. 1995. The cannibalistic behaviour of two *Gammarus* species (Crustacea: Amphipoda). – J. Zool. Lond. 236: 697–706.

- Dick, J. T. A. 1996a. Post-invasion amphipod communities of Lough Neagh, N. Ireland: influences of habitat selection and mutual predation. – *J. Anim. Ecol.* 65: 756–767.
- Dick, J. T. A. 1996b. Animal introductions and their consequences for freshwater communities. – In: Giller, P. S. and Myers, A. A. (eds), *Disturbance and recovery in ecological systems*, Royal Irish Academy, Dublin, pp. 47–58.
- Dick, J. T. A., Elwood, R. W. and Irvine, D. E. 1990a. Displacement of the native Irish freshwater amphipod *Gammarus duebeni* by the introduced *Gammarus pulex*. – *Ir. Nat. J.* 23: 313–316.
- Dick, J. T. A., Irvine, D. E. and Elwood, R. W. 1990b. Differential predation by males on moulted females may explain the competitive displacement of *Gammarus duebeni* by *G. pulex* (Crustacea: Amphipoda). – *Behav. Ecol. Sociobiol.* 26: 41–45.
- Dick, J. T. A., Montgomery, I. and Elwood, R. W. 1993. Replacement of the indigenous amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and mutual predation. – *J. Anim. Ecol.* 62: 79–88.
- Dick, J. T. A., Elwood, R. W. and Montgomery, W. I. 1994. Range expansion of the alien freshwater amphipod *Gammarus pulex* (L.) in the River Lagan, Co. Down. – *Ir. Nat. J.* 24: 403–404.
- Dick, J. T. A., Falloon, S. and Elwood, R. W. 1998. Active brood care in an amphipod: influences of egg-development, temperature and oxygen. – *Anim. Behav.* 56: 663–672.
- Drake, C., Behr, P. J. and Valiela, I. 1995. Effect of algal cover on size-selective predation of *Gammarus mucronatus* by the striped killifish, *Fundulus majalis*. – *Biol. Bull.* 189: 243–244.
- Fitter, R. and Manuel, R. 1994. Collins photo guide to lakes, rivers, streams and ponds. – Harper Collins.
- Fitzsimons, A. G. and Andrew, T. E. 1993. The seasonal succession of the zooplankton of Lough Neagh, 1968–1978. – In: Wood, R. B. and Smith, R. V. (eds), *Lough Neagh. The ecology of a multipurpose water resource*. Kluwer, pp. 281–326.
- Fowler, J. and Cohen, L. 1990. Practical statistics for field biology. – Open Univ. Press, Milton Keynes.
- Gee, J. H. R. 1982. Resource utilization by *Gammarus pulex* (Amphipoda) in a Cotswold stream: a microdistribution study. – *J. Anim. Ecol.* 51: 817–832.
- Gill, A. B. and Hart, P. J. B. 1994. Feeding behaviour and prey choice of the threespine stickleback: the interacting effects of prey size, fish size and stomach fullness. – *Anim. Behav.* 47: 921–932.
- Gledhill, T., Sutcliffe, D. W. and Williams, W. D. 1993. British freshwater Malacostraca: a key with ecological notes. – *Freshwat. Biol. Ass. Sci. Publ.* 52: 1–172.
- Goss-Custard, J. D. 1970. Feeding dispersion in some overwintering wading birds. – In: Crook, J. D. (ed.), *Social behaviour in birds and mammals*. Academic Press, pp. 3–35.
- Greenberg, L. A. 1994. Effects of predation, trout density and discharge on habitat use by brown trout, *Salmo trutta*, in artificial streams. – *Freshwat. Biol.* 32: 1–11.
- Hynes, H. B. N. 1956. British freshwater shrimps. – *New Biol.* 21: 25–42.
- Holomuzki, J. R. and Hoyle, J. D. 1990. Effect of predatory fish presence on habitat use and diel movement of the stream amphipod *Gammarus minus*. – *Freshwat. Biol.* 24: 509–517.
- Jeffries, M. 1988. Individual vulnerability to predation: the effect of alternative prey types. – *Freshwat. Biol.* 19: 49–56.
- Jenio, F. 1979. Predation on freshwater gammarids (Crustacea: Amphipoda). – *Proc. West Virginia Acad. Sci.* 51: 67–73.
- Kaiser, M. J., Gibson, R. N. and Hughes, R. N. 1992. The effect of prey type on the predatory behaviour of the fifteen-spined stickleback *Spinachia spinachia* (L.). – *Anim. Behav.* 43: 147–156.
- Kelsch, S. W. and Shields, B. 1996. Care and handling of sampled organisms. – In: Murphy, B. R. and Willis, D. W. (eds), *Fisheries techniques*. Am. Fish. Soc., MD, pp. 121–145.
- Kennedy, G. J. A. and Vickers, K. U. 1993. The fish of Lough Neagh. Part B. Investigations on salmon (*Salmo salar* L.) and eels (*Anguilla anguilla* L.) in the River Lower Bann. – In: Wood, R. B. and Smith, R. V. (eds), *Lough Neagh. The ecology of a multipurpose water resource*. Kluwer, pp. 397–417.
- Kinzelbach, R. 1995. Neozoans in European waters-exemplifying the worldwide process of invasion and species mixing. – *Experimentia* 51: 526–538.
- MacNeil, C. 1997. The ecology of freshwater amphipods: a study of invasive and native species. – Ph.D. thesis, Queen's Univ. of Belfast.
- MacNeil, C., Dick, J. T. A. and Elwood, R. W. 1997. The trophic ecology of freshwater *Gammarus* (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. – *Biol. Rev.* 72: 349–364.
- Metcalfe, N. B., Huntingford, F. A. and Thorpe, J. E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. – *Anim. Behav.* 35: 901–911.
- Mitchell, F. 1986. The shell guide to reading the Irish landscape. – Country House, Ireland.
- Nelson, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. – *J. Exp. Mar. Biol. Ecol.* 38: 225–245.
- Osenberg, C. W. and Mittelbach, G. G. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. – *Ecol. Monogr.* 59: 405–432.
- Pastorok, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. – *Ecology* 62: 1311–1324.
- Pinkster, S. et al. 1992. Drastic changes in the amphipod fauna (Crustacea) of Dutch inland waters during the last 25 years. – *Bijdr. Dierk.* 61: 193–204.
- Pinkster, S., Smit, H. and Brandse-De Jong, N. 1977. The introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands and its competition with indigenous species. – *Crust. Suppl.* 4: 91–105.
- Power, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. – *Ecology* 73: 1675–1688.
- Sih, A. and Moore, R. D. 1990. Interacting effects of predator and prey behaviour in determining diets. – In: Hughes, R. N. (ed.), *Behavioural mechanisms of food selection*. NATO, ASI ser. Springer, pp. 771–796.
- Sih, A. and Wooster, D. E. 1994. Prey behaviour, prey dispersal, and predator impacts on stream prey. – *Ecology* 75: 1199–1207.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry. The principles and practice of statistics in biological research*. 3rd ed. – W.H. Freeman.
- Spencer, C. N., McClelland, B. R. and Stanford, J. A. 1991. Shrimp stocking, salmon collapse, and eagle displacement. – *Bioscience* 41: 14–21.
- Stein, R. A. and Magnuson, J. J. 1976. Behavioral response of crayfish to a fish predator. – *Ecology* 57: 751–761.
- Stoner, A. W. 1982. Species-specific predation on amphipod crustacea by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. – *Mar. Biol.* 55: 201–207.
- Strange, C. D. and Glass, G. B. 1979. The distribution of freshwater gammarids in Northern Ireland. – *Proc. R. Irish Acad. (B)* 79: 145–153.

- Tikkanen, P. et al. 1997. The roles of active predator choice and prey vulnerability in determining the diet of predatory stonefly (Plecoptera) nymphs. – J. Ecol. 66: 36–48.
- Ware, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density and prey size. – J. Fish. Res. B. Can. 29: 1193–1201.
- Williams, D. D. and Moore, K. A. 1982. The effect of environmental factors on the activity of *Gammarus pseudolimnaeus* (Amphipoda). – Hydrobiologia 96: 137–147.
- Williams, D. D. and Moore, K. A. 1985. The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: a laboratory analysis. – Oikos 44: 280–286.

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.