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Habitat colonisation by amphipods: Comparison between native and alien algae

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ABSTRACT

Invasion of algal habitat by the alien alga *Caulerpa racemosa* results in changes to habitat structure, part of which may be due to accumulation of large amounts of detritus. In turn, such changes lead to alterations in the assemblage structure of associated invertebrates. The present study was aimed at testing the hypotheses that (i) invasion by *C. racemosa* will influence the assemblage structure of amphipods associated with vegetated habitats, since colonisation by the invertebrates will differ between native algal habitat and habitat invaded by the alien alga, and (ii) differences in colonisation are mainly due to accumulation of detritus by the alien alga. To test these hypotheses, field experiments on habitat colonisation were undertaken at two sites within each of two Mediterranean localities (Malta and Spain). Using mesh bags, 3 different habitats were introduced at each site: habitat with the native alga *Halopteris scoparia*, habitat with *C. racemosa*, and an artificial habitat resembling algal habitat. Additionally, empty mesh bags were deployed as controls. Mesh bags containing plant material were defaunated prior to deployment. For each of the three habitat types, three supplement treatments were used: (i) no detritus, (ii) low detritus, and (ii) high detritus. The bags were placed on a rocky substratum at a water depth of 4.5–5 m for a period of 14 days, after which they were collected and the amphipod assemblage was assessed. The results showed that, overall, amphipod species richness and abundance were higher in bags containing *H. scoparia* but some amphipods exhibited a broad capability to colonize new habitat such as *C. racemosa*. Accumulation of detritus by the alien alga may play an important role but small-scale physical or biological habitat features can affect its ecological role.

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1. Introduction

On shallow marine rocky bottoms, macrophytes are the most important organisms that contribute to habitat structural complexity and heterogeneity. Macrophytes act as ecosystem engineers by creating or modifying a habitat (Crooks, 2002). Several effects of habitat complexity on benthic ecosystems are recognised; two important ones being (i) habitat heterogeneity or patchiness of habitat across a landscape and (ii) habitat structure—the physical architectural component that contributes to complexity (Sebens, 1991). In general, Mediterranean rocky bottom algal habitats occur in mosaics and patches in which different algal species are spatially aggregated at various spatial scales. Habitat complexity differs between algal stands formed by different species and is influenced by factors such as whether the algae are encrusting or erect, tall or low lying (turf), or if they support epiphytes. Hence, algal habitats can be very heterogeneous such that the availability of habitat/microhabitat space for colonisation by other species varies greatly.

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Invasive marine algae can modify habitat structure and, consequently, result in large ecological effects (see review in Williams and Smith, 2007). The number of introduced species outside their natural ranges is rapidly increasing, although a relatively small proportion of transported and introduced species become invasive (Williamson and Fitter, 1996). However, the ability of such species to restructure and, hence, radically change the functioning of the recipient habitat is high (Crooks, 2002). Invasive species may (i) modify the availability and flow of nutrients in an ecosystem by altering biogeochemical cycling; (ii) contribute to changes in energy flow through a food web; and (iii) affect the availability or quality of resources, including the physical and chemical characteristics of a habitat such as available space, sediment properties, light regime and water quality (see Crooks, 2002; Vitousek, 1990). Frequently, an invasive species acts as an ecosystem engineer, hence influencing the biota that will become associated with the habitat. When this occurs, the resulting community will have mixed characteristics that are attributed to the initial pool of species and habitat preferences and to the colonization rate of the invasive species.

Amphipods are one of the most ubiquitous and abundant invertebrate groups in marine vegetated habitats, with densities often reaching several thousand individuals per square meter (Brawley, 1992; Vázquez-Luis

et al., 2008). They are important secondary producers (Carrasco and Arcos, 1984; Highsmith and Coyle, 1990; Sarvala and Uitto, 1991) and serve as food for a large variety of marine fauna (Beare and Moore, 1997; Sanchez-Jerez et al., 1999; Stål et al., 2007; Stoner, 1979), hence playing a key role in energy flow through food webs (Vázquez-Luis et al., 2010). Amphipods respond to habitat modification (Vázquez-Luis et al., 2008, 2009b); some species exhibit high habitat specificity, while others tolerate a range of habitat alteration that may result from pollution, invasion by alien species, and other disturbances, and can therefore be used as an indicator of disturbance of vegetated habitat (Bellan-Santini, 1980; Conradi et al., 1997; Sanchez-Jerez et al., 2000; Virnstein, 1987).

In the Mediterranean Sea, concerns on the appearance of the alien alga *Caulerpa racemosa* var. *cylindracea* (hereafter *C. racemosa*) have resulted in several studies on the ecology of this species (see Cavas et al., 2006; Ruitton et al., 2005). A main concern is that the fauna associated with native vegetation can change with the introduction of exotic algae (Schmidt and Scheibling, 2007; Wikström and Kautsky, 2004). As a result, several works have been focussed on assessing potential changes in the faunal assemblages associated with Mediterranean vegetated habitats when these are colonised by *C. racemosa* (Argyrou et al., 1999; Piazzini and Balata, 2008; Vázquez-Luis et al., 2008, 2009a,b). Results of previous studies on Mediterranean shallow rocky habitat indicated that the presence and amount of *C. racemosa* led to marked effects on the native macroalgal assemblage structure by affecting macrophyte species composition and biomass since the alien alga forms homogeneous monospecific stands in which detritus accumulates (Vázquez-Luis et al., 2008, 2009b). Such effects, brought about by changes to the structural complexity and to other physical attributes of the native algal habitat following invasion by *C. racemosa*, are reflected in the species composition, assemblage structure, and trophic dynamics of the associated amphipod assemblages (see Fig. 1). As a result, the amphipod assemblages associated with *C. racemosa* differ from those associated with native seaweeds; in addition to recorded differences in amphipod abundance and species richness, results also show

an increased abundance of detritivorous species and a decrease of herbivorous species. Furthermore, the presence of *C. racemosa* may affect the flow of matter and energy from invertebrates to higher trophic levels (Vázquez-Luis et al., 2010).

Studies on the ecology of macrofauna associated with *C. racemosa* stands have been mainly focussed on post-invasion assessment, while there is a dearth of data on the situation before invasion by the alien alga compared to that following invasion. The present study was aimed at testing the hypotheses that (i) invasion by *C. racemosa* will influence the assemblage structure of amphipods associated with vegetated habitats, since colonisation by the invertebrates will differ between native algal habitat and habitat invaded by the alien alga, and (ii) differences in colonisation are mainly due to accumulation of detritus by the alien alga. To test these hypotheses, we undertook colonisation experiments in the field, which were preceded by characterisation of the amphipod fauna associated with natural habitat at the study sites to enable comparison with the amphipod assemblages following colonisation of experimental units. Our experiments were replicated in two Mediterranean localities, separated by thousands of kilometres, to assess whether the same patterns occurred consistently over a large spatial scale.

2. Materials and methods

2.1. Study sites

The experiments were carried out in two Mediterranean localities: Malta and Spain. At each locality, two rocky sites with broadly similar environmental characteristics and supporting algal habitat that was not invaded by *C. racemosa* were selected (Fig. 2). The two Maltese sites – Ghallis and Pembroke – are both located on the northeastern coast, while the two Spanish sites – Albir and Sierra Helada – are both located on the Benidorm coast (Alicante), on the eastern coast of Spain. The four sites had similar water depth and habitat characteristics, which comprised a rocky bottom colonised by patchy beds of native algae. At

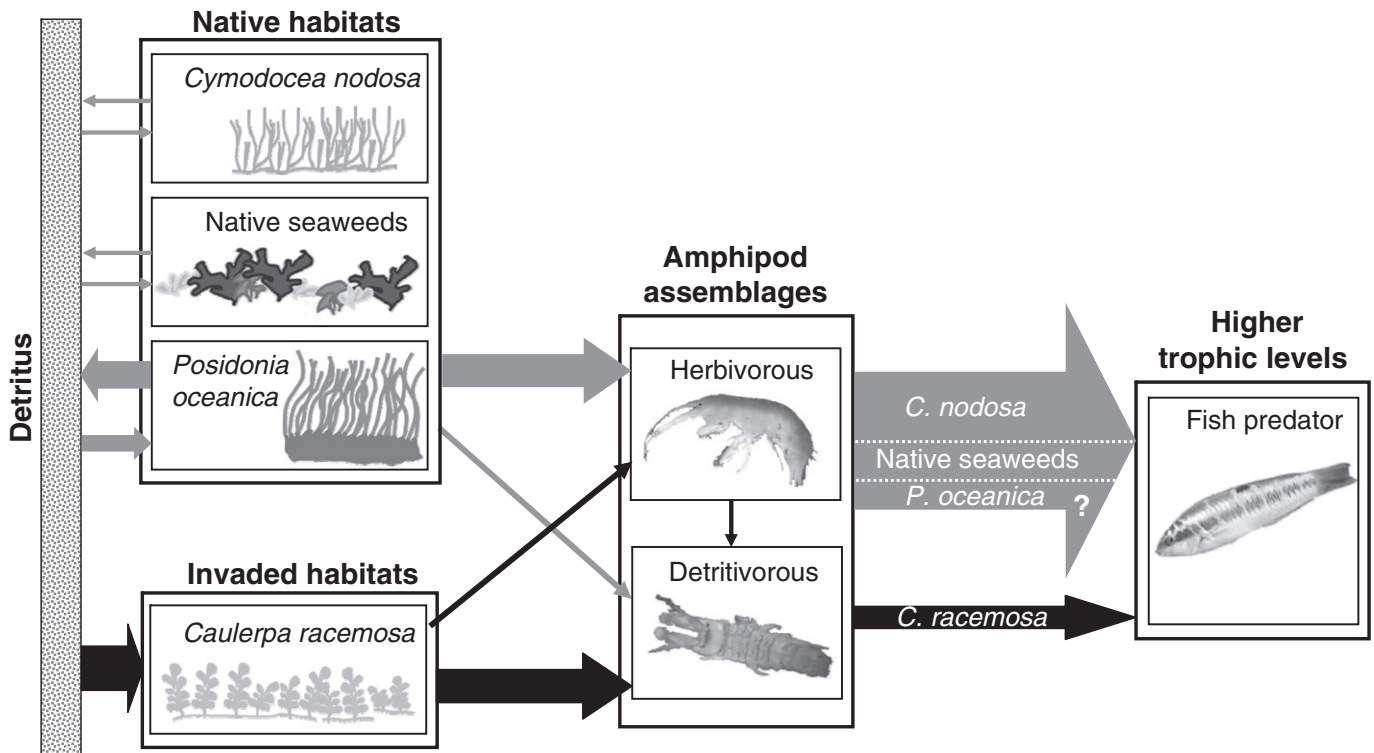


Fig. 1. Conceptual model of ecological effects of *C. racemosa* invasion through the trophic web on shallow Mediterranean habitats and associated fauna community. Grey arrows: interactions by native habitats. Black arrow: interactions by *C. racemosa* invaded habitats. The thickness of the arrows represents the importance of the influence between compartments.

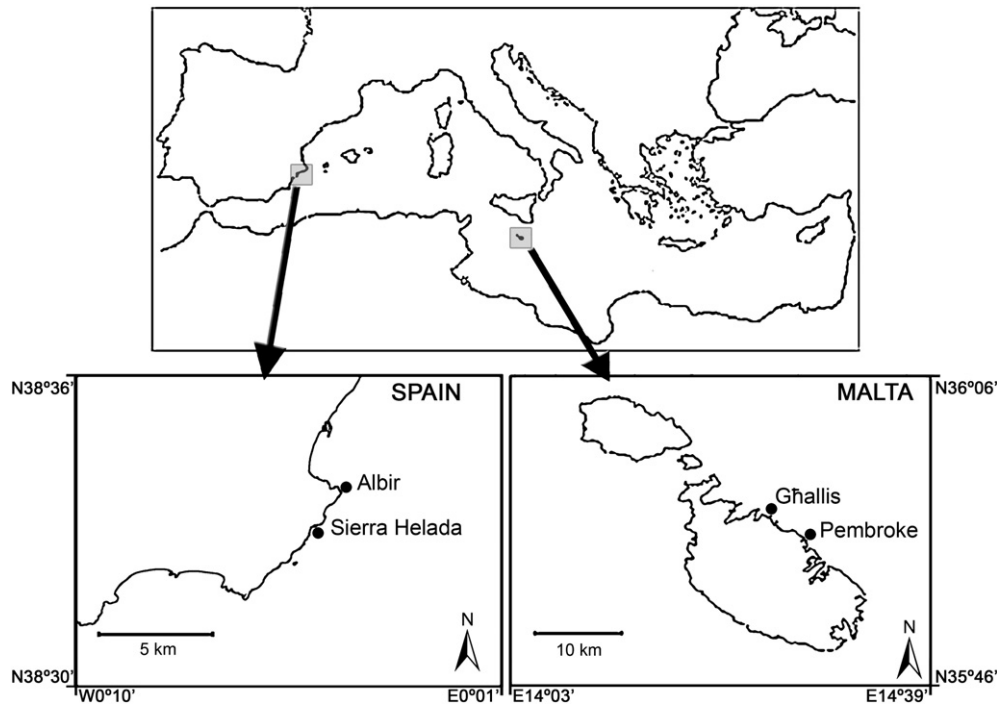


Fig. 2. Map showing the two localities and sites within each locality where the experiments were held: Albir and Sierra Helada, located in Spain, and Ghallis and Pembroke, located in Malta.

the Maltese sites, the dominant macrophytes were erect phaeophyceae that formed patches with *Cystoseira* spp., *Halopteris scoparia*, *Cladostephus spongiosus* and *Dictyopteris polypodioides*. Similarly, at the dominant algae at the Spanish sites were erect phaeophyceae, namely *H. scoparia* accompanied by red turf algae *Corallina elongata* and *Jania rubens*.

2.2. Characterisation of habitat features and amphipod fauna

To characterise the algae and amphipod fauna at the study sites, three random samples were taken by SCUBA divers at each site using a 20 × 20 cm quadrat. Samples were collected by scraping off all the vegetation enclosed by the quadrat. A 300 µm mesh net was attached to the quadrat to prevent escape of motile fauna during collection. Samples were preserved in 4% formalin in seawater. Each replicate was sieved in seawater using a 500 µm sieve. In the laboratory, the amphipods were separated, identified and counted. Algae were sorted and identified to species level and dried for 24 h in an oven at 80 °C to obtain dry weight.

2.3. Experimental setup and sampling design

For the field experiments, two algae were harvested: the native *Halopteris scoparia* and the alien *C. racemosa*, which have different habitat structure and complexity characteristics. *H. scoparia* was selected because it is ubiquitous in shallow water Mediterranean benthic habitats. It is a brown fern-like seaweed that grows to a height of some 20. In contrast, the invasive *C. racemosa* has slender thalli and is attached to the substratum by means of thin rhizoids that are closely arranged along the stolon.

In the laboratory, the algae were defaunated and their wet weight was recorded. Dry *Posidonia oceanica* 'balls' (Cannon, 1979) were used as source for the detritus stock. Mesh bags with different treatments (algae and detritus) were then prepared as follows. Bags containing algae (*H. scoparia* or *C. racemosa*) had a content weighing 80 g (wet weight) per bag, while those containing 'artificial algae' (synthetic garden shade fabric) had a volume equivalent to that of the algae. Two different treatments were used for bags with detritus: low detritus supplement (15 g wet weight) and high detritus supplement

(50 g wet weight). These detritus weights were chosen on the basis that they are equivalent to the amount of detritus found in habitats colonised by native algae and *C. racemosa*. Accordingly, 15 g represent around 15% detritus, which is the typical amount associated with native algae (Vázquez-Luis et al., 2008), while 50 g represent around 40% detritus, which is the amount typically associated with *C. racemosa* (Vázquez-Luis et al., 2008). Five replicate bags per category/treatment were prepared, such that a total of 120 bags per locality were used.

The initial analysis of variance (ANOVA) design for comparisons had the factors Locality, Habitat, Detritus and Sites. However, due to significant differences in the amphipod assemblages obtained for the factor Locality, separate ANOVAs were carried out for the two localities. Consequently the design was simplified to three factors: (i) 'habitat' (Ha), which was fixed and had 4 levels: *H. scoparia*, *C. racemosa*, artificial algae and control (only the mesh bag); (ii) 'detritus' (De), which was fixed and orthogonal and had 3 levels (without detritus, low detritus supplement and high detritus supplement); and (iii) 'site' (Si), which was random and orthogonal, and had two levels.

In the field, all bags were deployed randomly at each study site on a rocky bottom supporting algal habitat at a water depth of between 4.5 m and 5 m. Each bag had a mesh size of 1.6 cm, was 30 cm long and had a large pebble (collected from a coastal beach) inside to ensure it remained stationary on the seabed. The bag also contained the specific alga/*C. racemosa*/detritus treatment, and had its upper end closed. Deployment of the mesh nets was made during summer 2008. At each site, the area of seabed over which the mesh bags were spread was around 20 m². The mesh bags were then collected following 2 weeks from deployment. Immediately following collection of the bags, each one was placed in a plastic bag to avoid escape of macroinvertebrates. In the laboratory, the collected samples were first preserved in 4% formalin and later sieved through a 500 µm mesh sieve to retain the fauna and other material, which was then sorted. All amphipods were identified to species and counted. An index of complexity for the two different algal habitats was calculated as the ratio of surface area to volume (SA/V) for each algal species. This was done by placing the algae flat on graph paper (having graduations in mm) and drawing their outline. The area enclosed within the outline was then estimated using the graduations on the paper.

The volume of the algae was determined using the water displacement method, i.e. using a graduated measuring cylinder. A surface-to-volume ratio (SA/V) is a simple but practical measure of the complexity of biological habitats (Koukouras et al., 1992; Schmidt-Nielsen, 1984). *H. scoparia* had a higher structural complexity compared to *C. racemosa* (4.38 ± 0.06 and 6.45 ± 0.19 respectively, $n=4$).

2.4. Data analyses

For each locality (Malta and Spain), differences in number of species, total abundance of amphipods, and abundance of the most abundant amphipod species were tested using three-factor analysis of variance (ANOVA). Prior to carrying out the ANOVA, the data were tested for heterogeneity of variance using Cochran's *C*-test. Data were $\sqrt{x+1}$ or $\log(x+1)$ transformed in cases where the variances were significantly different at $P=0.05$. Where the variance remained heterogeneous following transformation, untransformed data were analysed since ANOVA is a robust statistical test that is relatively unaffected by heterogeneity of variances, particularly in balanced experiments (Underwood, 1997). However, in such cases, special care was taken in the interpretation of results, and to reduce type I error, α was reduced to 0.01. Where ANOVA indicated a significant difference for a given factor, the source of difference was identified using Student–Newman–Keul (SNK) tests (Underwood, 1981, 1997). Moreover, when the divisor for *F*-ratio was too small, and statistical differences were not found, pooling was applied for the main factors and interactions.

Non-parametric multidimensional scaling (MDS) was used as the ordination method for exploring differences in the amphipod assemblage composition (Clarke and Warwick, 1994). The similarity matrix, which was calculated using the Bray–Curtis index and using double square transformed data, was used to construct bivariate MDS plots. A permutational multivariate ANOVA (PERMANOVA software, Anderson, 2001) based on the same design used for the univariate analyses was carried out to test for differences in the species composition of the amphipod assemblage. Following the permutational test, a pairwise test was carried out to test differences among groups.

3. Results

3.1. Habitat and amphipod fauna

A total of 37 amphipod species were recorded from the Maltese sites and 34 from the Spanish ones. At both localities, the abundance of amphipods was high, with values of up to 5000 individuals m^{-2} being recorded but large differences in values were noted between different sites. In Malta the most abundant species were (in order of decreasing abundance) *Elasmopus brasiliensis* (602.34 ± 152.85 ind/ m^2), *Ampithoe ramondi* (485.38 ± 98.06 ind/ m^2), *Dexamine spiniventris* (362.57 ± 89.65 ind/ m^2), *Ericthonius punctatus* (347.95 ± 72.96 ind/ m^2), *Hyale camptonyx* (301.17 ± 104.03 ind/ m^2) and *Cymadusa crassicornis* (178.36 ± 113.01 ind/ m^2). In Spain, the most abundant species were *A. ramondi* (514.62 ± 119.98 ind/ m^2), *Microdeutopus* spp. (450.29 ± 80.61 ind/ m^2), *D. spiniventris* (400.58 ± 236.91 ind/ m^2), *Caprella grandimana* (391.81 ± 190.66 ind/ m^2), *Caprella acanthifera* (321.64 ± 60.38 ind/ m^2) and *Hyale schmidti* (201.75 ± 83.74 ind/ m^2).

3.2. Colonisation

Thirty-four amphipod species colonised the mesh bags in Malta and 33 in Spain. At both localities, species richness was significantly greater in bags containing *H. scoparia* compared to all other treatments (Malta: Ha, $P<0.01$; Table 1, Fig. 3a; Spain: Ha, $P<0.05$; Table 1, Fig. 3b). Total abundance was significantly higher at both localities for bags containing *H. scoparia* (Malta: Ha, $P<0.05$; Table 1, Fig. 3c and Spain: Ha, $P<0.05$; Table 1, Fig. 3d); the highest recorded values were for bags having a high content of detritus (95.7 ± 11.22 ind/bag).

No significant differences in total abundance and species richness were detected for the detritus treatment, except for species richness at the Maltese sites where bags having low and high detritus content had a significantly higher number of species (De, $P<0.05$; Table 1, Fig. 3a). At the Spanish sites, no significant differences were detected for the detritus treatment, but a pattern indicating an increase in amphipod abundance with an increase in the content of detritus was noted.

The two-dimensional MDS plot (Fig. 4) showed grouping of samples mainly by locality. At each locality, samples were grouped mainly by a combination of habitat and detritus content. The obtained multivariate pattern indicated a different response at the two localities (PERMANOVA, LoxHa, $P<0.01$, Table 2). The results of the pairwise test indicated that in Malta the contribution of *H. scoparia* was different between *C. racemosa* and control treatments, which were also different to the contribution of this species to the artificial units. For Spain, the contribution of *H. scoparia* was different from that of *C. racemosa*, which was different from that of the controls (and similar to the artificial substratum).

The most abundant amphipods recorded from the two study localities were *E. brasiliensis*, *Elasmopus pocillimanus*, *Gammarella fucicola*, *C. acanthifera*, and *Microdeutopus* spp., while the abundance of two *Lysianassa* species, *Lysianassa costae* and *Lysianassa longicornis*, differed between the two localities; the former being more abundant in Malta and the latter being more abundant in Spain. Collectively, these species comprised 82% and 54% of the amphipod fauna respectively from Malta and Spain. Abundance values of *E. brasiliensis* were significant higher in *H. scoparia* habitat in both Malta and Spain (Malta: Ha, $P<0.05$; Table 1, Fig. 5a; Spain: Ha, $P<0.01$; Table 1, Fig. 5b); for the factor 'detritus', the abundance of this species was significantly higher for low and high detritus content at the Maltese sites (De, $P<0.05$; Table 1, Fig. 5a). *E. pocillimanus* was more abundant in *H. scoparia* bags compared to the other substrata in Spain (Ha, $P<0.05$; Table 1, Fig. 5f).

The abundance of *G. fucicola* was high at both Maltese and Spanish sites, but was particularly so in bags containing *H. scoparia*. However, significant differences were detected only for Spain (Ha, $P<0.05$; Table 1, Fig. 5f). Furthermore, only one site in Malta showed significant differences for high detritus content (DexSi, $P<0.01$; Table 1, Fig. 5e). *C. acanthifera* had different patterns of abundance at the two study localities: in Malta it was more abundant on *C. racemosa* (Ha, $P<0.05$; Table 1, Fig. 5g) while in Spain it was more abundant on the artificial substratum at one site (HaxSi, $P<0.05$; Table 1 and Fig. 5h).

Species of the genus *Microdeutopus* were, in general, more abundant on *H. scoparia* and *C. racemosa*; in Malta, *Microdeutopus* spp. were significantly more abundant on *C. racemosa* at one site (HaxSi, $P<0.01$; Table 1, Fig. 5i). Furthermore, for bags from Malta, significant differences were found for the factor detritus, with the abundance of *Microdeutopus* spp. being higher in bags having high detritus content (De, $P<0.05$; Table 1, Fig. 5i). For Spain, significant differences in the abundance of these species were detected for habitat and detritus, but significant differences were recorded for only for one site. The abundance of *Microdeutopus* spp. was significantly higher on *H. scoparia* and *C. racemosa* at one of the Spanish sites, and higher on *C. racemosa* at the other site (HaxSi, $P<0.05$; Table 1, Fig. 5j). A significant interaction for detritus and site was also indicated for *Microdeutopus* spp.; at one of the Spanish sites, their abundance was higher in bags having a high content of detritus (DexSi, $P<0.05$; Table 1, Fig. 5j), while no differences in abundance were evident at the other site for the different detritus content levels (DexSi, $P<0.05$; Table 1, Fig. 5j). For *L. costae* in Malta and *L. longicornis* in Spain the abundance pattern was the same, with the species being more abundant in *H. scoparia* (Malta: HaxSi, $P<0.01$; Table 1, Fig. 5k; and Spain: HaxSi, $P<0.05$; Table 1, Fig. 5l).

4. Discussion

Overall, both the species richness and abundance of amphipods were higher in bags containing *H. scoparia*. Furthermore, for *C. racemosa* habitat, the results suggest that the presence of detritus results in increased

Table 1
Results of the three-factor ANOVA for species richness, total abundance, and species abundance of the most abundant amphipods. MS = mean square; *P* = level of significance; df = degrees of freedom; ns = not significant; * = significant (*P* < 0.05); ** = significant (*P* < 0.01); ^a = pooled data HaxSi; ^b = pooled data DexSi.

Malta										
Source of variation	df	Species richness		Total abundance		<i>Elasmopus brasiliensis</i>		<i>Elasmopus pocillimanus</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Habitat = Ha	3	91.88	0.0001 ^{***a}	17746.16	0.0221*	42.57	0.0259*	12.19	0.0516	Ha × Si
Detritus = De	2	87.06	0.0001 ^{**b}	11781.51	0.2333	31.1	0.0001 ^{**b}	9.58	0.111	De × Si
Site = Si	1	20.01	0.0123 ^{ab}	5057.01	0.0013 ^{**}	3.48	0.0678 ^b	25.52	0.0001 ^{**}	Res
Ha × De	6	5.66	0.3700	668.13	0.3921	2.53	0.3902	1.19	0.7662	Ha × De × Si
Ha × Si	3	0.69	0.8830	1053.87	0.0827	2.83	0.0455 ^b	1.35	0.1651	Res
De × Si	2	1.51	0.6241	3586.01	0.0007 ^{**}	0.49	0.6208	1.19	0.2192	Res
Ha × De × Si	6	4.26	0.2275 ^{ab}	529.07	0.3385	1.99	0.0791 ^b	2.22	0.0133	Res
Residual	96	3.18		459.16		1.03		0.78		
Cochran's C-test		C = 0.0942 ns		C = 0.1626 (<i>P</i> < 0.01)		C = 0.1541 ns		C = 0.1530 ns		
Transformation		–		–		Sqrt(<i>x</i> + 1)		Ln(<i>x</i> + 1)		
SNK		Ha: H > Ca = A > C De: L = H > Ø		Ha: H > Ca = A = C		Ha: H > Ca = A = C De: L = H > Ø				
Source of variation	df	<i>Gammarella fucicola</i>		<i>Caprella acanthifera</i>		<i>Microdeutopus spp.</i>		<i>Lyssianasa costae</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Habitat = Ha	3	25.96	0.1024	1.31	0.0062 ^{***a}	1.29	0.4595	30.79	0.3824	Ha × Si
Detritus = De	2	11.14	0.5807	0.18	0.5451 ^b	1.19	0.0143 ^{ab}	4.13	0.2832	De × Si
Site = Si	1	5.29	0.1733	5.28	0.0001 ^{***a,b}	4.72	0.0001 ^{**b}	42.01	0.0001 ^{**}	Res
Ha × De	6	1.57	0.9588	0.25	0.7638	0.1	0.6564	1.31	0.3297	Ha × De × Si
Ha × Si	3	4.91	0.1623	0.07	0.8722	1.14	0.0075 ^{**b}	21.14	0.0001 ^{**}	Res
De × Si	2	15.43	0.0055 ^{**}	0.05	0.8395	0.18	0.5111	1.63	0.1409	Res
Ha × De × Si	6	7.36	0.0213	0.46	0.1769 ^{ab}	0.14	0.7996 ^b	0.9	0.3669	Res
Residual	96	2.81		0.31		0.27		0.82		
Cochran's C-test		C = 0.1616 ns		C = 0.1093 ns		C = 0.1563 ns		C = 0.4439 (<i>P</i> < 0.01)		
Transformation		Sqrt(<i>x</i> + 1)		Sqrt(<i>x</i> + 1)		Ln(<i>x</i> + 1)		–		
SNK		De × Si: 2: H > L = Ø		Ha: Ca > H = A = C		De: H > L = Ø		Ha × Si: 1: H > Ca = A = C		
Spain										
Source of variation	df	Species richness		Total abundance		<i>Elasmopus brasiliensis</i>		<i>Elasmopus pocillimanus</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Habitat = Ha	3	55.09	0.0001 ^{***a}	4091.94	0.0001 ^{***a}	2.11	0.0002 ^{***a}	1.0179	0.0312 ^{**a}	Ha × Si
Detritus = De	2	13.41	0.3754	292.03	0.4656 ^b	0.25	0.4311 ^b	0.1218	0.6934 ^b	De × Si
Site = Si	1	14.01	0.0786 ^a	913.01	0.1238 ^{ab}	0.03	0.7750 ^{ab}	0.0991	0.5858 ^{ab}	Res
Ha × De	6	3.89	0.8588	249.9	0.4604	0.19	0.8446	0.2362	0.5790	Ha × De × Si
Ha × Si	3	2.09	0.7072	496.94	0.2782	0.01	0.9911	0.1183	0.7902	Res
De × Si	2	8.06	0.1679 ^a	85.73	0.7992	0.12	0.6709	0.2804	0.4406	Res
Ha × De × Si	6	9.88	0.0466 ^a	229.6	0.7253 ^{ab}	0.45	0.1767 ^{ab}	0.2799	0.5387 ^{ab}	Res
Residual	96	4.51		3381.55		0.31		0.3392		
Cochran's C-test		C = 0.1451 ns		C = 0.6525 (<i>P</i> < 0.01)		C = 0.1231 ns		C = 0.1326 ns		
Transformation		–		–		Sqrt(<i>x</i> + 1)		Ln(<i>x</i> + 1)		
SNK		Ha: H > Ca = A = C		Ha: H > Ca = A = C		Ha: H > Ca > C > A		Ha: H > Ca = C > A		
Source of variation	df	<i>Gammarella fucicola</i>		<i>Caprella acanthifera</i>		<i>Microdeutopus spp.</i>		<i>Lyssianasa longicornis</i>		<i>F</i> versus
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
Habitat = Ha	3	1015.84	0.0029 ^{*a}	1.47	0.4701	4.38	0.1801	4.05	0.1566	Ha × Si
Detritus = De	2	166.07	0.4461 ^b	0.29	0.7863	1.67	0.5523	0.96	0.345	De × Si
Site = Si	1	116.03	0.4526 ^{ab}	7.79	0.0001 ^{**}	23.41	0.0001 ^{**}	0.95	0.0792	Res
Ha × De	6	230.42	0.1855	0.49	0.5238	0.49	0.5661	0.65	0.0922	Ha × De × Si
Ha × Si	3	158.46	0.5143	1.34	0.0392*	1.35	0.0294*	0.1	0.0149*	Res
De × Si	2	174.56	0.4319	1.06	0.1064	2.07	0.0106*	0.51	0.1901	Res
Ha × De × Si	6	106.68	0.7899 ^{ab}	0.51	0.3627	0.57	0.2583	0.2	0.6663	Res
Residual	96	206.12		0.46		0.43		0.3		
Cochran's C-test		C = 0.8863 (<i>P</i> < 0.01)		C = 0.1524 ns		C = 0.1526 ns		C = 0.1527 ns		
Transformation		–		Sqrt(<i>x</i> + 1)		Sqrt(<i>x</i> + 1)		Ln(<i>x</i> + 1)		
SNK		Ha: H > Ca = A = C		Ha × Si: 1: A > H = Ca = C 2: H = Ca = A = C		Ha × Si: 1: H = Ca > A = C 2: Ca > H = A = C De × Si: 1: H > Ø = L 2: Ø = L = H		Ha × Si: 1: H > Ca = A = C		

values of amphipod species richness and abundance but with high spatial heterogeneity of these attributes. *H. scoparia* beds have a high structural complexity, and seem to serve as an important habitat for

amphipod assemblages, as shown by the very high values of species richness and abundance recorded for amphipods in the present study. Artificial substrata provide a refuge for amphipods, but natural vegetated

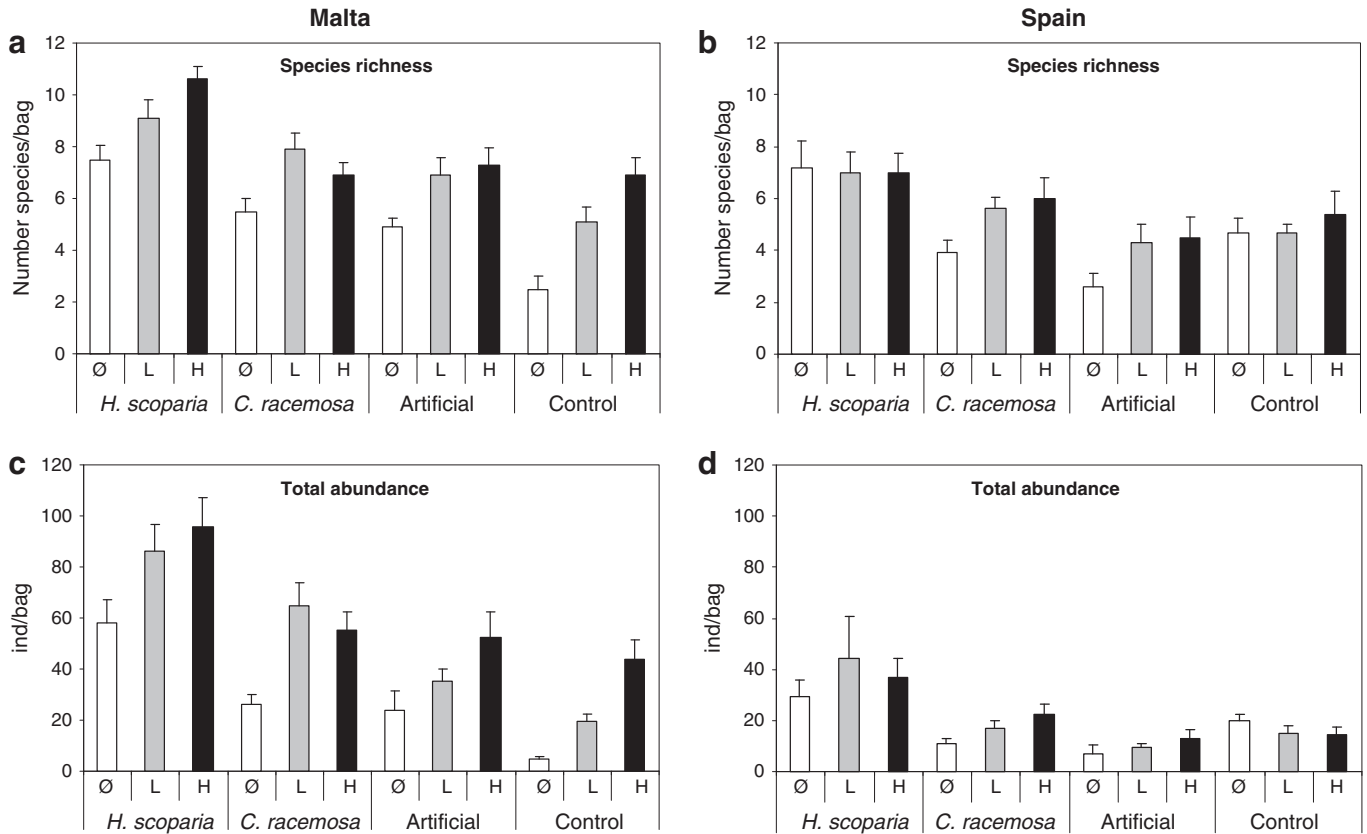


Fig. 3. Values (\pm SE) of mean number of amphipod species (a and b) and total amphipod abundance (individuals per bag) (c and d) recorded from each treatment in Malta (a and c) and Spain (b and d).

habitats are more attractive for the fauna. Some differences in the responses of amphipods were noted at the regional and local scale. However, such variation in the amphipods' response would be expected. Many studies have shown that the largest sources of spatial and temporal variability in the abundance of benthic organisms often occur at the smallest scales (Fraschetti et al., 2005), and this would be related to a number of biotic and abiotic variables. Such factors vary and interact at both the small spatial and temporal scales and may influence important habitat features such as detritus present.

In general, three main processes may account for faunal distribution patterns. One is different rates of settlement/recruitment; larvae or juveniles can recruit in larger numbers in one habitat compared to others (Dayton, 1975; Moore and Lopez, 1972). However, for peracarid crustaceans, it can indicate that juvenile amphipods may be actively seeking new habitats that have lower faunal abundance, thereby, avoiding competition with adults. An alternative explanation is that amphipod populations are distributed randomly in the available habitats but differential mortality leads to reduction in numbers in unfavourable habitats (Levins, 1968; Russo, 1987). Furthermore, previous studies have demonstrated that predation rates on amphipods differ depending on

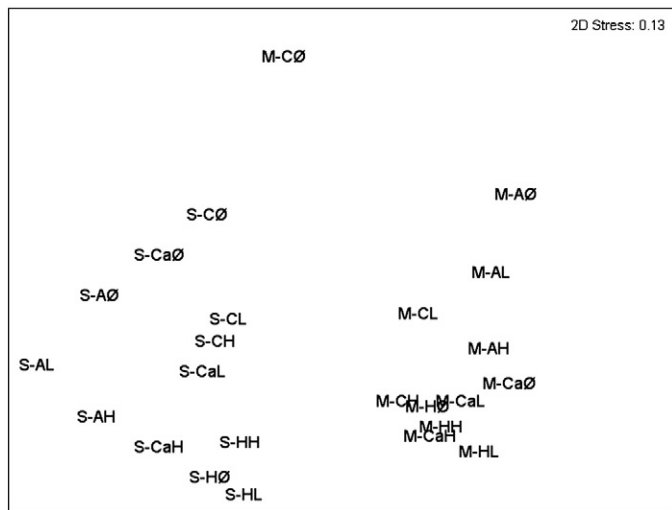


Fig. 4. Two-dimensional MDS plot for amphipod species abundance. M = Malta; S = Spain; H = *H. scoparia*; Ca = *C. racemosa*; A = artificial; C = control; Ø = without detritus; L = low detritus and H = high detritus content.

Table 2

Results of the multivariate analyse PERMANOVA for amphipod assemblage. MS = mean square; P = level of significance; df = degrees of freedom; * = significant ($P < 0.05$), ** = significant ($P < 0.01$).

Source of variation	df	Amphipod assemblage		F versus
		MS	P	
Locality = Lo	1	89690.63	0.0010**	Si (Lo)
Habitat = Ha	3	13356.26	0.1320	Lo × Ha
Detritus = De	2	3197.98	0.9080	Lo × De
Site = Si (Lo)	2	3126.08	0.0160*	Res
Lo × Ha	3	7827.47	0.0010**	Ha × Si (Lo)
Lo × De	2	6600.17	0.3850	De × Si (Lo)
Ha × De	6	2521.15	0.8280	Lo × Ha × De
Ha × Si (Lo)	6	1557.43	0.5050	Res
De × Si (Lo)	4	5882.81	0.0010**	Res
Lo × Ha × De	6	3351.99	0.1600	Ha × De × Si (Lo)
Ha × De × Si (Lo)	12	2621.91	0.0010**	Res
Residual	192	1583.72		
Transformation		Fourth root		

Post-hoc test (Lo × Ha): Malta: *H. scoparia* ≠ *C. racemosa* = Control ≠ Artificial. Spain: *H. scoparia* ≠ *C. racemosa* ≠ Control = Artificial.

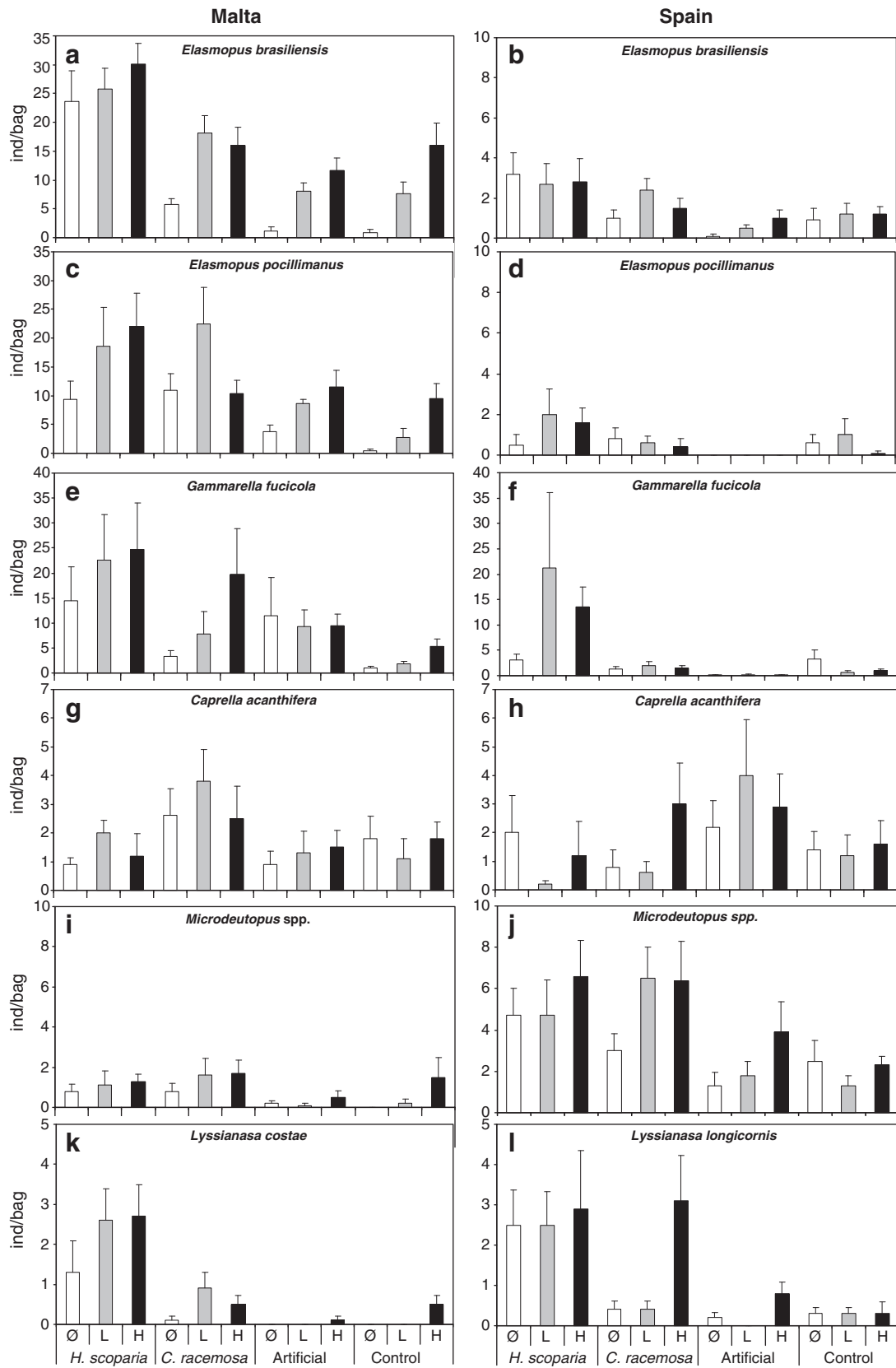


Fig. 5. Abundance (number of individuals \pm SE per bag) of *Elasmopus brasiliensis* (a and b), *Elasmopus pocillimanus* (c and d), *Gammarella fucicola* (e and f), *Caprella acanthifera* (g and h), *Microdeutopus* spp. (i and j), *Lyssianasa costae* (k) and *Lyssianasa longicornis* (l) recorded in Malta (a, c, e, g, i and k) and in Spain (b, d, f, h, j and l). Note that the different y-axis scale of plots for *Elasmopus brasiliensis* and *Elasmopus pocillimanus*.

species and on the habitat with which they associate (Poore, 2004; Vázquez-Luis et al., 2010). A third alternative is that following recruitment of juveniles, adults select favoured habitats (Crowe and Underwood, 1998). It has been demonstrated that amphipods can actively choose substrata and show high habitat fidelity (Poore and Hill, 2006; Roberts and Poore, 2005; Stoner, 1980). In our study, amphipods seem to prefer *H. scoparia* compared to the other habitats; however, since such processes are not exclusive, a combination of other factors and processes may also affect the observed patterns of distribution of amphipods.

Several studies highlight the importance of habitat structural complexity in determining the abundance and species richness of associated mobile epifauna (Beck, 2000; Chemello and Milazzo, 2001; Grabowski and Powers, 2004; Martin-Smith, 1993; Orth et al., 1984). The present results show that some amphipod species have a higher abundance in specific habitats. Some species (*E. brasiliensis*, *G. fucicola*, *L. costae* and *L. longicornis*) were associated with *H. scoparia* possibly because of the higher structural complexity of this alga. The importance of habitat physical structure compared with other features, such as chemical cues or micro-fouling as food resource, may be high because the artificial substratum used in our experiment had a higher abundance of some species. It should also be noted that the mesh per se serves as an ideal substratum for the attachment of caprellids using their pereopods, while amphipods belonging to this group are also predominantly found attached to the more exposed parts of plants (Aoki, 1999; Sudo and Azeta, 2001). *C. acanthifera* was consistently present in the mesh bags and the species has been reported to occur on many different substrata (see Guerra-García, 2001).

C. racemosa does not appear to be an unfavourable substratum for amphipods. *E. pocillimanus* and *Microdeutopus* spp. were more abundant in *H. scoparia* and *C. racemosa*. Moreover, species of the genus *Microdeutopus* are reported to have higher abundance values on substrata colonised by *C. racemosa* compared to ones colonised by native algae (Vázquez-Luis et al., 2008, 2009b). In contrast, *C. acanthifera* had different patterns of abundance at the two localities; in Malta it was more abundant in *C. racemosa* habitat, while in Spain it was more abundant on the artificial substratum.

Our results show that the species richness and abundance of amphipods may be affected by the presence of detritus but with high spatial heterogeneity. Detritus plays a very important role as a trophic resource for marine invertebrates and serves as one of the main trophic pathways in marine ecosystems (Valiela, 1995), while it is also one of the most important features of habitat structure in vegetated habitats (Allesina et al., 2005). It is suggested that amphipods do not consume algal biomass directly, but feed on associated material such as detritus (Enequist, 1949). The detritus stock associated with *C. racemosa* appears to play an important role for amphipod assemblages, as has been shown in other studies (Vázquez-Luis et al., 2008). It appears that gammarids are able to exploit the detritus as a microhabitat, while this is not as useful for caprellids which prefer the external canopy (Aoki, 1999) but Guerra-García and Tierno de Figueroa (2009) showed that detritus was clearly the main dietary component of caprellids.

Some species were abundant in their natural habitat but were absent in the mesh bags. One explanation is that the biology of a given species may be playing an important role. Herbivorous amphipods, such as those belonging to the family Ampithoidae and the genera *Hyale* and *Dexamine*, had high abundance values in their natural habitat but lower abundance values in the mesh bags at both study localities. Some species such as *A. ramondi*, *D. spiniventris*, *H. camptonyx* and *H. schmidtii* are strongly linked to the algal canopy and are very sensitive to habitat alteration; hence, they did not respond under experimental conditions. *A. ramondi* lives in transparent, gelatinous tubes on algae and seagrasses (Ruffo, 1982) and is therefore a sedentary species that does not move away from its host. In any case, lower abundance values of *A. ramondi* and *H. schmidtii* in habitats invaded by

C. racemosa and *C. prolifera* have been detected in some studies (Sánchez-Moyano et al., 2001; Vázquez-Luis et al., 2008, 2009b). Another possible explanation concerns the limitation of the methodology used in our experiment, since algae placed in our experimental bags did not necessarily retain the same morphology, and hence structural complexity, compared to the erect algae attached to the substratum in the natural habitat. However, in spite of this, the use of an appropriate experimental design to avoid confounding influences in studies of habitat selection as adopted in the present work is deemed very important (Olabarria et al., 2002).

In conclusion, when introduced, *C. racemosa* modifies rocky bottom algal habitats, which results in changes to the abundance and species richness of the associated amphipod assemblages. However, some amphipods fare better in algal habitat that has been invaded by the alien species. The present findings suggest that the total abundance and species richness of amphipods is higher in algal stands formed by the native *H. scoparia* but is also positively affected by the presence *C. racemosa*. Detritus may play an important role, depending on local environmental factors, since colonization of invertebrates is a complex process and local ecological conditions may also be very important in determining substratum selection by amphipods. Further experiments on habitat selection and the diet of amphipods are necessary to obtain a better understanding of such potential changes to benthic ecosystem functioning that may result from the spread of invasive species.

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