



Succession of macrofauna on macroalgal wrack of an exposed sandy beach: Effects of patch size and site

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Abstract

In this study, we used experimental manipulation of algal wrack to test hypotheses about influences on macrofaunal assemblages inhabiting the upper shore level of different sites along an exposed sandy beach. First, we hypothesized that decomposition of algal wrack depends on wrack patch size and site. With respect to macrofauna, we tested the hypotheses that (1) abundance of colonising individuals and species vary with wrack patch size, (2) succession (i.e. sequence of colonisation and species replacement) depends on time, and (3) as a result, macrofaunal assemblages associated with wrack patches vary with the patch size and time. We also predicted that responses could be different across sites because of their slightly different environmental conditions. The decomposition of wrack patches was similar in all sites and was dependent on wrack patch size. It was strongly influenced by time-specific environmental and/or biological factors. The pattern of colonisation, i.e. total number of species and individuals, varied among wrack patch sizes. Small patches had fewer species and individuals than medium and large patches. Nevertheless, pattern of colonisation varied among species, across sites and through time. Colonisation of wrack patches was rapid (i.e. within 3 days) for most species. There was some evidence to support the hypothesis that macrofaunal assemblages change in response to patch size and time.

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1. Introduction

In many shallow water marine habitats, a major natural disturbance is the stranding of mats of dead plant material, called wrack (Inglis, 1989; Ford et al., 1999; Rossi and Underwood, 2002). Disturbance by wrack has been implicated as a potentially important factor structuring local assemblages of invertebrates on sandy beaches (reviewed in Colombini and Chelazzi, 2003). In intertidal habitats (e.g. sandflats, salt-marshes, beaches), wrack is deposited throughout the entire intertidal range (e.g. Valiela and Reitsma, 1995). During this period the wrack beds are subjected to different processes such as dehydration, ageing, fragmentation, burial by sand, and decomposition. These processes are highly variable and influenced by both site- and time-specific environmental conditions and in most cases depend on the composition of the wrack itself (Colombini and Chelazzi, 2003).

In many temperate regions, the major sources of allocthonous organic material and carbon on exposed sandy beach macrofauna are phytoplankton and marine macrophytes (macroalgae, seagrasses) (e.g. Brown and McLachlan, 1990; Dugan et al., 2003). Hence, macrofaunal communities of exposed sandy beaches depend largely upon allocthonous inputs associated with oceanographic processes that deliver nutrients and transport phytoplankton onshore and macrophyte production within near-shore macroalgal and seagrass beds that arrive as stranded wrack (Dugan et al., 2003). Wrack also provides food and habitat to a diverse and abundant component of the macrofaunal communities, mainly terrestrial arthropods (Inglis, 1989; Polis and Hurd, 1996; Dugan, 1999; Colombini et al., 2000; Jedrzejczak, 2002b). The distribution and zonation of the macrofauna inhabiting the upper shore levels of exposed sandy beaches have been found to respond to spatio-temporal variability in the supply of drift macrophytes (e.g. Koop and Griffiths, 1982; Stenton-Dozey and Griffiths, 1983; McGwynne et al., 1988; Dugan et al., 2003).

Sandy beaches represent potentially ideal marine models for the study of the ecological concepts of patch-dynamics because disturbance by wrack creates a mosaic of bare and wrack occupied areas (Colombini et al., 2000; Rossi and Underwood, 2002). Seasonal, lunar, tidal and spatial fluctuations in beach wrack accumulations have been reported by many authors (e.g. Valiela and Reitsma, 1995; Colombini et al., 2000; Colombini and Chelazzi, 2003). Different dimensions and compactness of patches may create different microclimatic evolutions that influence the type and number of colonisers (Colombini et al., 2000). Patch size has been shown to influence the number of taxa present in terrestrial and marine habitats (e.g. Simberloff, 1976; Irlandi et al., 1995; Frost et al., 1999; Bowden et al., 2001), larger patches supporting greater numbers of species. This mosaic of patches on sandy beaches might influence the structure and function of animal assemblages and determine the taxonomic composition and diversity of species as shown in other marine coastal systems (e.g. Thrush, 1986; Irlandi et al., 1995; Valiela and Reitsma, 1995; Norkko and Bonsdorff, 1996; Bowden et al., 2001). To understand and model the functioning of mosaics of wrack patches (e.g. Paine and Levin, 1981), one must understand the mechanisms and rates of arrival of new organisms into disturbed patches. This phenomenon of species' arrival can have a number of important consequences for inter-specific interactions (Hodge and Arthur, 1997).

Despite the important influence of wrack on macrofaunal communities of different coastal systems (e.g. Ford et al., 1999; Rossi and Underwood, 2002; Dugan et al., 2003; Orr et al., 2005), relatively little attention has been paid to the responses of macrofaunal assemblages of exposed sandy beaches to macrophyte wrack supplies (reviewed in

Colombini and Chelazzi, 2003). Furthermore, the role of wrack size in determining patterns of macrofaunal distribution and abundance on sandy beaches has been not examined so far.

In this paper, we used experimental manipulation of algal wrack, i.e. artificial patches of *Saccorhiza polyschides*, to test hypotheses about influences on macrofaunal assemblages inhabiting the upper shore level of different sites along an exposed sandy beach. First, we hypothesized that decomposition of algal wrack (a time-dependent process) varies with patch size and among sites. Specifically, we tested the hypotheses that (1) abundance of colonizing individuals and species vary with wrack patch size, (2) succession (i.e. sequence of colonisation and species replacement) depends on time, and (3) as a result, macrofaunal assemblages associated with wrack patches vary with the size of wrack patch and time. Furthermore, we predicted that responses could differ among sites because of their slightly different environmental conditions.

2. Material and methods

2.1. Area of study

The study site of O Vilar (42°34'50"N; 9°08'45"W) is an exposed sandy beach located in the Corrubedo beach–lagoon complex. This complex, declared a Natural Park in 1992, is situated in an embayment on the northwestern coast of Spain. The geomorphological, climatic and vegetative characteristics of the beach-dune system have been extensively studied in other works (Vilas and Nombela, 1986; Calvo et al., 1999).

O Vilar beach is an intermediate-dissipative, exposed beach, about 10 km long and 140 m width (in low tides of spring tide), divided by rocky platforms (20–40 m wide) and backed by a large and active dune system, 9 km long and 16 m high (Calvo et al., 1999). The sandy shore is fringed from the dune by a scarp corresponding to the storm drift line. Tides are semi-diurnal with an approximate range of 2–4 m. On this beach the composition of the macrophyte wrack is very variable. During summer time, heterogeneous patches of algal wrack commonly range from 0.07 to 0.60 m² and are mainly composed of brown algae [e.g., *Saccorhiza polyschides* (>85% of biomass), *Sargassum muticum*, *Fucus* spp., and *Laminaria saccharina*] that are spread along the upper shore of the beach (personal observations).

2.2. Experimental design and sampling

The experiment started on 16 June 2004 and lasted for 21 days. Manipulative experiment was done in three different sites separated by about 150 m. A day prior to the experiment fresh seaweed, *Saccorhiza polyschides*, was collected by hand from surrounding intertidal areas, taken to the laboratory where it was washed with sea water to clean any organisms and then, weighed. Following measurement of patch sizes during initial observations in the area, small (0.09 m²; 1 kg ± 50 g wet weight), medium (0.25 m²; 3 kg ± 50 g wet weight) and large (0.49 m²; 5 kg ± 50 g wet weight) squared-patches of seaweed fronds and thalli were randomly placed at each site on the upper shore level of the beach (ca. 3 m above the drift line) parallel to the shoreline, i.e. 27 patches per site ($N = 81$). Patches were placed 2 m apart and their positions were marked with aluminium sticks stuck into the sand and located on the upper left corner of each patch. Patches

remained on the sand by day 7 and were partially buried by day 21. Patches were randomly placed and collected by calculating a random distribution by computer.

On day 3, 7 and 21 of the experiment, three randomly chosen replicate patches of each size were collected at each site. All samples were collected at low tide between 12.00 and 13.00 h. The associated fauna was retained by enclosing each patch within a 70 × 70 cm sieve of 1 mm mesh size. Insecticide was then sprayed to prevent mobile biota from escaping from the samples, and after 5 minutes, the seaweed and any visible fauna transferred to a plastic bag.

Macrofauna underneath each patch was also taken using a 10 cm diameter stainless-steel corer that was pushed into the sediment to a depth of 20 cm ($n = 4$). Samples were taken from the centre of the patches to avoid possible edge effects. To measure normal abundances of invertebrates in natural bare sediment, three replicates (4 cores per replicate) 50 cm apart from the wrack patches and separated by 1.5 m, were taken at each site.

At each site, three small cores (3 cm diameter, 5 cm depth) were taken for granulometric and water content analyses. The height above the low water line (LWL hereafter) was measured using a profiling technique (Emery, 1961) at spring and neap tides. The cover of naturally stranded seaweed was also determined (see below).

2.3. Laboratory analyses

Samples of sediment and seaweed were gently washed, sieved through a 0.5 mm mesh, and fixed in borax-buffered 4% formaldehyde in seawater. Then retained fauna was separated and stored in 70% ethanol. Macrofauna was identified to the lowest possible taxonomic level and counted. Seaweed from each patch was washed and, then oven-dried at 60 °C to a constant weight. The decomposition of seaweed was determined by calculations of dry weight differences using a conversion formula to estimate dry weight from initial wet weights based on drying and weighing five replicates of 1, 3 and 5-kg portions of fresh fronds and thalli (standard parts used in the experiment) of *S. polyschides* (Inglis, 1989).

Sediment samples were weighed and then oven-dried at 60 °C until a constant weight was obtained, and water content was estimated as the difference between these two values. Sediment particle-size distribution was determined using Coulter LS 200 laser diffraction particle size analyser and the coarser fraction (>2 mm) by dry sieving (Folk, 1980). To estimate the natural stranded seaweed, the cover and composition of wrack on the beach were estimated using a line intercept method (see Dugan et al., 2003).

2.4. Statistical analysis

Decomposition of algal wrack was evaluated following a single exponential decay model (Swift et al., 1979):

$$W_t = W_0 e^{-kt}$$

where W_t is the dry weight (g) of wrack remaining after time t , W_0 is the initial dry weight (g) of wrack, k is the decay coefficient (day^{-1}) and t is the time (days). This model does not discriminate between soluble and refractory material, nor does it distinguish microbial contributions.

The decay coefficient (k) was used to compare the decomposition rates among different wrack patch sizes and sites using a 2-factor orthogonal analysis of variance. Changes in number of individuals, number of species, abundance of main representative taxa and

diversity were investigated using a 3-factor orthogonal analysis of variance. The factors were patch size (3 levels), Sites (3 levels) and Time (3 levels). Patch size and time were fixed and site was random. Before analysis, the homogeneity of variances was evaluated by using Cochran's test (Winer et al., 1991) and data $\log(x + 1)$ -transformed when necessary. A *posteriori* multiple comparisons were done using SNK tests (Underwood, 1997).

Three factor orthogonal non-parametric multivariate analyses of variance (PERMANOVA, formerly NP-MANOVA) were used to test hypotheses about differences among macrofaunal assemblages (Anderson, 2001). When PERMANOVAs showed significant effects ($P < 0.05$), these were investigated further using a series of *a posteriori* pair-wise comparisons using the appropriate terms in the model. For these tests, only probability values are presented because the multivariate F -statistics and t -statistics are generated by permutations. Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations to show relationships among samples of macrofaunal assemblages. All multivariate analyses were done based on calculated Bray–Curtis similarity coefficients. Taxa that contributed the most to the dissimilarity/similarity among/within patches, sites and times were identified using SIMPER analysis (Clarke, 1993).

3. Results

3.1. Environmental characteristics of the area

The three sites differed slightly from each other in terms of the slope, water content of sediment, granulometry and algal cover. The slopes varied between 1/40 (Site 1) and 1/61 (Site 2). Sands from these three sites ranged from coarse ($573.9 \mu\text{m} \pm 83.09 \mu\text{m}$ at Site 1) to medium sands ($425.9 \mu\text{m} \pm 40.19 \mu\text{m}$ at Sites 2 and 3) and sediments were very poorly sorted, varying between 2.13 ϕ and 2.46 ϕ , indicating a poor grain selection at the three sites. Water content of sediment was very low ($<3\%$) at all sites except for time 2, i.e. 7 days after the start of the experiment, when water content increased considerably ($\sim 7\%$) due to a summer storm. In general, the percent cover of natural macrophyte wrack was low ($\leq 0.1\%$) at all sites. It consisted primarily of *S. polyschides* and *S. muticum* at times 1 and 3 by days 3 and 21, respectively, whereas at time 2, i.e. by day 7, was composed of a greater variety of species (*S. muticum*, *S. polyschides*, *Ulva* spp., *Himantalia elongata* and *Fucus* spp.).

3.2. Wrack decomposition

The pattern of weight loss of wrack patches over time was similar in all sites (Table 1), but the rate of wrack decomposition varied among wrack patches of different sizes (Table 1; Fig. 1). Small patches had a higher rate of decomposition than medium and large

Table 1
Analysis of the decomposition of macroalgal wrack (k coefficient) in the different patches at three sites

Source	df	MS	F ratio	P	F versus
Patch (Pa)	2	0.56	445.43	0.000	Pa \times Si
Site (Si)	2	0.00	0.01	0.993	Res
Pa \times Si	4	0.00	0.03	0.998	Res
Residual	72	0.05			

Patch size (Pa) is a fixed factor; site (Si) is a random factor ($n = 9$).

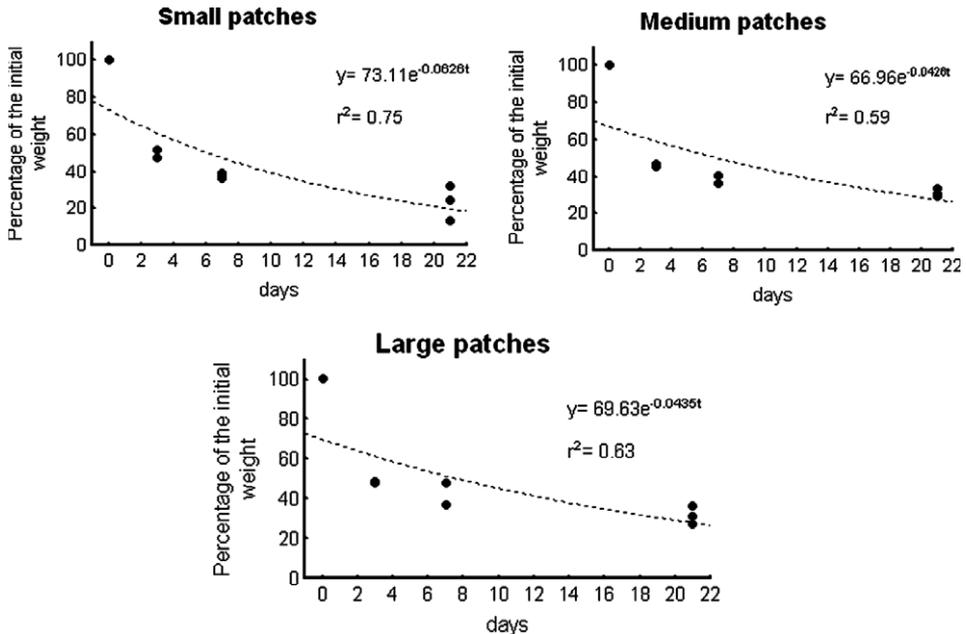


Fig. 1. Changes in the mean dry weight of *S. polyschides* in the wrack patches of different size through time ($n = 3$). Data from all sites have been pooled. Curves show an exponential decay model.

patches (small > medium > large; SNK tests, $P < 0.05$). Decomposition of all wrack patches was initially very rapid (i.e. by day 3), and then stabilised to be linear. By day 3, wrack patches had lost ~50% of their initial dry weight and by day 21, between ~76% and 86% of their initial dry weight (Fig. 1).

3.3. Natural abundances of invertebrates in bare sand

Control samples taken in bare sand had very few individuals and species. A total of 42 individuals belonging to 10 species were collected (Table 2). All these species were also found in the experimental wrack patches. The most abundant species in bare sediment also showed the highest abundances on the experimental patches and this was a coleopteran species, *Phaleria cadaverina* (43% of total individuals in bare sand). In general, a similar species composition was found in bare sand at all sites and times of sampling. Assemblages in bare sand were similar among sites at all times of sampling, i.e. no significant interaction (site \times time, $P > 0.05$).

3.4. Abundances of invertebrates in artificial wrack patches

A total of 7360 individuals belonging to 53 species colonised the wrack patches through time (Table 2). Two coleopteran species, the terebrionid *Phaleria cadaverina* and the staphilinid *Phytosus spinifer*, two dipteran species from the family Anthomyiidae, and the amphipod *Talitrus saltator* accounted for 77% of the total abundance. Two other species

Table 2
Total number and percent composition of macroinvertebrates found in wrack patches

Species	Number of individuals	% Community	Species	Number of individuals	% Community
Phylum Annelida			Melolonthidae		
Cl. Oligochaeta			<i>Anoxia (Anoxia) villosa</i> (Fabricius, 1781)	1	0.01
Enchytraeidae			Latridiidae		
Sp1	1	0.01	<i>Enicmus transversus</i> (Olivier, 1790)	1	0.01
Phylum Arthropoda			Tenebrionidae		
Supercl. Chelicerata			<i>Phylan gibbus</i> (Fabricius, 1775)	1	0.01
Ord. Aranei			^a <i>Phaleria cadaverina</i> (Fabricius, 1792)	2196	29.84
Lycosidae			<i>Tentyria curculionoides interrupta</i> (Latreille, 1807)	1	0.01
^a <i>Arctosa variana</i> (C.L. Koch, 1848)	148	2.02	Anthicidae	2	2.02
Linyphiidae			<i>Anthicus floralis</i> (Linnaeus, 1758)	17	0.23
Sp1	2	0.03	Chrysomelidae	2	0.03
Zoridae			<i>Leptinotarsa decemlineata</i> (Say, 1824)	1	0.01
<i>Zora</i> sp.	1	0.01	<i>Phyllotreta undulata</i> (Kutschera, 1860)	1	0.01
Salticidae			<i>Psylliodes marcidus</i> (Illiger, 1807)	2	0.03
<i>Euophrys frontalis</i> (Walckenaer, 1802)	1	0.01	Ord. Diptera	1	0.01
Araneidae			Subord. Nematocera		
<i>Araneus</i> sp.	1	0.01	Infraord. Bibiomorpha	1	0.01
Supercl. Crustacea			Mycetophilidae		
Ord. Amphipoda			Sp1	1	0.01
Oedicerotidae			Sciaridae		
^a <i>Pontocrates arenarius</i> (Bate, 1858)	1	0.01	Sp1	2	0.03
Talitridae			Subord. Brachycera		
<i>Orchestia gammarellus</i> (Pallas, 1766)	2	0.03	Sp1	1	0.01
^a <i>Talitrus saltator</i> (Montagu, 1808)	475	6.45	Infraord. Muscomorpha		
^a <i>Talorchestia brito</i> (Stebbing, 1891)	23	0.31	Sp1	5	0.07
^a <i>Talorchestia deshayesii</i> (Audouin, 1826)	15	0.21	Sp2	2	0.03
Ord. Isopoda			Empididae		
Tylidae			Sp1	80	1.1

(continued on next page)

Table 2 (continued)

Species	Number of individuals	% Community	Species	Number of individuals	% Community
^a <i>Tylos europaeus</i> (Arcangeli, 1938)	106	1.44	Sp2	26	0.35
Sphaeromatidae			Infraord. Schizophora		
<i>Sphaeroma rugicauda</i> (Leach, 1814)	3	0.041	Coelopidae		
Cirolanidae Dana, 1852			Sp1	3	0.04
^a <i>Eurydice affinis</i> (Hansen, 1905)	6	0.08	Sphaeroceridae		
Supercl. Insecta			Sp1	128	1.74
Ord. Dictyoptera			Sp2	2	0.03
Battellidae			Drosophilidae		
Sp1	2	0.03	Sp1	11	0.15
Ord. Thysanoptera			Infraord. Calyptratae		
Phlaeothripidae			Anthomyiidae		
Sp1	2	0.03	^a Sp1	1659	22.54
Ord. Coleoptera			Sp2	607	8.25
Hydrophilidae			Muscidae		
^a <i>Cercyon littoralis</i> (Gyllenhal, 1808)	129	1.75	Sp1	2	0.03
Histeridae			Limmoniidae		
<i>Hypocacculus rubripes</i> (Erichson, 1834)	4	0.05	Sp1	30	0.41
<i>Hypocaccus crassipes</i> (Erichson, 1834)	1	0.01	Ord. Hymenoptera Linnaeus, 1758		
<i>Hypocaccus dimidiatus maritimus</i> (Stephens, 1830)	119	1.62	Diapriidae		
Staphylinidae			Sp1	1	0.01
<i>Cafius (Cafius) xantholoma</i> (Gravenhorst, 1806)	358	4.86	Proctotrupidae		
<i>Aleochara (Emplenota) grisea</i> (Kraatz, 1856)	406	5.52	Sp1	1	0.01
<i>Phytosus (Phytosus) spinifer</i> (Curtis, 1838)	739	10.04	Ichneumonidae		
<i>Phytosus (Actosus) balticus</i> (Kraatz, 1859)	3	0.04	Sp1	1	0.01
<i>Leptacinus faunus</i> (Coiffait, 1956)	4	0.05			

Numbers are the pooled samples over all algal wrack patches, sites and times.

^a Species also found in the control samples.

belonging to the family Staphylinidae, *Aleochara grisea* and *Cafius xantholoma*, accounted for ~5% and ~4% of abundance, respectively. The arachnid *Arctosa variana*, two species of coleopteran *Cercyon littoralis* and *Hypocaccus dimidiatus maritimus*, and a dipteran species Sphaeroceridae sp1, accounted for a further ~7% of total abundance. Thirty species colonised wrack patches, but their occurrence was sporadic, i.e. one or two individuals in all (Table 2).

3.5. Pattern of colonisation in wrack patches

Wrack assemblages varied among patch sizes and through time. The number of species varied among patch sizes (Table 3; Fig. 2a), and this variation was consistent among sites. There were more species in medium and large patches than in small patches (SNK tests; $P < 0.05$). Similarly, the number of individuals varied among patch sizes (Table 3; Fig. 2b), and this variation was consistent across times and sites (i.e. no significant interactions between patch size and site or time; Table 3). The number of individuals per patch increased as patch size increased (Fig. 3). In contrast, there were no effects of patch size on Fisher's and Shannon's diversity indices (Table 3).

In general, all wrack patches were colonised rapidly. Pattern of colonisation of most abundant species varied among species, across sites and through time. *Arctosa variana* did not show significant variation among patch sizes (Table 4; illustrated for site 1 in Fig. 3a). Two species, Anthomyiidae sp2 and *T. saltator* showed significant differences among patch sizes, but these differences varied across sites and with length of time (i.e. a significant site \times patch size \times time interaction; Table 4). By day 7, abundances of *T. saltator* were significantly larger in medium and large patches than in small patches only

Table 3

Summary of analysis of variance for number of individuals, number of species, Shannon–Wiener's and Fisher's diversity indices

Source	Number of species				Number of individuals ^a		
	df	MS	F ratio	P	MS	F ratio	P
Site (Si)	2	0.90	0.21	Ns	0.67	2.67	ns
Patch (Pa)	2	30.61	14.17	<0.05	13.23	250.40	<0.001
Time (Ti)	2	367.64	46.42	<0.01	5.04	7.24	<0.05
Si \times Pa	4	2.16	0.51	Ns	0.05	0.21	ns
Si \times Ti	4	7.91	1.88	Ns	0.69	2.75	<0.05
Pa \times Ti	4	1.51	0.32	Ns	0.39	1.35	ns
Si \times Pa \times Ti	8	4.76	1.13	Ns	0.29	0.28	ns
Residual	54	4.20			0.25		
		Shannon's diversity index			Fisher's diversity index ^a		
Site (Si)	2	0.11	1.19	Ns	0.11	1.70	ns
Patch (Pa)	2	0.02	0.78	Ns	0.32	7.61	ns
Time (Ti)	2	8.21	125.14	<0.001	5.54	35.09	<0.01
Si \times Pa	4	0.02	0.25	Ns	0.04	0.66	ns
Si \times Ti	4	0.06	0.71	Ns	0.16	2.48	ns
Pa \times Ti	4	0.03	0.28	ns	0.12	1.52	ns
Si \times Pa \times Ti	8	0.12	0.14	ns	0.07	1.21	ns
Residual	54						

Patch size (Pa) and time (Ti) are fixed factors; site (Si) is a random factor.

^a Data were $\log(x + 1)$ -transformed prior to analysis.

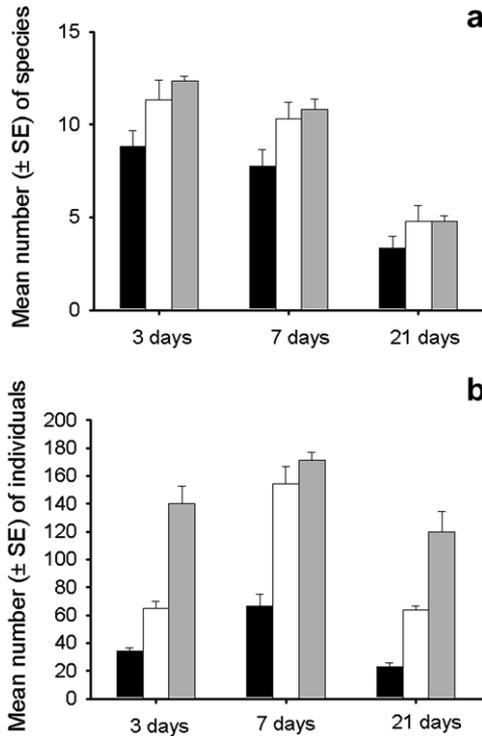


Fig. 2. The influence of patch size (averaged across sites) on the mean number (\pm SE; $n = 3$) of (a) species and (b) individuals in patches over time. ■: small patch; □: medium patch; ▒: large patch.

in Site 2 and Site 3 (illustrated for Site 2 in Fig. 3b). In contrast, abundances of Anthomyiidae sp2 varied among patches on day 21 in Site 1 and Site 2 (illustrated for Site 2 in Fig. 3c). Abundances of five species, *P. cadaverina*, *P. spinifer*, *A. grisea*, Sphaeroceridae sp1, and *C. xantholoma* varied among patch sizes although these variations were inconsistent through time (i.e. a significant interaction patch size \times time; Table 4). For example, by day 21, the abundances of *P. cadaverina* increased significantly with increasing patch size (small < medium < large; SNK tests, $P < 0.05$). In contrast, *C. xantholoma* and Sphaeroceridae sp1 showed the same patch size-related pattern, but only on day 3 (illustrated by *C. xantholoma*; Fig. 3d). Anthomyiidae sp1 was more abundant in medium and large patches than in small patches, and the magnitude of those differences was consistent across sites and time (i.e. no significant interactions between patch size and site or time; Table 4). Abundances of *C. littoralis* varied among patches, although these variations were inconsistent across sites (i.e. a significant site \times patch size interaction; Table 4). This species was more abundant in large patches than medium or small patches, but only in Site 1 (Fig. 3e).

3.6. Succession

Colonisation of wrack patches was rapid (i.e. within 3 days) for most species. The total number of species varied consistently among patches of different sizes, over time, and

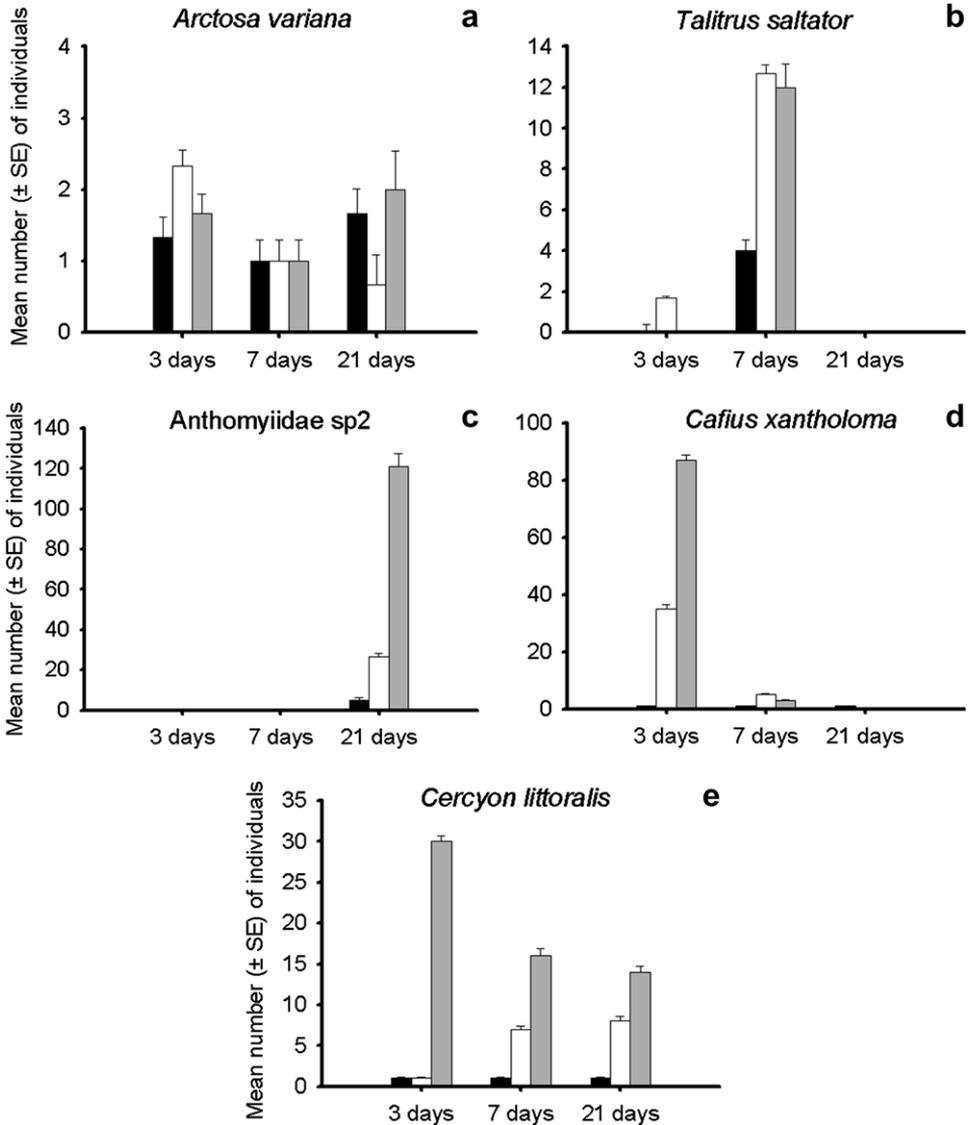


Fig. 3. The influence of patch size on the mean number (\pm SE) of individuals ($n = 3$) through time. (a) *A. variana* at Site 1; (b) *T. saltator* in Site 2; (c) *Anthomyiidae* sp2 at Site 2; (d) *C. xantholoma* averaged across sites; (e) *C. littoralis* in Site 1. ■: small patch; □: medium patch; ▒: large patch.

among sites (i.e. no significant interactions between time and patch size or site; Table 3). The number of species was smallest on day 21 (Fig. 2a). Most species colonised patches within 3 days (44 species, $\sim 83\%$) and only a few new species colonised by day 7 (5 species, 9.43%) and day 21 (4 species). The rate of species succession was very rapid with a high rate of species addition by day 3, and a high rate of species loss by 7 and 21 days (Fig. 4a). For example, by day 7 the rate of species addition decreased considerably, whereas the rate of species loss showed considerable increase with 19 and 37 species disappearing by days 7 and 21, respectively. The total number of individuals varied over time

Table 4
Summary of ANOVA for abundance of each species

Source	df	<i>P. cadaverina</i>	Anthomyiidae sp1 ^a	<i>P. spinifer</i> ^a	Anthomyiidae sp2	<i>T. saltator</i> ^a	<i>A. grisea</i> ^a	<i>C. xantholoma</i> ^a	<i>A. variana</i>	<i>C. littoralis</i>	Sphaeroceridae sp1 ^a
Site (Si)	2	1.96	1.35	0.57	6.23 ²	7.10 ²	0.33	0.55	2.59	8.52 ²	8.19 ²
Patch (Pa)	2	17.28 ¹	8.86 ¹	57.81 ²	4.34	1.73	31.06 ²	35.43 ²	0.34	2.12	13.75 ¹
Time (Ti)	2	7.69 ¹	62.55 ²	38.38 ²	7.65 ¹	20.12 ²	67.74 ³	345.36 ³	1.27	2.18	18.49 ²
Si × Pa	4	0.86	1.02	0.40	3.01 ¹	3.54 ¹	0.51	0.43	0.58	5.39 ²	1.26
Si × Ti	4	4.27 ²	2.70 ¹	1.05	11.59 ²	7.67 ²	0.88	0.19	4.94 ²	0.20	3.07 ¹
Pa × Ti	4	11.51 ²	0.64	5.76 ¹	2.91	1.15	14.58 ²	20.95 ³	0.42	0.94	12.24 ³
Si × Pa × Ti	8	0.76	1.63	0.65	3.18 ²	3.60 ²	0.28	0.42	1.79	1.04	0.63
Residual	54										

F-ratios and level of significance are shown ($n = 3$).

Site (three levels: site1, site2 and site 3) is a random factor, patch size (three levels: small, medium and large) and Time (three levels: 3, 7 and 21 days) are fixed factors.

^a Data were $\log(x + 1)$ -transformed prior to analysis.

¹ $P < 0.05$.

² $P < 0.01$.

³ $P < 0.001$.

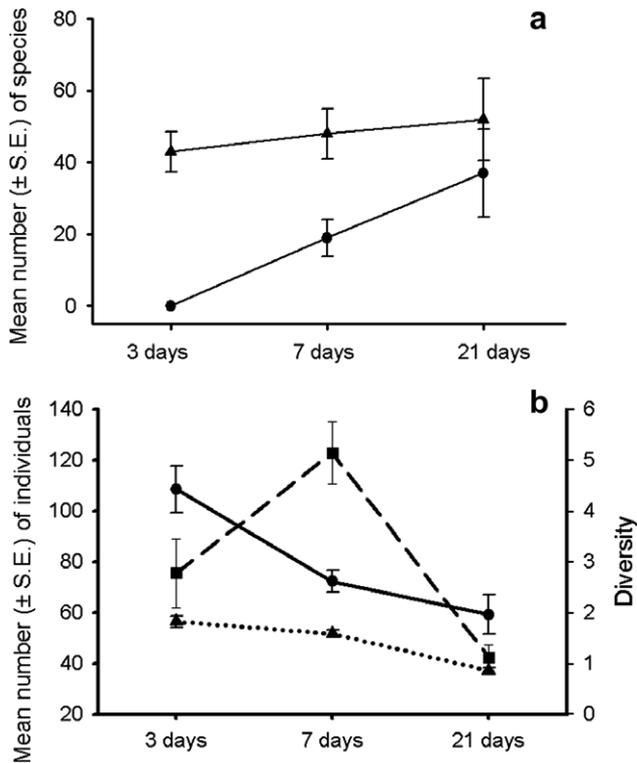


Fig. 4. (a) Cumulative addition and loss of species averaged across patches and sites by day 3, 7 and 21 ($n = 27$). ▲: cumulative species addition; ●: cumulative species loss. (b) Mean number (\pm SE) of individuals and Shannon–Wiener's and Fisher's diversity indices averaged across patches in Site 3 by day 3, 7 and 21. ■: abundance; ▲: Shannon–Wiener' index; ●: Fisher's index.

and, the magnitude of this variation was not consistent across sites (i.e. a significant site \times time interaction; Table 3). For example, abundances by day 7 were greater than by days 3 or 21 in Site 1 (day 7 > day 3 = day 21; SNK tests, $P < 0.05$). In Site 3, abundances by day 7 were greater than by days 3 and 21 (day 21 < day 3 < day 7; SNK tests, $P < 0.05$; Fig. 4b). In contrast, diversity varied over time consistently across sites and patch sizes (Table 3). Both diversity indices decreased steadily from an early maximum (day 3 > day 7 > day 21; SNK tests, $P < 0.05$; illustrated for Site 3 in Fig. 4b).

In general, successional patterns varied among patch sizes and sites, but trends were not consistent. Different patterns were observed in patches of same size at different sites. In addition, the most abundant species (Table 4) showed variable temporal trends in patterns of abundance.

C. littoralis colonised all patches rapidly and, patterns of abundance did not vary through time (Table 4). Abundances of Anthomyiidae sp1 and *A. variana* showed a significant variation over time, but this variation was inconsistent across sites (i.e. significant interaction site \times time; Table 4; illustrated by *A. variana*; Fig. 5a). *P. cadaverina* and Sphaeroceridae sp1 colonised all patches and sites within 3 days, but patterns of abundances in some patches and sites varied through time (i.e. significant interaction patch size \times Time and patch size \times site; Table 4). For example, abundances of both species in small patches

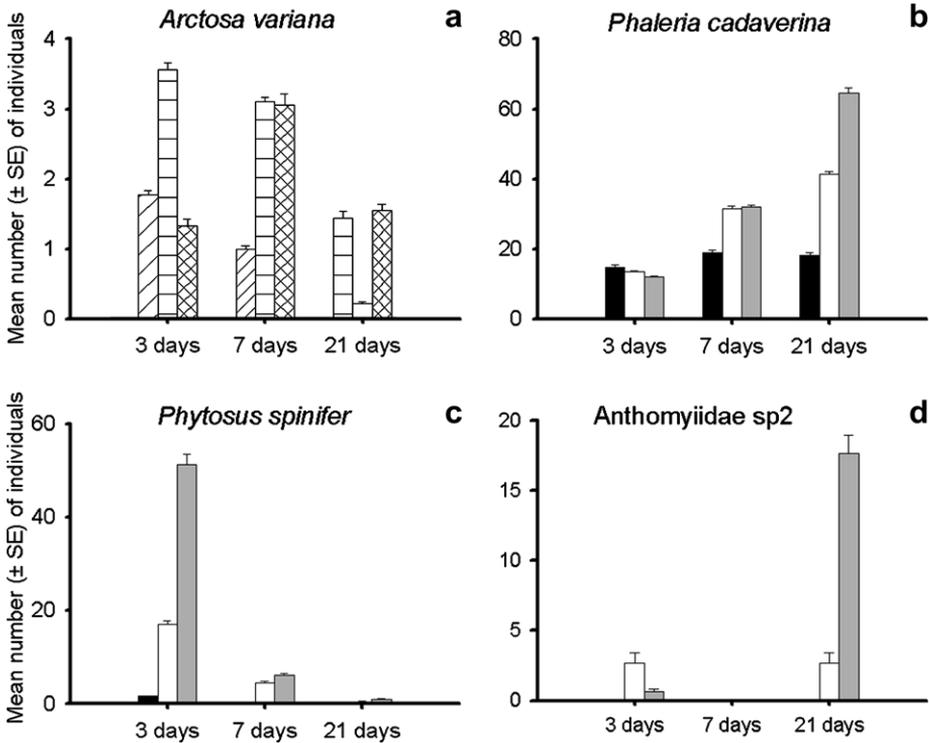


Fig. 5. Mean number (\pm SE) of individuals ($n = 3$) through time. (a) *A. variaria* averaged across patches at Site 1 \square ; Site 2 \square ; Site 3 \square . (b) *P. cadaverina* averaged across sites in small, medium and large patches. (c) *P. spinifer* averaged across sites in small, medium and large patches. (d) Anthomyiidae sp2 in small, medium and large patches in Site 1. \blacksquare : small patch; \square : medium patch; \square : large patch.

did not vary over time, whereas abundances in medium and large patches showed significant variation over time (medium patch: day 3 < day 7 = day 21; large patch: day 3 < day 7 < day 21; SNK tests, $P < 0.05$; illustrated by *P. cadaverina* in Fig. 5b). *P. spinifer*, *A. grisea* and *C. xantholoma* colonised patch of all sizes very quickly, but patterns of abundance were not consistent through time (i.e. a significant patch size \times time interaction; Table 4). For example, abundances of *P. spinifer* in small patches did not vary over time whereas its abundances in medium and large patches decreased over time (day 21 < day 7 < day 3, SNK tests, $P < 0.05$; Fig. 5c). Abundances of *C. xantholoma* in small and medium patches were significantly greater on day 3 (day 21 = day 7 < day 3, SNK tests, $P < 0.05$, whereas abundances in large patches decreased over time (day 3 > day 7 > day 21; SNK tests, $P < 0.05$). Anthomyiidae sp2 and *T. saltator* showed complex patterns (i.e. significant interaction site \times patch size \times time; Table 4). For example, Anthomyiidae sp2 only colonised quickly (i.e. by day 3) in medium and large patches at Site 1. Abundances of this species dropped to 0 in all patches by day 7. By day 21, the abundance of Anthomyiidae sp2 was greatest in large patches (Fig. 5d). *T. saltator* had only colonised some medium and large patches by day 3. By day 7, this species had colonised all patches, but its abundances in medium and large patches was greater than in small patches in all sites (small < medium = large; SNK tests, $P < 0.05$). Further, by day 21, the abundances of this species dropped to 0 in all patches and sites.

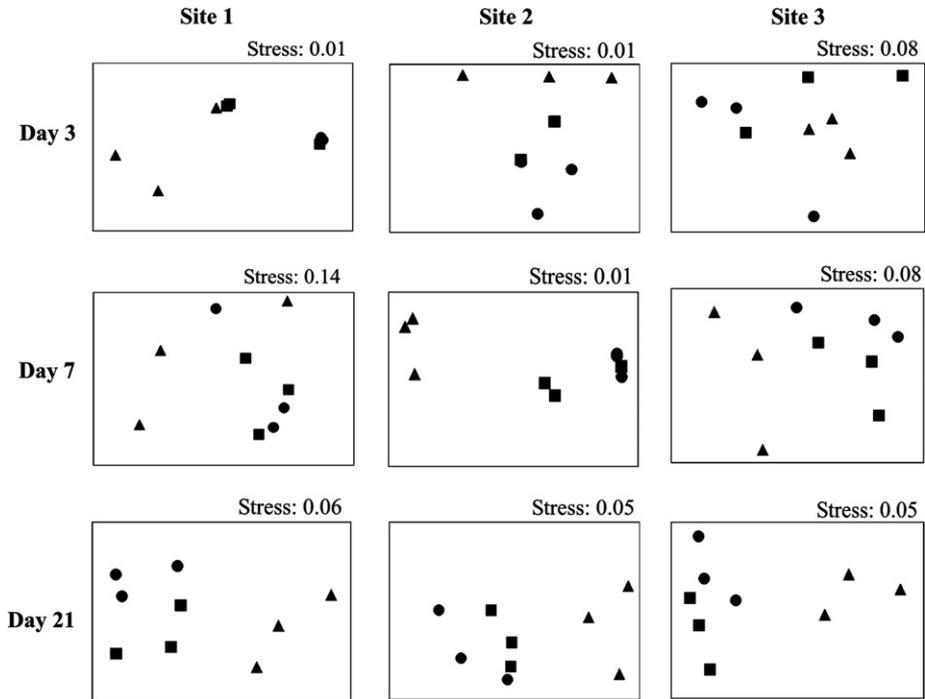


Fig. 6. Non-metric multi-dimensional scaling (nMDS) for differences in assemblages among patch sizes at each site and time ($n = 3$). ▲: small patch; ■: medium patch; ●: large patch.

3.7. Assemblages in wrack patches over time

There was some evidence to support the hypothesis that macrofaunal assemblages change in response to patch size and time. However, this response was not consistent across sites (i.e. a significant site \times patch size \times time interaction; $F_{8,54} = 1.36$, $P < 0.05$; Fig. 6). Post hoc comparisons showed that assemblages in small patches differed from those in medium and large patches although in different ways (Table 5). For example, on day 3 there was a clear difference between small and large patches in Site 1, although no clear alternative hypothesis could be defined because medium patches did not differ from either small or large patches. On day 7, small patches were significantly different from medium and large patches, but only in site 2. On day 21, small patches differed from medium and large patches in all sites.

4. Discussion

4.1. Decomposition of wrack

The decomposition of wrack patches was similar in all sites and depended on wrack patch size (see Table 1). It was strongly influenced by time-specific environmental and/or biological factors. All patches showed a rapid decline in dry mass with patches declining to $\sim 50\%$ of their initial mass by day 3. Small wrack patches had a higher rate of decomposition than medium and large patches. An increase in decomposition rate of small

Table 5

Mean Bray–Curtis dissimilarities (%) within and between patch sizes (small patch [S], medium patch [M] and large patch [L])

		Dissimilarity (%) within patches		Dissimilarity (%) among patches	<i>P</i>
<i>Day 3</i>					
Site 1	S	43.20	S vs M	50.62	<0.05
	M	38.95	S vs L	63.33	
	L	27.59	M vs L	39.17	
Site 2	S	49.12	S vs M	43.98	<0.05
	M	23.16	S vs L	53.26	
	L	29.48	M vs L	31.33	
Site 3	S	34.87	S vs M	43.78	<0.05
	M	52.39	S vs L	52.37	
	L	50.22	M vs L	52.40	
<i>Day 7</i>					
Site 1	S	44.22	S vs M	44.10	<0.05
	M	32.91	S vs L	44.10	
	L	33.44	M vs L	30.46	
Site 2	S	28.99	S vs M	39.43	<0.05
	M	29.40	S vs L	46.86	
	L	19.27	M vs L	27.55	
Site 3	S	34.03	S vs M	38.32	<0.05
	M	30.20	S vs L	42.18	
	L	28.85	M vs L	27.18	
<i>Day 21</i>					
Site 1	S	36.50	S vs M	41.28	<0.05
	M	39.06	S vs L	55.30	
	L	29.53	M vs L	42.66	
Site 2	S	32.23	S vs M	39.88	<0.05
	M	23.62	S vs L	49.36	
	L	36.31	M vs L	32.53	
Site 3	S	35.52	S vs M	62.95	<0.05
	M	37.98	S vs L	60.42	
	L	31.61	M vs L	35.38	

P indicates significant pairwise comparisons from PERMANOVA; 4999 permutations of the raw data to calculate significance. Data were log ($x + 1$)-transformed.

patches might be attributed to the more rapid drying process for small patches. Drying accelerates the release of cell contents by leaching, which contributes substantially to the total loss of the wrack's organic matter (e.g. Ochieng and Erfteimejjer, 1999). Wind exposure and sand abrasion are very important factors influencing the decomposition rates of wrack (Colombini and Chelazzi, 2003). Therefore, small patches with a larger surface area to volume ratio could be more affected by sand abrasion which also accelerated the decomposition process compared to medium and large patches.

Some studies have shown different phases (up to three phases) in the process of wrack decomposition (e.g. Valiela et al., 1985) whereas others have reported a linear trend in breakdown process (e.g. Inglis, 1989; Jedrzejczak, 2002a). In this study two different

phases were identified. Initially, there was a rapid desiccation and loss of organic material from the wrack by day 3, followed by a second slower phase. Great abundances of several invertebrates such as *T. saltator*, *C. littoralis*, *P. spinifer* and Anthomyiid flies were found in all wrack patches in this study and their role as algal wrack consumers might have been very important in the process of wrack decomposition (see Thrush, 1986; Lastra et al., 2005). Grazing by amphipods and other detritivores accelerates the decomposition of vascular plant material (e.g. Roberston and Mann, 1980; Inglis, 1989; Colombini et al., 2000; Pennings et al., 2000). Moreover, larvae may contribute greatly to the decomposition of wrack as a result of their own feeding activity and through the spread of microorganisms (Jedrzejczak, 2002a). Temperature during the experiment period could also be an important factor accelerating the decomposition process since maximum temperatures ranged from 18.4 °C to 29 °C during the experiment. Temperature can increase decay rates during the process of wrack breakdown (e.g. Valiela et al., 1985; Colombini and Chelazzi, 2003). Temperature may also affect daily activity of some macroinvertebrates such as amphipods and isopods (e.g. Scapini et al., 1992) and, consequently, influence their consumption rate (Lastra et al., 2005).

4.2. Patterns of colonisation and succession

Bare sediment was characterised by species-poor assemblages and low abundances of individuals. Input of algal wrack deposits might play an important role in determining the population abundances of upper shore communities on this exposed beach (see Griffiths and Stenton-Dozey, 1981; Dugan et al., 2000; Dugan et al., 2003; Jedrzejczak, 2002b). Several studies have found that supralittoral macrofaunal communities are more affected by food availability (wrack deposits) than by physical characteristics of the beach (e.g. Dugan et al., 2003). In addition, algal wrack can act as a refuge from predators (Inglis, 1989; Colombini et al., 2000).

The number of species found in this study (53) was higher than those reported in previous studies (e.g. Stenton-Dozey and Griffiths, 1983; Colombini et al., 2000; Colombini et al., 2002; Dugan et al., 2003; Jedrzejczak, 2002b). The major components of the algal wrack were coleopteran tenebrionid and staphylinid species, amphipods and dipteran flies. This is in contrast to what has been observed on other beaches (e.g. Behbehani and Crocker, 1982; Inglis, 1989; Shibata, 1993; Colombini et al., 2002; Jaramillo et al., 2003). Another striking result was the absence of Nematoda and Collembola in the macrofauna of algal wrack. These taxa have been reported to colonise older (i.e., >19 days) wrack (Colombini et al., 2000). It is possible that algal wrack in the experiment was not old enough to be colonised by these groups. Conversely, differences in fauna of beach-cast wrack may be related to location of algal deposits, beach morphology, season, climate and vegetation cover (Colombini and Chelazzi, 2003).

The pattern of colonisation varied among wrack patches of different sizes. Small patches had fewer species and individuals than medium and large patches. Patterns of colonisation varied among species, across sites and from time to time. The abundance of some species did not differ among patches of different sizes (e.g. *A. variana*), whereas the abundance of others varied with patch size, but not necessarily at all sites (e.g. *T. saltator* and Anthomyiidae) or times (e.g. *P. cadaverina*, *P. spinifer*, *A. grisea*, etc.). Species such as Anthomyiidae sp1 were more abundant in medium and large patches and the magnitude of those differences was consistent across sites and times.

Increasing algal wrack biomass provided a larger area for habitation by macroinvertebrates. Although the relationship between algal wrack biomass and associated macroinvertebrates was a species-area function, several mechanisms might be responsible for such a pattern, including environmental heterogeneity, sampling artefact, food supply, predation levels, an equilibrium between extinction and immigration (e.g. Rey, 1981; Castel et al., 1989; Koukouras et al., 1992; McCabe and Gotelli, 2000; Bowden et al., 2001; Rossi and Underwood, 2002). Different species showed different patterns of colonisation (see above) suggesting that life-history attributes and mobility of different taxa, such as their colonising and competitive abilities may be important in understanding the observed distributions among patch sizes (Wilson, 1994). For example, it is well known that large patches experience less environmental disturbance than do small patches (e.g. Irlandi et al., 1995). Thus, in large patches where disturbance is less frequent, species with limited dispersal and good competitive abilities would be likely to be present. In contrast, interactions in small patches with more frequent disturbances would be mostly among poor competitors with wide dispersal and rapid colonisation.

In general, all patches were rapidly colonised (within 3 days) by most species (44 of 53). The rate of species succession was very rapid with a high rate of species addition by day 3, and a high rate of species loss by days 7 and 21. Ephemeral resources such as algal wrack are an example of heterotrophic successions. They are generally characterised by a successional change of species associated with different qualitative stages of decomposition and ageing of wrack (Colombini and Chelazzi, 2003). Successional changes in algal wrack macrofaunal assemblages observed in the present study are characteristic of drift line communities (see Colombini et al., 2000; Jaramillo et al., 2003). Many species undergo tidal migrations of some sort that allow them to feed on freshly stranded debris (Inglis, 1989; Fallaci et al., 1999; Colombini et al., 2000). As a result, the population dynamics of many species are likely associated with maximising utilisation of food resources (Inglis, 1989; Rossi and Underwood, 2002).

Variations in the metabolic and trophic needs of the different colonizing species may be important in influencing the observed pattern of succession. Successional changes in the fauna of algal litter have been reported by other authors (e.g. Griffiths and Stenton-Dozey, 1981; Inglis, 1989; Marsden, 1991; Colombini et al., 2000; Dugan et al., 2003; Colombini and Chelazzi, 2003). These works have found that talitrid amphipods are the primary colonisers of newly deposited algal wrack, and that they are the most important consumers. In contrast, this study showed that the most abundant early colonisers included a dipteran (Sphaeroceridae sp1), several coleopteran species (*C. littoralis*, *P. cadaverina*, *C. xantholoma*, *A. grisea* and *P. spinifer*) and a spider, *A. variana*. Although *T. saltator*, *T. europaeus* and Anthomyiidae sp1 colonised the algal wrack by day 3 (very few individuals) and were very abundant by day 7. The other Anthomyiid fly (sp2) colonised algal wrack by day 21. *C. littoralis* and *P. spinifer* are herbivores, whereas *P. cadaverina* and *C. xantholoma* are scavengers (Ponel, 1993). Carnivorous species such as *A. variana* and *A. grisea* feed on larvae of dipterans and other insects (Colombini and Chelazzi, 2003; Jaramillo et al., 2003). Scavengers such as *P. cadaverina*, *T. europaeus* or *C. xantholoma* may feed on different sources of organic debris (Jaramillo et al., 2003). Adults Anthomyiid flies are insignificant consumers of algal-exuded substances but lay their eggs in wrack (Griffiths and Stenton-Dozey, 1981). Thus, their larvae that were very abundant by day 7 (pers. obs.) might have contributed to the breakdown of algal tissue (Inglis, 1989). The patterns of succession observed in the present study may be due in part to niche differences among the species

that were present, each exploiting space and time differently in order to avoid inter-specific interactions (Jaramillo et al., 2003). The appearance or disappearance of certain species may also be related to progressive microclimatic changes of the wrack deposits due to their varying position across the beach, i.e. three different sites that differed slightly in slope and topography (see area of study). A species' locomotory ability and behaviour are also very important in determining successional patterns (Fallaci et al., 1999; Scapini et al., 1992; Colombini and Chelazzi, 2003). Talitrid amphipods, tylid isopods and tenebrionid insects show patterns of distribution related to environmental variables such as the relative humidity of the air, sand temperature and moisture (e.g. Fallaci et al., 1999; Jaramillo et al., 2003). During the experiment period, air relative humidity, sand temperature and moisture changed due to weather conditions. In fact, *T. saltator* and *T. europaeus* showed peaks of abundance when sand moisture and relative humidity were higher (by day 7). Furthermore, talitrids and isopods have been found to show different movements and directions during neap and spring tides (Colombini et al., 2000; Jaramillo et al., 2003). In this study, day 3 was close to spring tide, whereas day 7 and day 21 were close to neap tide. It is possible that patterns of colonisation of some species such as *T. saltator* and *T. europaeus* could have been affected by the tidal phase.

There was some evidence to support the hypothesis that macrofaunal assemblages change in response to patch size and time. Nevertheless, this response was not consistent across sites. Different responses at different sites may be related to different environmental conditions among sites (e.g. Rossi and Underwood, 2002; Dugan et al., 2003; Colombini and Chelazzi, 2003). Species-specific strategies for exploiting the algal wrack (as refuges and/or as a feeding site), that vary in space and in time, and interactions between and within species may also lead to inconsistent changes in assemblages associated with different sizes of algal wrack patches and different sites.

This study shows the importance of time and size of wrack deposits in determining spatial and temporal patterns of macrofaunal distribution on exposed sandy beaches. For this reason, it is necessary to consider macrophyte wrack supply concomitantly with other physical factors (e.g. morphodynamics, sediment conditions) in order to better understand the processes that influence community structure on exposed sandy beaches. The assemblages supported by beach-cast macrophytes are important prey resources commonly exploited by a number of shorebirds and, therefore, are a basic element of food webs acting as important link between marine-terrestrial habitats (Ochieng and Erfemeijer, 1999; Colombini and Chelazzi, 2003; Hubbard and Dugan, 2003; Orr et al., 2005). Thus, wrack-cleaning activities done on beaches used as recreational areas might have important cascading effects on the strandline-related species diversity and abundance and, consequently, affect both terrestrial and marine habitats.

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