Recovery of macrobenthic assemblages following experimental sand burial*

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Abstract

Periodic inundation by sand is a very common feature of rocky coasts throughout the world. Even so, there have been few direct observations or experiments to investigate the role of sediments on intertidal rocky shores. We designed a field experiment in Mazatlán Bay, Mexico, to test the initial impact and subsequent

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recovery of intertidal macrobenthic assemblages exposed to sand burial at two sites of varying wave exposure. Both sites supported different natural assemblages. Treatment plots for the addition of sediment and control plots (50×50 cm), separated by at least 1.5 m, were randomly placed across the mid-water tidal level. The initial response of the resident macrobenthos and the subsequent recolonization was monitored over a period of 95 days. The main effect of sediment deposition at both sites was mortality and removal of biota due to smothering. The recovery process was rapid and may in part have been the result of the mechanism by which the small, disturbed patches were recolonized. Most of the invertebrates colonized the patches as adults; several seaweeds exhibited vegetative growth as the major mechanism of colonization (e.g., *Ulva lactuca* Linnaeus, 1753, *Amphiroa valonioides* Yendo, 1902 and *Chaetomorpha antennina* (Borgensen) Kutzing, 1849). The rate of recovery varied between the sites, however. Recovery of species numbers proceeded quickly at the sheltered site (day 7), but took 95 days at the exposed site. In contrast, biomass reached control levels by day 45 at the sheltered site, but already by day 15 at the exposed site. By day 95, the assemblages recovered to 83.5% and 81% similarity with the controls at the sheltered and exposed sites respectively. Although differences in wave exposure could be very important in determining the different patterns of recovery at both sites, other biological processes may also play an important part.

1. Introduction

The worldwide increase in sediment load in coastal areas as a consequence of anthropogenic activities has increased interest in the impact of sedimentation on rocky shore ecosystems (Newell et al. 1998). Natural factors such as wind-driven waves may also influence temporal fluctuations of sand movement in coastal areas (Anderson & Meyer 1986, Lund-Hansen 1991). In fact, periodic inundations by sand as a result of coastal currents or the action of storms are a very common abiotic disturbance of rocky coasts throughout the world (e.g., Littler et al. 1983, Pineda & Escofet 1989, Evans et al. 1993, Engledow & Bolton 1994, Moring 1996, Trowbridge 1996).

Sediments are added to a rocky coast and are redistributed as a function of sediment characteristics, hydrodynamic conditions, bottom heterogeneity and biological factors (Hiscock 1983). These factors operate over a wide range of spatial and temporal scales. Thus, while at large spatial and temporal scales sediment deposition may be relatively predictable, depending on the source and magnitude of sediment loads, at small scales, patterns may be highly heterogeneous and unpredictable (Airoldi & Virgilio 1998).

The importance of sediments as a major source of spatial and temporal heterogeneity for rocky coast organisms has only recently been fully recognized (Littler et al. 1983, McQuaid & Dower 1990, Trowbridge 1996, Airoldi 1998). Sediments may occur as a thin stratum, or form deposits

from a few to tens of centimeters thick. Depending on local hydrodynamic and topographic conditions, they may accumulate locally in crevices or be trapped in algal turfs, or be resuspended and transported above the substrata (Airoldi 2003). This heterogeneity results in a variety of possible effects on rocky coast organisms. For example, excessive sedimentation affects organisms directly by smothering or scouring them, although some authors have suggested that occasional burial by sand may be an important factor in maintaining diversity by permitting the co-existence of opportunistic species on patches of cleared substrate (Foster 1975, Taylor & Littler 1982) or by enhancing habitat heterogeneity (McQuaid & Dower 1990).

Be that as it may, most papers show that high levels of sediment deposition are detrimental to species richness and the diversity of hard-bottom communities (Littler et al. 1983, McClanahan 1990, Saiz-Salinas & Isasi-Urdangarin 1994, Naranjo et al. 1996, Carballo 2006). Burial may eliminate or reduce susceptible species, but may in turn increase the abundance of tolerant species, unless it becomes too severe or too prolonged, in which case even tolerant species are eliminated (Airoldi et al. 1996, Saiz-Salinas & Urkiaga-Alberdi 1999, Wesseling et al. 1999, Airoldi 2003). In addition, burial by sand may affect behavior patterns such as feeding activity and may cause physiological stress (Marshall & McQuaid 1993). Probably the most important stress animals experience during burial relates to reduced oxygen availability, which may be caused, for example, by lowered oxygen tension of the surrounding sediment water (Marshall & McQuaid 1989, Maun 1996). On the other hand, the movement of sediments in habitats subject to strong wave action or currents can seriously affect organisms by scouring or abrading them (Airoldi 2003). Scouring may damage and remove whole organisms or their parts and, depending on the duration and intensity of the water motion, the effects can be moderate damage or severe changes to the structure of the assemblages of organisms (Airoldi et al. 1996, Airoldi 1998).

Despite the extensive body of literature, there are few direct observations and experiments to investigate the effects of sedimentation on the organisms and assemblages inhabiting intertidal rocky shores (e.g., Taylor & Littler 1982, Littler et al. 1983, Marshall & McQuaid 1989, McQuaid & Dower 1990, Airoldi 1998, Crowe et al. 2000, Hutchinson & Williams 2003, Prathep et al. 2003, Zardi et al. 2006). For this reason, predicting the magnitude of the effects that different sedimentation regimes have on intertidal rocky-coast organisms and the critical levels above which detrimental effects become manifest remains an important issue for the ecology of rocky coasts (Airoldi 2003). A first step to understanding the ecological importance of

sediment deposition events on intertidal rocky shores is to determine the rate of recovery of macrobenthic assemblages and how the recovery process is influenced by environmental and biological processes operating at different spatial scales.

In this study we designed a field experiment to test the initial impact of sand burial on intertidal macrobenthic assemblages and their subsequent recovery at two sites on a rocky shore (Mazatlán Bay, Mexico). Both sites supported different natural assemblages and differed in wave exposure (see below). The hypotheses tested were that (1) the structure of assemblages, i.e., biomass, number and species composition and diversity, will vary as a consequence of the burial process, and that (2) the recovery process will differ between sites because of the variability in the physical and biological processes taking place at each site.

2. Material and methods

2.1. Study area

Mazatlán Bay is an open subtropical coastal embayment located on the southeast Gulf of California. The climate in the study area is warm and subhumid with wet summers and a mean annual rainfall of 800 mm (CNA 2004). In this area, we have observed that rocky intertidal ecosystems are seasonally influenced by sand deposition, partially generated by local variations in climate and fluctuations in wind-driven waves (Carballo 2006, Carballo et al. 2008). In summer, tropical waters from the south influence the bay, in contrast to sporadic wind-induced upwelling in winter. During the summer, rains coincide with the winds from the southwest (WSW) to produce a net sediment movement towards the open sea. During winter, however, most winds blow from the northwest, producing a net southward sediment movement that redistributes the sand, increasing deposition on rocky habitats (Peraza 1985). In some areas, sand deposition can produce a layer up to 60 cm thick that can remain for the whole season, i.e., 2–3 months. Local patterns of sediment deposition mostly vary on a scale of meters. For example, in Playa Norte over a distance of 10 m the sediment layer depth can vary between 16 and 50 cm (Yáñez, in preparation).

The study was done in the Cerro del Crestón (23°10′N; 106°25′W). The location selected for the study (Figure 1) is a gently sloping rocky shore ($\sim 0 - 2°$ incline), interrupted near the seaward margin by deeply cut surge channels that run perpendicular to the shoreline. The shore is exposed to direct wave action from all but the most westerly swells. Two sites 200 m apart and located on the same shore were chosen. Both
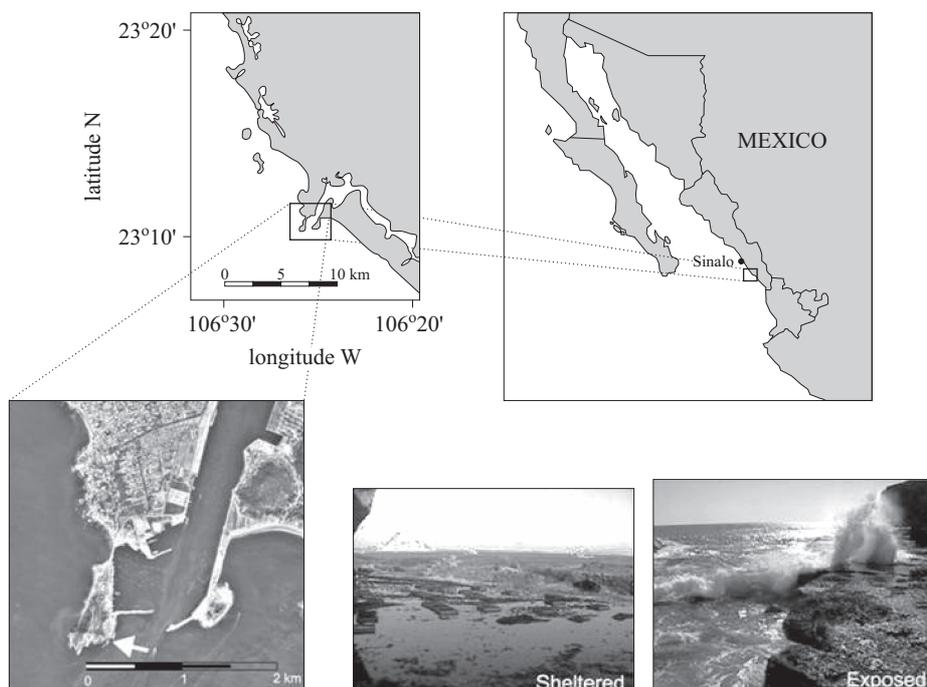
Figure 1. Location of the study area. The white arrow indicates the site locations

sites support different assemblages (see Results). Furthermore, both sites experience differences in wave exposure. Site 1 is located in a more sheltered position than Site 2 (hereafter referred to as the 'sheltered' and the 'exposed' site, respectively). Differences in wave action in this area were estimated using the plaster dissolution method (Gambi et al. 1989): two sets of four plaster spheres 5 cm in diameter were placed at each site during one week. The dissolution percentage was significantly higher for the exposed site than the sheltered one (ANOVA; site: $F_{1,6} = 6.29$; $P < 0.05$).

2.2. Experimental design

The aim of the experiment was to mimic a sedimentation event of moderate intensity when sediment is deposited on rocky shores in this area. A total of 80 experimental plots (50×50 cm) – 40 at each site – were established over two days (October 12–14, 2004). Treatments (20 sand addition plots) and controls (20 plots to which no sand was added), separated by at least 1.5 m, were randomly assigned and placed across the mid-water tidal level (Figures 2 and 3). All corners of both treatment and control plots were marked by stainless steel bolts drilled into the bedrock. To minimize edge effects, a band ~ 25 cm wide along the margins of the treatment
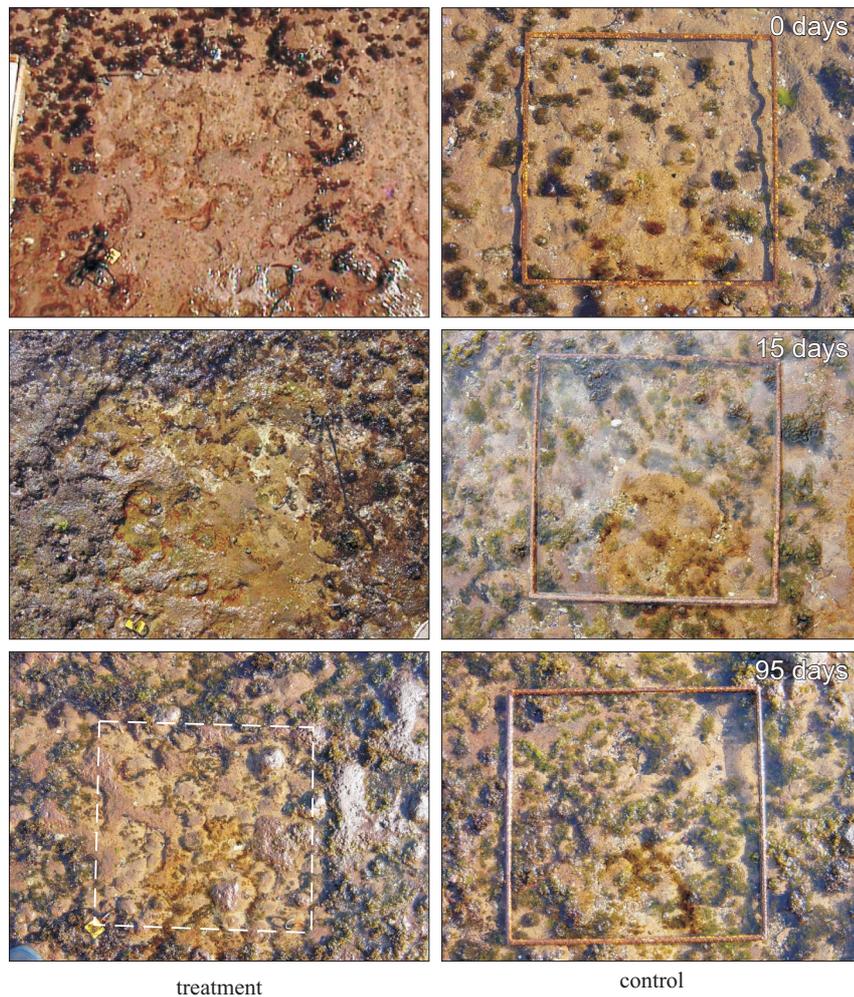
Figure 2. Treatment and control plots after 0, 15 and 95 days at the sheltered site

plots was cleared. To retain the sediment in the treatment plots a square wooden frame (5 cm height) was attached to the rock with lag bolts andexpanding lead anchors. Then, during the low-tide period, sediment was added to the treatment plots to produce a layer ~ 5 cm thick and kept there for 20 days. This thickness of sand was maintained daily during the whole experiment in that the sand blown/washed away was replenished (the layer was always thicker than 4 cm). After this period, the wooden frame was removed and the remaining sediment was washed away by waves at the exposed site or remained partially in the plots (small patches of sediment less than 2 cm thick) at the sheltered site.
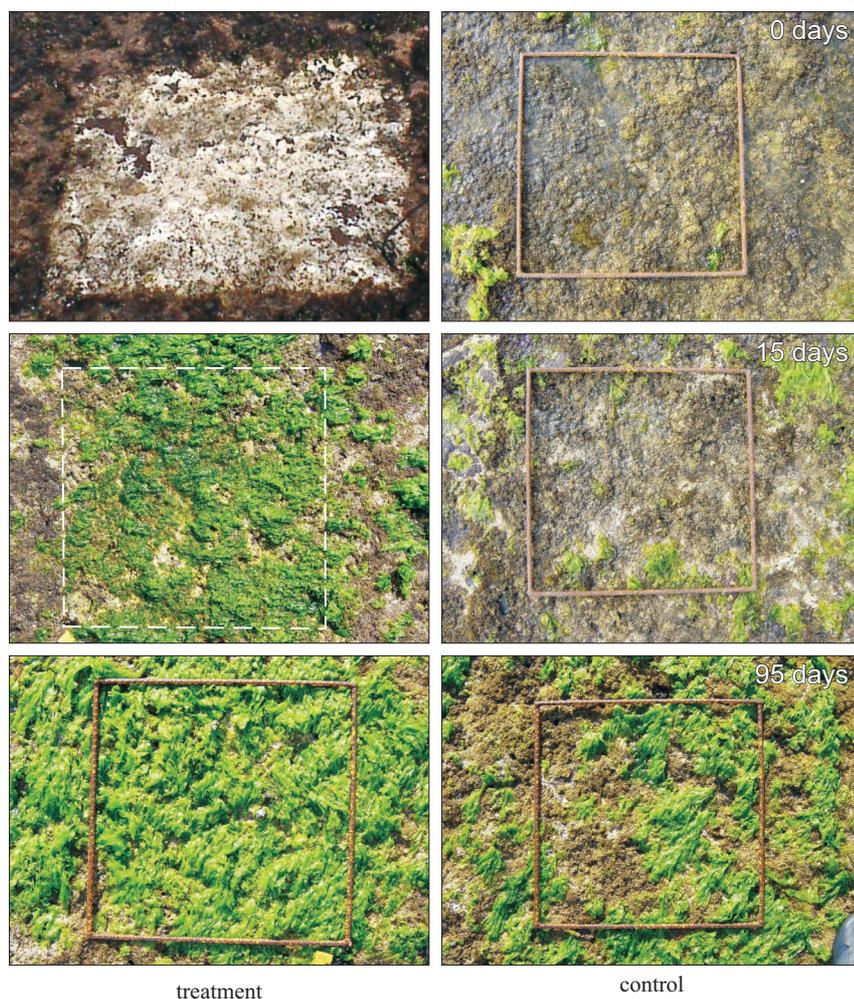
Figure 3. Treatment and control plots after 0, 15 and 95 days at the exposed site

Sediment was obtained from a nearby river. Particle size analysis of the material showed a similar composition and granulometry to the sand deposited naturally by waves and storms (fine sand 29.4% volume, medium sand 60.76% volume and coarse sand 10% volume).

Eight plots (4 treatment and 4 control) were randomly sampled on day 0, 7, 15, 45 and 95 following the deposition event. However, a storm washed away 5 treatment plots at the exposed site 20 days after the beginning of the experiment, so only 6 plots (3 treatment and 3 control) at the exposed site were sampled.

Because the wooden frame constituted a potential disturbance to macrofauna and might itself alter the assemblage, a procedural control was included: 3 frames similar to those used in the treatment plots but without sand were placed at each site. Because the wooden frame in the treatments was kept for 20 days, i.e., time 0, the effect of the wooden frame was tested by comparing assemblages in the procedural controls, controls and treatments on day 0, i.e., 20 days after the experiment had started. In addition, 4 plots of the same size were sampled at both sites before the beginning of the experiment in order to characterize the natural assemblages.

Sampling was destructive since it involved scraping the entire surface of each plot with a spatula. The samples were then taken to the laboratory. Seaweeds and invertebrates were examined under a stereomicroscope for sorting, drying and weighing. To estimate the biomass (g dry weight/0.25 m^2), all organisms were oven-dried at 60°C to constant weight.

2.3. Data analysis

Because the natural assemblages and the number of replicates both differed between sites, all statistical analyses were done at each site separately. Biomass, together with the univariate indices H' diversity ($\log_e$), J' evenness and number of species, were used to examine the structure of macrobenthic assemblages. Changes in these parameters were investigated using a 2-factor orthogonal analysis of variance. Treatments (2 levels) and Time (5 levels) were fixed and random factors, respectively. Prior to the analyses, homogeneity of variances was evaluated by using Cochran's test (Winer et al. 1991) and transformed when necessary. *A posteriori* multiple comparisons were done using SNK tests (Underwood 1997).

The structure of the assemblages was also analyzed using multivariate techniques. Changes in macrofaunal assemblages were assessed by 2-factor orthogonal non-parametric analysis, PERMANOVA (formerly NP-MANOVA; Anderson 2001), with *a posteriori* multiple comparisons, based on Bray-Curtis (dis)similarity measures calculated from square-root transformed data. A dendrogram (unweighted pair-group method algorithm) and non-metric multi-dimensional scaling (nMDS) were also used to plot the rank-order differences among treatments following square-root transformation of data. This reduced the effects of abundant species relative to rare species and thus minimized the possibility that significant differences among sites/time, etc., would be due simply to the chance abundance of highly variable species (Field et al. 1982, Underwood & Chapman 1998). The Kruskal stress coefficient was used to assess the adequacy of the ordination obtained by the nMDS (Clarke 1993). Taxa contributing most to

the dissimilarity/similarity among/within treatments were identified using SIMPER analysis (Clarke 1993).

3. Results

3.1. Natural assemblages

The natural assemblages differed between the sheltered and exposed sites (F = 11.61, $P = 0.006$). The differences were due mainly to 4 seaweeds (*Gymnogongrus leptophyllus* J. Agardh, 1876, *Amphiroa valonioides*, *Gelidium sclerophyllum* Taylor, W. R. 1945, and *Ulva lactuca*), and 4 invertebrate species, the molluscs *Cerithium menkei* Carpenter, 1857, *Nerita funiculata* Menke, 1851 and *Thais (Stramonita) biserialis* Blainville, 1832, and the sea urchin *Echinometra vanbrunti* Agassiz, 1863, which explained 82% of the dissimilarity between sites. *G. leptophyllus*, *G. sclerophyllum*, *C. menkei* and *N. funiculata* were the most abundant at the sheltered site, whereas *A. valonioides*, *U. lactuca*, *E. vanbrunti* and *T. (S.) biserialis* were the most abundant at the exposed site. Herbivores such as *Littorina aspera* Philippi, 1846 and Acmaeidae sp. were present at both sites, and predators such as *Pachygrapsus transversus* Gibbes, 1850 and *Acantholobulus mirafloresensis* Abele & Kim, 1989 were common at both sites, though slightly more abundant at the exposed site. Mussels (*Modiolus* sp.) were quite abundant at both sites but did not monopolize space.

3.2. Diversity and structure patterns of macrobenthic assemblages

3.2.1. Univariate indices, species composition and biomass

Diversity fluctuated greatly in the treatments (0–1.20 at the sheltered site and 0–1.19 at the exposed site), but also in the controls (1.12 –1.67 at the sheltered site and 0.35–1.51 at the exposed site) over time (Figures 4a,b). At the sheltered site, diversity remained similar from day 7 onwards, whereas at the exposed site diversity decreased steadily over time (Figures 4a,b). In addition, at the sheltered site, diversity in the controls did not differ significantly from the treatments except for day 0 (i.e., a significant Treatment × Time interaction; $F_{4, 30} = 40.59$, P < 0.001; Figure 4a), whereas at the exposed site diversity was consistently lower in the treatments than in the controls during the entire study ($F_{4, 20} = 18.34$, P < 0.001; Figure 4b). There were significant linear relationships between H' vs. J' for exposed (y = 0.3757× + 0.0422; $R^2 = 0.951$; P < 0.01) and sheltered sites (y = 0.3852× − 0.0001, $R^2 = 0.8837$; P < 0.01), but no significant correlation was found between diversity and number of species. This suggests that most changes in the assemblages were due to variation in evenness, rather
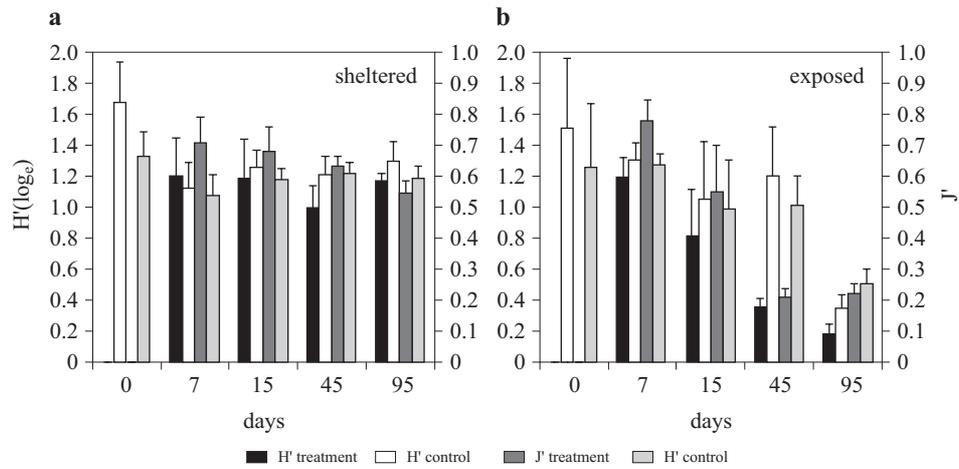
Figure 4. Mean variation ($\pm$SE) of diversity (H') and evenness (J') in treatment and control plots over time: sheltered site (n$=$4) (a); exposed site (n$=$3) (b)

than variation in the number of species. However, loss and substitution of species also occurred. For example, at the sheltered site, species such as *Chaetomorpha antennina* disappeared by day 15 and *Amphiroa valonioides* and *Ulva lactuca* appeared by the end of the experiment, i.e., by day 95. At the exposed site species such as *Echinometra vanbrunti* disappeared by day 7 and *Isognomon janus* Carpenter, 1857, *Acantholobulus mirafloresensis* and Nereidae sp. disappeared by day 95.

At the sheltered site, the number of species differed between treatments and controls, but this response was not constant over time (i.e., a significant Treatment x Time interaction; $F_{4,30} = 6.24$, $P < 0.001$). In fact, controls and treatments only differed significantly at time 0, and after this time there were no significant differences between controls and treatments (Controls $=$ Treatments, SNK tests $P > 0.05$; Figure 5a). The composition of species differed between treatments and controls. For example, species such as *Enteromorpha* sp. (Link) Nees, 1820, *Grateloupia filicina* (J. V. Lamouroux) C. Agardh, 1822, *Chiton articulatus* Sowerby, 1832, *Isognomon janus*, *Stenoplax sonorana* Berry, 1956, *Acantholobulus mirafloresensis* and *Pachygrapsus transversus* only appeared in the controls. No species was exclusive to the treatment plots at this site.

At the exposed site, the number of species differed significantly between treatments and controls at all sampling times except for day 95 (i.e., a significant Treatment $\times$ Time interaction; $F_{4,20} = 9.02$, $P < 0.001$; Figure 5b). SIMPER analysis revealed that the species responsible for these differences were three species of seaweeds and one invertebrate (*Ulva lactuca*,

a

b
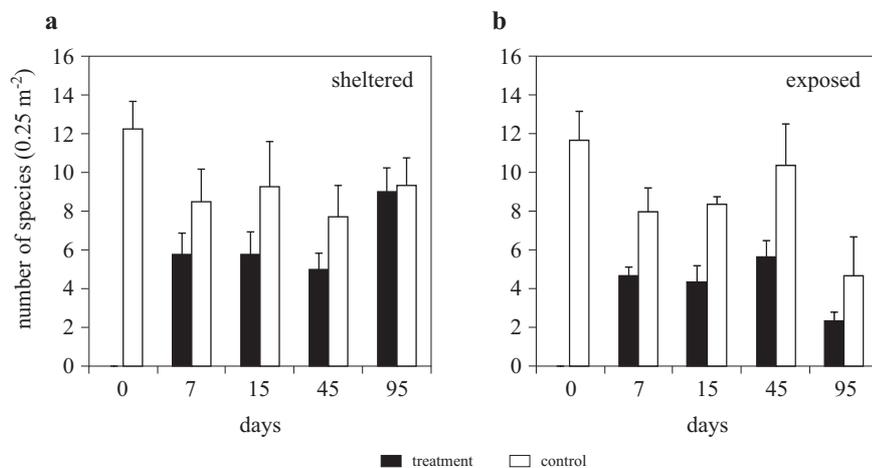
Figure 5. Total number ($\pm$ SE) of species in treatment and control plots over time: sheltered site (n = 4) (a); exposed site (n = 3) (b)

Amphiroa valonioides, *Gelidium sclerophyllum* and *Thais* (*Stramonita*) *biserialis*). At the exposed site, there were also differences in the composition of species between treatments and controls at all sampling times. For example, the seaweeds *G. sclerophyllum*, *Grateloupia abreviata* Kylin, 1941 and *Gymnogongrus leptophyllus* only appeared in the control plots, whereas the seaweed *Enteromorpha* sp., the mollusc *Nerita funiculata* and the sea urchin *Echinometra vanbrunti* only appeared in the treatment plots.

a

b
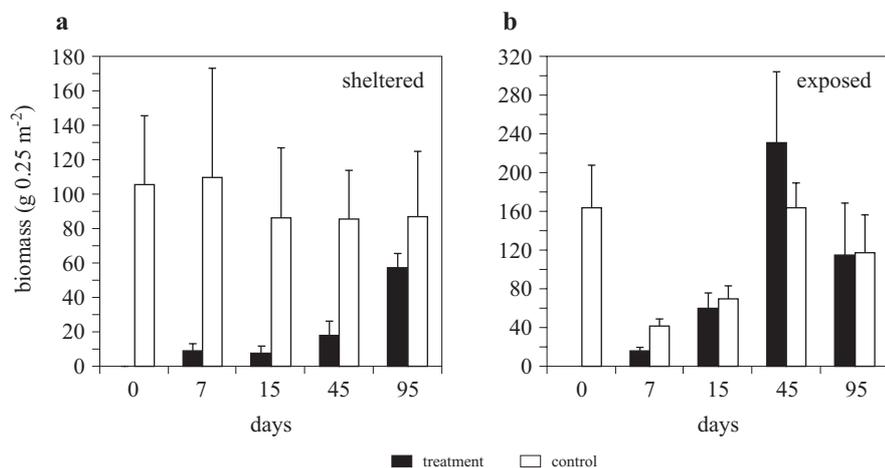
Figure 6. Total biomass ($\pm$ SE) in treatment and control plots over time: sheltered site (n = 4) (a); exposed site (n = 3) (b)

At the sheltered site, total biomass in the controls was significantly greater than in treatments for all sampling times except day 95 (i.e., significant interaction Treatment × Time; $F_{4,30} = 27.67$, $P < 0.001$; SNK tests, $P < 0.05$; Figure 6a). Total biomass in the controls decreased slightly by day 15, and this trend lasted until the end of the experiment. In contrast, total biomass in the treatments increased steadily over time. Several invertebrate species such as *Cerithium menkei*, *Nerita funiculata*, Acmaeidae sp. and *Cerithium* sp. were responsible for the increase in biomass in the treatments. The biomass of these species in the treatments increased to reach values similar to those observed in the controls (illustrated by *C. menkei* and *N. funiculata*; Figures 7a,b). In contrast, the biomasses of the most abundant seaweed species, i.e., *Gelidium sclerophyllum* and *Gymnogongrus leptophyllus*, were always lower in the treatments than the controls, except for day 95 when they were similar (i.e., < 1 g per 0.25 m^2, Figures 7c,d).
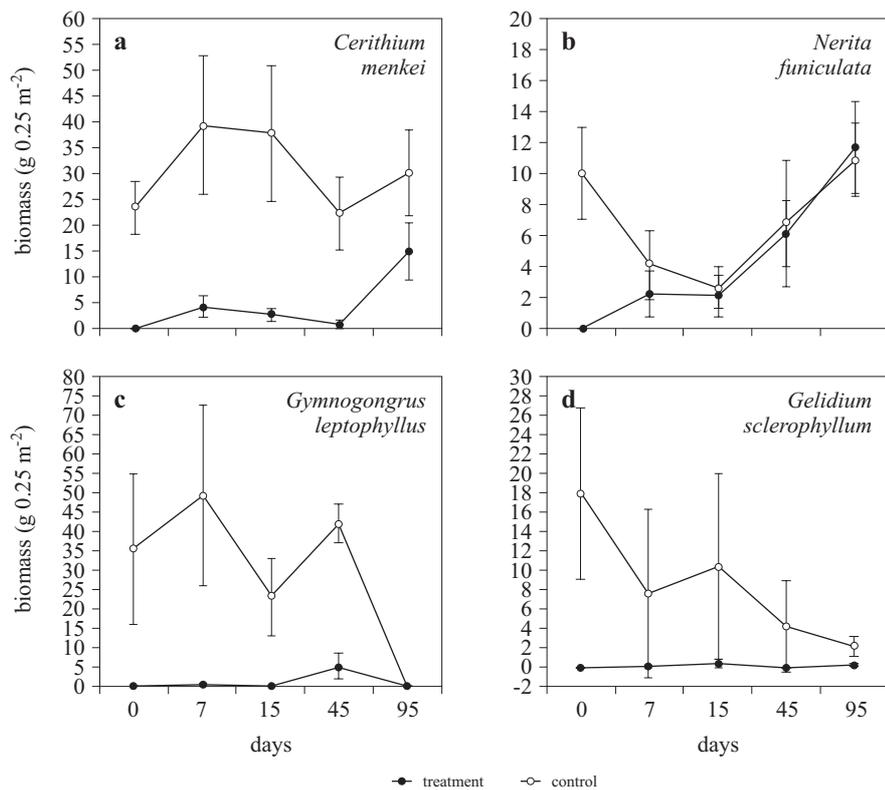
Figure 7. Mean biomass ($\pm$ SE; n = 4) of *Cerithium menkei* (a), *Nerita funiculata* (b), *Gymnogongrus leptophyllus* (c) and *Gelidium sclerophyllum* (d) in the treatment and control plots at the sheltered site over the 95 days

At the exposed site, total biomass in the treatments and controls differed significantly at the first two sampling times, i.e., 0 and 7 days (i.e., significant Treatment × Time interaction; $F_{4,20} = 17.59$, $P < 0.001$; Figure 6b). By day 15 the biomass in the treatments had recovered to reach values similar to those in the controls (SNK tests; $P > 0.05$). The seaweed *Ulva lactuca* was the species responsible for this increase of biomass in the treatments. The biomass of this species showed a complex pattern in the treatments which differed from that shown in the controls. In the treatments, the biomass of *U. lactuca* increased steadily during the first 15 days, then steeply until day 45, after which it decreased. However, biomass in the controls increased linearly over time (Figure 8a). Apart from *U. lactuca*, *Chaetomorpha antennina* and *Thais* (*Stramonita*) *biserialis*, which showed a higher biomass in the treatments than the controls on day 45 (illustrated by *U. lactuca* and *T. (S.) biserialis* in Figures 8a,b), the other abundant species displayed a lower biomass in the treatments than the
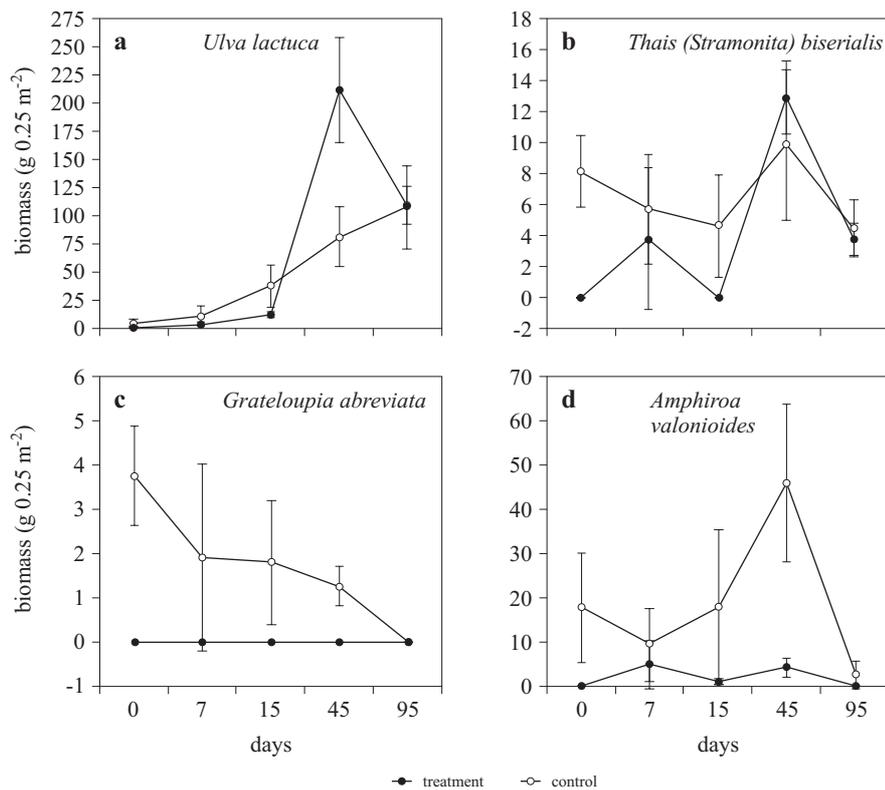
Figure 8. Mean biomass (± SE; n = 3) of *Ulva lactuca* (a), *Thais* (*Stramonita*) *biserialis* (b), *Grateloupia abreviata* (c) and *Amphiroa valonioides* (d) in the treatment and control plots at the exposed site over the 95 days

controls during the whole experiment (illustrated by *Grateloupia abreviata* and *Amphiroa valonioides* in Figures 8c,d).

3.2.2. Multivariate analysis

The wooden frame had no effect on assemblage structure (PER-MANOVA comparing assemblages in procedural control, control and treatment plots $F = 4.55$, $P = 0.019$ at the sheltered site: $F = 2.76$, $P = 0.03$ at the exposed site). Procedural control was similar to the control and differed from the treatment at both sites (SNK tests, $P < 0.05$; procedural control = control ≠ treatment).

The assemblages in the controls differed from those in the treatments at both sheltered and exposed sites, but these differences varied over time (i.e., significant Treatment × Time interactions; $F_{4, 30} = 2.45$, $P < 0.001$ at the sheltered site; $F_{4, 20} = 2.44$, $P < 0.001$ at the exposed site). Post hoc comparisons showed that the assemblages in the controls differed from those in the treatments until day 95 at both sites. These results were confirmed by the classification (Figure 9a) and nMDS (Figure 9b) analyses; these also differentiated clearly between the exposed and sheltered sites, and between the controls and treatments at each site. Ordination along the
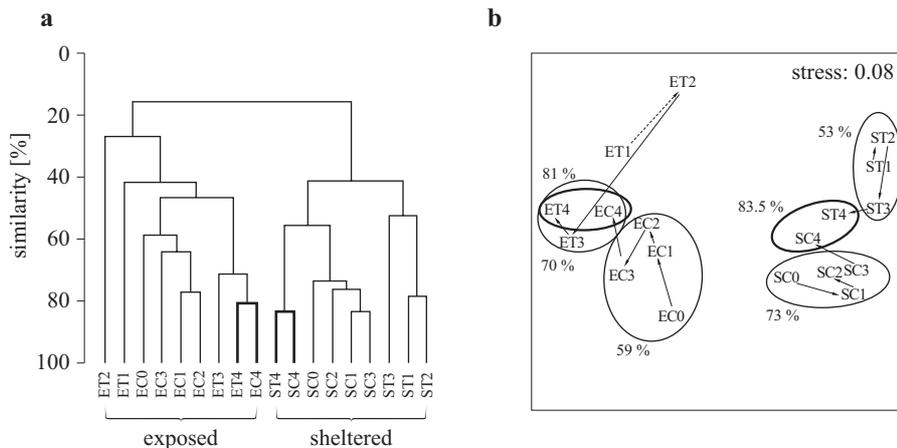
Figure 9. Dendrogram of group-average clustering of Bray-Curtis similarities (a); the thicker lines in the dendrogram show the assemblages of Control and Treatment at time 4. nMDS showing changes in assemblage structure in the two different treatments over time at the sheltered and exposed sites (b). (S) sheltered site, (E) exposed site, (T) treatment, (C) control; (0) after 0 days, (1) after 7 days, (2) after 15 days, (3) after 45 days, (4) after 95 days. Each point represents the average of the 3 or 4 replicates at each site. The lines in the nMDS plot indicate the degree of seriation by linking successive points over time from 0 to 95 days. Clusters from the dendrogram and similarity levels have been superimposed

horizontal axis clearly separated the exposed from the sheltered site. The ordination along the vertical axis showed the effect of burial by sand. At the sheltered site (nMDS plot, to the right), the assemblages in the treatment and control plots were different until day 45, after which the assemblages in the treatment started to resemble those of the control (see ST3 near controls). However, recovery was not complete until day 95, when the control (SC4) was similar to the treatment (ST4, 83.5% similarity). The same applies to the exposed site.

Another striking result was that the experimental burial clearly interrupted the successional sequence, although the interruption was more in evidence in the treatments from the exposed site (i.e., a distinct divergence in the ordination space between ET2 and ET3, Figure 9b).

4. Discussion

4.1. Initial effects of sand burial on macrobenthic assemblages

No differences in the initial tolerance of resident macrobenthic species to the sedimentation event were detected between the two sites, with a catastrophic loss of all species taking place at both sites after 20 days inundation by sediment. Thus, the main effect of sand deposition was mortality and removal of biota due to smothering. Duration of burial has been regarded as one of the most important factors determining the responses of rocky coast assemblages to stress by sediments (e.g., Airoldi & Virgilio 1998, Airoldi 2003). In this study, the duration of burial (20 days) severely affected assemblages at both sites.

4.2. Recovery process

Recovery patterns are dependent on the spatial scale of the disturbance and can involve different types of colonists, larval stages, post-settled juveniles and adults (Norkko et al. 2001). Recovery of macrobenthic invertebrates following sand deposition events can occur through passive and active migration from surrounding undisturbed areas or through larval colonization. In the case of seaweeds, vegetative growth or propagules supplied from nearby areas are probably the main mechanisms of colonization. Moreover, different models suggest that vegetative growth may be the major mechanism of seaweed colonization of small, disturbed areas (Airoldi 1998, 2000). According to these models, small clearings should exhibit fast rates of recovery because of their closeness to undisturbed thalli and their greater perimeter/area ratio. In the case of benthic invertebrates, different conceptual models dictate that larval stages will dominate following a large-scale disturbance, whereas post-larval stages play

a more important role when the scale of a disturbance is small (Günther 1992). In this study, recovery was rapid and assemblages at both sites had recovered by day 95. This fast recovery may be in part a result of the mechanism by which small, disturbed patches are recolonized. Most of the invertebrates colonized the patches as adults, and several seaweeds exhibited vegetative growth as an important mechanism of colonization (e.g., *Ulva lactuca*, *Amphiroa valonioides* and *Chaetomorpha antennina*) (pers. obs.). The ability of seaweeds to recover from disturbance through regrowth of previously damaged tissue was considered unimportant, since disturbance denuded patches completely.

The recovery process differed between the sheltered and the exposed site, and it also depended on the composition and structure of the natural assemblages at each site (see Foster et al. 2003). According to the resident assemblages and their location, there may be different pathways to recover from a disturbance (for review, see Schiel 2004). The number of species recovered quickly at the sheltered site (by day 7) but much more slowly at the exposed site (by day 95). In contrast, biomass at the sheltered site reached the control level by day 45, whereas at the exposed site it had reached that level already by day 15. Nevertheless, it is important to highlight that recovery of diversity and biomass at both sites was due to the recovery of invertebrate assemblages rather than of seaweed assemblages. Obviously, the responses of invertebrates and seaweeds to disturbance are very different (see Turner 1985, Menge & Sutherland 1987).

The dominant invertebrate species (e.g., *N. funiculata*, *C. menkei*, *T. (S.) biserialis*, etc.) are highly mobile: they colonized disturbed patches quite quickly. Individual growth rate, mobility and dispersal of species are very important factors influencing macrobenthic succession and recovery (e.g., Menge & Sutherland 1987, Olabarria 2002). Invertebrate species with different modes of life will have different potentials to be moved by waves, and thus a combination of behavior and resistance to transport by waves may result in species-dependent differences in colonization. In this study, most of the invertebrates colonized disturbed patches as adults (personal observations), and their responses to stress were probably more closely related to body size and mobility (see Menge & Sutherland 1987).

Seaweed biomass did not reach control levels until the end of the experiment, i.e., 95 days (apart from *Ulva lactuca*; Figure 8a), by which time the biomass of natural seaweed populations had fallen dramatically, i.e., <1 g per 0.25 m^2. This drop in biomass in natural assemblages may have been related to the life history of seaweed species rather than to any type of disturbance (Table 1). In fact, the winter die-off of algae on tropical shores has already been documented and occurs over a relatively

Table 1. General distribution/habitat and some life-history traits of the main species. S: sheltered site; E: exposed site

Species	Site	Distribution/Habitat	Life-history traits
Amphiroa valonioides Yendo 1902	S/E	Tropical and subtropical waters[6, 20]; inhabits the exposed rocky intertidal[12].	In some localities this species has been reported present during the whole year[1]. Reproduction is by means of cystocarps[12] or bisporangia[1].
Chaetomorpha antennina (Borgensen) Kutzing 1849	S/E	Tropical waters[20]; inhabits the exposed rocky intertidal[12]. Some species of this genus are dominant in areas routinely buried by sand[18].	The species of this genus reproduce vegetatively by fragmentation and sexually by means of biflagellated gametes[8,13]. Reproduction by fragmentation allows them to rapidly repopulate a space following mortality due to burial[18].
Enteromorpha sp. (Link) Nees 1820	S/E	This genus is cosmopolitan, with species in all oceans and estuaries of the world as well as in freshwater habitats[13]. Attached to a solid substrate, or forms tangled mats on mud and sand flats[13]. Some species of this genus are dominant in areas routinely buried by sand[18]; they have been ranked from sensitive to tolerant to sediments[7, 18, 2] and can also trap sediments[2].	The species of this genus reproduce vegetatively by fragmentation or by the growth of new upright thalli from basal cells and/or persistent holdfasts. Life history typically an alternation of isomorphic, unisexual haploid gametophytes and diploid sporophytes[8, 13]. Reproduction by fragmentation allows them to rapidly repopulate a space following mortality due to burial[18].
Gelidium sclerophyllum Taylor W. R. 1945	S/E	Tropical and subtropical waters[12, 24, 9]; inhabits the exposed rocky intertidal[12]. Some species of this genus have been ranked from sensitive to tolerant to sediments and can also trap sediments[2].	The species of this genus reproduce vegetatively by fragmentation[21] or by cystocarps or tetraspores[13].
Grateloupia abreviata Kylin 1941	E	Tropical[12]; inhabits the exposed rocky intertidal[12, 24].	Reproduction by means of cystocarps or tetraspores[1].

B. Yáñez, J. L. Carballo, C. Olabarria, J. J. Barrón

Table 1. (*continued*)

Species	Site	Distribution/Habitat	Life-history traits
Grateloupia filicina (J. V. Lamouroux) C. Agardh 1822	S/E	Tropical[12,20]; inhabits the exposed rocky intertidal[12].	In some places this species has been reported present during the whole year[1]. Reproduction by means of cystocarps or tetraspores during winter[1].
Gymnogongrus leptophyllus J. Agardh 1876	S/E	Subtropical to cool waters; commonly found as a perennial on rocks associated with sand[10]. Some species of this genus can survive sediment burial for over 6 months[2].	Perennial species[10]. Reproduction by means of cystocarps or tetraspores[13,10].
Ulva lactuca Linnaeus 1753	S/E	This species can be considered cosmopolitan; inhabits intertidal and subtidal waters, free or attached to diverse substrates[24]. Some species of this genus are dominant in areas routinely buried by sand[7]; they have been ranked from sensitive to tolerant to sediments[18] and can also trap sediments[2].	This species reproduces vegetatively by fragmentation or by the growth of new upright thalli from basal cells and/or persistent holdfasts. Life history typically an alternation of isomorphic, unisexual haploid gametophytes and diploid sporophytes[13]. Reproduction by fragmentation allows also them to rapidly repopulate a space following mortality due to burial[7, 18].
Cerithium menkei Carpenter 1857	S/E	Tropical and subtropical waters; inhabits sand pockets between rocks in the middle and low intertidal zones[4].	Sexual reproduction. Larval stages are free-swimming[16]. Species of this genus are generalized herbivores, browsing on small algae[4].
Cerithium sp. Bruguière 1789	S	Species of this genus are distributed in tropical and subtropical waters; they inhabit sand pockets between rocks in the middle and low intertidal zones[4].	Sexual reproduction. Larval stages are free-swimming[16]. Species of this genus are generalized herbivores, browsing on small algae[4].
Columbella sp. Lamarck 1799	S	Species of this genus are distributed in tropical and subtropical waters; they live under or between rocks and in tide-	Sexual reproduction. In some species the females have the ability to ingest spermatozoa within their pericardial cavity. The egg capsules are small and usually attached

Table 1. (*continued*)

Species	Site	Distribution/Habitat	Life-history traits
		pools in the middle and low intertidal zones[4].	to seaweeds. The veliger larva can be free-swimming or suppressed. Species of this genus are generalized herbivores[4].
Littorina aspera Philippi 1846	S/E	Tropical and subtropical waters; inhabits rocky intertidal and supralittoral[4].	Sexual reproduction. Larval stages are free-swimming[16]. Species of this genus are generalized herbivores[4]. Species of this genus can prevent the accumulation of sediments[3].
Nerita funiculata Menke 1851	S/E	Tropical and subtropical waters; inhabits the exposed rocky intertidal[17].	Sexual reproduction. This species has a veliger larva. Herbivorous; feeds mainly on crustose algae[17].
Thais (Stramonita) biserialis Blainville 1832	S/E	Tropical and subtropical waters; inhabits the rocky intertidal[4, 15].	Sexual reproduction. The species of this genus deposit attractive and sometimes intricate egg capsules on and under rocks. In many species the free-swimming veliger is suppressed and development occurs entirely within the egg capsule. These larvae then metamorphose into juvenile snails which hatch out of the capsule. The species of this genus are carnivorous, feeding on other molluscs, barnacles and mussels[4].
Acmaeidae	S/E	The species of this family are distributed in tropical and subtropical waters. They inhabit rocks, seaweeds or the shells of other molluscs in the intertidal zone[4].	Sexual reproduction. This family has a free-swimming trochophore larva. Species of this family are generalized herbivores. They scrape off algae with their radula[4].
Fissurellidae	S/E	The species of this family are distributed in tropical and subtropical waters. They inhabit rocks, seaweeds or other mollusc shells in the intertidal zone[4].	Sexual reproduction. This family has free-swimming veliger and trochophore larvae. Species of this family are generalized herbivores. They scrape off algae with their radula[4].

Table 1. (*continued*)

Species	Site	Distribution/Habitat	Life-history traits
Isognomon janus Carpenter 1857	S/E	Tropical and subtropical waters; inhabits tidal flats and mud-rock intertidal regions and offshore in very shallow water[4].	Sexual reproduction. The species of this genus have free-swimming veliger larvae[16]. They are sessile filter feeders[19].
Modiolus sp. Lamarck 1799	S/E	Species of this genus are distributed in subtropical to cool waters. They live in the intertidal zone, on rocks or half-buried in the mud[4].	Sexual reproduction. The species of this genus have free-swimming larvae[11]. They are sessile filter feeders, and tend to aggregate in large masses[4].
Chiton articulatus Sowerby 1832	S	Tropical and subtropical waters; inhabits rock surfaces and crevices in the exposed intertidal[15].	Sexual reproduction[4]. This species has a free-swimming trochophore larva[16]. Herbivorous; feeds on crustose filamentous algae and diatoms[14].
Stenoplax sonorana Berry 1956	S	Subtropical waters; lives in the rocky intertidal or under rocks[4, 15].	Sexual reproduction[4]. This species has a free-swimming trochophore larva[16]. Herbivorous[4].
Acantholobulus mirafloresensis Abele & Kim 1989	S/E	Common in tropical and temperate waters. Inhabits coastal lagoons (mangrove prop roots and hard substrata, including bivalves) or the rocky intertidal[23].	Sexual reproduction; this species has a free-swimming zoea larva[23] and breeds all the year round[22].
Pachygrapsus transversus Gibbes 1850	S/E	Tropical and subtropical waters; inhabits mainly rocky shores and the roots of mangroves. It is also found on coral outcrops, sandy beaches, and even clinging to floating clumps of Sargassum[4].	Sexual reproduction; this species has a free-swimming zoea larva[4, 23] and is primarily herbivorous[4].

Table 1. (*continued*)

Species	Site	Distribution/Habitat	Life-history traits
Clibanarius albidigitus Nobili 1901	S	Tropical and subtropical waters; inhabits the rocky intertidal, but may also be found on sandy beaches with rocky outcrops[4].	Sexual reproduction; this species has a free-swimming zoea larva[23]. It clusters in groups under boulders at low and high tide. During the ebb- and flood-tide, individuals disperse onto substrate surfaces to scavenge and filter feed[4].
Amphinomidae	S/E	Species of this family are distributed in tropical and subtropical waters. They live under boulders and buried in sand in the intertidal and subtidal zone[4].	Some species of this family reproduce sexually and asexually during summer. Some species are highly gregarious and slow-moving. They feed on soft-bodied animals, plant matter and sediments[4].
Nereidae	S/E	Species of this family are distributed in tropical, subtropical and temperate waters. They inhabit rocky crevices, algae, sandflats, and are also associated with other animals, in the intertidal and subtidal zones[4].	Members of this family undergo a remarkable morphological change with sexual development. The end result is a heteronereid that is well adapted for swimming. The heteronereid usually dies after spawning on the surface of the water. They can be carnivorous, herbivorous or omnivorous; they can also feed on detritus and particulate matter[4].
Haliclona sp. Grant 1836	S/E	Species of this genus are cosmopolitan, inhabiting the rocky low intertidal and subtidal areas, especially where the water is clean and devoid of excessive silt[4].	Species of this genus can reproduce sexually, or asexually by fragmentation. They are sessile filter feeders[4, 5].
Echinometra vanbrunti Agassiz 1863	E	Tropical and subtropical waters; occurs in the lower mid intertidal zone. Prefers crevices and cavities in rocks	Sexual reproduction; it has a free-swimming larva (Echinopluteus)[23]. Herbivorous; feeds on macroalgae[4].

Table 1. (*continued*)

Species	Site	Distribution/Habitat	Life-history traits
		and reefs. Occasionally found on exposed rock surfaces where the surf is calm. It can be found singly or in aggregations[4].	

[1]Aguilar-Rosas et al. (2000)
[2]Airoldi (2003)
[3]Bertness (1984)
[4]Brusca (1980)
[5]Brusca & Brusca (2003)
[6]Casas-Valdez et al. (2000)
[7]Daly & Mathieson (1977)
[8]Dawson (1944)

[9]Dawson, 1953
[10]DeCew & West (1981)
[11]Farfan et al. (1998)
[12]Galindo-Villegas et al. (1997)
[13]Guiry et al. (2007)
[14]Holguin-Quiñones & Morfin (2002)
[15]Keen (1971)
[16]Levin & Bridges (1995)

[17]Levings & Garrity (1983)
[18]Littler et al. (1983)
[19]Ringwood (1991)
[20]Riosmena-Rodríguez & Paul-Chávez (1997)
[21]Rodríguez (1996)
[22]Salgado-Barragán & Hendrickx (2002)
[23]Salgado-Barragán & Ruiz-Guerrero (2005)
[24]Taylor (1945)

short period of time (Hutchinson & Williams 2003). The low biomass of seaweed species such as *G. sclerophyllum* and *G. leptophyllus* in the treatments may have been related to the negative influence of sediment deposition on spore settlement and recruitment (see Renaud et al. 1996). The responses of colonizing seaweeds to sediment accumulation could also have been complicated by a potential variation in their rates of growth related to the time of year when colonization started (Airoldi & Cinelli 1997, Airoldi & Virgilio 1998, Hutchinson & Williams 2003).

4.3. Looking for differences between sites

Differences in wave exposure may have caused variation in the supply of colonists and given rise to different patterns of recovery between the exposed and sheltered sites, located only a few meters apart (Sousa 1979, Underwood & Jernakoff 1984, Petraitis et al. 1989, Kendrick 1991, Menge 1991, Kaehler & Williams 1997, Minchinton 1997, Hunt & Scheibling 1998, Williams et al. 2000, Hutchinson & Williams 2003).

Other site-dependent factors, such as gradients in the intensity of biological processes like predation and/or grazing, are likely to have had an effect on recovery at both sites (see Littler et al. 1983, Sousa 1984, Engledow & Bolton 1994, Hutchinson & Williams 2003, Prathep et al. 2003). In this context, an interesting model needs to be looked at: it is the one proposed by Palmer et al. (1996), in which the local biological interactions (predation/grazing and competition) that structure marine communities are influenced by regional dispersal. The differences in the recovery process between the two sites could be related to dispersal as a factor driving local population and assemblage dynamics (see Palmer et al. 1996). The exposed site is a system experiencing higher levels of disturbance (e.g., wave impacts) than the sheltered site. At the exposed site, the assemblage structure will be highly variable, have a high turnover rate, and will be determined largely by the 'lottery' effects of arrival and establishment of species. In contrast, the sheltered site experiences lower levels of disturbance, i.e., wave exposure, which permits local interactions such as predation or competition to play a more substantial role. In fact, recovery at the sheltered site was gradual, i.e., a linear increase in biomass and number of species over time. In contrast, this process at the exposed site exhibited stochastic fluctuations (see Figures 5b, 6b). The most dominant feature of recovery at this latter site was the rapid colonization of the treatment plots by the seaweed *Ulva lactuca*. This species was also the one dominant in the natural assemblages at the exposed site and monopolized space, contributing greatly to the recovery process in terms of biomass. But with its high capacity for rapid recruitment, growth, and reproduction

(Cruz-Ayala et al. 2001), this ephemeral and opportunistic species has been shown to inhibit colonization by other seaweed species (Sousa 1979); it was probably responsible for the low number of species and biomass at the exposed site throughout the recovery process. In the inhibition model, species arriving later cannot recruit and mature in the presence of earlier colonists (*U. lactuca*) until a physical and/or biological disturbance occurs.

This field experiment showed that sediment burial affected the structure of benthic assemblages (number of species, species composition and biomass) at both sites. Although the assemblages had recovered by day 95, the recovery process was site-dependent and varied at a small spatial scale. The data suggest that differences in wave exposure may have played an important role in determining the different patterns of recovery at the sheltered and exposed sites. This conclusion has to be treated with caution, however, since we would need to replicate the experiment at several exposed and sheltered sites to see whether or not wave exposure or yet other factors affecting different shores influence the recovery process. In the meantime, however, this study can be used as a working hypothesis in future studies that seek to assess the importance of community-structuring mechanisms following a natural disturbance such as sand burial.

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