

## Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain

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### Abstract

The mobile epifauna colonizing the invasive brown alga *Sargassum muticum* (Yendo) Fensholt was compared with assemblages inhabiting two locally established seaweeds (*Fucus vesiculosus* L. and *Cystoseira nodicaulis* (Whit.) Roberts) in a sheltered locality of northern Spain. The epifauna colonizing *S. muticum* was studied in both the shallow subtidal and intertidal pools at mid shore. The main aims of this study were to: (i) determine the host-plant specificity of the mobile epifauna; (ii) estimate the impact of the invasion on these animal assemblages. The mobile epifauna was not highly host-plant specific; very few taxa were found in just one algal species. Herbivorous species (mesograzers) were very abundant, accounting for 58–98 % of the characterized epifauna. *Sargassum muticum* was successfully colonized by the assemblages inhabiting local seaweeds, and this was probably due to: (i) the presence of epifaunal species that use plant epiphytes as habitat and food rather than the macroalga itself; (ii) morphological and chemical similarities between the invasive and the local seaweeds; (iii) generalist habits of mesograzers consuming the host plant itself. The impact of *S. muticum* invasion on the epifauna depends on the degree of host-plant specificity of animals as well as on the effect of the invader on macroalgal assemblages. The results of this study support the existence of a labile association between seaweeds and the invertebrates inhabiting them. ©1999 Elsevier Science B.V. All rights reserved.

*Keywords:* Amphipods; Epifauna; Invasion; Mesograzers; *Sargassum muticum*

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### 1. Introduction

Marine macroalgae and seagrasses harbor an abundant and diverse assemblage of invertebrates, very frequently motile species such as small crustaceans (amphipods, isopods)

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and gastropods (see for example Dean and Connell, 1987a; Arrontes and Anadón, 1990a, 1990b; Taylor and Cole, 1994). These animals exhibit a wide range of trophic habits. Some species are filter feeders or detritivores, or prey upon other epifauna, but commonly many of them are herbivores (mesograzers sensu Brawley, 1992), consuming epiphytic algae or the host plant itself (Duffy, 1990; Bell, 1991; Duffy and Hay, 1991a). Macrophytes may also provide refuge for animals from physical stress (desiccation, wave impact) and protection from predators.

Patterns of distribution and abundance of epifauna differ among marine macrophytes. These differences may be related to variation in the physical environment and the physiological tolerance of the animals (Holdich, 1976; Williams, 1992; Lancelloti and Trucco, 1993). However, the epifaunal assemblages also differ among macroalgae or seagrasses inhabiting the same tidal height or wave exposure (Young, 1981; Taylor and Cole, 1994). Different patterns of distribution and abundance of mobile epifauna are very often the result of an active host selection instead of the effect of differential mortality among host plants (Leber, 1985; Dean and Connell, 1987b; Hacker and Steneck, 1990; Edgar, 1992).

Epifaunal abundances and species composition can be strongly influenced by host plant architecture; macroalgae with higher morphological complexity are usually preferred by animals (Hacker and Steneck, 1990; Gee and Warwick, 1993; Jacobi and Langevin, 1996). For some animals, the presence of algal epiphytes is the determinant of their habitat preferences (Schneider and Mann, 1991a, 1991b; Martin-Smith, 1993). The distribution among host plants may change during developmental phases (Salemaa, 1987; Hacker and Steneck, 1990; Gee and Warwick, 1994).

Despite the presence of different patterns of abundance and distribution among macroalgae, motile epifauna seem to present a low degree of host-plant specificity. Even mesograzers feeding on the host plant itself are rarely specialists, confined to a sole macrophytic species (Arrontes, 1990; Duffy and Hay, 1991b). However, the studies are biased towards the more abundant or widespread species and descriptions of the total assemblages inhabiting different host plants are rare (but see Taylor and Cole, 1994). The pattern of colonization of an invasive seaweed by the local epifauna constitutes a great opportunity to study the degree of specialization in host utilization in these marine systems. The study of the colonization by herbivorous species may provide insights into the ecology and evolution of plant–herbivore interactions. The degree of host-plant specificity will, moreover, determine the local impact of the invasion on the epifaunal assemblages.

On the northern Spanish coast, the brown algae *Sargassum muticum* Yendo (Fensholt) invaded the rocky shores in the 1980s (Fernández et al., 1990). The species has mainly colonized the shallow subtidal level of sheltered shores and rock pools in the mid shore of sheltered and more exposed locations (Andrew and Viejo, 1998). Some other studies of the epifauna inhabiting this invasive algae have been carried out on British (Withers et al., 1975; Jephson and Gray, 1977) and North American shores (Norton and Benson, 1983). However, quantitative comparisons with the epifauna associated to indigenous algae are unknown. In the present study, quantitative sampling was carried out on the invasive *S. muticum* and two local brown algae: *Fucus vesiculosus* L. and *Cystoseira nodicaulis* (Whit.) Roberts. The patterns of distribution and abundance of the epifauna were studied throughout an annual cycle in a sheltered location. The main goal of the present study was to characterize the epifaunal assemblages inhabiting the local species and the invasive *S. muticum*, in order

to: (i) determine the degree of host-plant specificity of the animals; (ii) estimate the local impact of the invasion on the epifaunal assemblages.

## 2. Materials and methods

### 2.1. Study site and seaweeds

Samples of *Sargassum muticum*, *Fucus vesiculosus* and *Cystoseira nodicaulis* were collected for identification and quantification of the mobile epifauna in El Truhán Inlet, on the North coast of Spain (43°36'41"N, 5°46'29" W), from April 1991 to March 1992. The invasive seaweed *Sargassum muticum* is abundant in this sheltered area in tidepools and at low intertidal–shallow subtidal level (Fernández et al., 1990; Andrew and Viejo, 1998). *S. muticum* was sampled at two tidal levels: tidepools near the *F. vesiculosus* zone (0.9–1.2 m above lowest astronomical tide) and the low intertidal–shallow subtidal where *C. nodicaulis* is also present (–0.2–0.4 m LAT). The studied seaweeds will be referred to as *Sargassum* ‘tidepools’, *Sargassum* ‘low’, *Fucus* and *Cystoseira* respectively.

### 2.2. Sampling protocol

Plants were collected one day every month, during low water of spring tides. The samples of *Sargassum* ‘low’ in October 1991 and of *Sargassum* ‘tidepools’ from June to October 1991 had very low biomass (less than 5 g dry weight) and were not considered in this study. The low biomass of these samples was related to: (a) the phenology of *S. muticum* in this area, with senescence of reproductive plants in summer, and settlement of new individuals in early autumn (Fernández et al., 1990); (b) the smaller dimensions of *S. muticum* individuals growing in tidepools in comparison with the plants growing in the shallow subtidal.

Four samples were collected per day and seaweed species; thalli (1–3 per sample) were carefully removed from the substratum, and placed in plastic bags with 4% formalin. Samples were frozen (–16°C) until they were sorted.

The seaweeds were then vigorously washed in a bucket containing freshwater and carefully examined to collect all visible animals. The animals were collected with forceps and stored in 70% ethanol prior to identification and counting. The macroscopic algal epiphytes were removed from macroalgae and epiphytes and macroalgae were weighed separately after drying at 60°C for 72 h. The abundance of mobile animals was quantified. Counts were done using a dissecting microscope and the abundances were all standardized to numbers per 10 g algal dry weight (without algal epiphytes). In the case of fragmented animals (such as Polychaeta), only heads were counted. Copepoda (Crustacea), though present in some of the samples, were not quantified nor considered in this study. Animals included in the study were within a size range from roughly 0.1 to 10 cm (from small isopods to fishes of genus *Nerophis*).

The most abundant groups, Isopoda, Amphipoda Gammaroida and Gastropoda, were identified, whenever possible, to species level using dissecting and light microscopes. In

some amphipods, such as the genus *Ericthonius*, only males could be determined to species using the morphology of their second gnathopod.

### 2.3. Feeding habits of the epifauna

The feeding habits of the mobile epifauna were determined using bibliographic references, in order to establish the percentage of herbivores (mesograzers) inhabiting the seaweeds. Species or taxonomical groups were categorized as herbivores, predators or detritivores. Omnivores were species or taxa that fell into two or more of the above categories.

The diet of gammarid amphipods, the most abundant group of animals on *Sargassum* 'low' and *Cystoseira*, was investigated by analysis of gut contents when its abundance was highest (July, August and September 1991 samples). 10–20 amphipods with full guts were chosen per date. Each whole gut was observed through a microscope at a magnification of 400 $\times$ . Food items were grouped into four categories: macroalgae (*Fucus*, *Sargassum*, etc.), filamentous algae (*Audouinella*, *Sphacelaria*, etc.), detritus (material with sand, sponges, benthic diatoms, etc.) and unidentified material. The relative abundance of each category of food was roughly estimated by eye.

### 2.4. Body size of isopods inhabiting *Sargassum* 'tidepools' and *Fucus*

The body size of the most abundant species on *Fucus* and *Sargassum* 'tidepools', the isopod *Dynamene bidentata*, was estimated for each seaweed and date. The length, from cephalon to the end of pleotelson, was measured with a dissecting microscope and a calibrated ocular.

### 2.5. Statistical analysis

Canonical discriminant analysis (CDA) was used to examine the uniqueness of the epifaunal assemblages on the different algal hosts, and to identify the epifaunal taxa which best discriminated between algae. The 18 most abundant species or taxonomic groups of invertebrates were selected for the analysis. Samples from June to October 1991 were not included in the analysis, in order to balance the number of samples of *Sargassum* 'tidepools' in relation to the other three groups. Data were  $\log_{10}(x + 0.1)$  transformed to fit the linear model used in CDA, homogenize variances and reduce emphasis on species with very high abundances (see Pielou, 1984).

Differences between *Sargassum* 'low' and *Cystoseira* in the abundance of the most common groups of animals were analysed by two-way analysis of variance, with date and alga as orthogonal factors. Data were transformed prior to analysis as required by Cochran's test for homogeneity of variances and the transformations are indicated in the relevant tables. Unifactorial analysis of variance were used to compare the peaks of abundance of amphipod species between *Sargassum* 'low' and *Cystoseira* and their mean abundances throughout the year.

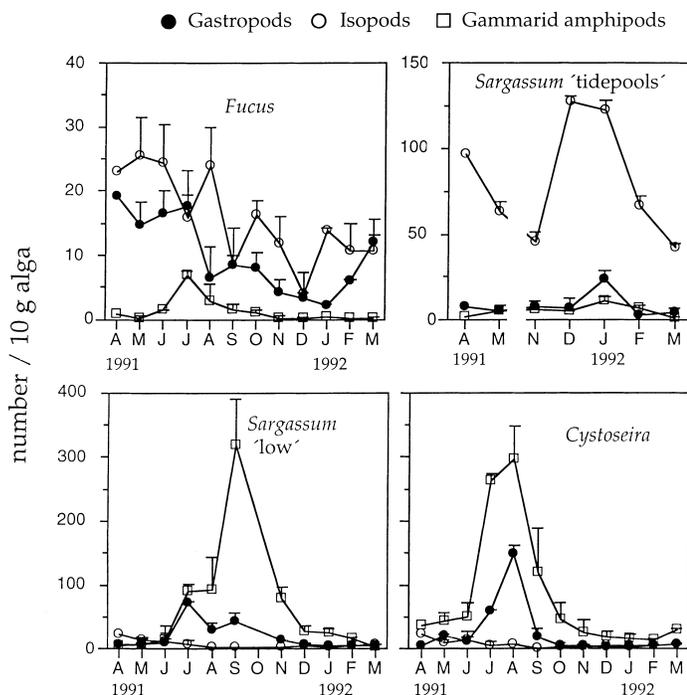


Fig. 1. Mean densities ( $\pm$ SE) of the most abundant groups of invertebrates (isopods, gastropods and gammarid amphipods) on *Fucus*, *Sargassum* 'tidepools', *Sargassum* 'low' and *Cystoseira*. Note different y axes scales between seaweeds.

The body size of the isopod *D. bidentata* in *Fucus* and *Sargassum* 'tidepools' was also analysed with a two-factor (alga and date) analysis of variance. Only eight dates were used in the analysis, in order to balance the number of samples per seaweed.

### 3. Results

#### 3.1. General patterns of distribution and abundance of the epifauna

The total density of mobile epifauna varied among seaweeds. *Fucus* had the lowest epifaunal densities through the year, with a mean abundance ( $\pm$ SE) of 33 individuals per 10 g of alga ( $\pm 2$ ) (pooled data). Gastropods, isopods and gammarid amphipods accounted for 90–95% of the total number of vagile invertebrates, but the relative importance of groups varied among seaweeds. On *Fucus* and *Sargassum* 'tidepools', the isopods were the most abundant taxa, whereas on *Sargassum* 'low' and *Cystoseira* gammarid amphipods constituted the dominant group (Fig. 1). A considerable variation in epifaunal densities was observed through time, mainly in gammarid amphipods colonizing *Sargassum* 'low' and *Cystoseira* (Fig. 1).

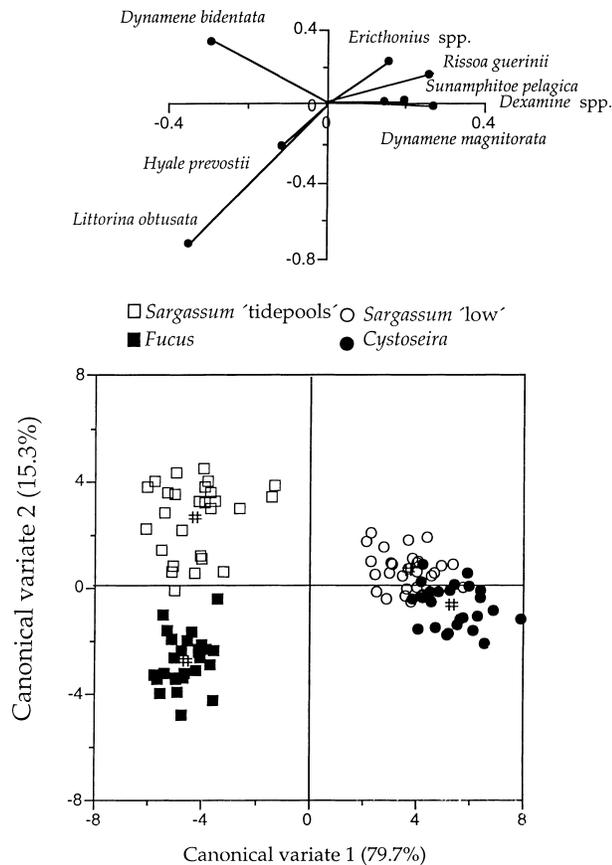


Fig. 2. Canonical discriminant analysis (CDA) plot of the first 2 canonical variates summarising trends in densities of the 18 commonest epifaunal taxa on *Fucus*, *Sargassum* 'tidepools', *Sargassum* 'low' and *Cystoseira*. Symbol # represent the centroids for each group (seaweed). Percentages associated with each canonical variate refer to the proportion of total variation accounted for that canonical variate. Some of the pooled within-groups correlations between epifaunal taxa and canonical variates are also shown.

The epifaunal taxa found on seaweeds are shown in Table 1. Focusing on the dominant groups (gammarid amphipods, isopods and gastropods), *Fucus* had the lowest number of taxa (21) in comparison with 30 taxa found on *Sargassum* 'tidepool', 39 on *Cystoseira* and 37 on *Sargassum* 'low' (Table 1). Overall, the epifauna was not highly host-plant specific. Very few taxa were found on just one algal species. Most of these cases, such as the gammarid amphipods *Hyale prevostii* and *Amphitolina cuniculus* were found just on *Fucus* (Table 1).

CDA analysis on densities of the 18 commonest taxa showed that samples of *Fucus* and *Sargassum* 'tidepools' were clearly differentiated from those of *Sargassum* 'low' and *Cystoseira* along canonical axis 1, which explained the 79.73% of total variance (Fig. 2). Furthermore, *Sargassum* 'tidepools' and *Fucus* presented distinct epifaunas. The gam-

Table 1

Mean abundance per 10 g of alga (SE) of epifaunal species (pooled samples across dates). The abundances lower than 1 per 10 g of seaweed were classified in two groups: abundances < 1 but > 0.1 (labelled < 1) and abundances < 0.1 (labelled +)

	<i>Fucus</i>	<i>Sargassum</i> 'tidepools'	<i>Sargassum</i> 'low'	<i>Cystoseira</i>
Total number of samples	48	28	42	46
<b>Gastropoda</b>				
<i>Gibbula</i> spp. <sup>a,b</sup>	3 (0.5)	<1	<1	<1
<i>Rissoa parva</i> (da Costa) <sup>a</sup>	<1	4 (1.3)	<1	<1
<i>R. guerinii</i> (Recluz) <sup>a</sup>	+	<1	2 (0.3)	3 (0.5)
<i>Ocenebra aciculata</i> (Lamarck)			+	+
<i>Bittium reticulatum</i> (da Costa) <sup>a</sup>		<1	11 (3.5)	10 (3.1)
<i>Cerithiopsis</i> spp.		<1		
<i>Cingula trifasciata</i> (J. Adams)		<1		2 (0.7)
<i>Cingula</i> spp.	+		<1	+
<i>Barleeia unifasciata</i> <sup>a</sup> (Montagu)	+	<1	<1	<1
<i>Tricolia pullus</i> (Linné)	+	<1	<1	<1
<i>Skeneopsis planorbis</i> (Fabricius)		+	+	+
<i>Hinia</i> spp. <sup>c</sup>		+	+	+
<i>Littorina obtusata</i> (Linné) <sup>a</sup>	1 (0.2)			
<i>L. fabalis</i> (Turton) <sup>a</sup>	<1			
<i>Littorina</i> spp. <sup>a</sup>	7 (1.2)	<1	1 (0.3)	2 (1.3)
<i>Helcion pellucidum</i> (Linné)	+	+	<1	<1
Opisthobranchia	+	+	+	+
<b>Polyplacophora</b>				
<b>Amphipoda Gammaroidea</b>				
Lysianassidae			+	
<i>Amphilocheus neapolitanus</i> Della Valle			<1	<1
Stenothoidae		+	+	<1
<i>Orchestia gammarellus</i> (Pallas)	+			
<i>Hyale prevostii</i> Milne Edwards <sup>a</sup>	1 (0.4)			
<i>Hyale</i> spp.		+		+
<i>Gammarus</i> spp.	+	<1	1 (0.7)	+
<i>Apherusa bispinosa</i> (Bate) <sup>a</sup>		+	6 (3.1)	2 (0.4)
<i>A. jurinei</i> (Milne-Edwards) <sup>a</sup>		+	<1	<1
Pleustidae		<1	+	+
<i>Atylus swammerdami</i> (Milne-Edwards)			1 (0.5)	+
<i>Atylus</i> spp.		<1		
<i>Dexamine spinosa</i> (Montagu) <sup>a</sup>		<1	13 (4.3)	26 (6.5)
<i>D. thea?</i> Boeck <sup>a</sup>			+	<1
<i>D. spiniventris</i> (A. Costa) <sup>a</sup>				+
<i>Amphitolina cuniculus</i> (Stebbing)	+			
<i>Amphithoe ramondi</i> Audouin <sup>a</sup>			9 (3.3)	8 (2.8)
<i>A. helleri</i> G.Karaman <sup>a</sup>	+	<1	10 (3.8)	22 (6.2)
juvenile <i>Amphithoe</i> spp. <sup>a</sup>	+	<1	7 (3)	2 (1)
<i>Sunamphithoe pelagica</i> (Milne-Edwards) <sup>a</sup>	+	+	1 (0.3)	3 (0.7)
<i>Corophium volutator</i> (Pallas)	+	<1		
Isaeidae				<1
<i>Aora typica</i> Kröyer <sup>a</sup>	+	<1	2 (0.7)	<1
<i>Erichthonius punctatus</i> Bate <sup>a,*</sup>		(*)	(*)	(*)
<i>E. difformis</i> Milne-Edwards <sup>a,*</sup>			(*)	(*)
<i>Erichthonius</i> spp. <sup>a</sup>	+	1 (1.06)	10 (3.0)	5 (1.4)
<i>Jassa pusilla</i> (Sars) <sup>a</sup>		+	2 (0.7)	+
<i>Podocerus variegatus</i> Leach <sup>a</sup>				+

Table 1  
Continued

	<i>Fucus</i>	<i>Sargassum</i> 'tidepools'	<i>Sargassum</i> 'low'	<i>Cystoseira</i>
<b>Amphipoda Caprelloidea</b>		<1	<1	<1
<b>Isopoda</b>				
<i>Dynamene bidentata</i> (Adams) <sup>a</sup>	16 (1.6)	80 (7.5)	3 (0.6)	2 (0.3)
<i>D. magnitorata</i> Holdich <sup>a</sup>		+	4 (0.8)	5 (1.1)
<i>Cymodoce truncata</i> Leach			+	+
<i>Synisoma acuminatum</i> Leach			<1	<1
<i>Idotea granulosa</i> Rathke		+	+	
<i>Paranthura nigropunctata</i> Lucas			+	
<i>Eurydice</i> spp.			+	+
<b>Cumacea</b>			+	
<b>Tanaidacea</b>			+	<1
Decapoda Natantia <sup>a,d</sup>		<1	<1	<1
Reptantia	+	<1	<1	<1
<i>Pachygrapsus marmoratus</i> (Fabricius)	+			
<i>Carcinus maenas</i> (Linné)	+			
<i>Pisa tetraodon</i> (Pennant)		+	+	+
<i>Clibanarius erythropus</i> (Latreille)		<1	+	<1
Megalopa (larval phase)			+	+
<b>Pycnogonida</b>	+	+	+	+
<b>Arachnida</b>	+	+	+	+
<b>Insecta (Chironomidae larvae)</b>	2 (1.0)	+	<1	2 (0.9)
<b>Polychaeta (Errantia)<sup>a</sup></b>	+	1 (0.4)	8 (2.1)	5 (1.3)
<b>Cnidaria</b>				
<i>Haliclystus auricula</i> (Rathke)		+	<1	<1
<i>Anemonia viridis</i> (Forskål)			+	
<b>Echinodermata</b>				
<i>Asterina gibbosa</i> (Pennant)			+	
Ophiuroidea		+		+
<b>Chordata</b>				
Pisces		<1	+	+
Total abundance	33 (2.3)	101 (9.1)	106 (22.2)	105 (19.3)

<sup>a</sup> The species or groups used in the canonical discriminant analysis (CDA, Fig. 2).

<sup>b</sup> *Gibbula umbilicalis* (da Costa) and *G. pennanti* (Philippi).

<sup>c</sup> *Hinia incrassatus* (Ström) and *H. reticulata* (Linné).

<sup>d</sup> Natantia: Families Palaemonidae, Pasiphaeidae, and Hippolytidae.

\* Presence of males.

marid amphipod *Hyale prevostii* and the gastropod *Littorina obtusata* were important for distinguishing the epifauna of *Fucus*, while the isopod *Dynamene bidentata* clearly characterized *Sargassum* 'tidepools' (Fig. 2). The invasive *S. muticum* had different epifaunal composition and abundance depending on the tidal level where it colonized, with samples of *Sargassum* 'tidepool' and *Sargassum* 'low' clearly differentiated (Fig. 2). *Sargassum* 'low' presented an epifaunal assemblage close to the assemblage associated to *Cystoseira* (Fig. 2). Both seaweeds were characterized by most of the species of gammarid amphipods, the gastropod *Rissoa guerini*, and the isopod *Dynamene magnitorata* (Fig. 2).

Table 2

Analysis of variance table for differences between seaweeds and dates on mean densities of gastropods, isopods and gammarid amphipods<sup>a</sup>

Source	df for F	Gastropods		Isopods		Gammarid amphipods	
		MS	F	MS	F	MS	F
Alga (A)	1, 64 <sup>b</sup>	0.03	0.41 <sub>ns</sub>	22.02	41.00***	1.89	14.25***
Date (D)	10, 64	1.67	25.16***	12.43	23.15***	2.11	15.92***
A x D	10, 64	0.22	3.37**	1.18	2.20 <sub>ns</sub>	0.57	4.30***
Residual		0.07		2.23		0.13	
Transformation		none		square root			log <sub>10</sub> (x + 0.1)

<sup>a</sup>\*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; ns: non-significant.

<sup>b</sup> Four values were replaced by the mean of the group and four df subtracted from the residual.

### 3.2. Predominant feeding habits of the mobile epifauna inhabiting the invasive and local seaweeds

The trophic status of a high percentage of the epifauna was characterized (around 95% on *Fucus* and *Sargassum* 'tidepools', more than 82% on *Sargassum* 'low' and *Cystoseira*) (bibliographic references are given in App. A). Herbivores were very abundant on the studied seaweeds; 58.2% of all the mobile epifauna characterized on *Sargassum* 'low', 75.7% on *Cystoseira*, 75.1% on *Sargassum* 'tidepools' and 98.6% on *Fucus* (pooled samples). Some taxonomic groups were considered omnivores, though they may include herbivorous species (for example, the polychaetes). Real percentages of herbivores on the epifaunal assemblages may be even higher than those estimated here.

### 3.3. The epifaunal assemblages inhabiting *Sargassum* 'low' and *Cystoseira*

Though the epifaunal assemblage that colonized *Sargassum* 'low' was similar to that inhabiting *Cystoseira*, some differences were found between seaweeds in the temporal patterns and densities of the most abundant groups. Densities of isopods were higher on *Cystoseira* (mean  $\pm$  SE =  $15 \pm 2.0$  individuals per 10 g of alga) in relation to *Sargassum* 'low' ( $8 \pm 0.2$ ) (Table 2), whereas differences between seaweeds in the densities of gammarid amphipods and gastropods were very dependent on the date (Fig. 1; Table 2). Abundance peaks of these two groups were observed on different dates in *Sargassum* 'low' and *Cystoseira* (Fig. 1; interaction alga  $\times$  date, Table 2).

#### 3.3.1. Abundances and temporal patterns of gammarid amphipods

Gammarid amphipods constituted the most abundant group of mobile epifauna on both *Cystoseira* and *Sargassum* 'low'. The families Ampithoidae and Ischyroceridae (genera *Erichthonius* and *Jassa*) and the genera *Dexamine* spp. and *Apherusa* spp. were the most abundant taxa within the group (Table 1). Abundance of the families Ampithoidae and Ischyroceridae and the genus *Dexamine* spp. peaked at different dates in the two seaweeds (Fig. 3). No significant differences were found either between peaks of abundance of these groups (Ampithoidae  $F_{1,4} = 2.05$ , ns; Ischyroceridae  $F_{1,4} = 0.55$ , ns; *Dexamine*  $F_{1,4} = 0.53$ , ns)

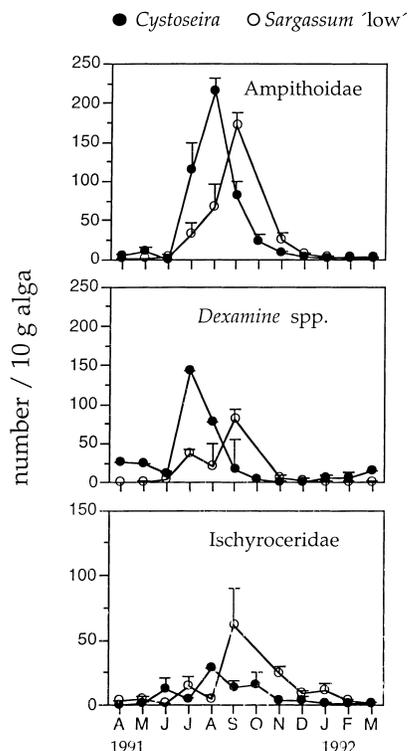


Fig. 3. Mean densities ( $\pm$ SE) of the most abundant groups of gammarid amphipods on *Sargassum* 'low' and *Cystoseira* (Amphithoidae, *Dexamine* spp. and Ischyroceridae). Note different y axes scales between the different groups.

or mean abundances of these groups throughout the year (Amphithoidae  $F_{1,21} = 0.19$ , ns; Ischyroceridae,  $F_{1,21} = 0.91$ , ns; *Dexamine*  $F_{1,21} = 0.83$ , ns).

Within the family Amphithoidae, abundance peaks were displaced in the most abundant species, *Amphithoe helleri* and *A. ramondi*; the juvenile *Amphithoe* spp. peaked in abundance in *Sargassum* 'low' in September 1991 (Fig. 4).

### 3.3.2. Gut contents of gammarid amphipods

Filamentous algae (such as *Elachistea flaccida* (Dillwyn) Areschoug, *Sphacelaria* spp., *Ceramium* spp.) were the most frequent components in the gut contents of gammarid amphipods during July, August and September, frequently constituting 100% of the gut content (Table 3).

### 3.3.3. Percentage of algal epiphytes on seaweeds

The peak of abundance of algal epiphytes was one month later in *Sargassum* 'low' than in *Cystoseira* (Fig. 5). The qualitative composition of algal epiphytes was very similar between the two seaweeds, with the presence of both filamentous and foliose species. *Leathesia difformis* (L.) Areschoug, *Sphacelaria* spp., *Elachistea flaccida* (Dillwyn) Areschoug,

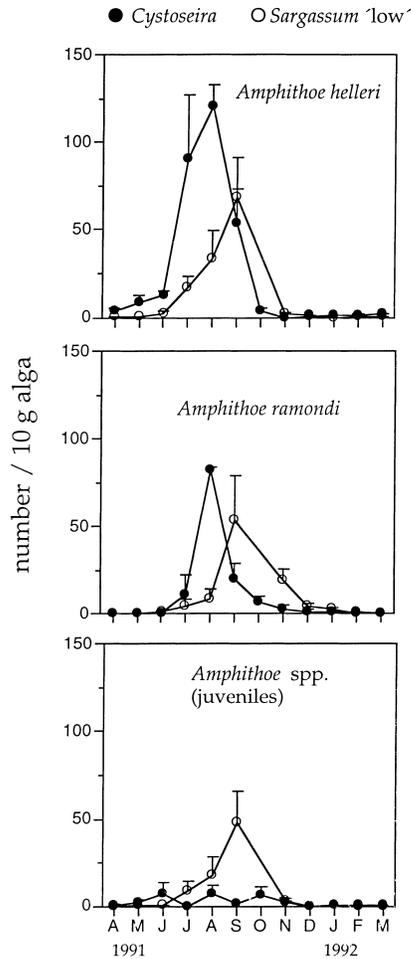


Fig. 4. Mean densities ( $\pm$ SE) of the species of genus *Amphithoe* and *Amphithoe* spp. juveniles on both *Sargassum* 'low' and *Cystoseira*.

*Ceramium* spp. *Calliblepharis jubata* (Good. and Woodw.) Kütz., *Ectocarpus* spp. and Ulvaceae were the most abundant taxa.

### 3.4. *Sargassum* 'tidepools': the abundance and size distribution of the isopod *D. bidentata* on the invasive alga in relation to *Fucus*

*Sargassum* 'tidepools' was mainly colonized by isopods (Fig. 1), and specifically by the species *D. bidentata* (Table 1). This isopod was present at higher densities on the invasive seaweed than on *Fucus* (Table 1), but the individuals were smaller on *Sargassum* 'tidepools' (Table 4). The body size of individuals is related to their developmental stage (Holdich, 1968); only the individuals above 4 mm length had sexual features (personal observation). These sizes were rare in *Sargassum* 'tidepools' (Fig. 6).

Table 3

Analysis of the gut contents of gammarid amphipods collected on *Sargassum* 'low' and *Cystoseira* during July, August and September 1991<sup>a,b</sup>

	<i>Sargassum</i> (low)						<i>Cystoseira</i>					
	July (n=21)		August (n=10)		Sept (n=23)		July (n=20)		August (n=20)		Sept (n=10)	
	% ind	%100	% ind	%100	%ind	%100	% ind	%100	% ind	%100	%ind	%100
Filamentous	61.9	38.1	80.0	40.0	82.6	30.4	100.0	70.0	90.0	35.0	90.0	50.0
Detritus	19.1	9.5	50.0	20.0	39.1	13.0	10.0	0.0	70.0	5.0	30.0	0.0
Unidentified material	33.3	19.1	10.0	0.0	26.1	4.3	5.0	0.0	5.0	5.0	30.0	20.0
Macroalgae	9.5	9.5	0.0	0.0	4.3	0.0	10.0	0.0	0.0	0.0	0.0	0.0

<sup>a</sup> % ind: Percentage of individuals with presence of the correspondent category of food in their gut contents.

<sup>b</sup> %100: Percentage of individuals with 100% of one category of food in their gut contents.

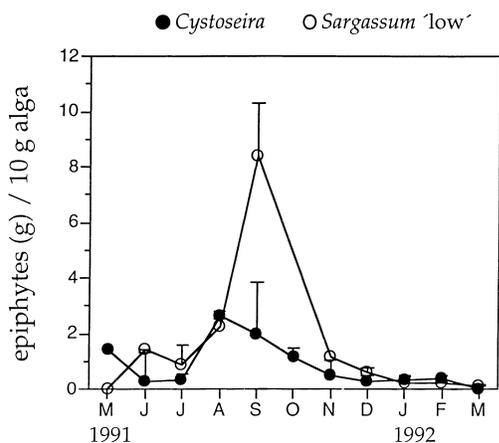


Fig. 5. Mean biomass of epiphytic algae (per 10 g of alga  $\pm$  SE) through time on both *Sargassum* 'low' and *Cystoseira*.

Table 4

Analysis of variance table for differences on mean lengths of the isopod *D. bidentata* between *Fucus* and *Sargassum* 'tidepools'<sup>a</sup> and mean lengths  $\pm$  SE, data pooled across dates<sup>b</sup>

Source	df for F	MS	F	p
Alga	1,7 <sup>c</sup>	0.9211	9.36	*
Date	7,219 <sup>d</sup>	0.0732	5.20	***
A $\times$ D	7,219	0.0224	1.59	ns
Residual		0.0141		
Mean $\pm$ SE	<i>Fucus</i>	3.2 $\pm$ 0.2 mm (n = 48)		
	<i>Sargassum</i> 'tidepools'	2.2 $\pm$ 0.2 mm (n = 28)		

<sup>a</sup> Log transformed data.

<sup>b</sup> \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; ns: non-significant

<sup>c</sup> Date was considered a random factor and the effect of alga tested against the interaction MS.

<sup>d</sup> Five values were replaced by the mean of the group and five df subtracted from the residual.

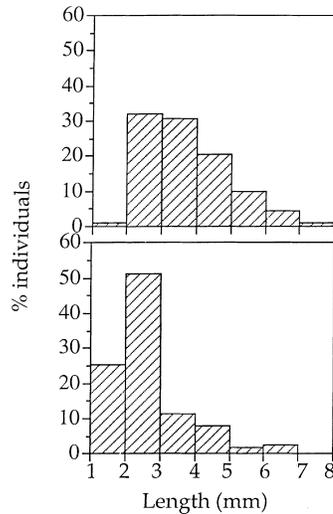


Fig. 6. Size frequency distributions of the isopod *D. bidentata* on both *Fucus* and *Sargassum* 'tidepools' (data pooled across dates).

#### 4. Discussion

##### 4.1. Colonization of *S. muticum* by invertebrates inhabiting local macroalgae: degree of host-plant specificity

The results of this study support the existence of a labile association between macroalgae and the invertebrates inhabiting them; the composition of the epifaunal assemblages associated to the invasive *Sargassum muticum* and the local *C. nodicaulis* were very similar.

One of the possible causes of the low specificity of the epifauna to the host plant is the existence of an indirect relationship, mediated by the presence of epiphytic algae. The abundance peaks of gammarid amphipods on *C. nodicaulis* and *S. muticum* concurred with the peaks of epiphytic algae. This result suggests that there is a habitat change in gammarid amphipods, from *C. nodicaulis* to *S. muticum*, in response to the availability of food (epiphytic algae) at the end of summer. The most abundant amphipods, those of the genus *Dexamine* and the family Ampithoidae, are mainly grazers (App. A). Gut content analysis indicates that gammarid amphipods feed on epiphytic algae during summer. The relationship between the abundance peaks of epiphytic algae and gammarid amphipods is not, however, necessarily related to the trophic habits of the species. The epiphyte load increase the structural complexity of the habitat (Martin-Smith, 1993) and consequently may reduce the susceptibility to predation (see for example Edgar, 1983) or simply increase the living space (Hacker and Steneck, 1990; Gee and Warwick, 1993). In domicolous amphipods such as Ischyroceridae and Ampithoidae, epiphytic algae may be used as material for tube building or as a sediment trap (Johnson and Scheibling, 1987; Schneider and Mann, 1991a).

The structural similarities of *S. muticum* and *C. nodicaulis*, both having complex morphology, is another possible cause of the similarities between their epifaunal assemblages.

In the present work, samples were collected during the day. Some mobile species can separate the resource refuge from the resource food in time (day and night), selecting algae of high food quality at night and algae with complex structure (such as *S. muticum* or *C. nodicaulis*) as refuge during the day (Buschmann, 1990).

Some of the species that colonized *S. muticum* certainly feed on it. Damaged thalli of *S. muticum* were frequently observed in the field (personal observation), with superficial scrapings or small holes, similar to the grazing marks detected in *F. vesiculosus* by Viejo and Arrontes (1992). The isopod *D. bidentata*, for instance, commonly feeds on the macroalgae that it inhabits (Arrontes, 1990; Viejo and Arrontes, 1992) and it grazed on *S. muticum* in the laboratory (personal observation). This isopod was present on *S. muticum* in the shallow subtidal and extensively colonized the invasive seaweed in intertidal pools.

If the invertebrates can colonize and feed on an invasive species, the practise of feeding on host plants must be an ecologically dynamic process and not the result of a long evolutionary history between the plant and animal. However, in this study, the use of *S. muticum* as a feeding source may reflect the generalist habits of mesograzers as well as the chemical and structural similarities between the invasive species and the local seaweeds. The similarity between the fauna inhabiting *S. muticum* and that inhabiting seagrasses (see Caine, 1980) support the existence of a labile plant–animal association in these marine systems dominated by macrophytes.

Despite the low host specificity of the epifauna, the abundance of several species differed between seaweeds or between tidal levels. *S. muticum* plants in the low intertidal had a higher number of epifaunal species than those living in tidepools. Fluctuations in physical factors such as salinity or temperature are significant in intertidal pools (Metaxas and Scheibling, 1993); tolerance ranges of animals to these changes determine their patterns of distribution through the tidal gradient. The different colonization of *S. muticum* in the low intertidal and rock pools can also be influenced by differences in the epiphyte load or the smaller size of the rock pool plants. The complexity of the seaweeds, as biomass, was very often related to the number of animal species associated with them (Gunnill, 1982; Dean and Connell, 1987a; Schneider and Mann, 1991a).

The most abundant species colonizing *S. muticum* in intertidal pools was the isopod *D. bidentata*. The individuals colonizing the invasive alga were smaller than those living on *F. vesiculosus*, being juveniles of the first post-marsupial stages whereas individuals living on *F. vesiculosus* belonged to later developmental phases. The physical environment of *F. vesiculosus* is harsher, with emersion periods close to six hours twice a day. A late recruitment in this seaweed may be an advantageous strategy in minimizing stress upon early, presumably more sensitive growth stages of the fauna, as suggested by Arrontes and Anadón (1990b).

The more branched and apparently less tough thalli of *S. muticum* may also influence the body-size distribution of the isopod. The accumulation of smaller individuals of isopods and gammarid amphipods in more finely filamentous algae can be due to age-dependent changes in diet (Salemaa, 1987), or to body-size scaling to habitat dimensions (Edgar, 1983; Leber, 1985; Hacker and Steneck, 1990; Gee and Warwick, 1994). In a similar way, the abundance peak of juvenile *Ampithoe* spp. on *S. muticum* at low intertidal may also reflect body-size-dependent host selection. The abundance of algal epiphytes would determine

host selection in juveniles, whereas in the larger specimens additional factors, such as the structure of the macroalgae, or their temporal permanence, may also be important.

Summarizing, *S. muticum* has been successfully colonized by the epifauna inhabiting local seaweeds. This is probably due to: (i) presence of epifaunal species that use plant epiphytes growing on the macroalga as food resource and/or living space rather than the macroalga itself; (ii) morphological and chemical similarities between the invasive and the local seaweeds (iii) generalist habits of mesograzers consuming the host plant itself.

Despite the low specificity of the epifauna by the host plant, the abundance distributions of animals among seaweeds suggest the presence of mechanisms of host selection, which are probably different for each species and even for each developmental stage within a species.

#### 4.2. *Impact of the invasion of S. muticum on the epifaunal assemblages*

The impact of *S. muticum* invasion on the epifaunal assemblages depends on the host-plant specificity of the animals and the similarities between the invasive and the local seaweeds, but it is also related to the impact of the invasion on the macroalgal assemblage. In the studied locality, as on other European shores (Fletcher and Fletcher, 1975; Jephson and Gray, 1977; Critchley, 1983), *S. muticum* colonized areas with low initial cover of macroalgae (Fernández et al., 1990). In this case, the presence of the invasive seaweed supplies a new and additional habitat for the local epifauna. The establishment of the species, with its cover of epiphytes, sediment and harpacticoid copepods, will increase the temporal and spatial availability of food resources. The seasonal decrease of epifaunal species has been related to food limitations (Edgar, 1990). The invertebrates inhabiting macroalgae are the prey of omnivorous fishes and decapods (Leber, 1985; Brawley, 1992; Williams, 1992), and, therefore, *S. muticum* invasion will result, ultimately, in an increase in the secondary production in the local benthic system. However, the effect of the introduction of *S. muticum* on the epifauna may be very different at other sites, where *S. muticum* reduces the abundance of indigenous perennial macroalgae (see Viejo, 1997). *S. muticum* has high growth rates and annual losses of considerable parts of the thalli (Norton, 1977) in contrast with other perennial seaweeds. At these other sites the invasion would increase the seasonality of the macroalgal biomass and the abundance of animals with long life cycles may be negatively affected.

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## Appendix A. Feeding habits of the epifaunal species found in this study and the references including these feeding modes

### Herbivores

- Helcion pellucidum* ('parasite' of algae) (Graham and Fretter, 1947)  
*Littorina obtusata* (Viejo and Arrontes, 1992)  
*L. fabalis* (Williams, 1992; Watson and Norton, 1985)  
*Gibbula umbilicalis* (Graham, 1971; Withers et al., 1975)  
*Rissoa parva* (Borja, 1986)  
*Amphitolina cuniculus* ('parasite' of algae) (Lincoln, 1979)  
 Genus *Amphithoe* (Duffy, 1990)  
*Amphithoe ramondi* (Zimmerman et al., 1979; Edgar, 1992)  
*Sunampithoe pelagica* (Withers et al., 1975)  
*Hyale prevostii* (Viejo and Arrontes, 1992)  
*Dexamine spinosa* (Greeze, 1968; Zimmerman et al., 1979)  
*Dynamene bidentata* (Holdich, 1976; Arrontes, 1990; Viejo and Arrontes, 1992; Morán and Arrontes, 1994)  
*D. magnitorata* (Arrontes, 1990)  
*Idotea* spp. (Nicotri, 1980; Kangas et al., 1982; Salemaa, 1987)  
 Chironomidae larvae (Brawley, 1992)

### Predators

- Cerithiopsis* spp. (Graham, 1971)  
*Paranthura nigropunctata* (Wägele, 1982)  
*Eurydice* spp. (Naylor, 1972)  
 Tanaidae (Barnes, 1984)  
*Carcinus maenas* (Cohen et al., 1995)  
 Pycnogonida (Barnes, 1984)  
 Opisthobranchia (Thompson and Brown, 1976)  
*Nerophis* spp. (Piscis) (Bauchot and Pas, 1987)

### Detritivores

- Atylus* spp. (Edgar, 1992)  
*Orchestia* spp. (Behbehani and Croker, 1982)  
*Corophium* spp. (Barnes, 1984)  
*Aora* spp. (Barnes, 1984)  
*Clibanarius erytrophus* (Barnes, 1984)  
*Barleeia unifasciata* (Borja, 1986)  
*Tricolia pullus* (Fretter and Manly, 1977)  
*Hinia* spp. (Hyman, 1967)

### Omnivores

- Genus *Cymodoce*: herbivores and predators of sponges (Arrontes, 1987)  
*Jassa (falcata)*: filter feeder and herbivore (see ref. in Duffy, 1990)  
*Palaemon serratus*: predator and herbivore (Smaldon, 1979)  
*Bittium reticulatum*: detritivore and herbivore (Borja, 1986)  
*Erichtonius (brasiliensis)*: filter feeder and detritivore? (Duffy, 1990)

*Gammarus (locusta)*: detritivore and herbivore (Greeze, 1968)  
 Polychaeta Errantia: predators; herbivores; filter feeders (Fauchald and Jumars, 1979)  
 Ophiuroidea: predators and detritivores (Lawrence, 1987)  
 Caprellioidea: filter feeders and predators (see ref. in Duffy, 1990); herbivores (ref. in Brawley, 1992)

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