Predatory nature of the littoral amphipod *Echinogammarus marinus*: gut content analysis and effects of alternative food and substrate heterogeneity

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ABSTRACT: Interspecific interactions are major structuring forces in marine littoral communities; however, it is unclear which of these interactions are exhibited by many key-component species. Gut content analysis showed that the ubiquitous rocky/cobble shore amphipod *Echinogammarus marinus*, often ascribed as a mesograzer, consumes both algae and macroinvertebrates. Further, laboratory experiments showed that *E. marinus* is an active predator of such macroinvertebrates, killing and consuming the isopod *Jaera nordmanni* and the oligochaete *Tubificoides benedii*. Predatory impacts of *E. marinus* were not alleviated by the presence of alternative food in the form of alga discs. However, in the presence of prey, consumption of alga by *E. marinus* was significantly reduced. Further, survival of prey was significantly higher when substrate was provided, but predation remained significant and did not decline with further increases in substrate heterogeneity. We conclude that such amphipods can have pervasive predatory impacts on a range of species, with implications for community structure, diversity and functioning.

KEY WORDS: Littoral communities · Predation · Gut content · Amphipods · Heterogeneity · *Echinogammarus marinus*

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INTRODUCTION

Marine littoral communities are structured by a combination of physical factors and biotic interactions (Little & Kitching 1996). Classically, it is recognised that organisms on rocky/cobble shores such as algae, barnacles and mussels compete for space, with further structuring influences of predators such as crabs, dogwhelks and starfish (e.g. see Paine 1980, Bertness 1999). However, the roles of many other key component species in structuring such communities remain unclear, particularly where there is uncertainty regarding the types of interspecific and trophic interactions in which they engage. Amphipods are ubiquitous in the marine littoral zone and many species are clearly able to utilise plant material in their diet (e.g. Pavia et al. 1999, Duffy & Hay 2000, Karez et al. 2000,

Duffy & Harvilicz 2001). However, the emphasis on a 'mesograzer' lifestyle of widespread species such as *Gammarus locusta* and *Echinogammarus marinus* has led to neglect of the potential predatory impact of such gammarids in aquatic communities (Kelly et al. 2002a). Indeed, freshwater community ecology offers many lessons in this respect, with the presumed herbivorous/detritivorous 'functional' role of freshwater *Gammarus* species challenged by both field and laboratory studies (reviewed by MacNeil et al. 1997, see also Kelly et al. 2002a). In particular, freshwater *Gammarus* spp. are now viewed as predators of a range of macroinvertebrates (Kelly et al. 2002a,b), with major community structuring influences (Kelly et al. 2003). Recognition of the potential predatory role of marine littoral amphipods is important if the range of lethal, non-lethal, direct and indirect consequences of preda-

tion (e.g. see Lima 1998) is to be appreciated in such communities. It is thus now timely to explore predatory interactions among marine littoral amphipods and potential prey species.

A number of techniques can be employed to examine the predatory nature of a particular species. Gut content analyses can provide evidence of consumption of animal material, and can indicate a 'carnivorous' diet (e.g. see Yu et al. 2003). Whilst such analyses cannot discriminate between active predation and scavenging of cadavers, they can provide support for or against active predation. Clearly, if no animal material is ever found in the gut of a particular species, then predation can be discounted; however, presence of animal material in the gut can stimulate further research into potential predatory behaviour. Stable isotope ratios offer an alternative, with one study showing that a freshwater amphipod, *Dikerogammarus villosus*, is on the same trophic level as some predatory fish species (Marguillier 1998). However, this technique may suffer inaccuracies in elucidating trophic pathways (Hart & Lovvorn 2002) and is less useful in identifying which species of prey are actually consumed and how such predation may impact by structuring the wider community. Laboratory experiments offer close control of confounding variables and confidence in ascribing cause-and-effect relationships, but may be criticised on the grounds of lack of realism (see Huston 1999, Kelly et al. 2002a). However, micro- and mesocosm studies are increasingly recognised as being of high fidelity in extrapolation to field patterns and processes (e.g. Bergstrom & Englund 2002, Dick et al. 2002).

Herein, we examine the predatory nature of a ubiquitous marine littoral amphipod, *Echinogammarus marinus*. This species is found along NE Atlantic coasts from Norway and Iceland to the north coast of Portugal (Lincoln 1979). It inhabits the intertidal zone among stones, shingle and algae and is often highly abundant (Maranhao et al. 2001, Martins et al. 2002). First, we conducted gut content analysis of freshly caught individuals. Second, we used a laboratory microcosm experiment to elucidate the relative balance of predatory and herbivorous feeding behaviour by offering alternative foodstuffs. Third, we mimicked levels of physical heterogeneity encountered in the rocky littoral zone and examined predatory impacts that may reasonably be extrapolated to the field.

MATERIALS AND METHODS

General. All algae and animal collections took place by searching over and under cobbles on 'Walter's Shore' (54° 22.95′ N, 5° 33.3′ W) in front of the Marine Laboratory of Queen's University Belfast at Portaferry,

County Down, Northern Ireland, from September to March of 2002 to 2003 and 2003 to 2004; laboratory work was conducted within the facility. We found 3 abundant algae growing on the cobbles: *Ulva lactuca* (green), *Palmaria palmata* (red) and *Fucus vesiculosus* (brown). Of the variety of macroinvertebrates observed when turning over cobbles, *Echinogammarus marinus* was very abundant, together with 3 other species which were judged as potential prey of *E. marinus*, since they were smaller than and in close proximity to the amphipod. These were the isopod *Jaera nordmanni*, the tubificid oligochaete *Tubificoides benedii* and the collembolan insect *Anurida maritima*.

Gut content analyses. In order to quantify the diets of *Echinogammarus marinus* in the field, we examined gut content of freshly collected specimens and related these to the gut content of individuals fed known diets in the laboratory.

First, 40 *Echinogammarus marinus* (20 male + 20 female adults, 10 to 16 mm body length) were starved individually in plastic containers (5 cm diameter) with 8 cm depth seawater (8 to 12°C) and a continuous flow of filtered seawater, gauze near the bottom allowed faeces to sink out of reach of the amphipods and gauze over the top prevented escape. Each day, 4 individuals were killed in warm water and their guts dissected, until all specimens killed on 2 consecutive days had empty guts. From this, we determined that 7 d was the optimal period to ensure that individual *E. marinus* had fully evacuated their guts.

Second, 120 (60 male + 60 female) *Echinogammarus marinus* starved for 7 d were individually isolated (as above) and randomly allocated to 6 groups representing the 3 algae and 3 invertebrates (see preceeding subsection). Algae was presented as 1 cm^2 sections and (live) prey body lengths were 3 to 5 mm (*Jaera nordmanni*), 5 to 10 mm (*Tubificoides benedii*) and 3 to 4 mm (*Anurida maritima*). Once each *E. marinus* had partially or wholly consumed its allocated food item, it was killed in warm water and its gut immediately dissected and examined to provide 'signatures' for each food type.

Third, 116 *Echinogammarus marinus* (sizes as above) were collected in small batches of 10 to 20 individuals d^{-1} following tidal exposure, their guts were dissected, and individuals were sexed (presence/absence of penile papillae and brood pouches). Gut material was compared to reference 'signature' samples (see preceeding paragraph). Percentage contribution (volume) to the entire gut content was estimated for each food type (including 'unidentified'). Means (raw data arcsine-transformed; Sokal & Rohlf 1995) were compared with respect to food type by a 1-factor repeated-measures ANOVA, with Fisher's protected least significant difference (FPLSD) post-hoc tests (in Fig. 1 means of raw percentages are shown for clarity). Chi-square

analyses were conducted on the raw count data to test for sex differences in gut contents.

Microcosm experiments. For the laboratory experiments, we chose 2 representative potential prey species, the hard-bodied isopod *Jaera nordmanni* and the soft-bodied worm *Tubificoides benedii*, and the most abundant alga, *Fucus vesiculosus*, all of which appeared in *Echinogammarus marinus* guts. In the laboratory, for 24 h prior to experiments, individuals of each species were housed separately in pots (15 cm diam. × 10 cm height) supplied with substrate, alga (*F. vesiculosus*) and a continuous flow of filtered seawater at *in situ* temperatures (6 to 12°C) and a light:dark regime of 10:14 h.

For experiment 1, the pots were supplied with 2 mm depth of sand, 5 pebbles (2 × 1.5 cm) and a continuous flow of filtered seawater, the outflow being a 1 cm gauze-covered hole, maintaining pot water volume at 500 ml and preventing escape of animals over the top of the pot or through the outflow. A clear plastic vial of 1.5 cm diameter and 6 cm depth, perforated with 20 small holes, was placed within each pot, allowing 2 *Echinogammarus marinus* to be physically 'isolated' from or 'free' within the main body of the pot. This design allowed us to distinguish between predatory acts and scavenging following deaths due to unknown causes (see also Dick & Platvoet 2000, Kelly et al. 2002a). Discs of alga (*Fucus vesiculosus* fronds) and plastic of 2 cm diameter were cut with a cork borer. The latter controlled for substrate heterogeneity in experimental groups lacking alga discs. There were 9 experimental treatments (n = 10 each), arranged into 5 groups for analyses. Group 1: 2 isolated *E. marinus* + 6 *Jaera nordmanni* or *Tubificoides benedii* + 2 alga discs + 2 plastic discs; Group 2: 2 free *E. marinus* + 6 *J. nordmanni* or *T. benedii* + 2 alga discs + 2 plastic discs; Group 3: 2 free *E. marinus* + 6 *J. nordmanni* or *T. benedii* + 4 plastic discs; Group 4: 2 free *E. marinus* + 4 alga discs; Group 5: 4 alga discs + 6 isolated *J. nordmanni* or *T. benedii*. Replicates were checked after 96 h and live individuals counted; the remaining alga disc area was assessed by placement under a transparent 1 mm square grid.

Group 1 was used to assess first, any effect of experimental conditions on survival of the 3 species and second, survival of the 2 prey species when *Echinogammarus marinus* were unable to interact with them, such that any reduced survival of prey in Groups 2 and 3 (i.e. predator free to interact) could be attributed to predation by *E. marinus*. Comparisons of Groups 2 and 3 assessed predation on each species by *E. marinus* in the presence and absence of alga (the plastic discs controlling for any effects of habitat heterogeneity). Comparison of Groups 2 and 4 assessed *E. marinus'* consumption of alga in the presence and absence of potential prey. Group 1 also allowed assessment of any

alga consumption by prey species, while Group 5 assessed any natural alga decay in the presence of, but isolated from, the prey species.

Percentage prey survival (arcsine-transformed; see Sokal & Rohlf 1995) was examined by a 2-factor ANOVA with respect to 'group' (1, 2 and 3) and 'prey species'. The percentage remaining alga area (arcsine-transformed) was examined in a 2-factor ANOVA with respect to 'group' (1, 2, 4 and 5) and 'prey species' (in Figs. 2 & 3 means of raw percentages are shown for clarity).

For experiment 2, *Echinogammarus marinus* were either isolated or free in pots, with 1 of the 2 prey species separately, and supplied with 4 levels of substrate heterogeneity (graded stones), giving 16 experimental groups (n = 8 each). Heterogeneity was classified as zero (with no stones), low (60 stones of 10 mm), medium (60 stones of 10mm + 60 stones of 14 mm) and high (60 stones of 10 mm + 60 stones of 14 mm + 10 stones of 20 mm). Thus, substrate surface area, complexity and heterogeneity increased from zero to high. Prey individuals were allowed to disperse within pots overnight before addition of *E. marinus*, then each replicate was examined and survivors counted after 96 h.

Percentage prey survival (arcsine-transformed) was examined in a 3-factor ANOVA with respect to predator status (isolated & free), heterogeneity (zero, low, medium and high), and prey species (*Jaera nordmanni* and *Tubificoides benedii*: in Fig. 4 means of raw percentages are shown for clarity).

RESULTS

Gut content analyses

The 3 algae formed straightforward signatures in *Echinogammarus marinus* guts by retaining their distinct colouration. The 3 invertebrate signatures were dark grey, mottled and irregular pieces of exoskeleton for the isopod *Jaera nordmanni*, pale red pieces of integument with some gelatinous material for the oligochaete *Tubificoides benedii* and black/blue pieces of exoskeleton for the collembolan *Anurida maritima*.

Of 116 *Echinogammarus marinus* collected and immediately dissected, 71 were male and 45 female. Both sexes clearly consumed algae and animal material (Table 1), with the majority consuming both, but also significant numbers consuming either algae only or animal material only. Females consumed 'animals only' significantly more frequently than males, as a result of consuming *Palmaria palmata* significantly less frequently and having '*Jaera nordmanni* only' significantly more frequently in their guts (Table 1). All 3 algae were consumed, with *Ulva lactuca* being highest

Table 1. *Echinogammarus marinus*. Percentage consuming algae and animal (macroinvertebrates) material (ns: not significant; na: not applicable)

|	Both sexes (n = 116)	Males (n = 71)	Females (n = 45)	χ^2 M vs. F
Algae only	30.2	35.2	22.2	ns
Animals only	20.7	14.1	31.1	<0.05
Algae + animals	49.1	50.7	46.7	ns
Prevalence in guts				
Algae				
Ulva lactuca	44.8	42.3	48.9	ns
Palmaria palmata	37.1	50.7	15.6	<0.01
Fucus vesiculosus	25	26.8	22.2	ns
Animals				
Jaera nordmanni	56	56.3	55.6	ns
Tubificoides benedii	25	25.4	24.4	ns
Anurida maritima	19.8	14.1	28.9	ns
Unknown items	6.9	7	6.7	na
Algae: 1 species as sole item				
U. lactuca only	6	5.6	6.7	na
P. palmata only	1.7	2.8	0	na
F. vesiculosus only	2.6	2.8	2.2	na
Animal: 1 species as sole item				
J. nordmanni only	9.5	4.2	17.8	<0.05
T. benedii only	0	0	0	na
A. maritima only	0	0	0	na
Unknown only	0	0	0	na
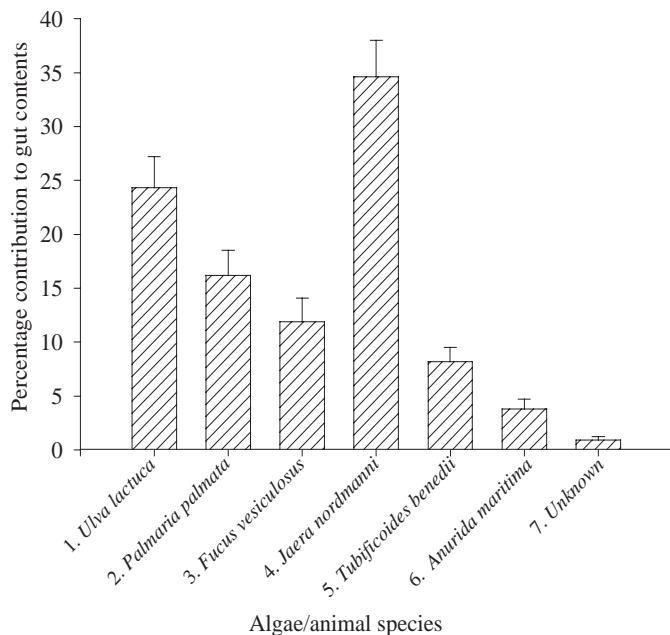
Fig. 1. *Echinogammarus marinus*. Mean (+SE) percentage contribution of 3 algae and 3 macroinvertebrate species to amphipod gut contents. All means are significantly different from each other (Fisher's PLSD test) except for Species 5 vs. 6, 3 vs. 5, 6 vs. 7 and 2 vs. 3

in prevalence. All 3 invertebrates were consumed, with over 50% of individuals consuming *J. nordmanni*. Indeed, nearly 10% of *E. marinus* had only this isopod in their guts, a much higher value than for the other invertebrates or algae (Table 1).

Mean percentage contribution to the gut content varied significantly among the 6 food types ($F_{6,690} = 25.8$, p < 0.0001; Fig. 1), with *Jaera nordmanni* and *Ulva lactuca* contributing significantly more than the other types (Fig. 1), reflecting the higher gut prevalence of these food items (Table 1).

Expt 1

There was no mortality of *Echinogammarus marinus* during the experiment. There was a significant difference in prey survival among Groups 1 to 3 ($F_{2,54} = 176.5$, p < 0.0001; Fig. 2). Fisher's PLSD tests showed that prey survival was significantly lower when *E. marinus* were free than when isolated, in both the presence and absence of alga (all p < 0.0001; Fig. 2). There were no significant differences in prey survival when alga was present or absent (see Fig. 2). There was significantly lower survival of *Tubificoides benedii* than of *Jaera nordmanni* ($F_{1,54} = 8.3$, p < 0.005), but no significant group × prey interaction ($F_{2,54} = 2.4$).

Alga discs showed minimal natural decay and impact of prey species (Fig. 3). There was a significant difference in remaining alga disc area among Groups 1, 2, 4 and 5 ($F_{3,72} = 666.3$, p < 0.0001; Fig. 3). Fisher's PLSD tests showed that remaining alga area was significantly lower when *Echinogammarus marinus* were free than when isolated, in both the presence and absence of prey (all p < 0.0001; Fig. 3). However, remaining alga area was significantly higher when prey (both species) were present than when absent (both p < 0.0001; Fig. 3). There was no significant difference in remaining alga area between the 2 prey species ($F_{1,72} = 0.01$, ns) and no significant group × prey interaction ($F_{3,72} = 0.5$, ns).

Casual observations revealed that *Echinogammarus marinus* were consuming live prey, with pots often littered with the body parts of the 2 prey species. Alga discs were also actively consumed.

Expt 2

Again, there were no deaths of *Echinogammarus marinus* during this experiment. Significantly fewer prey survived when *E. marinus* were free than when isolated ($F_{1,112} = 282.3$, p < 0.0001;
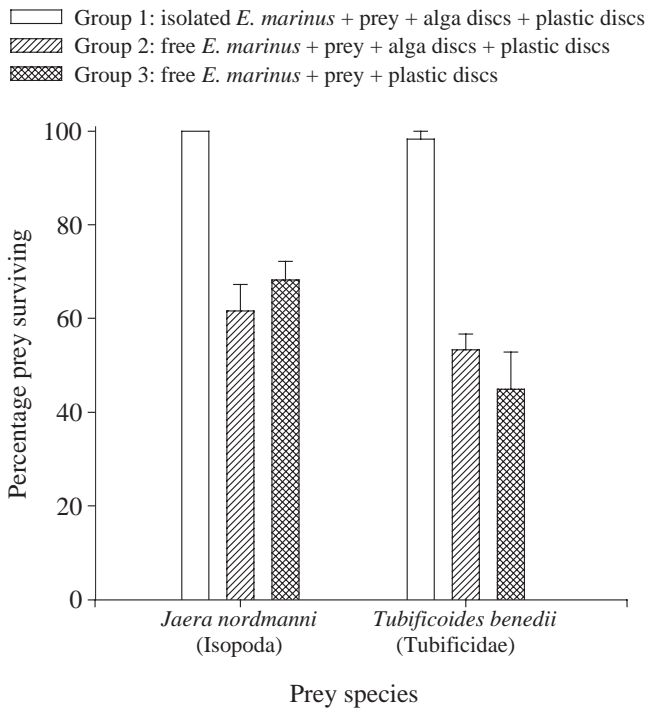
Fig. 2. *Jaera nordmanni* and *Tubificoides benedii*. Mean (+SE) percentage survival of the 2 prey species when *Echinogammarus marinus* were 'isolated' and 'free' and in presence and absence of seaweed (*Fucus vesiculosus*) discs
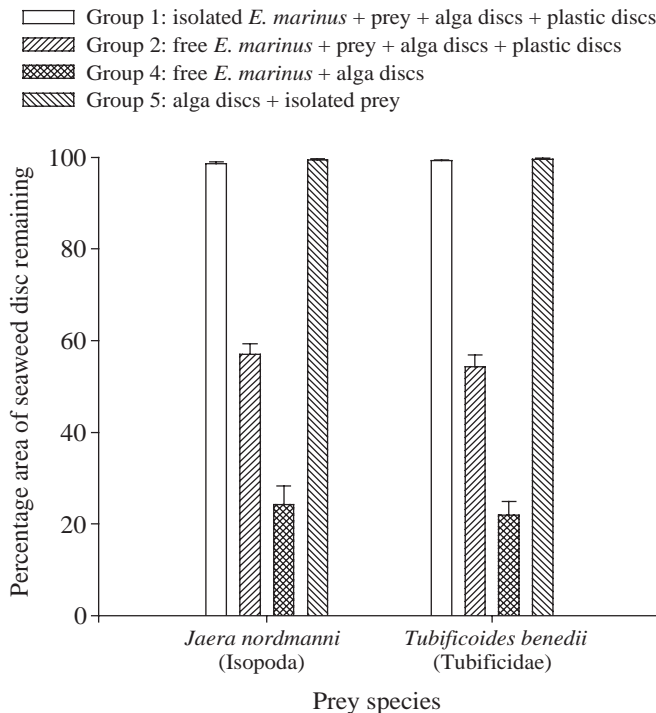

Fig. 3. *Fucus vesiculosus*. Mean (+SE) percentage remaining seaweed area when *Echinogammarus marinus* were isolated and free and in presence and absence of prey

Fig. 4). There was a significant difference in prey survival among the 4 levels of substrate heterogeneity ($F_{3,112} = 8.2$, p < 0.0001; Fig. 4). Fisher's PLSD tests showed that prey survival was significantly lower for zero than for low, medium and high heterogeneity (all p < 0.001), but there were no significant differences among the latter 3 conditions (Fig. 4). There was no significant difference in survival of the 2 prey species ($F_{1,112} = 0.53$, ns; Fig. 4). There was a significant amphipod status × heterogeneity interaction effect ($F_{3,112} = 4.6$, p < 0.005), driven by the very low survival of prey in the free predator condition in the 'zero' as compared to low, medium and high heterogeneity (Fig. 4). Acts of predation and the littering of pots with prey body parts was again observed.

DISCUSSION

Our gut content analysis of freshly caught *Echinogammarus marinus* clearly indicate that a range of algae and macroinvertebrate species is consumed. The presence in the guts of animal remains could be attributed to scavenging of cadavers or coincidental ingestion of body parts whilst, for example, feeding on detritus. However, the very high prevalence of macroinvertebrates in *E. marinus* guts, including the finding that nearly 10% of individuals had consumed nothing but the isopod *Jaera nordmanni*, rather suggests more active predatory behaviour. That females appeared to consume more animal material at the expense of algae (Table 1) is interesting, if difficult to explain. Being significantly smaller than males, females may often utilise different microhabitats, or forage for high protein foodstuffs in order to invest in egg production. This sex difference in the balance of animal:plant consumption clearly merits further study.

Further, in both experiments, the significantly lower survival of the isopod *Jaera nordmanni* and the oligochaete *Tubificoides benedii* when the *Echinogammarus marinus* was free to interact with them (as compared to isolated) indicates that the amphipod is capable of predation. This is supported by observations of *E. marinus* killing and consuming prey, and the littering of experimental containers with prey body parts. Further, however, the degree of predatory impact of *E. marinus* was not alleviated by the presence of alternative food, indicating that predation is a normal component of the behaviour of *E. marinus* and not induced simply through lack of other feeding opportunities. Neither was predation a forced switch in feeding behaviour, as algae remained in the experimental containers in excess throughout the experiment. It is notable also, however, that while *E. marinus* consumed algae, this feeding mode was

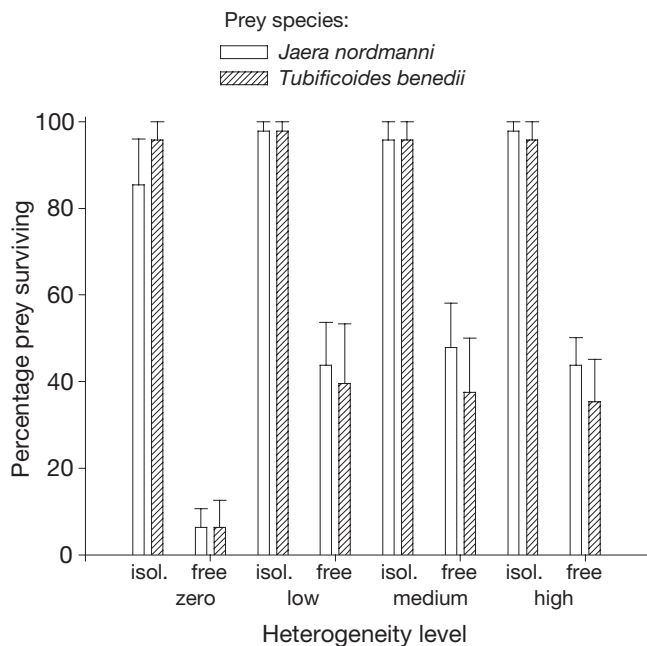Prey species:

☐ *Jaera nordmanni*
▨ *Tubificoides benedii*

Fig. 4. *Jaera nordmanni* and *Tubificoides benedii*. Mean (+SE) percentage survival of the 2 prey species when *Echinogammarus marinus* were isolated and free at increasing levels of substrate heterogeneity

significantly reduced when alternative food, i.e. the prey, were present, similar to the food-choice of some decapods in the presence of live animal and plant-based diets (Buck et al. 2003). This indicates that prey may be selected as higher-quality food over plant material, and that *E. marinus* is indeed truly omnivorous, utilising a wide variety of foodstuffs to maximise fitness (see also Vassallo & Steele 1980, Delong et al. 1993, Cruz-Rivera & Hay 2000). Previous studies demonstrating positive effects of food selection and diet mixing on the fitness of marine amphipods (Cruz-Rivera & Hay 2000, 2003), focused on artificially assembled foods or a suite of macroalgal species without consideration of live animal prey. Our results with live prey have implications for the impact of amphipods as mesograzers (e.g. see also Viejo & Åberg 2003), as rates of grazing and damage to algae may fluctuate depending on the availability of prey. On the other hand, our results also indicate that the predatory impacts of such amphipods will not be reduced by an over-abundance of plant material. Further, an appreciation of the true trophic roles of individual species in marine communities is clearly required if we are to resolve inconsistencies and deviations in the results of studies linking biodiversity and ecosystem functioning. For example, Duffy et al. (2003) postulated that interference competition and/or intraguild predation among grazers may be operating and that this would explain why ecosystem responses

at high grazer diversity differ from those predicted from the sum of impacts of individual species.

Interspecific interactions such as competition and predation may be mediated by the physical structuring of the environment (e.g. Petren & Case 1998, Bartholomew et al. 2000, Lewis & Eby 2002). If amphipods such as *Echinogammarus marinus* display predatory behaviour only as a laboratory artefact due to lack of substrate heterogeneity, then we should expect to see predation decline as levels of heterogeneity increase. Indeed, we might expect to see any anomalous predatory behaviour disappear where potential prey have an abundance of refuges, since we would expect only true predators to exhibit behaviour such as searching for and actively capturing prey. In experiment 2, we increased the surface area, complexity and heterogeneity of the environment within which the amphipods and potential prey could interact. We found significantly reduced predation when heterogeneity was increased from zero to low, but predation remained significant and did not decline over low, medium and high levels of heterogeneity. This indicates that *E. marinus* actively search for and will capture and consume prey even when faced with highly complex substrates. Although the effects of diet mixing in marine amphipods may be species-specific, our findings support the supposition that highly mobile amphipod species should have a more diverse food base as they have better searching ability than sedentary species (Cruz-Rivera & Hay 2000). The maintenance of predatory impact over a range of habitat heterogeneity is further strong evidence that *E. marinus* acts as a predator in marine littoral communities. Indeed, our results mirror those of Ray-Culp et al. (1999), who showed that a known predatory xanthid crab was effective in its predatory behaviour regardless of experimentally manipulated habitat structure.

Amphipods such as *Echinogammarus marinus* are ubiquitous in marine littoral communities; this particular species is distributed throughout the NE Atlantic from Iceland to Portugal, and can reach extremely high densities (Lincoln 1979, Maranhao et al. 2001). Whilst it is clear that marine amphipods forage on plant material, their ability to actively prey upon other community members has thus far been neglected. Studies of animal remains in the guts of marine amphipods are unable to ascribe predation as causal (Nyssen et al. 2002, Yu et al. 2002). Our study strongly supports the proposition that members of this group may be capable of active predation, and indicates that *E. marinus* in particular preys on a range of marine macroinvertebrates from hard-bodied and mobile isopods to soft-bodied oligochaetes. It follows that many other invertebrate species may be subject to amphipod predation, with even vertebrates at risk where vulnerable life

stages such as eggs and larvae are encountered (see also Brown & Diamond 1984, Deblois & Leggett 1991, 1993). As mesograzers, amphipods may structure macroalgae communities (Duffy & Hay 2000, Haggitt & Babcock 2003); however, their potential role of predators has not been addressed. Such predation clearly has implications for individuals, populations and communities, particularly when we appreciate that predators exert lethal, non-lethal, direct and indirect effects (Kelly et al. 2002b). For example, the traditional view of freshwater *Gammarus* species as herbivorous shredders has been replaced by an appreciation of widespread impacts at many trophic levels. These include the predatory elimination of other species, reduction in numbers and biomass, and radical shifts in community structure dependent on which *Gammarus* species is present (Kelly et al. 2003, Kelly & Dick 2005). Further, aquatic habitats are increasingly subject to species invasions and replacements, with both marine and freshwater amphipods a prominent group in many such invasions (Conlan 1994, Ricciardi & Rasmussen 1998, Ruiz et al. 2000, Dick et al. 2002). Thus, now that the potential predatory nature of amphipods such as *E. marinus* is recognised, it is time to investigate the pervasive influence of these species in the marine littoral and elsewhere. This is important for both understanding community structure and function and in protecting marine biodiversity from environmental and biotic change.

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