



## ORIGINAL ARTICLE

**Selection of habitat by a marine amphipod**

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**Abstract**

Marine algae are known to provide habitats for a wide range of marine organisms. Populations of marine epiphytal invertebrates are generalists and are less adapted to live in only one macroalga species. However, there are some examples of local adaptation and, in particular, amphipods have shown strong host specificity. *Amphitholina cuniculus*, an amphipod with an alga-burrowing habit, has been mainly observed in *Bifurcaria bifurcata* mats on the intertidal rocky shores of the southern region of the Galician coast (NW Spain; 42°11.27' N, 8°48.25' W). We designed a laboratory experiment conducted in June 2009 to analyse the association between the amphipod and the macroalga. In particular, we hypothesised that (i) this species would exhibit different behaviour during the day and at night, and (ii) adults of *A. cuniculus* would prefer *B. bifurcata* as habitat rather than *Fucus vesiculosus* or *Sargassum muticum*. Results supported the hypothesis that adults of *A. cuniculus* preferred *B. bifurcata*, although such preferences did not show the day/night variability predicted. This amphipod might be considered a specialist species, at least on rocky intertidal shores along the Galician coast.

**Introduction**

The association of small invertebrates with larger sessile organisms such as plants or macroalgae that provide habitat and/or food has been a major topic in ecological and evolutionary studies, in both terrestrial and marine systems. However, patterns of habitat use in terrestrial and marine systems differ. For example, most species of terrestrial herbivorous insects show habitat specialisation (Fox & Morrow 1981), whereas most marine invertebrates are associated with multiple macroalgal families as habitats (Hay & Fenical 1988). Some marine invertebrates, however, are specialised and it has been argued that an understanding of these rare cases may provide insight into the ecology and evolution of feeding and habitat specialisation in general (Poore *et al.* 2000; Sotka 2007).

For small mobile epifauna, seaweeds are a refuge from stressful conditions associated with life on rocky intertidal shores. For example, seaweeds can provide cool and protective canopies and interstices and ameliorate the

influence of rapid changes in temperature, desiccation and hydrodynamic forces on intertidal shores (Bates 2009). In addition, seaweeds may also offer shelter from predation and food for some species of invertebrates (Cronin *et al.* 1995; Bates 2009).

Patterns of distribution of mobile epifauna are frequently explained by the behaviour of the species under consideration, or of those with which they interact (Chapman 2000). Preference for different habitats, for example, may occur during site selection and settlement of larvae (Highsmith 1982), during exploratory behaviour of post-larvae and juveniles (Pardo *et al.* 2007), and during the period of adult life (Aikins & Kikuchi 2001). Changes in behaviour may also occur during a daily cycle due to changes in patterns of activity of epifauna. For example, small soft-bodied herbivores tend to move at night when predators are less active (Hay *et al.* 1987; Bell 1991; Brawley 1992). In contrast, large herbivores such as fishes, urchins and some gastropods exhibit high mobility with relatively little probability of being successfully attacked by their predators (Hay *et al.* 1987). In

particular, some amphipods are more active at night than during the day. For example, the filter-feeding amphipod *Erichthonius brasiliensis* lives in domiciles it constructs by curling terminal segments of its host seaweed *Halimeda tuna*, but exclusively at night (Sotka *et al.* 1999). Criteria for epifauna host choice include intrinsic factors of the host such as cell wall components, defensive biochemistry, nutritive value and palatability, toughness and architectural complexity of seaweeds (Hawkins & Hartnoll 1983; Chémello & Milazzo 2002; Van Alstyne & Houser 2003). In addition, habitat selection may be determined by abundance, size and patchiness of habitat (Kumagai 2008).

When animals are associated with a particular habitat, it is often assumed that they have actively 'selected' that habitat. A common problem is the probable or actual misuse of the term 'preference'. It is always necessary to test (and be able to provide evidence to support) the model that behaviour of the animals can indeed account for the observed patterns (see Olabarria *et al.* 2002 and references therein). To avoid confounding preference (an active behaviour) with other causes of greater numbers being found in some habitats, it is also necessary to determine the pattern of occupancy of each type of habitat when available alone (i.e. when there is no choice and therefore no preference). If organisms choose a certain habitat (i.e. show a preference) they should select more of that habitat when presented with a mixture than would be the case when each of the various choices is presented alone. Therefore, experiments to demonstrate preferences are quite complex.

On intertidal shores, amphipods are often among the most dominant macroepifauna on macroalgae and seagrasses (Hay *et al.* 1987; Bell 1991; Aikins & Kikuchi 2001; Bates 2009). Despite generalist habits of most species of this group, some organisms have shown a strong host specificity (Duffy & Hay 1991; Poore *et al.* 2000), and they have been suggested to play a similar role to insects in terrestrial habitats because they are locally abundant, small relative to the host that they use for both habitat and food, and can have large impacts on host assemblage structure (Duffy & Hay 2000). An interesting group of amphipods that has been used as a model in evolutionary approaches and in several studies on ecology and behaviour is the family Ampithoidae (Arrontes 1999; Poore & Steinberg 1999; Cruz-Rivera & Hay 2001; Sotka 2003; Poore & Hill 2006). Previous studies have revealed that ampithoid amphipods differ in host specificity and composition (Poore *et al.* 2008), suggesting that evolutionary history may affect the ability of this family to colonise diverse algal taxa. As an example, the genus *Peramphithoe* rarely uses available macrophytes in the order Dictyotales, and as a consequence, displays a more restricted host range than other genera. However, other species from the

family are very often associated with the host genus *Sargassum* (Poore *et al.* 2008).

*Amphitholina cuniculus* (Stebbing 1874) is a small species that belongs to the family Ampithoidae and exhibits an alga-burrowing habit (Myers 1974). This species has been found burrowing into the thalli of different macroalgae such as *Alaria esculenta* (Linnaeus) Greville, *Fucus vesiculosus* Linnaeus or *Bifurcaria bifurcata* R. Ross (Myers 1974; Viejo 1999; Gestoso *et al.* 2010). A previous study done on the Galician coast showed that this species was especially abundant in *B. bifurcata*, although it also appeared sporadically associated with *Sargassum muticum* Yendo (Fensholt) (Gestoso *et al.* 2010) and with *F. vesiculosus* (I. Gestoso, personal observation). Due to this differential pattern of distribution, the study suggested that *A. cuniculus* could exhibit a preference for certain habitats.

Based upon these observations we designed a laboratory experiment in which we analysed the association of *A. cuniculus* with the most abundant algae that form mixed stands on low intertidal rocky shores along the Galician coast (Northwest Spain). An important aspect of the experimental design used here was the unconfounding of preference (active behavioural choice) from any other reasons for different occupancies of different types of habitat (e.g. differences in accessibility). Many studies on selection of habitats by different invertebrates have not used an experimental design like that used here, i.e. also determining the pattern of occupancy of each habitat when there is no choice (Durante & Chia 1991; McDonald & Bingham 2010). Here, we tested the hypotheses that (i) this species would exhibit different behaviour during the daily cycle (day *versus* night), and (ii) adults of *A. cuniculus* would prefer *B. bifurcata* as habitat rather than *F. vesiculosus* or *S. muticum*.

## Material and Methods

### Collection of amphipods and macroalgae

Amphipods and macroalgae (i.e. *Bifurcaria bifurcata*, *Fucus vesiculosus* and *Sargassum muticum*) were collected on a semi-exposed intertidal rocky shore in the southern region of the Galician coast (42°11.27' N, 8°48.25' W) during the low tide in June 2009. Macroalgae were carefully removed from the substratum and taken to the laboratory in insulated containers filled with seawater.

More individuals of *B. bifurcata* were collected because amphipods were more abundant in this species. Apical parts of *B. bifurcata* were examined carefully under a light microscope to pick up amphipods. After being removed from the algae, amphipods were kept in small containers filled with seawater until the experiment started (within 2 h). All amphipods used in the experiments were

adults with ~ 4 mm total length (Myers 1974; Lincoln 1979). Individuals of *B. bifurcata* that were used to collect amphipods were discarded and were not used as habitats in the laboratory experiments.

Because amphipods used in the experiments were collected from *B. bifurcata*, there might be a predisposition to be attracted to their original host. Prior to the experiment we conducted a pilot experiment to test whether amphipods collected from *B. bifurcata* were able to burrow indiscriminately in the three selected macroalgae. For that, we put ~ 50 g of each species of algae in two replicated 3-l circular plastic containers filled with seawater. Then we added four amphipods (collected in *B. bifurcata*) in each replicate and, after 12 h, we counted the individuals of *Amphitholina cuniculus* that were able to burrow into each alga. We also filmed the burrowing behaviour in the three species of algae. Results indicated that amphipods burrowed indiscriminately in the three algae ( $F_{2,3} = 0.50$ ,  $P = 0.645$ ). In addition, recorded films showed that amphipods were able to burrow in all algae within 2 h, although they were faster when burrowing in *B. bifurcata* or *F. vesiculosus* than in *S. muticum*.

#### Set-up of habitats

Macroalgae were kept in transparent 3-l circular plastic containers that were divided into three equal sections (using a plastic template) (Fig. 1), each containing an experimental habitat: B was *Bifurcaria bifurcata*, F was *Fucus vesiculosus* and S was *Sargassum muticum*. Pieces of approximately 10 g wet weight of alga were used as habitats. Containers were filled with filtered seawater and randomly placed on a table. Each experiment was run for 4 h because previous observations indicated that an amphipod could burrow into a thallus in 2 h, and it therefore was not unreasonable to think that they would demonstrate any choice of a habitat within 4 h.

#### Experimental design

Six individuals of *Amphitholina cuniculus* were placed into one experimental habitat (i.e. one of the three pieces of alga) using a paintbrush. Prior to the experiment, amphipods from 10 individuals of *Bifurcaria bifurcata* were counted and biomass of each alga was determined. Then, the maximum number of individuals per 1 g wet weight of alga was calculated to use similar densities to those found in the field ( $2.04 \pm 0.94$  per 1 g wet weight of alga).

The experimental design consisted of six different treatments, three of multiple choice and three others of no choice (see treatments in Fig. 2;  $n = 6$  replicates of each treatment). The experiment compared the proportion of individuals of *A. cuniculus* in each of the habitats when

presented together (treatments 1–3) or alone (treatments 4–6). At the end of the experiment in each treatment, we calculated the proportion of all amphipods found in each habitat, included the one in which they were initially placed (shown with a circle for each treatment in Fig. 2). Dead or swimming individuals were discarded from analyses. The experiment was run during the day and at night to test the first hypothesis that *A. cuniculus* exhibits different behaviour in a daily cycle. Each experiment was repeated twice (15 June 2009 and 23 June 2009) to check the consistency of results.

Preference for *B. bifurcata* would be reflected by a greater proportion of the amphipods in this habitat at the end of the experiment, compared with what is expected by chance if no preference is expressed. The chance of occurrence in habitats at the end of the experiment is estimated from the treatments where there is no choice (4–6; see Fig. 2). Preference for *B. bifurcata* involves acceptance of the following hypothesis:

$$\text{Hypothesis 1: } nB/N_1, nB'/N_4 > nS/N_2, nF/N_3$$

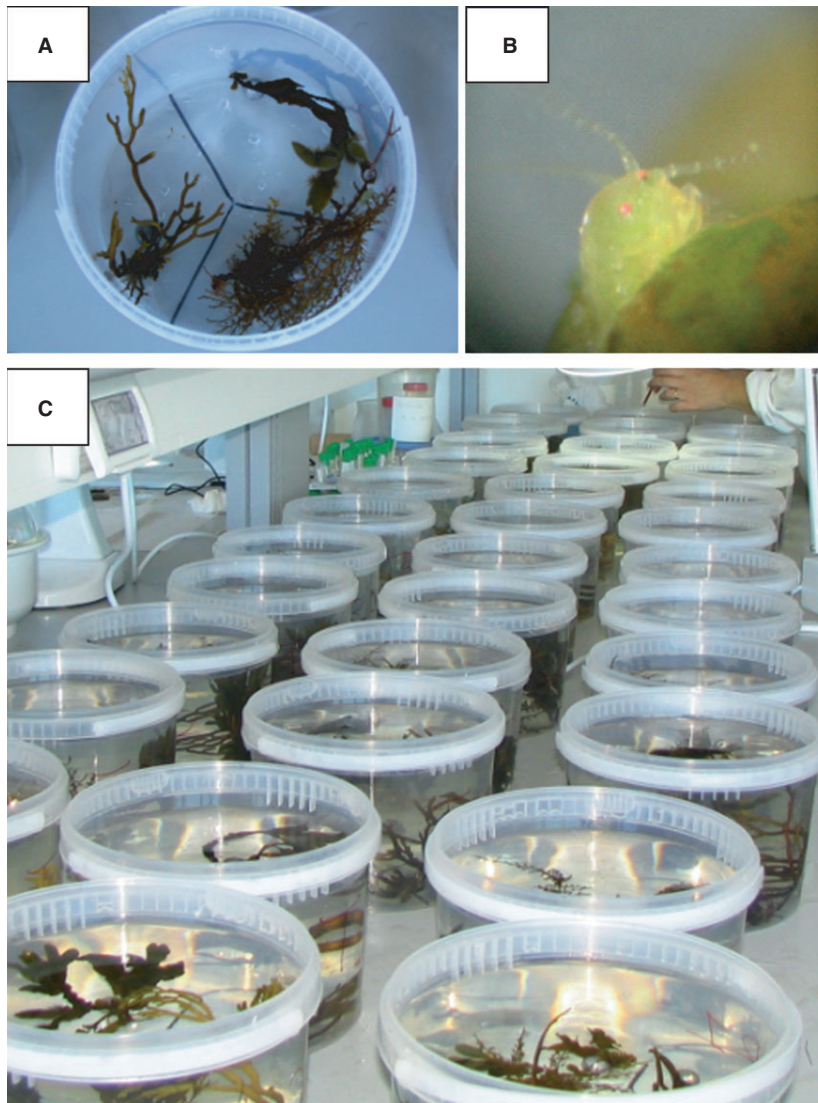
Where, at the end of the experiment,  $nB$ ,  $nB'$ ,  $nS$  or  $nF$  is the number of individuals in the macroalgae where they were initially placed (*B. bifurcata*, *Sargassum muticum* or *Fucus vesiculosus*);  $N$  is the total number of individuals recovered from that container at the end of the experiment,  $i = 1 \dots 6$ , indicates the treatment.

The proportion of individuals in *B. bifurcata* (if amphipods really prefer this habitat) should be greater than in the other macroalgae. Thus, in treatments 1 and 4 this proportion will be significantly greater than in treatments 2 and 3 (non-preferred habitats) because in these two cases the amphipods should move to the preferred habitat and, therefore, out of *S. muticum* and *F. vesiculosus*, where they were placed initially (Fig. 2). There are different possibilities for differences among treatments 1–4. For instance, amphipods in treatment 4 may move to random positions because they have other individuals of *B. bifurcata* apart from the initial one where they were placed, resulting in  $nB/N_1 > nB'/N_4$ . Alternatively, they may not move out of their starting habitat because they would be already in their preferred habitat, resulting in  $nB/N_1$  and  $nB'/N_4$  being similar. In both cases, preference requires a smaller proportion of amphipods in S and F of treatments 2 and 3 than in B and B' of treatments 1 and 4, respectively.

$$\text{Hypothesis 2: } nS'/N_5 > nS/N_2$$

$$\text{Hypothesis 3: } nF'/N_6 > nF/N_3$$

because amphipods are more likely to move from S in treatment 2 and F in treatment 3 into the preferred macroalga (B), than into non-preferred habitats ( $S''$  and  $S'''$ ) in treatment 5 and ( $F''$  and  $F'''$ ) in treatment 6.



**Fig. 1.** Montage showing (A) the arrangement of macroalgae in containers, (B) one specimen of *Amphitholina cuniculus* (10 ×) and (C) the random set-up of containers on a table.

Treatments 5 and 6 do not have *B. bifurcata*, so amphipods should not move from initial macroalga, whereas in treatments 2 and 3, individuals have a choice and would move into the preferred *B. bifurcata*.

#### Analyses of data

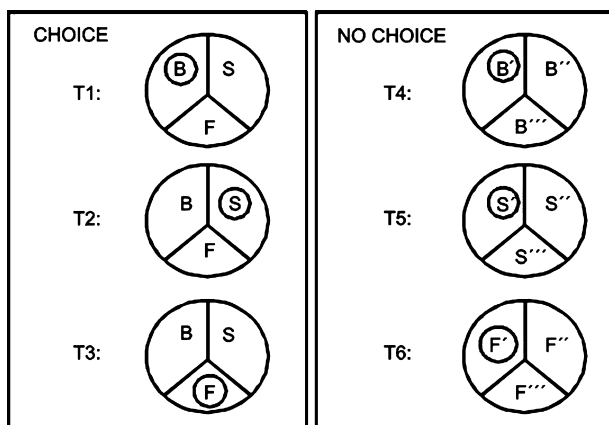
To test the hypothesis that *Amphitholina cuniculus* exhibit different behaviour during a daily cycle, data were analysed using three orthogonal analyses of variance (ANOVA). Treatment (six levels, fixed), Time of day (two levels: day versus night, fixed), and Trial (two levels, random) were orthogonal factors. The hypotheses of preference were tested by analyses of variance which, when designs are balanced (as in this case), are robust to violations of assumptions of normality and homoscedasticity (Olabarria *et al.* 2002).

#### Results

A total of 864 individuals of *Amphitholina cuniculus* were placed into different habitats at the beginning of the experiments but only 763 individuals (88%) were recovered in any of the three habitats at the end of experiments (i.e. after 4 h).

The hypothesis that *A. cuniculus* exhibit different preference behaviour during the day than at night was not supported. Although proportions of amphipods varied significantly among treatments, this variation was consistent during the daily cycle (i.e. no significant main effect of Time of day, or significant interaction of Time of day with any other factor; Table 1). In addition, response was consistent in the two trials (i.e. no significant main effect of Trial, or interaction of Trial with any other factor; Table 1).

As Trial and Time of day did not have any effect on the proportions of amphipods found in each habitat, replicates



**Fig. 2.** Experimental design with six treatments ( $n = 6$ ). B is *Bifurcaria bifurcata* habitat, S is *Sargassum muticum* habitat and F is *Fucus vesiculosus* habitat. The circle indicates the place where the individuals of *Amphitholina cuniculus* were placed at the beginning of the experiment.

**Table 1.** ANOVA analysis of proportions of *Amphitholina cuniculus* in experimental treatments. Time of day (day versus night) and treatment (six levels) were fixed factors, and Trial (two levels) was a random factor ( $n = 6$ ).

Source	df	MS	F	P
Trial	1	0.1726	3.72	0.0560
Time of day	1	0.0508	2.19	0.3785
Treatment	5	0.4433	7.00	<b>0.0261</b>
Trial × Time of day	1	0.0232	0.50	0.4804
Trial × Treatment	5	0.0633	1.37	0.2420
Time of day × Treatment	5	0.0939	4.06	0.0752
Trial × Time of day × Treatment	5	0.0231	0.50	0.7762
Residual	120	0.0463		
Total	143			

of the different trials and different experiments (day and night) were pooled for analyses of preference ( $n = 24$ ).

There were significant differences among the proportions of individuals in different habitats (Table 2). All analyses supported the hypotheses derived from the model in which adults of *A. cuniculus* prefer *Bifurcaria bifurcata*.

To test the second hypothesis of preference (see Material and Methods), *a priori* determined contrasts were used which demonstrated that a greater mean proportion of the individuals were recovered of those initially placed in *B. bifurcata* habitat (B in treatments 1 and 4; Fig. 3A) than in *Sargassum muticum* (S in treatment 2) or *Fucus vesiculosus* habitats (F in treatment 3) (contrast:  $nB/N_1, nB/N_4$  versus  $nS/N_2, nF/N_3$ ;  $F_{1,92} = 16.1769$ ;  $P = 0.0001$ ). This was entirely consistent with the hypothesis. There were also greater proportions of *A. cuniculus* in *B. bifurcata* when choices of preferred habitat were available (treatment 1) than when choices were not available (treatment 4) (con-

**Table 2.** ANOVA analyses of proportions of *Amphitholina cuniculus* in experimental treatments. Data from the two experiments (day and night) and two trials were pooled ( $n = 24$ ).

	df	MS	F	P
Hypothesis 1: $nB/N_1, nB/N_4 > nS/N_2, nF/N_3$ (more in preferred habitat)				
Among treatments	3	0.7169	15.48	<b>0.0000</b>
Residual	92	0.0463		
Hypothesis 2: $nS/N_5 > nS/N_2$ (fewer in non-preferred habitats where there is choice)				
Among treatments	1	0.4020	6.39	<b>0.0150</b>
Residual	46	0.0629		
Hypothesis 3: $nF/N_6 > nF/N_3$				
Among treatments	1	0.4134	7.37	<b>0.0093</b>
Residual	46	0.0561		

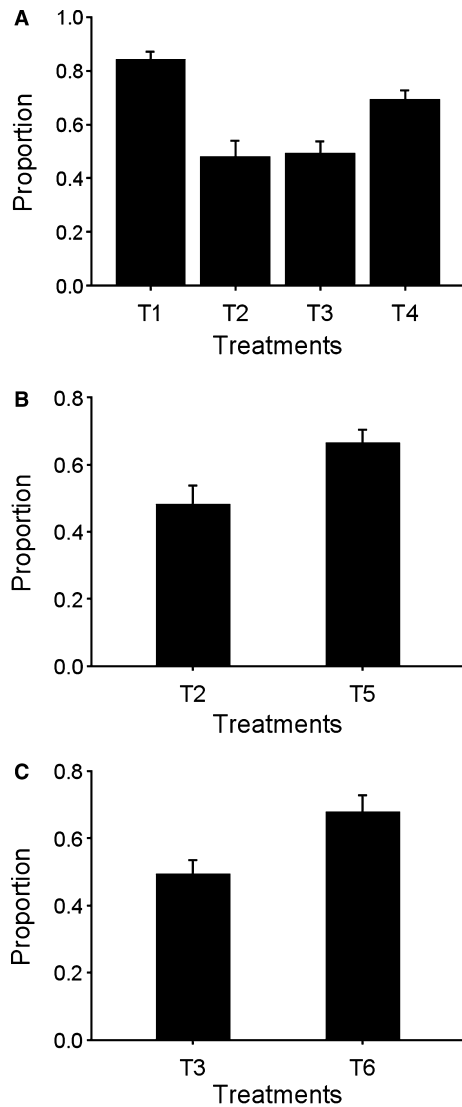
[Correction added after online publication, 22 May 2013: in Hypothesis 2, col. 1, 'no choice' changed to 'choice'.]

= 0.0177), probably due to the random movement of amphipods. Choice treatments of non-preferred habitats showed similar proportions (treatments 2 and 3) (contrast:  $nS/N_2$  versus  $nF/N_3$ ,  $F_{1,92} = 0.3732$ ;  $P = 0.5428$ ). [Correction added after online publication, 22 May 2013: 'No' deleted from start of preceding sentence.] In addition, there were smaller proportions of amphipods in non-preferred habitats when choices were available (treatments 2 and 3) than in those habitats when choices were not available (treatments 5 and 6) (Table 2, Fig. 3B,C). [Correction added after online publication, 22 May 2013: text '(treatments 5 and 6)' and '(treatments 2 and 3)' transposed in preceding sentence]. These results, therefore, supported hypotheses 2 and 3.

### Discussion

The hypothesis that this species exhibits different behaviour during the daily cycle was not supported. In contrast, results confirmed the hypothesis that adults of *Amphitholina cuniculus* show a preference for *Bifurcaria bifurcata* habitat.

Previous studies have found that marine invertebrates may exhibit different behaviour during a daily cycle (Hay *et al.* 1987). In particular, amphipods are more active at night than during the day (e.g. Edgar 1983; Hay *et al.* 1987; Sotka *et al.* 1999). These organisms may constrain their foraging movements to avoid predators because the risk of predation increases when moving between seaweeds. However, our results indicated that *A. cuniculus* did not change patterns of selection of habitat during the daily cycle. In general, individuals were quite active during the day and at night in both trials (I. Gestoso, personal observation). Nevertheless, we have to take into account that experiments under laboratory conditions have certain constraints. For



**Fig. 3.** Mean (+ SE) proportion of *Amphitholina cuniculus* remaining in treatments in the habitats where they were initially placed: (A) proportion of individuals in multiple choice and no choice treatments; (B) proportion of individuals remaining in *Sargassum muticum* habitat in choice (T2) and no choice (T5) treatments; (C) proportion of individuals in *Fucus vesiculosus* habitat in choice (T3) and no choice (T6) treatments.

example, the absence of large predators in the laboratory experiments might have an effect on the behaviour of this species because individuals may change behaviour in response to stimuli from predators (Chapman 2000).

In marine habitats, small herbivorous invertebrates tend to be generalists and very few species are host-plant specialists (Hay & Steinberg 1992; McDonald & Bingham 2010). In addition, most amphipods associated with seaweeds are habitat generalists (Duffy & Hay 1991). However, *A. cuniculus* might be considered a specialist species at least on

rocky intertidal shores along the Galician coast (Gestoso *et al.* 2010). The active behaviour shown by this species in the experiments may explain in part the distribution of this amphipod. For example, after widespread recruitment, adults of *A. cuniculus* could choose the favoured habitats (Underwood & Denley 1984). Alternatively, populations could distribute randomly across available habitats, but differential mortality would lead to a decrease of individuals in unfavourable habitats (Russo 1987).

Several works have pointed out that distributions of amphipods are rarely determined by differential mortality due to predation, active selection of habitat being a more important factor in determining patterns of distribution (Duffy & Hay 1991; Aikins & Kikuchi 2001; Poore 2004). Many factors related to intrinsic characteristics of macroalgae such as morphology, toughness, longevity, nutritional value or content of polyphenols may influence the choices of species (Hawkins & Hartnoll 1983; Chemello & Milazzo 2002; Van Alstyne & Houser 2003; McDonald & Bingham 2010). More complex morphologies may allow amphipods to escape detection or attack by visual predators (Hay 1991) or prevent dislodgement by waves (Sotka 2007). In this particular case, morphological complexity did not seem to play an important role. Although not formally analysed, *Fucus vesiculosus* and *Sargassum muticum* have a more complex morphology than *B. bifurcata*, which was the preferred habitat. *Fucus vesiculosus* and *S. muticum* are more branched and present vesicles, whereas *B. bifurcata* is a less frondose and cylindrical macroalga. Furthermore, algal toughness and stability of habitat (influenced by longevity of algae) have been reported to be more important factors than morphology (McDonald & Bingham 2010). A greater stability of habitat might favour certain species of amphipods, especially in habitats where risk of predation is high or environmental conditions are stressful (Duffy & Hay 1991). The fact that *B. bifurcata* is a perennial alga might explain why the amphipod *A. cuniculus* prefers this species over the pseudoperennial *S. muticum*.

The chemical traits of the host may also affect the susceptibility of amphipods to predation, and predation on small invertebrates may be reduced due to their association with chemically rich hosts that are avoided by omnivorous fish (Poore *et al.* 2000). *Bifurcaria bifurcata* is well known for its capacity to synthesise a wide variety of acrylic diterpenes (Ortalo-Magné *et al.* 2005). *Amphitholina cuniculus* might be able to tolerate these compounds because it supposes a lower risk of being consumed than if it selects more palatable species (Taylor & Steinberg 2005). Nevertheless, within the family Ampithoidae, responses to non-polar metabolites in host algae are very variable, with species showing negative relationships (*Peramphithoe*, *Biancolina*), positive relationships (*Exampithoe*) or no relation (*Ampithoe* spp.) (Poore *et al.* 2008). In addition, the nutritional

value of host seaweeds may influence the selection of host alga (Cruz-Rivera & Hay 2000).

In conclusion, it is very likely that the amphipod should get some benefit from selecting *B. bifurcata* against *F. vesiculosus* and *S. muticum*. For example, the amphipod might have greater fitness (i.e. maximising growth or mate encounter rates), get a good quality food and refuge from abiotic stress and predators, or avoid competition with other species, among other possibilities. Unfortunately, this experiment did not allow us to determine the underlying mechanisms of habitat choice and, therefore, the evolutionary forces that maintain this restricted host choice are unclear.

Preference experiments in the laboratory should be extrapolated to natural systems with caution (Chapman 2000). For example, the laboratory preference assays were conducted on small scales that may not represent the scales on which organisms discriminate among hosts in the field. Therefore, factors such as availability of preferred habitat or proximity of available hosts (Jonsen *et al.* 2001) might influence the distribution of amphipods in the field. Indeed, the spatial arrangement of plants affects strongly patterns of colonisation of marine invertebrates associated with vegetated substrates (Bell *et al.* 2001). Not only colonisation, but also post-colonisation processes (competition, predation, disturbance, immigration/emigration, etc.) may be important in determining patterns of spatial distribution of these organisms (Olabarria 2002, and references therein). Thus, it is essential that laboratory studies be accompanied by field tests of related hypotheses, so that differences between field-based behaviour and laboratory-based behaviour can be measured and the relevance of the laboratory studies sensibly evaluated. We are concerned about these difficulties but tried to make the conditions as realistic as possible, maintaining amphipods in the laboratory along with natural algae prior to the experiment. The experiments were also repeated twice to examine the consistency of patterns. In addition, these experiments were based on observations from a previous field study in which the distribution of mobile epifauna, including this species, was evaluated at different spatio-temporal scales. It would be desirable to carry out some parts of these experiments in the field if logistic problems could be overcome, using the information gained here as a guide. Nevertheless, results suggested that the behaviour of these amphipods may explain in part their distribution in the field.

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### References

- Aikins S., Kikuchi E. (2001) Studies on habitat selection by amphipods using artificial substrates within an estuarine environment. *Hydrobiologia*, **457**, 77–86.
- Arrontes J. (1999) On the evolution of interactions between marine mesoherbivores and algae. *Botanica Marina*, **42**, 137–155.
- Bates C.R. (2009) Host taxonomic relatedness and functional-group affiliation as predictors of seaweed-invertebrate epifaunal associations. *Marine Ecology Progress Series*, **387**, 125–136.
- Bell S.S. (1991) Amphipods as insect equivalents? An alternative view. *Ecology*, **72**, 350–354.
- Bell S.S., Brooks R.A., Robbins B.D., Fonseca M.S., Hall M.O. (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation*, **100**, 115–123.
- Brawley S.H. (1992) Mesoherbivores. In: John D.M., Hawkins S.J., Price J.H. (Eds), *Plant-animal Interactions in the Marine Benthos*. Clarendon Press, Oxford: 235–263.
- Chapman M.G. (2000) Poor design of behavioural experiments gets poor results: examples from intertidal habitats. *Journal of Experimental Marine Biology and Ecology*, **250**, 77–95.
- Chemello R., Milazzo M. (2002) Effect of algal architecture on associated fauna: some evidence from phytal mollusks. *Marine Biology*, **140**, 981–990.
- Cronin G., Lindquist N., Hay M.E., Fenical W. (1995) Effects of storage and extraction procedures on yields of lipophilic metabolites from the brown seaweeds *Dictyota ciliolata* and *Dictyota menstrualis*. *Marine Ecology Progress Series*, **119**, 265–273.
- Cruz-Rivera E., Hay M.E. (2000) The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. *Oecologia*, **123**, 252–264.
- Cruz-Rivera E., Hay M.E. (2001) Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. *Marine Ecology Progress Series*, **218**, 249–266.
- Duffy J.E., Hay M.E. (1991) Food and shelter as determinant of food choice by an herbivorous marine amphipod. *Ecology*, **72**, 1286–1298.
- Duffy J.E., Hay M.E. (2000) Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs*, **70**, 237–263.
- Durante K.M., Chia F.-S. (1991) Epiphytism on *Agarum fimbriatum*: can herbivore preferences explain distributions of epiphytic bryozoans? *Marine Ecology Progress Series*, **77**, 279–287.

- Edgar G.J. (1983) The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of amphitoid amphipods among algae. *Journal of Experimental Marine Biology and Ecology*, **70**, 205–225.
- Fox L.R., Morrow P.A. (1981) Specialization: species property or local phenomenon? *Science*, **211**, 887–893.
- Gestoso I., Olabarria C., Troncoso J.S. (2010) Variability of epifaunal assemblages associated with native and invasive macroalgae. *Marine & Freshwater Research*, **61**, 724–731.
- Hawkins S.J., Hartnoll R.G. (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology*, **21**, 195–282.
- Hay M.E. (1991) Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, CA: 96–119.
- Hay M.E., Fenical W. (1988) Marine plant–herbivore interactions: the ecology of chemical defense. *Annual Review of Ecology and Systematics*, **19**, 111–145.
- Hay M.E., Steinberg P.D. (1992) The chemical ecology of plant–herbivore interactions in marine versus terrestrial communities. In: Rosenthal G.A., Berenbaum M.R. (Eds), *Herbivores: Their Interactions with Secondary Plant Metabolites: Evolutionary and Ecological Processes*. Academic Press, San Diego, CA: 371–413.
- Hay M.E., Duffy J.E., Pfister C.A. (1987) Chemical defenses against different marine herbivores: are amphipods insect equivalents? *Ecology*, **68**, 1567–1580.
- Highsmith R.C. (1982) Induced settlement and metamorphosis of sand dollar (*Dendraster ecentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology*, **63**, 329–337.
- Jonsen I.D., Bouchier R.S., Roland J. (2001) The influence of matrix habitat on *Aphthona* flea beetle immigration to leafy spurge habitats. *Oecologia*, **127**, 287–294.
- Kumagai N.H. (2008) Role of food source and predator avoidance in habitat specialization by an octocoral-associated amphipod. *Oecologia*, **155**, 739–749.
- Lincoln R.J. (1979) *British Marine Amphipoda: Gammaridea*. British Museum (Natural History), London: 658 pp.
- McDonald P.S., Bingham B.L. (2010) Comparing macroalgal food and habitat choice in sympatric, tube-building amphipods, *Ampithoe lacertosa* and *Peramphithoe humeralis*. *Marine Biology*, **157**, 1513–1524.
- Myers A.A. (1974) *Ampitholina cuniculus* (Stebbing), a little-known marine amphipod crustacean new to Ireland. *Proceedings of the Royal Irish Academy Section B: Biological, Geological, and Chemical Science*, **74**, 463–469.
- Olabarria C. (2002) Role of colonization in spatio-temporal patchiness of microgastropods in coralline turf habitat. *Journal of Experimental Marine Biology and Ecology*, **274**, 121–140.
- Olabarria C., Underwood A.J., Chapman M.G. (2002) Appropriate experimental design to evaluate preferences for microhabitat: an example of preferences by species of microgastropods. *Oecologia*, **132**, 159–166.
- Ortalo-Magné A., Culioli G., Valls R., Pucci B., Piovetti L. (2005) Polar acyclic diterpenes from *Bifurcaria bifurcata* (Fucales, Phaeophyta). *Phytochemistry*, **66**, 2316–2323.
- Pardo L.M., Palma A.T., Prieto C., Sepulveda P., Valdivia I., Ojeda F.P. (2007) Processes regulating early post-settlement habitat use in a subtidal assemblage of brachyuran decapods. *Journal of Experimental Marine Biology and Ecology*, **344**, 10–22.
- Poore A.G.B. (2004) Spatial associations among algae affect host use in a herbivorous marine amphipod. *Oecologia*, **140**, 104–112.
- Poore A.G.B., Hill A.N. (2006) Sources of variation in herbivore preference: among individual and past diet effects on amphipod host choice. *Marine Biology*, **149**, 1403–1410.
- Poore A.G.B., Steinberg P.D. (1999) Preference–performance relationships and effects of host plant choice in an herbivorous marine amphipod. *Ecological Monographs*, **69**, 4443–4464.
- Poore A.G.B., Watson M.J., Nys R., Lowry J.K., Steinberg P.D. (2000) Patterns of host use among alga- and sponge-associated amphipods. *Marine Ecology Progress Series*, **208**, 183–196.
- Poore A.G.B., Hill A.N., Sotka E.E. (2008) Phylogenetic and geographic variation in host breadth and composition by herbivorous amphipods in the family Amphithoidae. *Evolution*, **62**, 21–38.
- Russo A.R. (1987) Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods. *Marine Ecology Progress Series*, **36**, 101–105.
- Sotka E.E. (2003) Genetic control of feeding preference in the herbivorous amphipod *Ampithoe longimana*. *Marine Ecology Progress Series*, **256**, 305–310.
- Sotka E.E. (2005) Local adaptation in host use among marine invertebrates. *Ecology Letters*, **8**, 448–459.
- Sotka E.E. (2007) Restricted host use by the herbivorous amphipod *Peramphithoe tea* is motivated by food quality and abiotic refuge. *Marine Biology*, **151**, 1831–1838.
- Sotka E.E., Hay M.E., Thomas J.D. (1999) Host-plant specialization by a non-herbivorous amphipod: advantages for the amphipod and costs for the seaweed. *Oecologia*, **118**, 471–482.
- Taylor R.B., Steinberg P.D. (2005) Host use by Australasian seaweed mesograzers in relation to feeding preferences of larger grazers. *Ecology*, **86**, 2955–2967.
- Underwood A.J., Denley E.J. (1984) Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong D.R. Jr, Simberloff D., Abele L.G., Thistle A.B. (Eds), *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, NJ: 151–180.
- Van Alstyne K.L., Houser L.T. (2003) Dimethylsulfide release during macroinvertebrate grazing and its role as an activated chemical defense. *Marine Ecology Progress Series*, **250**, 175–181.
- Viejo R.M. (1999) Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquatic Botany*, **64**, 131–149.