

# Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches

Iván F. Rodil\*, Celia Olabarria, Mariano Lastra, Jesús López

Departamento de Ecología y Biología Animal, Universidad de Vigo, Campus As Lagoas-Marcosende, 36310 Vigo (Pontevedra), Spain

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## Abstract

Many sandy beaches worldwide receive large amounts of drift seaweed, known as wrack, from offshore algal beds and closer rocky intertidal shores. Despite the important influence of algal wrack on macrofaunal assemblages from different coastal systems, relatively little attention has been paid to the macrofaunal responses in sandy beaches to macrophyte wrack supplies. Algal wrack is a key resource, i.e. for food and/or refuge, for beach invertebrates while its availability can affect diversity and abundance of intertidal animals including shorebirds, but the role of certain types of wrack and its location on the shore has not been examined experimentally to date. In this paper, we use experimental manipulation of two species of brown seaweeds, i.e. artificial wrack patches made up of the native macroalgae *Saccorhiza polyschides* and the invasive species *Sargassum muticum*, to test hypotheses about influences on macrofaunal assemblages inhabiting the drift line and supratidal levels of exposed beaches. Results pointed out that different types of wrack deposits were not used uniformly by invertebrates. Nutritional value differed between the two species of wrack. In most cases, the carbohydrates, lipids and organic carbon content were greater in patches of *S. muticum* than in patches of *S. polyschides*. Data also provided evidences that nutritional content and microclimatic conditions of wrack deposits, i.e. temperature and humidity, might affect macrofaunal assemblages.

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**Keywords:** Experimental manipulation; Invasive species; Macroalgal wrack; Macrofaunal assemblages; Sandy beaches

## 1. Introduction

Many sandy beaches worldwide receive large amounts of drift seaweed from offshore algal beds and closer rocky intertidal shores (Inglis, 1989; Rossi and Underwood, 2002; Dugan et al., 2003). The importance of beach accumulations of wrack on the ecology of sandy beaches has been previously documented in the literature (see Colombini and Chelazzi, 2003 and references therein). Algal wrack deposits represent the main food resource for upper shore detritus feeders such as talitrid amphipods, tyloid and oniscoid isopods besides tenebrionid and staphylinid beetles (Colombini et al., 2000; Dugan et al., 2003). Wrack also acts as a refuge for the supralittoral fauna, mainly terrestrial and semi-terrestrial arthropods, providing an opportunity to study seaweed debris both as a food resource and shelter habitat (Inglis, 1989; Colombini et al., 2000; Jędrzejczak, 2002a,b; Olabarria et al., 2007).

Despite the important influence of algal wrack on macrofaunal assemblages from different coastal systems, relatively little

attention has been paid to the macrofaunal responses in sandy beaches to macrophyte wrack supplies (see Olabarria et al., 2007). On sandy beaches, wrack is deposited throughout the entire intertidal range creating a patchy scene of bare and wrack occupied areas (Valiela and Rietsma, 1995; Colombini et al., 2000; Rossi and Underwood, 2002). The spatial distribution of wrack debris along the beach profile should be a very important factor since the higher the seaweed is located on the beach, the longer it is presumably present on the intertidal zone. Close to the swash zone, in the lower part of the intertidal zone, mats of wrack are driven mainly by the physical forces of waves, tides and sediment movement during the entire period of stranding. Wrack deposits at the supratidal zone undergo dehydration, ages and finally become covered by wind-blown sand. After a period of decomposition and decay, wrack releases nutrients, particularly N and P, which can enhance benthic microalgae and stimulate growth of aerobic and anaerobic bacteria. Processes are complex and depend on the amount and taxonomic composition of wrack (Rossi and Underwood, 2002; Jędrzejczak, 2002a). For example, different seaweeds may vary in physical structure (levels of branching, toughness), nutritional values and decomposition rates, which could potentially influence wrack-

\* Corresponding author. Tel.: +34 986812588; fax: +34 986812556.

E-mail address: iredil@uvigo.es (I.F. Rodil).

associated macrofauna. Different physical structures of seaweeds may also modify microclimatic conditions, i.e. temperature and humidity of wrack deposits. Therefore, different types of wrack might influence the structure and function of animal assemblages and determine taxonomic composition, number and turnover of species (e.g. Valiela and Rietsma, 1995; Colombini et al., 2000; Pennings et al., 2000; Goecker and Käll, 2003).

Accumulations of dead seaweed on the beach face are a ubiquitous feature of Galician sandy beaches (NW Spain), where heaps of macroalgae frequently appear stranded, mainly consisting of brown macrophytes such as *Saccorhiza polyschides*, *Sargassum muticum*, *Fucus* spp., and *Laminaria saccharina* (Olabarria et al., 2007). The amount and type of stranded material also vary at different spatio-temporal scales. In summer, for example, considerable amounts of *S. polyschides* and *S. muticum* are stranded on beaches, creating a mosaic of bare and wrack affected areas (pers. obs.). In this context, it would be interesting to take heed of the effect of both species on the macrofaunal assemblages inhabiting exposed sandy beaches. Another important point to consider is the origin of both species, since *S. polyschides* is a native seaweed species, whereas *S. muticum* is an invasive species. This species was first observed on the Galician coast in 1986 (see Pérez-Cirera et al., 1989) and since then has successfully colonised most of the Galician estuaries, increasing its abundance rapidly. The rapid spread of *S. muticum* might have important effects on the composition, structure and organization of local assemblages on rocky shores and sandy beaches (via stranded seaweed). Invasive species have been reported to have strong impacts on local ecosystems, changing species diversity, trophic structure and dynamics of populations, negatively affecting ecosystem processes (Carlton, 1996). So far, no studies have compared the effects of types of stranded seaweed (native versus exotic species) on macrofaunal assemblages dwelling on exposed sandy beaches.

In this paper, we used experimental manipulation of two types of brown seaweeds, i.e. artificial wrack patches comprising the native macroalgae *S. polyschides* and the invasive species *S. muticum*, to test hypotheses about influences on macrofaunal assemblages inhabiting the drift line and supratidal zone (i.e. dune) at two different sites along an exposed sandy beach. In particular, we test the hypothesis that (1) the microclimatic conditions, i.e. temperature and humidity, vary between both types of wrack, (2) the nutritional content of the two types of wrack is different, (3) abundance of colonising individual and species differ in the two types of wrack, (4) succession varies between wrack types, and (5) as a result, macrofaunal assemblages are different in each type of wrack. Furthermore, we predicted that responses in wrack patches located at the drift line would differ from the patches located at the supratidal because wrack patches placed at this level remain longer on the beach. Finally, we predicted that responses could differ among sites because of their slightly different environmental conditions.

## 2. Methods

### 2.1. Study area

The study site of Ladeira (42° 34' 33" N; 9° 3' 16" W) is an intermediate exposed sandy beach, about 1400 m long and 130 m

wide (low spring tide), backed by a large and active dune system located in the Corrubedo beach–lagoon complex. This beach is influenced by a mesotidal regime with a medium tidal range of 3 m.

Two sites about 500 m apart were chosen for this experiment (Site A and Site B, hereafter). Site A was located at the northern part of the beach, while site B was located at the southern part. The environmental characteristics of the two sites differed slightly in terms of the slope, granulometry, temperature and wind exposure. The slopes varied between 1/27 (Site A) and 1/24 (Site B). Sand was mainly made of fine fraction ranging from  $251.2 \pm 24.8$  (Site B, Drift) to  $182.4 \pm 1.34$   $\mu\text{m}$  (Site A, Drift) and sediments were well sorted varying between  $1.34 \pm 0.07$  and  $1.56 \pm 0.02$   $\phi$  at Sites A and B respectively. Temperature in the sediment underneath wrack patches ranged from  $30.6 \pm 0.47$  (Site A, Dune) to  $31.6 \pm 0.94$  °C (Site B, Dune), whereas temperature in bare sediment ranged from  $29.7 \pm 0.94$  (Site A, Dune) to  $30.1 \pm 0.73$  °C (Site B, Dune). The predominant wind was from northerly ( $F_{3,3} = 12.26$ ;  $P < 0.05$ ) being more intense at Site A ( $F_{1,64} = 8.71$ ;  $P < 0.01$ ; SNK tests,  $P < 0.05$ ).

### 2.2. Experimental design

The experiment started on 13 June 2006 and lasted for 21 days. Manipulative experiment was performed at Sites A and B. The day before starting the experiment, 250 kg of fresh seaweeds, *S. polyschides* and *S. muticum*, were collected by hand from surrounding rocky intertidal areas, taken to the laboratory, weighed and separated in plastic bags of  $2.5 \text{ kg} \pm 0.50 \text{ g}$ . At the field, medium squared-patches ( $0.25 \text{ m}^2$ ;  $2.5 \text{ kg} \pm 0.50 \text{ g}$  wet weight) of the two types of seaweed (twelve patches of each type) were haphazardly placed on the highest mark of the drift line and on the base of the dune parallel to the shoreline, i.e. 24 patches per tidal level ( $N = 48$  per site). Each patch was placed 1 to 2 m apart and its location on the beach determined by calculating a random distribution on the computer.

On days 3, 7, 12 and 21 of the experiment, three randomly chosen replicate patches of each type of wrack were collected at each site from the dune and also from the drift line. The associated fauna was retained by enclosing each patch within a  $50 \times 50$  sieve of 1 mm mesh size. Then insecticide was sprayed to prevent mobile fauna, such as adult dipterans and coleopterans, from escaping, and after 5 min, the seaweed and any visible fauna transferred to a plastic bag. Macrofauna underneath each wrack patch was also collected with a 10 cm diameter stainless-steel corer penetrating 20 cm depth into the substratum ( $n = 3$ ). Samples were taken from the centre of the patches to avoid possible edge effects. Three control replicates (3 cores per replicate), 50 cm apart from the wrack patches and separated by 1 m, were also taken at each site in order to measure the normal abundance of invertebrates in nearby bare sediment.

Subsamples of wrack ( $\pm 5 \text{ g}$ ) for biochemical composition analysis were collected ( $n = 3$ ) at each time and frozen at  $-30$  °C until further processing. In addition, temperature (°C) was measured inside the wrack patches ( $n = 3$ ). Four aeolian sediment traps were buried vertically with their rims flush with the beach surface in the dune of both sites surrounding the wrack patches. An inlet and an outlet tube, connected to the chamber trap, were exposed and orientated to the main wind directions. These devices were designed as sediment collectors in order to assess the intensity of

aeolian processes and to measure horizontal sediment transport by wind (Goossens et al., 2000). The amount of sand collected on sampling days was measured as relative total grain mass ( $\text{g day}^{-1}$ ) and the predominant wind direction was established. During the whole experiment none of the sediment traps were found totally filled up by wind action.

### 2.3. Laboratory analysis

Sediment samples ( $n=3$ ) from underneath wrack patches were weighed and then oven-dried at  $60\text{ }^{\circ}\text{C}$  until a constant weight was obtained. Sediment water content; i.e. humidity, was estimated as the difference between wet and dry weight.

Wrack was collected, washed and sieved through a 1 mm mesh. The retained macrofauna was sorted and identified to the lowest possible taxonomic level. The total organic matter of wrack was measured as the difference of dried seaweed ( $60\text{ }^{\circ}\text{C}$  to a constant weight) before and after ignition in a muffle furnace at  $500\text{ }^{\circ}\text{C}$  for 4 h. Nutritional value of the wrack during the decay process was determined through the analyses of the main biochemical classes of organic compounds (i.e. carbohydrates, proteins and lipids), which are assumed to estimate the food potentially available for consumers (Fichez, 1991; Fabiano et al., 1995; Dugan et al., 2003). All biochemical analyses were conducted on samples previously oven-dried at  $60\text{ }^{\circ}\text{C}$  until constant weight was achieved and finely powdered with a pestle. Total lipids (Bligh and Dyer, 1959; Marsh and Weinstein, 1966), carbohydrates (Dubois et al., 1956) and proteins (Markwell et al., 1978) were analysed and measured as  $\mu\text{g g}^{-1}$ . The sum of the main biochemical classes was reported as the biopolymeric carbon (BPC *sensu* Fichez, 1991) assumed as a reliable estimate of the labile fraction available to benthic consumers. Analyses of dry weight samples ( $n=3$ ) of Chlorophyll *a* (Chl *a*,  $\mu\text{g g}^{-1}$ ) from seaweed fronds were extracted following Lorenzen (1967). Chl *a* can be used as a surrogate of benthic microalgae biomass (Rossi and Underwood, 2002).

### 2.4. Statistical analysis

Changes in number of individuals, number of species, abundance of main representative species and diversity (Shannon–Weaver index) were analysed using a 4-factor orthogonal analysis of variance. Moreover, changes in the content of organic matter, carbohydrates, lipids, proteins and chlorophyll *a* in the wrack were also analysed following the same model. Type of wrack (2 levels), Height on the shore (2 levels), Time (4 levels) were fixed factors and Site (2 levels) was random. Any interaction that was sufficiently small with a probability  $\geq 0.25$  was pooled. Before analysis, the homogeneity of variances was evaluated with Cochran's test (Winer et al., 1991) and data were transformed when necessary. *A posteriori* multiple comparisons were done using Student–Newman–Keul's (SNK) tests ( $\alpha=0.05$ ).

Four factor orthogonal non-parametric multivariate analyses of variance (PERMANOVA) were used to test the hypothesis about differences among wrack-associated macrofaunal assemblages (Anderson, 2001). Only significant effects ( $p<0.05$ ) were further investigated through a series of pair-wise comparisons using the appropriate terms in the model. This statistical method was used

because experiment designs were relatively complex (involving four factors) and because, similar to most other studies on assemblages, the data did not meet the assumptions of traditional multivariate statistical analyses (e.g., MANOVA). This method improves on previous ones because it allows the direct additive partitioning of variation, which enables tests of multivariate interactions in complex experimental designs. The statistic test (*pseudo-F*) is calculated from a symmetric dissimilarity matrix. *P*-values are then obtained by permutation tests. Here, the *P*-values for each term in the model were generated using 5000 permutations. To graphically visualize multivariate patterns in assemblages, non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordination plots. Species that mostly contributed to the dissimilarity/similarity among the two types of wrack were identified using SIMPER analysis (Clarke, 1993). The BIO-ENV analysis (PRIMER) was used as an exploratory tool to define suites of abiotic variables that best determine the macrofaunal assemblages. For that purpose, biotic and abiotic matrices were constructed using Bray–Curtis dissimilarity (square-root transformed) and Euclidean distances, respectively.

To compare the relationships between presence/absence of main taxa, total number of individuals, total number of species, diversity and abiotic variables, two types of regression models were used. Firstly, we used the logistic regression model, which falls within the general framework of GLMs (McCullagh and Nelder, 1989), to analyse the relationship between a binary response variable (presence/absence) and several explanatory variables (abiotic predictors). All variables were simultaneously used in a forward multiple logistic regression analysis to derive a multivariate model that would predict the presence or absence of main taxa. The odds of an event occurring (i.e. the probability of an event occurring relative to its converse) were calculated in order to know if there was a relationship between the presence of the species and each of the predictor variables. Secondly, we used a GLM with a Poisson

Table 1

Summary of analyses of variance for Temperature ( $^{\circ}\text{C}$ ) and Humidity (%) in wrack patches at the different sites and heights on the shore

Source	Humidity			Temperature <sup>a, b</sup>	
	<i>df</i>	MS	<i>F</i>	MS	<i>F</i>
Wrack (W)	1	1027.75	84.81	0.0092	49.33
Site (S)	1	0.938	1.08	0.0701	54.86***
Height (H)	1	1.281	0.29	0.0013	0.77
Time (T)	3	3.61	0.95	0.0429	0.86
W × S	1	12.119	14.01***	0.0002	0.15
W × H	1	1.629	0.40	0.0006	19.70
W × T	3	2.491	4.85	0.0297	14.40*
S × H	1	4.459	5.16*	0.0017	1.31
S × T	3	3.795	4.39***	0.0500	39.14***
H × T	3	0.284	0.22	0.0000	0.00
W × S × H	1	4.046	4.68*	0.0000	0.02
W × S × T	3	0.513	0.59	0.0021	1.61
W × H × T	3	0.393	1.49	0.0154	2.77
S × H × T	3	1.322	1.53	0.0016	1.26
W × S × H × T	3	0.264	0.31	0.0055	4.33**
Residual	64	0.864		0.0013	

\* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$ .

<sup>a</sup>  $\ln(x+1)$  transformed data.

<sup>b</sup> Significant differences with control (bare sediment).

Table 2  
Summary of analyses of variance for the organic matter, proteins, carbohydrates, lipids, biopolymeric carbon (BPC) and chlorophyll *a* (Chl *a*) in wrack patches

Source	Organic matter			Proteins <sup>b</sup>		Carbohydrates <sup>a,b</sup>		Lipids <sup>a,b</sup>		BPC <sup>b</sup>		Chl <i>a</i>	
	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Wrack (W)	1	500,673	46.3	374.06	925.96***	2.25	178.1 <sup>+</sup>	0.75	123.5 <sup>+</sup>	6,096,570.5	429.8*	141,189.4	199.9*
Site (S)	1	1485.8	4.45*	66,881.8	12.32***	0.01	0.92	0.05	2.14	155,102.05	6.34*	12,732.8	6.8*
Height (H)	1	1530.5	1.12	219,564.6	3.33	0.35	354.3*	0.13	3.10	633,101.8	3.62	1513.7	0.41
Time (T)	3	2376.8	14.14*	1,754,970.4	95.8***	6.37	40.74***	6.64	104.6**	8,756,419.6	252.1***	543,716.7	681.7***
W×S	1	10,806.2	32.3***	0.076	0.00	0.01	1.12	0.01	0.25	2509.11	0.10	706.33	0.4
W×H	1	3521.3	1.3	54,116.7	6.01	0.08	2.27	0.18	4.45	117,452.3	0.74	2285.4	21.94
W×T	3	469.5	0.72	14,951.1	0.99	0.31	29.11*	0.11	13.72*	954,517.5	25.93*	28,373.6	81.1**
S×H	1	1361.3	4.1	65,976.9	12.2***	0.001	0.09	0.04	1.84	174,917.15	7.2**	3690.24	1.96
S×T	3	168.04	0.5	18,322.7	3.4*	0.01	0.54	0.06	2.65 <sup>+</sup>	74,414.5	3.04*	797.58	0.42
H×T	3	70.1	1.9	4999.72	0.11	0.05	9.01 <sup>+</sup>	0.29	8.1 <sup>+</sup>	29,116.9	0.24	1386.94	0.17
W×S×H	1	2702.7	8.1**	9003.56	1.7	0.04	3.4	0.04	1.7	158,740.7	6.5*	104.2	0.06
W×S×T	3	652.6	1.95	15,070.1	2.8 <sup>+</sup>	0.01	0.94	0.01	0.32	36,814.2	1.51	349.8	0.2
W×H×T	3	373.6	1.7	1377.7	0.7	0.01	0.50	0.014	0.6	5584.2	0.15	1633.9	0.5
S×H×T	3	35.2	0.11	43,981.9	8.1***	0.01	0.51	0.04	1.52	120,442.3	4.93**	8364.8	4.45**
W×S×H×T	3	220.9	0.7	1955.6	0.4	0.01	0.93	0.025	1.1	36,706.2	1.5	3322.82	1.7
Residual	64	334.25		5427.9		0.01			0.024	24,444.8		1879.11	

Type of wrack (W), Height on the shore (H), Time (T) are fixed factors and Site (S) is a random factor.

<sup>+</sup>marginally significant ( $0.04 < p < 0.05$ ); \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; <sup>a</sup>ln ( $x+1$ ) transformed data; <sup>b</sup>significant differences with control.

error term and a log link function, known as a log-linear model, which can be used effectively when the predictors are continuous and the response variable is a count (Quinn and Keough, 2002). This model is more flexible and better suited for analyzing ecological relationships that can be poorly represented by classical Gaussian distributions (Guisan et al., 2002 and references therein). The significance of the independent variables was tested using the  $\chi^2$ -test ( $P < 0.05$ ) on the Wald statistic (Statistica 6.0).

### 3. Results

#### 3.1. Microclimatic conditions of wrack patches: humidity and temperature

Humidity varied between wrack patches, but the variation was not consistent across heights on the shore and sites (i.e. a significant Wrack × Site × Height interaction,  $P < 0.05$ ; Table 1).

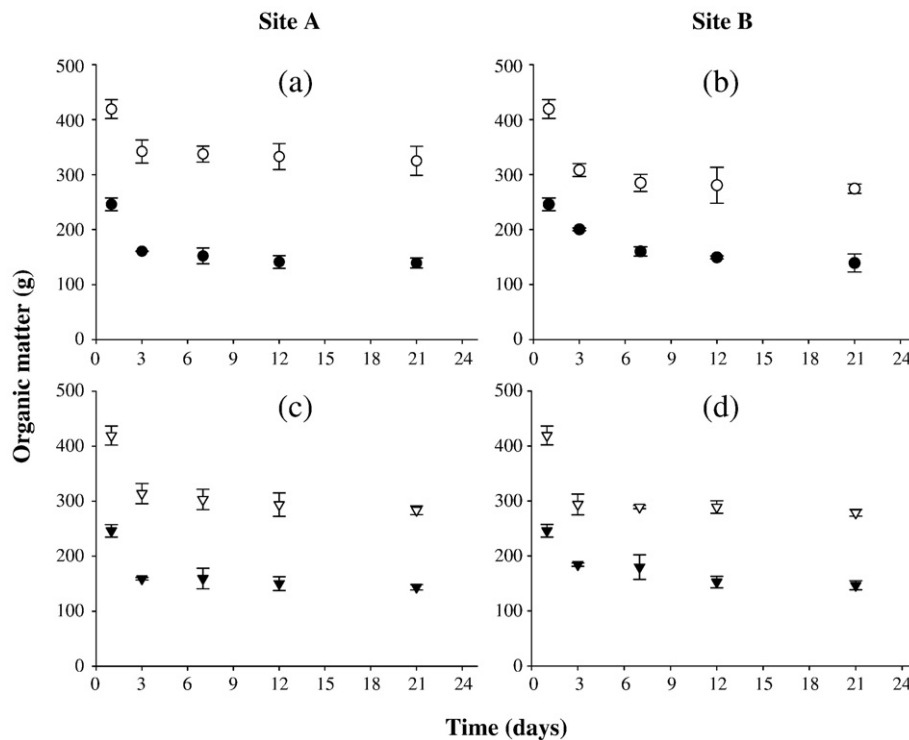


Fig. 1. Mean ( $\pm$ SD;  $n=3$ ) amount of organic matter (g) in wrack patches across heights on the shore (Dune and drift levels), sites (A and B) and over time. Points show an exponential decay model for the two types of wrack: [*S. polychides*: a)  $y=197.1e^{-0.021x}$   $R^2=0.51$ ; b)  $y=219.3e^{-0.026x}$   $R^2=0.77$ ; c)  $y=198.5e^{-0.019x}$   $R^2=0.48$ ; d)  $y=216.5e^{-0.022x}$   $R^2=0.73$ ] and *S. muticum*: a)  $y=378e^{-0.008x}$   $R^2=0.47$ ; b)  $y=354.5e^{-0.015x}$   $R^2=0.5$ ; c)  $y=361.8e^{-0.014x}$   $R^2=0.53$ ; d)  $y=348.9e^{-0.013x}$   $R^2=0.4$ ]. ●: *S. polychides* dune level; ○: *S. muticum* dune level; ▼: *S. polychides* drift level; ▽: *S. muticum* drift level.



Humidity was higher in patches of *S. polyschides* than *S. muticum*, but only in the dune at Site A (SNK tests,  $P < 0.05$ ). Temperature measured inside the patches differed between wrack types, but, once again, differences were not consistent over space and time (i.e. significant Wrack  $\times$  Site  $\times$  Height  $\times$  Time interactions; Table 1). For example, at site A, temperature in patches of *S. polyschides* was higher than in patches of *S. muticum*, but only in the dune on day 12 and in the drift line on day 3 (SNK tests,  $P < 0.05$ ). At site B, temperature in patches of *S. polyschides* was higher than in patches of *S. muticum* in the drift line on days 3 and 12 and in the dune on day 12 at Site B.

### 3.2. Analysis of the total organic matter and nutritional value

Total organic matter varied significantly among wrack types (Table 2), but this variation was not consistent between sites and heights on the shore (i.e. a significant Wrack  $\times$  Site  $\times$  Height interaction,  $P < 0.05$ ). The total organic matter was greater in patches of *S. muticum* than in *S. polyschides* at all sites and heights on the shore (Fig. 1a, b, c, d). However, there was more organic matter content in patches of *S. muticum* in the dune at Site A than at Site B (Fig. 1a, b; SNK tests,  $P < 0.05$ ). In contrast, patches of *S. polyschides* in the dune had more organic matter content at site B than at Site A. (Fig. 1a, b; SNK tests,  $P < 0.05$ ).

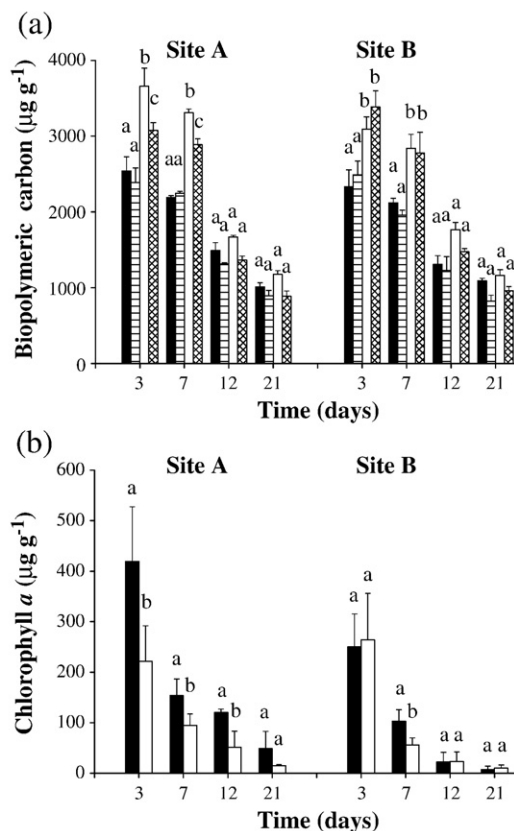


Fig. 2. Mean ( $\pm$ SD;  $n = 3$ ) amount of a) Biopolymeric carbon across sites (A and B) and heights on the shore (Dune and drift levels); b) Chlorophyll a concentrations in the dune level at the two sites over time. Different letters represent significant differences and same letters represent no significant differences. ■ *S. polyschides* dune; ■ *S. polyschides* drift; □ *S. muticum* dune; ▨ *S. muticum* drift.

Table 3

Total number and percent composition (in brackets) of macroinvertebrates in wrack patches

Species	<i>S. polyschides</i>	<i>S. muticum</i>	Bare sediment
<i>Phylum Annelida, Cl. Oligochaeta, Enchytraeidae</i>			
Sp1	1(0.02)	1 (0.06)	
<i>Phylum Arthropoda, Supercl. Chelicerata, Ord. Aranei, Lycosidae</i>			
<i>Arctosa varinana</i> (C.L. Koch, 1848)	59 (0.95)	5 (0.32)	2 (1.56)
<i>Thomisidae</i>			
<i>Xysticus</i> sp. (C.L. Koch, 1835)	1(0.02)		
<i>Supercl. Crustacea, Ord. Amphipoda, Talitridae</i>			
<i>Talorchestia deshayesii</i> (Audouin, 1826)	36 (0.58)	33 (2.1)	
<i>Ord. Isopoda, Tylidae</i>			
<i>Tylos europaeus</i> (Arcangeli, 1938)	2 (0.03)	2 (0.13)	1 (0.78)
<i>Cirolanidae Dana, 1852</i>			
<i>Eurydice affinis</i> (Hansen, 1905)	5 (0.08)	5 (0.32)	
<i>Supercl. Insecta, Ord. Coleoptera, Hydrophilidae</i>			
<i>Cercyon littoralis</i> (Gyllenhal, 1808)	107 (1.72)	82 (5.2)	13 (10.2)
<i>Histeridae</i>			
<i>Hypocacculus rubripes</i> (Erichson, 1834)	466 (7.47)	251 (15.9)	5 (3.91)
<i>Hypocaccus dimidiatus maritimus</i> (Stephens, 1830)	162 (2.6)	13 (0.82)	3 (2.34)
<i>Staphylinidae</i>			
<i>Aleochara (Emplenota) grisea</i> (Kraatz, 1856)	2 (0.03)		
<i>Cafius (Cafius) xantholoma</i> (Gravenhorst, 1806)	116 (1.86)	101 (6.4)	2 (1.56)
<i>Phytosus (Phytosus) spinifer</i> (Curtis, 1838)	3 (0.05)	2 (0.13)	
Sp1	4 (0.06)	4 (0.25)	
<i>Tenebrionidae</i>			
<i>Phaleria cadaverina</i> (Fabricius, 1792)	2062 (33.05)	990 (62.7)	86 (67.2)
<i>Phylan gibbus</i> (Fabricius, 1775)	5 (0.08)	5 (0.32)	
<i>Ord. Diptera, Subord. Nematocera, Infraord. Muscomorpha</i>			
Sp1	8 (0.13)	4 (0.25)	
Sp2	3(0.05)		
<i>Empididae</i>			
Sp1	18 (0.29)	9 (0.57)	2 (1.56)
Sp2		6 (0.38)	
<i>Drosophilidae</i>			
Sp1	2 (0.03)		
<i>Infraord. Calypttratae, Anthomyiidae</i>			
Sp1	3009 (48.23)	11 (0.7)	1 (0.78)
Sp2	99 (1.55)	2 (0.13)	9 (7.03)

(continued on next page)

Table 3 (continued)

Species	<i>S. polyschides</i>	<i>S. muticum</i>	Bare sediment
<i>Muscidae</i>			
Sp1	23 (0.37)	20 (1.27)	
Sp2	2 (0.03)	2 (0.139)	
<i>Infraord. Tabanomorpha, Fam Tabanidae</i>			
Sp1	29 (0.46)	20 (1.27)	4 (3.13)
<i>Infraord. Bibionomorpha, Bibionidae</i>			
Sp1	1 (0.02)		
<i>Infraord. Tipulomorpha, Limoniidae</i>			
Sp1	15 (0.24)	8 (0.51)	
<i>Ord. Neuroptera, Myrmeleionidae</i>			
<i>Myrmelon (Myrmeleon) formicarius</i> (Linnaeus, 1767)	4 (0.06)	2 (0.13)	
<i>Ord. Orthoptera, Fam. Acrididae</i>			
Sp1	1(0.02)		
<i>Ord. Trichoptera</i>			
Sp1	1 (0.02)	1 (0.06)	

Nutritional value, i.e. proteins, carbohydrates and lipids, varied significantly between wrack types, but patterns differed (illustrated by biopolymeric carbon concentration in Fig. 2; Table 2). Protein concentrations ( $\mu\text{g g}^{-1}$ ) were found significantly greater in patches of *S. muticum* than in *S. polyschides*, but this pattern was not consistent across sites and over time (i.e. a significant Wrack  $\times$  Site  $\times$  Time interaction,  $P < 0.05$ ). For example, protein concentrations were greater in patches of *S. polyschides* than in *S. muticum* at Site B on day 3. Although lipids and carbohydrates tended to be more abundant in patches of *S. muticum* than in patches of *S. polyschides*, this trend was

not consistent over time (i.e. Wrack  $\times$  Time interaction,  $P < 0.05$ ). Lipids showed this pattern on days 3, 7 and 21, whereas carbohydrates followed this pattern on days 12 and 21. The nutritional composition of wrack measured as biopolymeric carbon concentration (BPC), varied among wrack patches although this pattern was not consistent over space (i.e. Wrack  $\times$  Site  $\times$  Height interaction,  $P < 0.05$ ) nor over time (i.e. Wrack  $\times$  Time interaction,  $P < 0.05$ ) (Fig. 2a). There was more BPC in patches of *S. muticum* than in patches of *S. polyschides*, but this trend varied between heights on the shore and sites. For example, there was more BPC in patches of *S. muticum* in the dune than in the drift line at Site A (SNK tests,  $P < 0.05$ ). Moreover, BPC in patches of *S. muticum* was more abundant than in patches of *S. polyschides*, but only on days 3 and 7 (SNK tests,  $P < 0.05$ ).

Chlorophyll *a* concentration varied significantly among wrack patches, but this variation was not consistent over time (i.e. a significant interaction Wrack  $\times$  Time interaction,  $P < 0.01$ ; Table 2). Chlorophyll *a* was in greater concentration in patches of *S. polyschides* than in patches of *S. muticum* on days 3, 7 and 12 (SNK tests,  $P < 0.05$ , illustrated in Fig. 2b by wrack patches located in the dune).

### 3.3. Patterns of colonisation and succession

A total number of 7820 individuals belonging to 29 species were collected in wrack patches (Table 3). Larval stages of different species accounted for 66% of total number of individuals. Two coleopteran species, the tenebrionid *Phaleria cadaverina* and the histrid *Hipocacculus rubripes*, and two dipteran species from the family Anthomyiidae in larvae stage accounted for 90% of the total abundance. The arachnid *Arc-tosa variana* and three species of coleopteran *Cercyon littoralis*, *Hipocaccus dimidiatus maritimus* and *Cafius xantholoma* accounted for  $\sim 4\%$  of the total abundance.

Table 4

Summary of analyses of variance (total number of individuals, larvae abundance, species richness and Shannon–Wiener's diversity index) and PERMANOVA (entire assemblage) ( $n = 3$ )

Source	Total abundance <sup>a,b</sup>			Larvae abundance <sup>a,b</sup>		Species richness <sup>b</sup>		Diversity <sup>a,b</sup>		Entire assemblage <sup>a</sup>	
	df	MS	F	MS	F	MS	F	MS	F	MS	Pseudo-F
Wrack (W)	1	12.03	233.4*	68.02	275.35*	18.37	12.25	0.01	0.92	15495	1.9
Site (S)	1	0.94	4.18*	0.03	0.08	2.66	0.87	0.05	2.17	12433	20.96***
Height (H)	1	1.98	0.73	22.32	7.84	1.04	0.69	0.03	301.1*	6485.1	1.91
Time (T)	3	7.71	88.24**	12.88	44.48**	75.29	44.43**	0.016	3.05	601	7.86***
W $\times$ S	1	0.05	0.23	0.24	0.54	1.5	0.49	0.012	0.52	8153	13.74***
W $\times$ H	1	0.62	229.3*	9.82	43.84	1.04	6.25	0.003	0.8	1591.5	1.26
W $\times$ T	3	3.87	25.72*	5.32	23.84*	22.46	13.25*	0.790	42.44**	3219	3.56*
S $\times$ H	1	2.70	11.97**	2.84	6.28*	1.50	0.49	0.000	0.00	3402.4	5.73***
S $\times$ T	3	0.08	0.39	0.29	0.64	1.69	0.55	0.005	0.23	457.84	0.77
H $\times$ T	3	0.01	0.06	1.21	8.69 <sup>+</sup>	2.79	0.44	0.027	0.53	717.45	0.41
W $\times$ S $\times$ H	1	0.003	0.01	0.22	0.49	0.16	0.05	0.003	0.15	1263.2	2.13
W $\times$ S $\times$ T	3	0.15	0.67	0.22	0.49	1.69	0.55	0.018	0.81	904.8	1.52
W $\times$ H $\times$ T	3	0.47	27.95*	0.99	4.47	1.62	1.24	0.000	0.00	1425	1.5
S $\times$ H $\times$ T	3	0.16	0.72	0.14	0.31	6.36	2.07	0.051	2.23	1758	2.96***
W $\times$ S $\times$ H $\times$ T	3	0.01	0.07	0.22	0.49	1.30	0.42	0.034	1.48	955.2	1.61
Residual	64	0.22		0.45		3.07		0.023		593.3	

Type of wrack (W), Height on the shore (H), Time (T) are fixed factors and Site (S) is a random factor.

<sup>+</sup>marginal significant ( $0.04 < p < 0.05$ ); \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; <sup>a</sup> $\ln(x+1)$  transformed data; <sup>b</sup>significant differences with control.

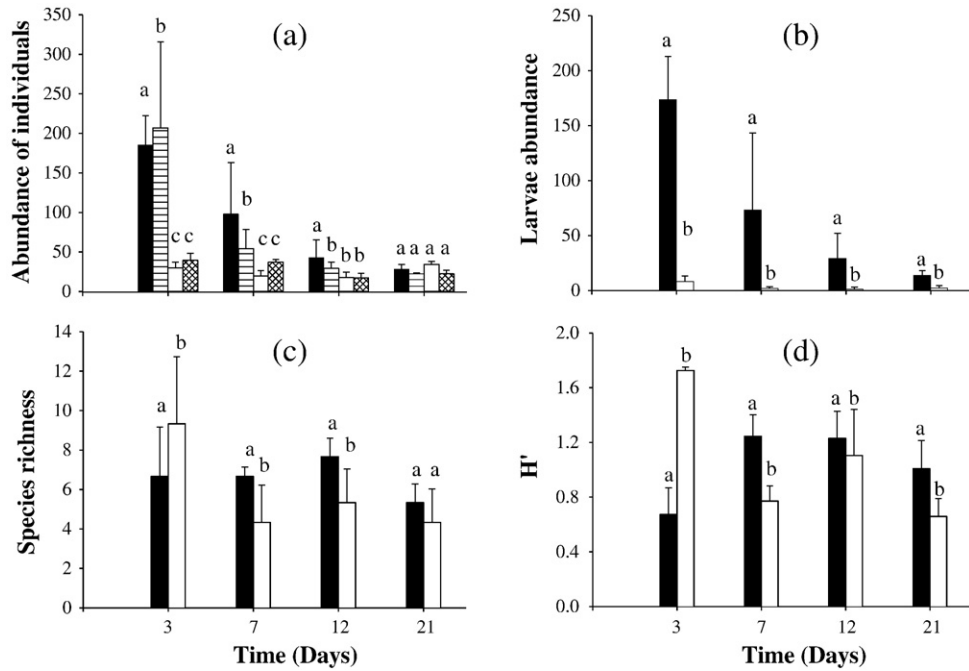


Fig. 3. Mean ( $\pm$ SD;  $n=3$ ) of a) abundance of individuals in the dune and drift levels at Site A; b) abundance of larvae in the dune at site A; c) number of species in the drift at site B; d) diversity in the drift level at site B over time. Different letters represent significant differences and same letters represent no significant differences. ■ *S. polyschides* dune; ▒ *S. polyschides* drift; □ *S. muticum* dune; ▨ *S. muticum* drift.

Colonisation of all wrack patches was very rapid. Most species colonised patches within 3 days (25 species) and only a few new species colonised by day 7 (2 species), 12 (1 species) and 21 (1 species). Abundances varied significantly between both types of wrack, but this variation was not consistent between heights

on the shore over time (i.e. a significant Wrack  $\times$  Height  $\times$  Time interaction,  $P < 0.05$ ; Table 4). Abundances in patches of *S. polyschides* were larger than in patches of *S. muticum* in the dune on days 3, 7 and 12 and in the drift line on days 3 and 7 (shown in Fig. 3a; SNK tests,  $P < 0.05$ ). Abundance of larvae was

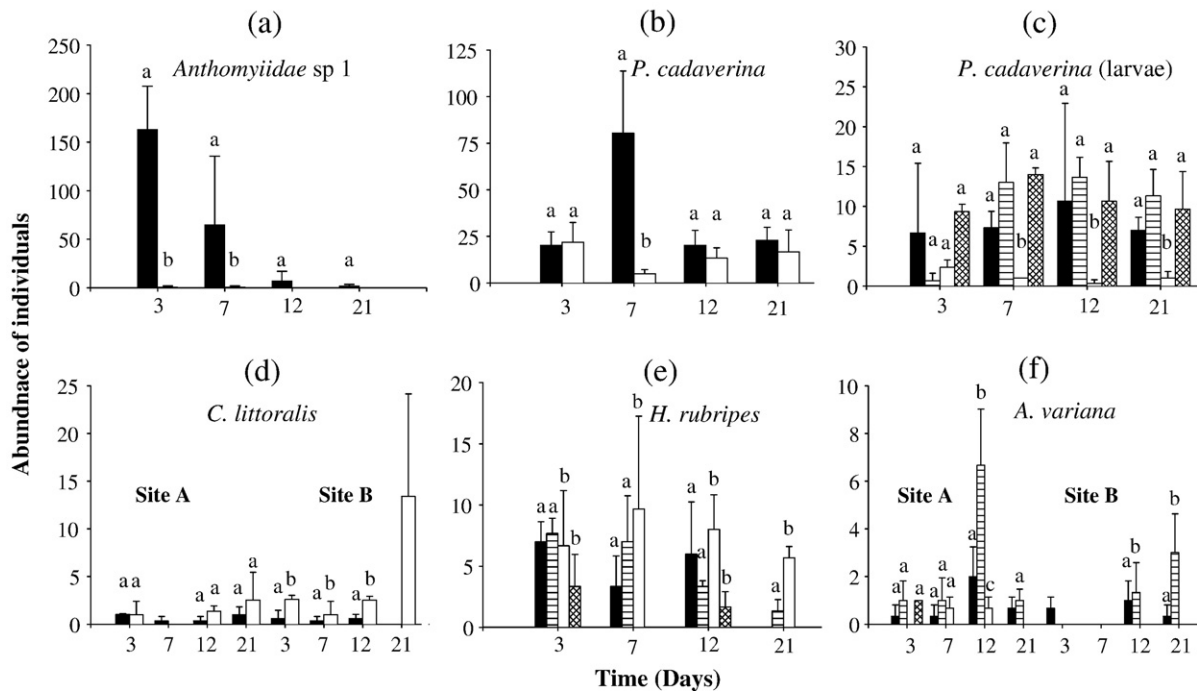


Fig. 4. Mean ( $\pm$ SD;  $n=3$ ) number of individuals over time. a) Anthomyiidae sp 1 in the dune level at site A; b) *P. cadaverina* averaged in the dune at site B; c) *P. cadaverina* (larvae stage) averaged in the dune and drift levels at site A; d) *C. littoralis* in the dune across sites (A and B); e) *H. rubripes* in the dune and drift levels at site B; f) *A. variana* across heights on the shore and sites. Different letters represent significant differences and same letters mean no significant differences. ■ *S. polyschides* dune; ▒ *S. polyschides* drift; □ *S. muticum* dune; ▨ *S. muticum* drift.

Table 5  
Summary of analyses of variance for abundance of each species

Source	Anthomyiidae sp1			<i>P. cadaverina</i>		<i>P. cadaverina</i> (larva)		<i>C. littoralis</i>		<i>H. rubripes</i>		<i>A. variana</i>	
	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Wrack (W)	1	30.8	221.9*	0.77	2.87	5.77	20.26	2.37	1.67	0.11	0.44	2.5	51.5
Site (S)	1	0.54	3.98	4.71	7.33*	2.93	6.89*	0.34	1.13	0.23	0.63	0.41	6.8*
Height (H)	1	0.38	2.15	5.32	2.03	3.26	36.6	0.08	206.6**	11.6	25.7	0.55	4.36
Time (T)	3	9.22	64.4**	3.66	22.8*	0.2	0.11	1.09	1.49	3.35	4.0	0.53	1.62
W×S	1	0.14	1.03	0.27	0.41	0.28	0.67	1.42	4.71*	0.24	0.65	0.05	0.8
W×H	1	0.07	0.56	6.24	44.1	1.43	913.9*	0.08	0.17	1.94	266.2*	0.43	5.9
W×T	3	7.86	85.8**	2.9	2.28	2.18	2.31	0.61	1.47	2.47	10.4*	0.62	2.30
S×H	1	0.18	1.32	2.62	4.1*	0.89	2.09	0.00	0.00	0.45	1.23	0.12	2.07
S×T	3	0.14	1.06	0.16	0.25	1.73	4.06*	0.74	2.45	0.84	2.27	0.33	5.39**
H×T	3	0.01	0.44	0.74	1.9	1.89	12.41*	0.16	0.36	0.39	6.10	0.10	0.45
W×S×H	1	0.12	0.89	0.14	0.22	0.01	0.01	0.44	1.46	0.01	0.02	0.07	1.2
W×S×T	3	0.09	0.68	1.27	1.98	0.94	2.22	0.42	1.38	0.24	0.64	0.27	4.47**
W×H×T	3	0.22	2.18	2.01	1.95	0.44	0.68	0.25	0.75	1.39	6.13	0.24	1.08
S×H×T	3	0.015	0.12	0.39	0.61	0.15	0.36	0.44	1.47	0.06	0.18	0.23	3.85*
W×S×H×T	3	0.101	0.75	1.03	1.6	0.64	1.51	0.33	1.10	0.23	0.61	0.22	3.7*
Residual	64	0.135		0.64		0.42		0.3		0.37		0.06	

Type of wrack (W), Height on the shore (H), Time (T) are fixed factors and Site (S) is a random factor. Data were  $\ln(x+1)$  transformed.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

significantly larger in patches of *S. polyschides* on day 3 (Fig. 3b; Table 4), whereas the number of larvae in patches of *S. muticum* did not vary over time (SNK tests,  $P > 0.05$ ). Number of species and diversity varied between wrack types, but this pattern was not consistent over time (i.e. significant Wrack×Time interactions; Table 3). The number of species was larger in patches of *S. muticum* on day 3, whereas it was larger in *S. polyschides* than *S. muticum* on days 7 and 12 (Fig. 3c). Diversity followed the same trend as the number of species, except for day 21 when diversity varied significantly between wrack types (Fig. 3d).

Colonisation patterns in the most abundant species (Fig. 4) varied between heights on the shore levels, sites and over time. For example, Anthomyiidae sp1 (3009 individuals, 48% of the

total abundance) was the most abundant species in patches of *S. polyschides*, contributing with the highest dissimilarity among wrack types (17.33%), but this pattern was not consistent over time (i.e. a significant Wrack×Time interaction,  $P < 0.05$ ; Table 5). This species was more abundant in patches of *S. polyschides* than in patches of *S. muticum* only on days 3 and 7 (SNK tests,  $P < 0.05$ ; Fig. 4a). The pattern of this variation was consistent across heights on the shore and sites (i.e. no significant interaction). The contribution of the rest of the species was very similar between wrack patches. Adults of *P. cadaverina* did not show significant differences among wrack patches consistently over space and over time (i.e. no significant interactions; Table 5). However, abundance of this species

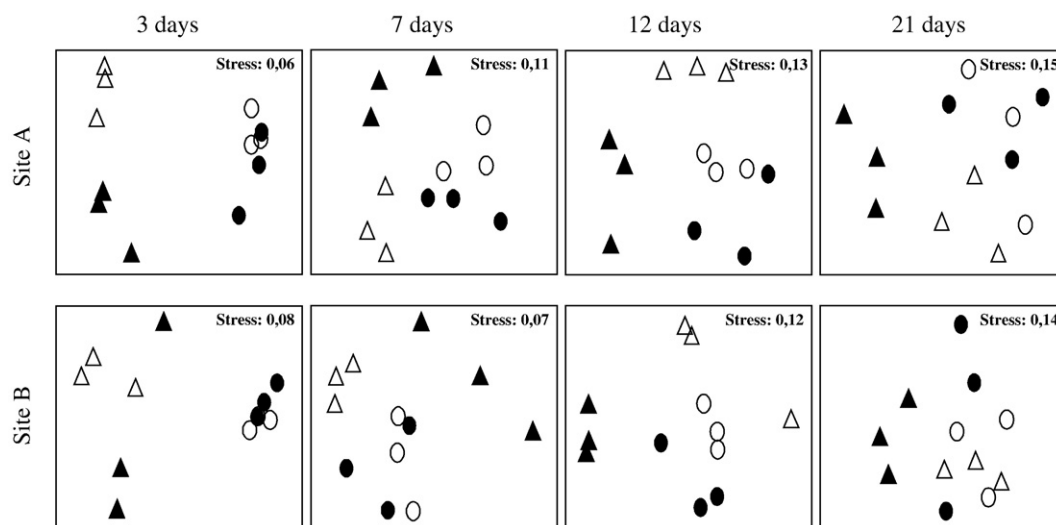


Fig. 5. Non-metric multidimensional scaling (nMDS) for differences in assemblages among wrack patches across heights on the shore (dune and drift), sites (A and B) and over time ( $n=3$ ).  $\blacktriangle$ : *S. muticum* dune;  $\triangle$ : *S. muticum* drift;  $\bullet$ : *S. polyschides*;  $\circ$ : *S. polyschides* drift.



Table 6  
Mean Bray–Curtis dissimilarities (%) between wrack patches (*S. muticum* versus *S. polyschides*)

Time (days)	Dissimilarity (%) between wrack
3	61
7	55
12	61
21	50
<i>Site</i>	
A	63
B	52

Pairwise comparisons from PERMANOVA; 4999 permutations of raw data. Data were square-root transformed.

varied over time (7 days > 21 days > 12 days > 3 days; SNK tests,  $P < 0.05$ ; Fig. 4b). Larvae of *P. cadaverina* followed a different pattern from adults varying between wrack patches, but inconsistently across heights on the shore (i.e. Wrack × Height interaction,  $P < 0.05$ ). Larvae were more abundant in patches of *S. polyschides* than in *S. muticum* in the dune, whereas this pattern was the opposite in the drift line (Fig. 4c). Abundance of *C. littoralis* varied between wrack patches, although this variation was not consistent across sites (i.e. significant Wrack × Site interaction;  $P < 0.05$ ; Table 5). This species was more abundant in patches of *S. muticum* than in *S. polyschides*, but only at Site B (SNK tests,  $P < 0.05$ ; Fig. 4d). *H. rubripes* varied significantly between wrack patches, but there was no consistency between heights (i.e. Wrack × Height interaction,  $P < 0.05$ ; Table 5), nor over time (i.e. Wrack × Time interaction,  $P < 0.05$ ; Table 5). This species was more abundant in patches of *S. polyschides* than in *S. muticum* in the drift line, whereas the pattern was the opposite in the dune (SNK tests,  $P < 0.05$ ; Fig. 4e). In addition, *H. rubripes* was more abundant in patches of *S. polyschides* on days 3, 7 and 12, whereas the pattern was the opposite on day 21 (SNK tests,  $P < 0.05$ ; Fig. 4e). Abundance of the arachnid *A. variana* differed between wrack patches, but this variation was not consistent over space and over time (i.e. significant Wrack × Site × Height × Time interaction,  $P < 0.05$ ; Table 5). For example, this species was more abundant in patches of *S. polyschides* than in patches of *S. muticum* on day 12 in the drift and dune line at both sites, and only in the drift line at Site B on day 21 (Fig. 4f).

### 3.4. Analysis of assemblages in wrack patches

Macrofaunal assemblages varied between types of wrack, but the direction and magnitude of these differences were inconsistent between sites (i.e. significant Wrack × Site interaction,  $pseudo-F_{(1,64)} = 18.84$ ;  $P < 0.001$ ; Table 4) and over time (i.e. significant Wrack × Time interaction,  $pseudo-F_{(3,3)} = 3.58$ ,  $P < 0.01$ ; Table 4). The interactions were caused by variation in direction and magnitude of differences among wrack patches (see Fig. 5; Table 6). First, the dissimilarity between macrofaunal assemblages in patches of *S. polyschides* and those in *S. muticum* was greater at Site A than B. Second, the

dissimilarity between macrofaunal assemblages in patches of *S. polyschides* and those in *S. muticum* was greater on days 3 and 12 than on days 7 and 21. Finally, the magnitude of change between assemblages in patches of *S. polyschides* and *S. muticum* was similar on days 3 and 12 and on days 7 and 21 (Table 6).

### 3.5. Influence of environmental variables on macrofauna assemblages

The total organic matter content of wrack, concentrations of carbohydrates and Chl *a* best explained the pattern of macrofaunal assemblages (Table 7). Carbohydrates content accounted for as much variance alone as when combined with total organic content and Chl *a*. Nevertheless, the best combination overall did not explain a high percentage of variance ( $\rho_s = 0.335$ ;  $P < 0.01$ ).

For each main species, a multiple stepwise logistic regression was run with all abiotic variables together (Table 8). Several of the environmental variables included in this analysis explained variation for five species. For example, the effect of temperature and chlorophyll *a* in patches of *S. polyschides* on the probability of *P. cadaverina* larvae being present, were significant. This means that for a 1% increase in temperature and chlorophyll *a* content, a patch of *S. polyschides* has a 0.436 and 1.014 more chance of having a larva than not, respectively (Table 8). Effects of temperature, humidity, chlorophyll *a* and carbohydrates in patches of *S. muticum* on the probability of *C. littoralis* being present were also significant. However, only the effect of carbohydrates content in wrack was relatively stronger on the presence of this species. In general, although the effects were significant for some environmental predictors, the effect size was small. In contrast, total abundance of individuals and total abundance of larvae showed significant effects with most of the environmental predictors in both types of wrack (see log-linear models; Table 8). However, the environmental predictors explaining variability of total abundance and abundance of larvae varied between types of wrack, i.e. lipids content for total abundance and chlorophyll *a* for larvae abundance. Results of the log-linear model for total number of species and diversity were omitted since there were no significant effects for any of the predictor variables tested.

Table 7

Combinations of environmental variables, taken *k* at a time, giving largest rank correlation  $\rho_s$  between biotic and abiotic similarity matrices; bold indicates best combination overall

<i>K</i>	Best variable combinations ( $\rho_s$ )
1	CHO (0.326)
2	<b>O.M., CHO</b> <b>(0.335)</b>
3	O.M., CHO, Chl <i>a</i> (0.323)
4	H, O.M., CHO, Chl <i>a</i> (0.309)

CHO: carbohydrate; O.M.: organic matter; Chl *a*: chlorophyll *a*; H: humidity.

Table 8  
Summary of the generalised linear models indicating significant variables in bold

Logistic regression		<i>Sacchoriza polyschides</i>								<i>Sargassum muticum</i>							
		Intercept	T	H	O.M.	prot	cho	Lip	Chl <i>a</i>	Intercept	T	H	O.M.	prot	cho	Lip	Chl <i>a</i>
Anthomyiidae sp1	Estimate	48.98	0.73	-0.72	0.084	-0.03	0.002	-0.004	0.004	60.9	-0.4	-0.47	-0.001	-0.01	0.001	-0.001	-0.01
	Wald st.	0.66	2.41	0.96	2.29	<b>4.58</b>	0.334	0.201	0.141	0.195	1.45	0.11	0.001	2.86	0.91	0.056	0.77
	Odds ratio	–	2.08	0.48	1.09	0.971	1.001	0.996	1.004	–	0.67	0.625	0.999	0.99	1.001	0.999	0.993
<i>P. cadaverina</i> (larvae stage)	Estimate	21.3	-0.83	0.76	-0.03	-0.01	-0.000	-0.001	0.014	-8.44	0.57	-0.18	0.014	0.01	0.001	-0.001	-0.05
	Wald st.	3.97	<b>4.23</b>	0.41	0.252	0.983	0.001	0.021	<b>3.87</b>	0.014	1.47	0.07	0.27	0.98	0.14	0.043	3.55
	Odds ratio	–	0.44	2.14	0.97	0.993	0.999	0.999	1.014	–	1.77	0.835	1.014	1.01	1.000	0.999	0.955
<i>C. littoralis</i>	Estimate	6.87	-0.11	-0.07	0.021	0.001	0.001	-0.002	-0.01	176.9	-0.73	-1.62	-0.05	-0.01	0.002	-0.001	-0.02
	Wald st.	0.03	0.53	0.025	0.681	0.032	0.535	0.239	1.941	<b>4.39</b>	<b>5.40</b>	<b>3.87</b>	2.11	2.21	<b>4.78</b>	0.161	<b>4.93</b>
	Odds ratio	–	0.9	0.932	1.021	1.000	1.001	0.998	0.994	–	0.484	0.197	0.952	0.992	1.002	0.998	0.983
<i>H. rubripes</i>	Estimate	91.45	-0.3	-0.79	-0.05	-0.01	0.001	0.008	-0.03	484.7	0.199	-4.81	-0.204	-0.03	0.002	0.01	-0.02
	Wald st.	2.03	1.51	1.422	1.31	1.323	0.06	0.835	<b>5.08</b>	<b>6.87</b>	0.284	<b>6.69</b>	<b>7.40</b>	<b>5.52</b>	3.541	1.65	2.57
	Odds ratio	–	0.74	0.467	0.951	0.992	1.000	1.01	0.972	–	1.22	0.01	0.815	0.972	1.002	1.01	0.98
<i>A. variana</i>	Estimate	21.52	-0.01	-0.33	0.02	0.001	0.002	-0.002	-0.01	230.5	0.66	-2.41	-0.13	-0.001	0.001	0.005	-0.02
	Wald st.	0.53	0.01	0.8	0.762	0.02	<b>5.1</b>	0.312	2.01	1.19	1.63	1.241	1.79	0.003	0.063	0.404	2.563
	Odds ratio	–	0.99	0.72	1.02	1.0	1.002	0.998	0.994	–	1.93	0.1	0.88	0.999	1.0	1.005	0.98
<i>Log-linear model</i>																	
Abundance	Estimate	11.13	-0.04	0.006	-0.04	0.001	-0.00	0.00	0.001	-1.54	-0.09	0.07	0.01	-0.001	0.00	-0.001	-0.001
	Wald st.	<b>2378.7</b>	<b>37.9</b>	0.212	<b>1163.1</b>	<b>96.7</b>	<b>72.2</b>	2.21	<b>46.41</b>	0.117	<b>29.9</b>	2.43	<b>18.02</b>	<b>13.91</b>	<b>6.64</b>	<b>17.1</b>	<b>10.85</b>
Abundance (larvae stage)	Estimate	-15.4	0.03	0.161	0.012	0.001	-0.00	0.001	0.003	43.65	0.026	-0.39	-0.02	-0.02	0.00	0.001	-0.001
	Wald st.	<b>44.2</b>	<b>17.7</b>	<b>43.44</b>	<b>124.3</b>	<b>18.45</b>	<b>4.8</b>	<b>140.4</b>	<b>211.5</b>	<b>34.02</b>	0.98	<b>26.32</b>	<b>47.3</b>	<b>19.4</b>	<b>10.6</b>	<b>15.33</b>	1.21

T: temperature; H: humidity; O.M.: organic matter; prot: proteins; cho: carbohydrates; lip: lipids; Chl *a*: chlorophyll *a*.

## 4. Discussion

### 4.1. Patterns of colonisation and succession

Results indicate that abundances of individuals were significantly larger in wrack patches than those found in bare sand, i.e. controls located nearby wrack patches. It is clear that algal wrack indeed promotes an increase in population abundances of sandy beach macrofauna, either because it provides their main source of food or refuge from environmental conditions and/or due to predation (e.g. Inglis, 1989; Colombini et al., 2000). The number of species found in this study (29) is similar to those reported in previous studies elsewhere (Jędrzejczak, 2002b; Dugan et al., 2003), but lesser in number than in a previous work conducted in an adjacent beach (Olabarria et al., 2007). In our study, the major components of the algal wrack were dipteran flies and tenebrionid and staphylinid beetles. Several authors have noticed that talitrid amphipods are considered primary macroinfaunal colonisers of fresh algal wrack stranded on sandy beaches (e.g. Griffiths and Stenton-Dozey, 1981; Inglis, 1989; Colombini et al., 2000). The scarcity of these amphipods in the area of study might be related to the specific environmental conditions in the beach during the sampling period, when high temperatures and very strong winds following the first sampling day dried off most of the wrack patches. In fact, previous studies have shown that locomotory behaviour of talitrids is strongly influenced by weather conditions such as relative humidity of air, sand temperature and moisture (e.g. Colombini et al., 1998; Fallaci et al., 1999).

The pattern of colonisation varied between wrack types. The total number of individuals was larger in patches of *S. polyschides* than in patches of *S. muticum*. This difference in abundance became more evident within 3 days and diminished over time, although the sharpest differences occurred in the abundance of several larvae species. It is interesting to highlight that the number of species and diversity reached higher values in patches of *S. muticum* than in *S. polyschides* on day 3, but this pattern was reverted from day 7 onwards. On day 3, the largest abundances in native wrack patches were related mainly to larvae belonging to the same species, i.e. Anthomyiidae sp1. Thus, dominance of larvae, can explain the small number of species and low diversity found in native patches at that time. After day 3, larvae abundance dropped, and both number of species and diversity increased to reach higher values in patches of *S. polyschides* than those in *S. muticum*. Reproduction, larval settlement or recruitment can be stimulated by an increase in food (Ford et al., 1999; Bolam et al., 2000). In the case of flies, adults are insignificant consumers of algae-exuded substances, but lay eggs in wrack which may contribute greatly to the breakdown of kelp tissue as a result for their own feeding activity and through the spread of microorganisms (Griffiths and Stenton-Dozey, 1981; Inglis, 1989). Within the first days of experiment, the increase in number of fly larvae could be related to the movements of adults towards patches of *S. polyschides*, which can offer a more suitable habitat and constitute a source of food for these species (see Norkko and Bonsdorff, 1996). For example, the physical structure and/or specific microclimatic conditions in native wrack patches might favour chiefly dipteran oviposition and breeding.

Most species (87%) colonised the wrack patches within 3 days. Different species showed different patterns of colonisation suggesting that life-history attributes, such as their colonising and competitive abilities, and mobility of different taxa, may be important factors contributing to explain such patterns (see Wilson, 1994). Changes in habitat quality also affect dynamics of local populations (Bonte et al., 2003). Variations in trophic habitats of different species may play an important role in the pattern of succession, together with different qualitative stages of decomposition and ageing of wrack (Olabarria et al., 2007). Herbivorous species such as *C. littoralis* rapidly colonised all the patches and remained present over time. The scavenger *P. cadaverina* that feeds on different sources of organic debris (Jaramillo et al., 2003) peaked on day 7. Carnivorous species such as the histerid *H. rubripes* and the spider *A. variana* were early colonisers in both types of wrack, but their abundances were larger on days 7 and 21. This increase in abundance of predators may be related to the increase in abundance of larvae and immature individuals, which are likely to act as food source. Apart from Anthomyiidae sp1 that was clearly more abundant in patches of *S. polyschides* on day 3, abundances of rest of species showed differences between wrack types, but this trend was not consistent over space and/or over time. This suggests that other factors, apart from the type of wrack, are influencing the patterns of colonisation and succession. For example, variation may be related to progressive microclimatic changes of wrack accumulations due to their different position across the beach, i.e. dune and drift at the two sites slightly varied in environmental conditions (e.g. Colombini et al., 2002; Jędrzejczak 2002a,b). In fact, several studies have pointed out that responses of macrofaunal assemblages to wrack deposits vary depending on sites located a few metres or kilometres apart (Rossi and Underwood, 2002; Colombini and Chelazzi, 2003; Dugan et al., 2003) and on seasonality (Ford et al., 1999).

### 4.2. Abiotic factors affecting macrofaunal assemblages

There were some evidences to support the hypothesis that macrofaunal assemblages changed in response to the wrack type, but patterns varied over space and over time. Results indicated that carbohydrates, organic matter and chlorophyll *a* variables best described the observed patterns in macrofaunal assemblages. Moreover, temperature and humidity had some influence on the presence of some species in wrack patches (see Table 8).

Different types of wrack can offer different quality and/or quantity of food availability for macrofauna, which leads to complex patterns of macrofaunal response (Ford et al., 1999; Rossi and Underwood, 2002). Results indicated that nutritional value of wrack (mostly carbohydrates and lipids) and total organic matter content differed between the two types of wrack. In most cases, the carbohydrates, lipids and organic matter content were greater in patches of *S. muticum* than in patches of *S. polyschides*. In contrast, the chlorophyll *a* concentration (used as a proxy of benthic microalgae biomass) was greater in patches of *S. polyschides* than in patches of *S. muticum* in most cases. Benthic microalgae may account for a large proportion of the carbon budget of a detrital food-web and may play an important role in moderate fluxes of carbon in coastal sediments (e.g. Herman et al., 2000). In fact, a

greater concentration of benthic microalgae in *S. polyschides* might be related to a lesser content of polyphenols in laminarian seaweeds since the colonization process of these organisms is related to the polyphenol content (Van Alstyne et al., 1999). In this context, the role of microphytobenthos in the flux of nutrients in sediment is very important. Nutrients can be released from wrack patches and are likely to be used by microphytobenthos, which may play a major role in the flux of nutrients in the sediments, representing a direct or indirect source of food for some invertebrates (Rossi and Underwood, 2002). Strong variation in patch quality, i.e. nutritional value, may give rise to source-sink dynamics affecting the local macrofaunal assemblages inhabiting patches of wrack (see Bonte et al., 2003).

Although temperature and humidity influenced the presence of some species (e.g. *C. littoralis* and *H. rubripes* in patches of *S. muticum*, total abundance in the two types of patches; Table 8), the effect was not very strong. Temperature and humidity varied between the two types of wrack, although inconsistently over space and over time. Slight differences in these parameters could affect colonisation by different invertebrate species. In fact, variation in microclimatic conditions of wrack deposits has been considered an important factor affecting behaviour, locomotory activity and distribution of several arthropod species inhabiting beach–dune systems (e.g. Colombini et al., 1998; Fallaci et al., 1999).

Apart from differences in nutritional value and microclimatic conditions between the two types of wrack, differences in structure, i.e. complexity, of wrack patches might play an important role in variability of macrofaunal assemblages. Different structures due to morphological differences of seaweeds cause variability in habitat quality, i.e. shelter from predation (e.g. Vandendriessche et al., 2006). In some cases, preference of invertebrates for certain seaweed species seems to be related to factors such as availability, habitat provision or refuge from predation rather than nutritional value (e.g. Wakefield and Murray, 1998).

In summary, this study indicates that the different wrack deposits, i.e. native versus invasive algal wrack, were not used uniformly by invertebrates. Data also provide evidences that nutritional content and microclimatic conditions of wrack deposits, i.e. temperature and humidity, could affect macrofaunal assemblages. It is important to emphasize that since correlation does not prove causation, the conclusions from this study should be treated as predictions that point to the most important experimental manipulation to be conducted next, not as conclusions to be set in stone. Experimental manipulation to test hypotheses regarding the physical structure of wrack and stable isotope analyses to provide clues about the origin of invertebrate's food sources and trophic flows in beaches are the next step. In addition, results indicate that replacement of native wrack deposits by invasive wrack may have important effects on macrofaunal assemblages on sandy beaches. A change in the type (or amount) of seaweed wrack entering a beach may alter the macrofaunal assemblages and ecosystem function. Thus, the effect of the invasive seaweed *S. muticum* may have an effect that is spread away from the points of invasion, i.e. intertidal and subtidal rocky shores. An assessment of impact on different marine ecosystems must be important criteria in assessing the impact of this invasive species and the prioritization of invasive species management.

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