Vol. 368: 9–22, 2008
doi: 10.3354/meps07625

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 25

Assessing the consequences of sea level rise: effects of changes in the slope of the substratum on sessile assemblages of rocky seashores

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ABSTRACT: Sea level rise can affect the biodiversity of coastal areas through alterations of features of the substratum, including the geometry of shorelines. Field measurements on the rocky shore of Calafuria (NW Mediterranean Sea) showed that a rise in sea level in the range of 5 to 50 cm would increase the availability of steep substrata (>40°) for assemblages of algae and invertebrates by up to 58% compared to current conditions. Comparisons between assemblages on horizontal and vertical substrata revealed clear differences in the composition and abundance of common taxa. Clearing experiments replicated on vertical and gently sloping surfaces at 2 heights on the shore were performed to test hypotheses about the role of recruitment and post-recruitment processes in maintaining differences between substrata. Comparisons of recolonizing assemblages with unmanipulated controls allowed us to test the hypothesis that a change in slope of the substratum affected the ability of assemblages to recover after a disturbance. Results indicated that differences in the structure of assemblages between vertical and horizontal substrata were maintained by a combination of recruitment and post-recruitment processes, although the relative importance of these processes differed among taxa. Nonetheless, patterns of recovery of assemblages were comparable between the 2 substrata. These findings suggested that sea level rise, by increasing the proportion of vertical substrata at the expense of horizontal surfaces, will lead to the expansion of assemblages dominated by encrusting coralline algae and grazing gastropods, and the reduction of abundance of filamentous forms and barnacles. The resilience of assemblages, however, appeared unaffected by the aspect of the substratum.

KEY WORDS: Sea level rise · Habitat structure · Resilience · Rocky shores · Recruitment · Mediterranean Sea

INTRODUCTION

Over the last 100 yr sea levels have risen between 10 and 25 cm (Houghton 1997, Michener et al. 1997) and, despite uncertainties in projections, they are predicted to rise further about 12 cm by 2030 and by about 50 cm by 2100, at a rate of about 4 to 5 cm per decade (IPCC 1996). It is widely recognized that the predicted rise in sea level will have considerable impacts on the coastal zone, altering the thermal and osmotic environment, changing sediment dynamics and drastically modifying the position and geometry of shorelines (Chappell 1990, IPCC 1996, Crooks & Turner 1999, Pethick 2001). It is conceivable that sea level rise will have important consequences for patterns of distribution and abundance of assemblages living at the boundary between marine and terrestrial realms (Denny & Paine 1998). In particular, organisms are expected to shift their upper limits of distribution higher up the shore, where they will face new habitats that may or may not be suitable

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for colonization (Oertel et al. 1992, Bird 1993, Bijlsma 1997). Such shifts in distribution could be hindered by human interventions like the construction of bulkheads, breakwaters and installations aimed at reducing sedimentation, or by natural changes in the morphology of the coast (Titus 1988). The physical aspect of the substratum would change considerably for shores that are nearly flat at their seaward end and become steeper towards the landward end, a characteristic of many rocky coasts around the world. In this case, sea level rise would change the proportion of vertical and horizontal surfaces available for colonization of intertidal organisms.

Inclination of the substratum is an important determinant of the structure of assemblages of rocky shores. Previous studies conducted mostly in subtidal habitats (but see Benedetti-Cecchi 2001, Benedetti-Cecchi et al. 2000a, 2001, Knott et al. 2004), indicated differences in composition and abundance of species occurring on surfaces of different inclination (Harris & Irons 1982, Wendt et al. 1989, Hurlbut 1991, Baynes 1999, Connell 1999, Glasby 2000, Knott et al. 2004, Balata et al. 2007). Macroalgal cover was generally shown to be higher on horizontal substrata such as reef platforms and boulders, while the cover of sessile invertebrates tended to be larger on vertical walls in a variety of benthic habitats (McLean 1962, Foster 1975, Sebens 1986, Vance 1988, Chadwick 1991, Chapman et al. 1995, Bruno & Witman 1996, Baynes 1999, Goldberg & Foster 2002). The causes of these differences are not clear, but may involve factors such as incidence of light (Kennelly 1989, Baynes 1999, Glasby 2000), temperature (Williams 1994, Williams & Morritt 1995, Helmuth & Hofmann 2001), larval behaviour (Meadows & Campbell 1972, Raimondi & Keough 1990, Hurlbut 1991), water flow at micro and meso scales (Eckman 1983, Mullineaux & Garland 1993, Breitburg et al. 1995, Guichard & Bourget 1998, Glasby & Connell 2001), and sedimentation (Airoldi 2003, Balata et al. 2007). Although potential explanations for differences in structure of assemblages between vertical and horizontal substrata have been suggested in all these studies, experimental tests of causal effects are much less common and have usually focused on artificial substrata (Glasby 2000, Glasby & Connell 2001).

Even less is known about the consequences of changes in the physical aspect of the shore for the functional properties of assemblages, like productivity and resilience, i.e. the ability of organisms to recover after events of disturbance (Grimm & Wissel 1997). Understanding the processes that maintain differences in assemblages between substrata of different slope in natural habitats and the functional consequences of these changes is important to make better predictions on the consequences of sea level rise on assemblages of rocky sea shores.

In this study we first examined the consequences of sea level rise in terms of changes in the physical aspect of the shoreline (Calafuria, Italy), by profiling the slope of the substratum at intervals of 5 cm from the mean low-water level (MLWL) to 50 cm above the upper limit of distribution of barnacles, the dominant organisms in high-shore habitats. In this way we quantified the proportion of vertical and horizontal surfaces that would be available to populations of algae and invertebrates currently distributed between low-shore and high-shore habitats, under different scenarios of sea level rise. We also tested whether vertical and gently sloping (hereafter horizontal) substrata supported distinct assemblages of algae and invertebrates using a multifactorial sampling design with spatial and temporal replication. We then replicated a clearing experiment on vertical and horizontal substrata to test hypotheses about the role of recruitment and post-recruitment processes in maintaining the differences in assemblages between these habitats, as revealed by the sampling programme. If recruitment was solely responsible for the observed differences, patterns of recovery in cleared plots would be expected to differ between habitats from the early stages of colonization. If, in contrast, post-recruitment processes were more important than recruitment, assemblages on horizontal and vertical substrata would be more similar at early rather than later stages of colonization. A combination of recruitment and post-recruitment processes likely generated temporal variation in the pattern of differences between vertical and horizontal surfaces, although our experimental design was not able to determine the relative importance of these processes if they operated simultaneously. Finally, we compared the resilience of assemblages between vertical and horizontal substrata as a test of the functional consequences of a change in slope of the substratum. We had no basis to anticipate a particular direction for this effect.

MATERIALS AND METHODS

Study location. This study was carried out at Calafuria, a rocky coast a few km south of Livorno, Italy (43° 30′ N, 10° 20′ E), in the northwest Mediterranean, between January 2002 and October 2006. The shore is made of sandstone and exposed mainly to western winds due to its southwest orientation. In general, the highest part of the shore (0.3 to 0.5 m above MLWL) is dominated by the barnacle *Chthamalus stellatus* (Poli). The most common organisms at mid-shore heights (0.1 to 0.3 m above MLWL) are barnacles, cyanobacteria of the genus *Rivularia* and the fleshy red alga *Rissoella verruculosa* (Bertoloni) J. Agardh. Lower on the shore (–0.1 to 0.1 m with respect to MLWL) the rock is characterized by filamentous algae, articulated corallines and coarsely branched algae. At all heights on the shore encrusting coralline algae are present. The most common herbivores are the limpets *Patella aspera* Roding, *P. caerulea* Linné, *P. rustica* Linné and the topshell *Osilinus turbinatus* (Von Born). Detailed descriptions of these assemblages are reported elsewhere (Menconi et al. 1999, Benedetti-Cecchi et al. 2000a,b).

Changes in the inclination of the substratum. We conducted a study to assess the proportion of the coastline that, following a rise in sea level from 5 to 50 cm (the maximum value predicted by climate models by the end of this century), would be changed from a mainly horizontal inclination to a mainly vertical one. Projections were made of 3 positions on the shore where the substratum was mostly horizontal: the MLWL (low-shore habitat), 20 cm on average above MLWL (mid-shore habitat) and 40 cm on average above MLWL (high-shore habitat). Results were given as percentage of the transect displaying an increase in slope of the substratum >40° at given vertical heights. To determine this, the slope of the substratum that would become available for organisms with 50 cm increase in sea level was measured at 5 cm intervals (Fig. 1). The topographical measurements were conducted using an Automatic Level (C330, Sokkia Instruments) held on a tripod and a stadia rod. Measurements were taken along transects perpendicular to the shore. Four transects were chosen at random within each of 3 areas (stretches of coast about 20 m long, 30 to 50 m apart) randomly selected at each of 4 sites (stretches of coast about 100 m long, 100s of m apart) distributed along the coast of Calafuria. The tripod holding the Automatic Level was located in the middle of each transect, while the stadia rod was moved from the one end of the transect to the other, recording any visible change in the slope of the substratum. The horizontal distance between 2 consecutive points and their difference in height allowed us to calculate, by means of simple trigonometric formulae, the slope of the interposed substratum and to reconstruct the profile of the transect.

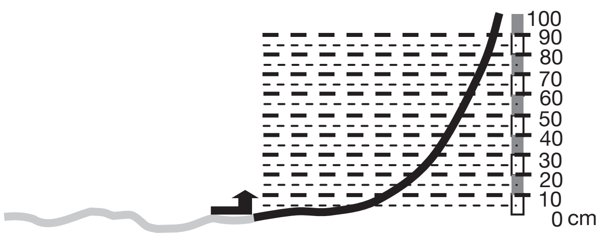

Fig. 1. 'L' shape of hypothetical coast (sea surface: grey; rocky shore: black). Hatched lines indicate the heights of projection of the sea level above the mean low-water level. Further details in 'Materials and methods'

Comparison of assemblages on vertical and horizontal substrata. The sampling programme was conducted between January 2002 and October 2003. Sessile organisms were visually sampled on vertical and horizontal substrata in 4 areas (stretches of coast about 5 m long, 10s of m apart) selected at random at each of 4 times: January and February 2002, and May and October 2003. In each area, 6 quadrates were randomly sampled in the mid-shore habitat (between 0.1 and 0.3 m above the MLWL) at each time. Estimates of abundance of algae were obtained using quadrats of 20 × 20 cm divided into twenty-five 4 × 4 cm subquadrats, assigning each taxon a score ranging from 0 to 4 in each subquadrat, and adding up the 25 estimates (Dethier et al. 1993, Benedetti-Cecchi et al. 1996). Final abundance was expressed as percentage cover. Densities of limpets and other mobile animals were determined as number of individuals in each quadrat. When possible, organisms were identified in the field to species or genus; in other cases, taxa were lumped into morphological groups (Littler & Littler 1980, Steneck & Dethier 1994).

Data were analyzed by Permutational Analysis of Variance (PERMANOVA, Anderson 2001) aimed at testing spatial and temporal differences in structure of assemblages between vertical and horizontal substrata. The analysis included the following factors: (1) Time (4 levels, random), (2) Slope (2 levels, vertical vs. horizontal, fixed and crossed with Time), (3) Area (4 levels, random, nested in the interaction between Time and Slope). SIMPER analysis (Clarke 1993) was used to identify the percentage contribution (δ_i%) of each species (or morphological group) to the Bray-Curtis dissimilarity between the average of vertical and horizontal substrata (δ_i). Taxa that contributed most to variation between vertical and horizontal substrata ($\delta_i > 3\%$) were analyzed individually with ANOVA, using the same factors as in PERMANOVA. Before each analysis, Cochran's *C*-test was used to assess the assumption of homogeneity of variances and data were Ln(x + 1)-transformed, if necessary (Winer 1971, Underwood 1997).

Clearing experiment. The clearing experiment started in June 2004 and was designed to examine the hypotheses that recruitment, post-recruitment or a combination of these processes caused the differences between assemblages of vertical and horizontal substrata observed in the sampling programme.

Four sites (stretches of coast 10 to 20 m long, 100s of m apart) consisting mainly of vertical substrata and 4 sites where the substratum was almost horizontal were selected along about 3 km of coast. Within each site, 8 quadrats of 14 × 10 cm were established at each of 2 heights on the shore (about 0.1 m and 0.3 m above MLWL, respectively) and marked at corners with epoxy putty. We will refer to these heights as the lower mid-shore and upper mid-shore habitats, respectively. Four of the 8 quadrats were cleared to bare rock with a chisel mounted on a battery drill, while the remaining 4 quadrats were left undisturbed as controls. Some sites were large enough to accommodate all the quadrats, whilst in other sites quadrats were established only at 1 of the 2 heights.

Organisms occurring in treatments and controls were sampled 7 times over 29 mo, using a 12 × 8 cm metal frame sub-divided into twenty-four 2 × 2 cm quadrats and placed in the centre of each plot. Estimates of abundance of algae and invertebrates were obtained as described in the previous section.

Collected data were analyzed, separately for each height, from 3 dates (September 2004, July 2005 and October 2006) by univariate (ANOVA) and multivariate procedures (PERMANOVA). It was necessary to analyze data from 3 out of the 7 sampling dates to avoid the uncontrolled increase of Type I error that occurs when repeating tests on data that are not independent in time (Underwood 1997). In order to test hypotheses about recruitment and/or post-recruitment processes, analyses were conducted only on data from cleared quadrats and included the following factors: (1) Slope (2 levels, horizontal vs. vertical, fixed) and (2) Site (4 levels, random and nested in Slope), with 4 replicate units in each site.

The analyses examining the resilience of assemblages in relation to inclination of the substratum included both cleared and control quadrats in a 3-way design with the following factors: (1) Slope (2 levels, horizontal vs. vertical, fixed), (2) Site (4 levels, random) and (3) Treatment (2 levels, cleared vs. control, fixed). Site was nested within Slope and Treatment was crossed with both Slope and Site; there were 4 replicate units for each treatment in each site.

SIMPER analysis was used to identify those taxa that contributed to variation between vertical and horizontal substrata and between cleared and control plots (δ_i > 3%). Univariate analyses were run on those taxa that were abundant enough to be analyzed individually and that were indicated as important by SIMPER. Student-Newman- Keuls (SNK) tests were used for *a posteriori* comparisons of means. Multivariate patterns were displayed graphically by plotting the centroids of sites in a non-metric Multidimensional Scaling (NMDS) based on Euclidean distances. Centroids were obtained by first calculating principal coordinate axes from the original Bray-Curtis similarity matrix (Bray & Curtis 1957) and then averaging these values across replicate quadrats (Legendre & Anderson 1999).

RESULTS

Changes in the inclination of the substratum

The rocky coast of Calafuria becomes steeper towards its landward end (Table 1). The proportion of transects that displayed an increase in slope >40° varied, on average, between 6% (5 to 20cm above the mid-shore habitat) and 29% (45 cm to 50 cm above the high-shore habitat), with a maximum value of 58% observed at some sites 50 cm above the high-shore habitat (Table 1).

Table 1. Means, SE (n = 48: data averaged across sites and shores) and range of the percentage of transects that displayed an increase in slope of the substratum >40° at given vertical heights of the shore above low-shore (mean low-water level, MLWL), mid-shore (0.2 m above MLWL) and high-shore (0.4 m above MLWL) habitats

Height	Low-shore			Mid-shore			High-shore		
(cm)	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
5	13	1.56	0–25	6	0.60	0–8	25	1.01	17–42
10	13	1.56	0–25	6	0.60	0–8	25	1.01	17–42
15	17	1.39	8–25	6	0.60	0–8	25	1.15	8–50
20	19	1.16	8–25	6	0.60	0–8	27	1.19	8–50
25	19	1.16	8–25	10	1.16	0–17	25	1.08	8–50
30	13	0.70	8–17	8	0.99	0–17	25	1.08	8–50
35	13	1.21	8–25	8	0.99	0–17	25	1.12	8–50
40	15	1.16	8–25	10	1.16	0–17	23	1.06	8–50
45	13	1.21	8–25	10	1.16	0–17	29	1.26	17–58
50	17	1.40	8–25	10	1.16	0–17	29	1.28	8–58

Table 2. PERMANOVA examining temporal and spatial differences in structure of assemblages of vertical and horizontal substrata. **Bold:** significant

Source of variability	df	MS	Pseudo *F*	p	Permutable units and denominator for *F*
Time (T)	3	11903.0	2.76	**0.001**	32 Area (T × S)
Slope (S)	1	20214.0	5.94	**0.004**	8 T × S
T × S	3	3405.1	0.79	0.694	32 Area (T × S)
Area(T × S)	24	4315.4	3.64	**0.001**	192 Residual
Residual	160	1186.5	–	–	–

Comparison of assemblages on vertical and horizontal substrata

Assemblages on vertical and horizontal substrata differed consistently with time (Fig. 2, Table 2). Eight taxa out of the 26 identified contributed more than 3% and cumulatively accounted for >88% of dissimilarities between substrata of different slope (Table 3). Among such taxa, *Chthamalus stellatus* was more abundant on horizontal substrata (Fig. 2A, Table 4). Filamentous algae also were more abundant on horizontal than vertical substrata, although these algae fluctuated considerably in time; therefore, the differences between inclinations also were temporally variable (Fig. 2F, Table 4). By contrast, encrusting corallines, *Rissoella verruculosa*, *Ralfsia verrucosa*, *Polysiphonia sertularioides* and *Patella aspera/caerulea* were more abundant on vertical than horizontal substrata (Fig. 2B,D,E,G,H). Differences between slopes were statistically significant for *R. verrucosa* and *P. aspera/caerulea* (Table 4).

Clearing experiment

Upper mid-shore habitat

Multivariate and univariate analyses showed temporally consistent differences between assemblages on vertical and horizontal substrata and that these differences were mainly driven by 3 taxa: *Rivularia* spp., *Chthamalus stellatus* and encrusting coralline algae.

PERMANOVA on data from cleared quadrats indicated differences in assemblages between vertical and horizontal substrata throughout the study period (Table 5). The NMDS plots showed clear separation among centroids representing each combination of treatments, both in Sep 2004 — despite the interaction Tr × Si(Sl) detected by the analyses (Table 5) — and in July 2005. In Oct 2006, assemblages in cleared quadrats converged with unmanipulated assemblages, but some degree of separation between inclinations was still evident (Table 5, Fig. 3A).

SIMPER identified 3 taxa as the most important in determining differences among experimental conditions throughout the experiment: *Rivularia* spp., *Chthamalus stellatus* and encrusting coralline algae. *Polisiphonia sertularioides* and *Patella rustica* further contributed to differentiation in vertical and horizontal substrata, occurring

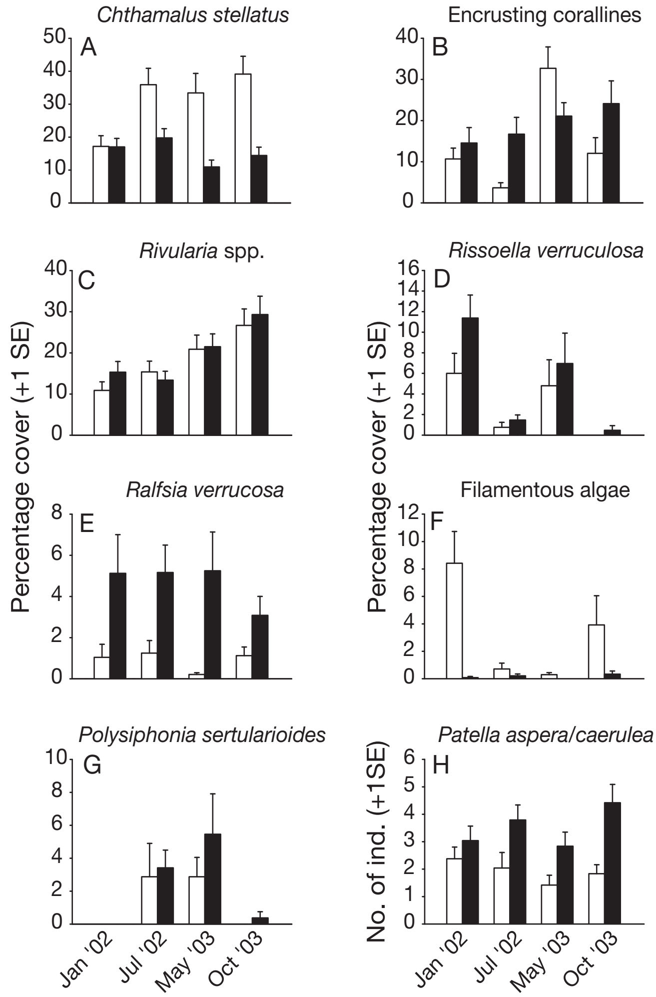

Fig. 2. Abundance (mean ± SE, n = 96, data averaged across Replicates, Areas and Times) of common taxa on horizontal (white) and vertical (black) substrata of mid-shore habitats

Table 3. Results of SIMPER analysis. H and V: average abundance of taxa on horizontal and vertical substrata, respectively; δ_i: contribution of each taxon to the average Bray-Curtis dissimilarity between horizontal and vertical substrata. Values of $\delta_i/SD(\delta_i) \geq 1$ indicate that the contribution of a given taxon to percentage dissimilarity was consistent among pairwise comparisons of samples between horizontal and vertical substrata. Each taxon was considered important if its contribution to percentage dissimilarity exceeded the arbitrary value of 3%

	H	V	δ_i	$\delta_i/SD(\delta_i)$	Cumulative % of δ
Chthamalus stellatus	31.41	15.53	26.21	1.19	26.21
Encrusting corallines	14.77	19.11	21.20	1.10	47.41
Rivularia spp.	18.45	19.86	18.66	1.23	66.07
Rissoella verruculosa	2.89	5.06	7.29	0.61	73.37
Ralfsia verrucosa	0.91	4.66	5.03	0.67	78.39
Filamentous algae	3.33	0.16	3.78	0.42	82.17
Polysiphonia sertularioides	1.44	2.31	3.34	0.42	85.52
Patella aspera/caerulea	1.92	3.52	3.20	1.15	88.71

Table 4. ANOVA examining temporal and spatial differences in percentage cover and number of individuals of taxa on vertical and horizontal substrata. *p < 005; **p < 0.01; ***p < 0.001; NS: p > 0.05. When necessary, pooling procedures were applied according to Winer et al. (1991)

Source	df	*Chthamalus stellatus* MS	*Chthamalus stellatus* F	Encrusting corallines MS	Encrusting corallines F	*Rivularia* spp. MS	*Rivularia* spp. F	*Rissoella verruculosa* MS	*Rissoella verruculosa* F
Time (T)	3	2.83	1.15	2637.14	2.58	2267.36	4.84**	769.45	5.24**
Slope (S)	1	15.04[a]	6.09*	905.67	0.58	96.33	1.06	227.51	3.71
T × S	3	3.01	Eliminated	1563.10	1.53	91.04	0.19	61.35	0.42
Area(T × S)	24	2.47	3.89***	1023.18	3.86***	468.51	2.27**	146.74	2.35***
Residual		160	0.63	264.82		206.10		62.56	
Cochran's test		C = 0.120, NS		C = 0.112, NS		C = 0.115, NS		C = 0.324, p < 0.01	
Transformation		Ln(x + 1)		None		None		None	

Source	df	*Ralfsia verrucosa* MS	*Ralfsia verrucosa* F	Filamentous algae MS	Filamentous algae F	*Polysiphonia sertularioides* MS	*Polysiphonia sertularioides* F	*Patella aspera/caerulea* MS	*Patella aspera/caerulea* F
Time (T)	3	0.67	0.26	170.12	3.46*	211.68	1.81	8.91	0.55
Slope (S)	1	31.67	89.32**	484.51	2.87	36.75	2.27	123.52	16.30*
T × S	3	0.35	0.14	168.98	3.44*	16.18	0.14	7.58	0.47
Area (T × S)	24	2.56	4.89***	49.15	1.67*	117.00	4.40***	16.27	3.57***
Residual		160	0.52	27.79		26.58		4.56	
Cochran's test		C = 0.098, NS		C = 0.322, p < 0.01		C = 0.393, p < 0.01		C = 0.109, NS	
Transformation		Ln(x + 1)		None		None		None	

[a]Tested on Area (T × S)

Table 5. PERMANOVA examining the effects of the slope of the substratum and treatment on assemblages at 2 heights on the shore. Sl: Slope; Si: Site; Tr: Treatment. Significant effects are indicated in **bold**

Source of variability	df	Sep 2004 Pseudo F	Sep 2004 p	Jul 2005 Pseudo F	Jul 2005 p	Oct 2006 Pseudo F	Oct 2006 p
Upper mid-shore habitat							
Sl	1	4.85	**0.032**	5.51	**0.037**	3.56	**0.037**
Si(Sl)	6	1.87	**0.016**	1.01	0.445	1.85	**0.016**
Tr	1	10.98	**0.001**	6.71	**0.003**	0.79	0.537
Sl × Tr	1	0.52	0.672	1.45	0.233	2.53	0.063
Tr × Si(Sl)	6	1.90	**0.016**	1.55	0.066	1.49	0.077
Residual	48						
Lower mid-shore habitat							
Sl	1	5.82	**0.032**	3.20	0.060	7.33	**0.037**
Si(Sl)	6	2.01	**0.004**	1.48	0.066	2.65	**0.002**
Treatment (Tr)	1	16.08	**0.001**	2.99	**0.029**	3.58	0.058
Sl × Tr	1	0.04	0.996	1.17	0.345	1.38	0.255
Tr × Si(Sl)	6	0.87	0.641	1.04	0.440	0.64	0.896
Residual	48						

only on flat surfaces 2 yr after the start of the experiment (data not shown). Univariate analyses showed higher recruitment of *Rivularia* spp. on horizontal than vertical substrata, but this difference was not maintained at later stages of colonization (Table 6, Fig. 4A). Differently, initial patterns of recruitment of the barnacle *C. stellatus* were independent of the slope of the substratum, but the abundance of this species increased significantly more on horizontal than on vertical substrata during colonization (Table 6, Fig. 4B). Although not statistically significant, patterns of colonization of encrusting corallines in cleared quadrats showed a temporally consistent trend of higher abundance on horizontal than vertical substrata (Table 6, Fig. 4C).

Analyses including control quadrats indicated differences in abundance between cleared and unmanipulated plots for *Rivularia* spp. and *Chthamalus stellatus*, but not for encrusting corallines algae by September 2004 (Fig. 4, Table 7). A significant main effect of Treatment was still present for *C. stellatus* by July 2005, while this factor was not significant for all the response variables analyzed by the end of the study. There was large variability in the differences between cleared and control quadrats among sites for encrusting coralline algae at all dates, as revealed by the significant Treatment × Site

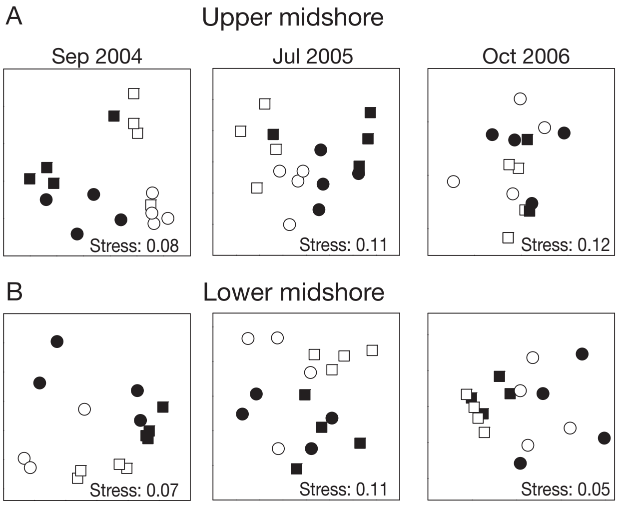

Fig. 3. Non-metric multidimensional scaling plots comparing (A) Upper and (B) Lower mid-shore assemblages on cleared (white) and control (black) quadrats established on horizontal (circle) and vertical (square) substrata. Each symbol is the centroid of each site

(Slope) interactions in Table 7. Spatial variability in the effect of treatment was also significant for barnacles in October 2006 (Table 7). This variability may explain the lack of significance of the Slope × Treatment interaction suggested by Fig. 4B, where barnacles are shown to have attained large abundance values in all treatments, except in the cleared quadrats on vertical surfaces. The lack of a significant Slope × Treatment interaction for *Rivularia* spp. and encrusting coralline algae indicated that the patterns of recovery of these taxa did not differ between horizontal and vertical substrata.

Lower mid-shore habitat

Results were similar to those described for the upper mid-shore habitat, with temporally consistent differences between assemblages on vertical and horizontal substrata. In addition to *Rivularia* spp., *Chthamalus stellatus* and encrusting coralline algae, *Chaetomorpha aerea* contributed to variation between substrata in the low-shore habitat.

Multivariate patterns of recruitment and recovery resembled those observed for the upper mid-shore habitat, with distinct early assemblages colonizing clearings established on vertical and horizontal substrata, and cleared quadrats converging towards controls only in Oct 2006, independently of Slope (Fig. 3B, Table 5).

SIMPER identified 4 taxa as the most important in determining differences among experimental conditions at each date of sampling: encrusting coralline algae, *Rivularia* spp., *Chaetomorpha aerea* and *Chthamalus stellatus*. Additional taxa that contributed to variation among treatments were *Cladophora* spp. in September 2004 and July 2005 and filamentous and coarsely branched algae in July 2005 and October

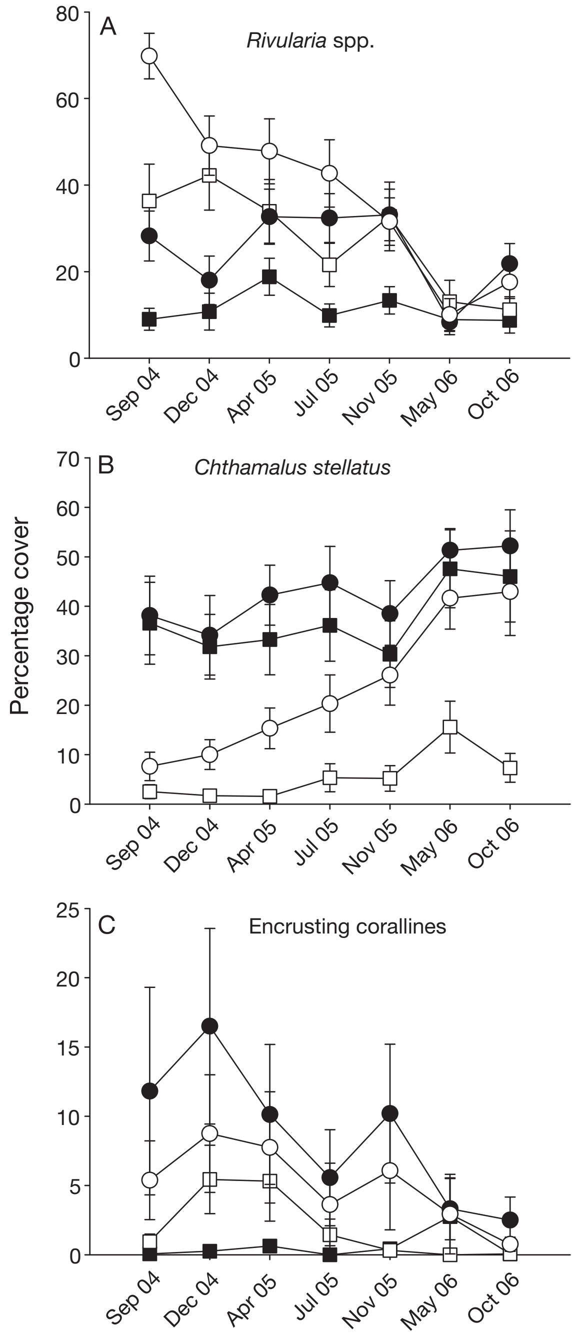

Fig. 4. Abundance (mean ± SE, n = 16, data averaged across Replicates and Sites) of common taxa through the study period in each combination of treatments established in the upper mid-shore habitat in June 2004. Symbols and shadings as in Fig. 3

Table 6. ANOVA examining the effects of slope of substratum on individual taxa in cleared quadrats. Sl: Slope; Si: Site *p < 005; **p < 0.01; ***p < 0.001; NS: p > 0.05

Source of variability	df	Sep 2004 MS	Sep 2004 F	Jul 2005 MS	Jul 2005 F	Oct 2006 MS	Oct 2006 F
Upper mid-shore habitat							
***Rivularia* spp.**							
Sl	1	8978.00	8.19*	3570.13	3.38	325.13	0.85
Si(Sl)	6	1096.48	1.51	1055.48	1.79	384.56	2.80*
Residual	24	728.38	590.35	137.29			
Cochran's test		*C* = 0.274, NS		*C* = 0.213, NS		*C* = 0.294, NS	
Transformation		None		None		None	
Chthamalus stellatus							
Sl	1	4.12	4.25	15.29	18.01**	22.12	8.79*
Si(Sl)	6	0.97	0.84	0.85	0.55	2.52	2.11
Residual	24	1.16	1.53	1.19			
Cochran's test		*C* = 0.244, NS		*C* = 0.227, NS		*C* = 0.276, NS	
Transformation		Ln(*x* + 1)		Ln(*x* + 1)		Ln(*x* + 1)	
Encrusting corallines							
Sl	1	157.53	1.18	38.28	0.41	3.78	1.32
Si(Sl)	6	133.74	2.63*	92.91	1.19	2.86	1.47
Residual	24	50.76	78.26	1.95			
Cochran's test		*C* = 0.923, p < 0.01		*C* = 0.862, p < 0.01		*C* = 0.920, p < 0.01	
Transformation		None		None		None	
Lower mid-shore habitat							
Encrusting corallines							
Sl	1	17112.50	13.78*	7750.13	4.25	9180.13	12.38*
Si(Sl)	6	1242.25	3.00*	1823.48	3.23*	741.73	1.14
Residual	24	414.25	563.94	647.96			
Cochran's test		*C* = 0.295, NS		*C* = 0.414, NS		*C* = 0.394, NS	
Transformation		None		None		None	
***Rivularia* spp.**							
Sl	1	2610.03	5.98*	351.13	0.53	3.53	2.40
Si(Sl)	6	436.11	0.48	658.88	0.96	1.47	3.56*
Residual	24	908.47	683.60	0.41			
Cochran's test		*C* = 0.192, NS		*C* = 0.337, NS		*C* = 0.318, NS	
Transformation		None		None		Ln(*x* + 1)	
Chaetomorpha aerea							
Sl	1	790.03	3.41	3.81	37.50***	124.03	6.52*
Si(Sl)	6	231.86	1.38	0.10	0.11	19.03	0.79
Residual	24	168.07	0.90	24.11			
Cochran's test		*C* = 0.822, p < 0.01		*C* = 0.356, NS		*C* = 0.664, p < 0.01	
Transformation		None		Ln(x+1)		None	
Chthamalus stellatus							
Sl	1	413.28	2.72	6.98	2.09	8.73	6.61*
Si(Sl)	6	151.91	1.07	3.35	2.98*	1.32	1.83
Residual	24	142.53	1.12	0.72			
Cochran's test		*C* = 0.922, p < 0.01		*C* = 0.317 NS		*C* = 0.344, NS	
Transformation		None		Ln(*x* + 1)		Ln(*x* + 1)	

2006, respectively (data not shown). Univariate analyses on data from cleared quadrats indicated that encrusting coralline algae were more abundant on vertical than horizontal substrata throughout the study (Table 6, Fig. 5A). *Rivularia* spp. was also significantly more abundant in quadrats cleared on vertical surfaces than on horizontal surfaces, but this effect was more evident at early stages of colonization and vanished with time (Table 6, Fig. 5B). *C. aerea* was absent from quadrats established on vertical substrata, while it intermittently colonized the horizontal clearings, with the result that differences between slopes were temporally variable (Table 6, Fig. 5C). Finally, barnacles were significantly more abundant on horizontal than vertical substrata throughout the study (Table 6, Fig. 5D).

Analyses including unmanipulated quadrats indicated that encrusting corallines were generally more abundant in clearings than in controls and confirmed the large cover of these algae on vertical surfaces (Table 8, Fig. 5A). Patterns of recovery were, however, similar between vertical and horizontal substrata, as indicated by the lack of a significant Slope × Treatment interaction (Table 8). In contrast, a significant Slope × Treatment interaction was observed for *Rivularia* spp. in September 2004, reflecting the large cover of these algae in quadrats cleared on vertical substrata and the lack of a difference between inclinations for unmanipulated plots (Table 8, SNK tests). This interaction disappeared at later stages of colonization, with a significant main effect of Treatment reflecting the larger cover of *Rivularia* in cleared than in control plots in July 2005, and complete convergence resulting by October 2006 (Table 8, Fig. 5B). The filamentous alga *Chaetomorpha aerea* was only present on horizontal surfaces and displayed temporally variable patterns of abundance (Fig. 5C). Although this species was absent from vertical surfaces, neither the main effect of Treatment, nor its interaction with the other factors were significant (Table 8). Finally, *Chthamalus stellatus* showed lower abundances in quadrats cleared on vertical substrata than in any other treatment combination throughout the study, analogous to what was described for the upper mid-shore environment (Table 8, Fig 5D).

Table 7. ANOVA examining the effects of slope of substratum and treatment on individual taxa in the upper mid-shore habitat. Sl: Slope; Si: Site; Tr: Treatment. *p < 005; **p < 0.01; ***p < 0.001; NS: p > 0.05

Source of variability	df	Sep 2004 MS	Sep 2004 F	Jul 2005 MS	Jul 2005 F	Oct 2006 MS	Oct 2006 F
***Rivularia* spp.**							
Sl	1	11130.25	12.40*	7612.56	8.79*	1511.26	4.70
Si(Sl)	6	897.86	1.77	866.19	2.06	321.74	1.76
Tr	1	18975.06	29.53**	1936.00	2.63	13.14	0.04
Sl × Tr	1	812.25	1.26	7.56	0.01	178.89	0.49
Tr × Si(Sl)	6	642.53	1.27	735.36	1.75	365.84	2.01
Residual	48	507.80	421.36	182.33			
Cochran's test		*C* = 0.197, NS		*C* = 0.150, NS		*C* = 0.227, NS	
Transformation		None		None		None	
Chthamalus stellatus							
Sl	1	178.89	0.19	2232.56	4.14	6993.14	5.43
Si(Sl)	6	923.55	1.97	539.28	0.95	1288.24	1.83
Tr	1	16673.26	16.42**	12210.25	14.84**	9192.01	4.39
Sl × Tr	1	50.76	0.05	162.56	0.20	3466.26	1.65
Tr × Si(Sl)	6	1015.22	2.17	822.73	1.44	2094.51	2.98*
Residual	48	467.80	569.82	702.08			
Cochran's test		*C* = 0.225, NS		*C* = 0.159, NS		*C* = 0.170, NS	
Transformation		None		None		None	
Encrusting corallines							
Sl	1	1048.14	2.03	240.25	2.16	39.06	1.82
Si(Sl)	6	517.22	2.87*	111.40	1.51	21.43	2.29
Tr	1	123.77	0.20	1.00	0.01	12.25	0.49
Sl × Tr	1	213.89	0.34	45.56	0.24	12.25	0.49
Tr × Si(Sl)	6	625.66	3.48**	186.78	2.53*	25.12	2.68*
Residual	48	180.02	73.71	9.36			
Cochran's test		*C* = 0.858, p < 0.01		*C* = 0.4654, p < 0.01		*C* = 0.892, p < 0.01	
Transformation		None		None		None	

These figures, combined with the well-documented differences in structure of assemblages between vertical and horizontal substrata (Benedetti-Cecchi et al. 2000a, Chapman & Bulleri 2003, Knott et al 2004, present study), suggest that sea level rise may have drastic and immediate effects on the structure of assemblages of rocky shores.

The clearing experiment showed a clear separation in the structure (composition and relative abundance of species) of assemblages between vertical and horizontal substrata at every stage of colonization. These differences were caused mainly by changes in the relative abundance of the most common taxa (barnacles, cyanobacteria and encrusting coralline algae) and, to a lesser extent, by changes in the identity of colonizers at later stages of recovery. Collectively, these findings indicate that differences in assemblages in relation to the inclination of the substratum are generated and maintained by a combination of differential recruitment and post-recruitment processes. It should be noted that our experiment was not replicated in time, so results are conditional on the particular environmental conditions occurring during the experiment. Seasonality or other temporal patterns of variation in recruitment might have led to different outcomes had the experiment started in other periods. Nonetheless, the experiment lasted long enough (2 yr) to show that assemblages in clearings converged towards unmanipulated ones, despite any uncertainty that episodic events of recruitment may have introduced during the recovery period.

Univariate analyses helped to identify the taxa responsible for the observed multivariate patterns. In the upper mid-shore habitat, encrusting corallines and *Rivularia* spp. were more abundant on horizontal than vertical substrata during the first year of the experiment, but differences decreased with time. This pattern was in agreement with the findings of Kaehler & Williams (1997), who suggested that strong wave action and water turbulence could dislodge settling propagules of encrusting corallines from vertical substrata. On horizontal substrata, in contrast, less desiccation due to water retention and more light compared to vertical surfaces might have favored the colonization of these organisms. A similar explanation was proposed by Thompson et al. (2005), who invoked light

DISCUSSION

Sea level rise is a slow process compared to the rates of recruitment and mortality that drive the dynamics of assemblages of algae and invertebrates of rocky shores (Harley et al. 2006). As a consequence, the impact of sea level rise on rocky shore organisms is expected to be lower than the effect of other phenomena associated with climate change, such as warming and storminess (Thompson et al. 2002). On topographically complex shores, however, a rise in sea level may cause drastic changes in the type of environment that becomes available to sessile organisms. The coast of Calafuria, for example, becomes steeper on the landward side, so that the proportion of vertical and subvertical substrata would increase with sea level rise. Our data indicated that an increase in sea level of 5 cm would enhance the availability of substrata with slope >40° compared to current slope by 13 and 25% for lower and upper mid-shore organisms, respectively.

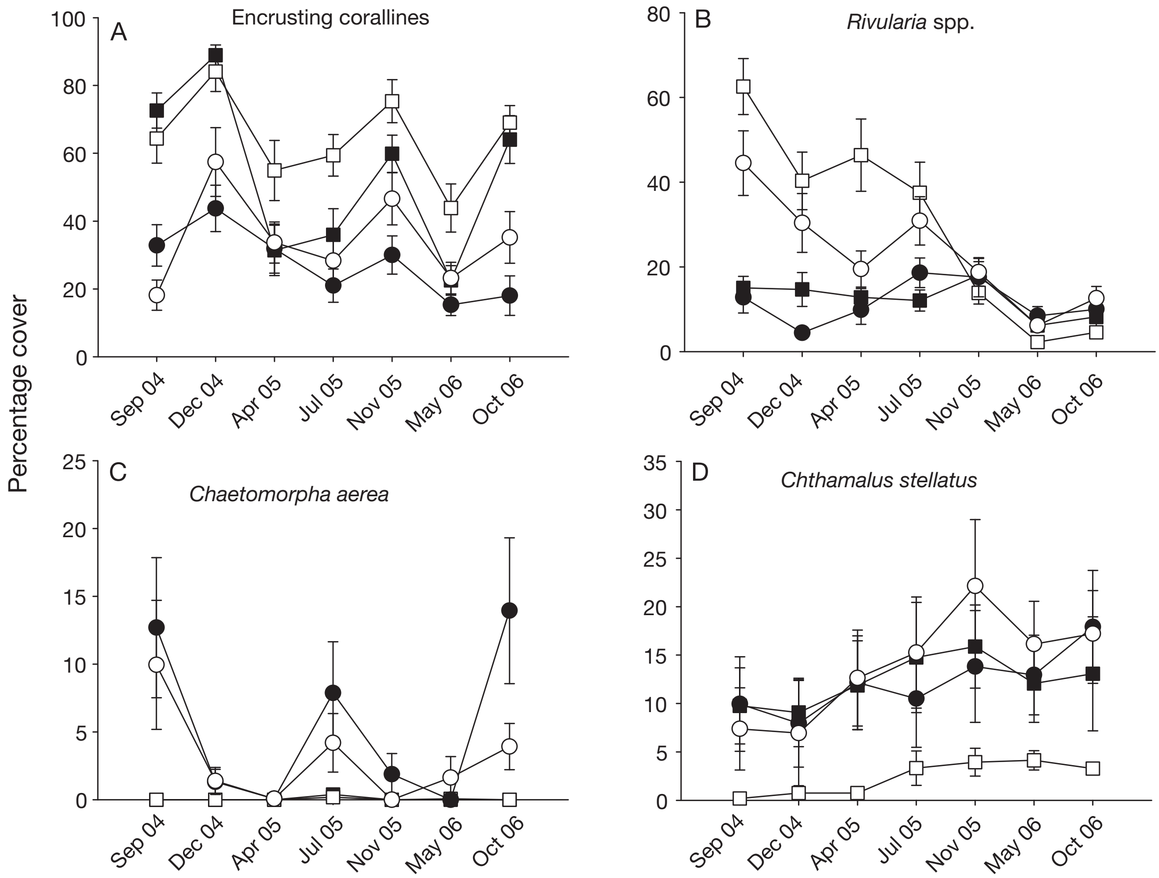

Fig. 5. Abundance (mean ± SE, n = 16, data averaged across Replicates and Sites) of common taxa through the study period in each combination of treatments established in the lower mid-shore habitat in June 2004. Symbols and colors as in Fig. 3

limitation to explain the lower abundance of cyanobacteria on sheltered than exposed shores in the UK.

A different result was observed for the barnacle *Chthamalus stellatus*, which showed lower abundances in quadrats cleared on vertical surfaces than in any other treatment throughout the study. The bulldozing effect of limpets (Denley & Underwood 1979, Branch 1981), which were more abundant on vertical than horizontal substrata, in combination with the active selection of the relatively wetter horizontal substrata by cyprids (Strathmann & Branscomb 1979), provided valid arguments to explain the observed pattern both in the upper and the lower mid-shore habitats.

Several authors have observed that limpets are more abundant on vertical than horizontal substrata. The common explanation is that on vertical surfaces limpets experience reduced solar radiation, greater recruitment and less competition compared to horizontal surfaces (Foster 1975, Garrity 1984, Sebens 1986, Williams & Morritt 1995, Vance 1988, Benedetti-Cecchi et al. 2000a, Benedetti-Cecchi 2001).

Encrusting coralline algae recruited more heavily on vertical than horizontal substrata in the lower mid-shore habitat, in contrast to what was observed higher on the shore. This result could reflect a positive indirect effect of limpets through their top-down control on other algae (Menge et al. 1999). These herbivores may have removed propagules of filamentous algae from vertical substrata, providing free space available for recruitment of encrusting algae, which are resistant to the effects of grazers (Lubchenco & Cubit 1980, Underwood & Jernakoff 1981, Steneck & Dethier 1994, Benedetti-Cecchi et al. 2000a). This interpretation is consistent with the large abundance of limpets observed on vertical surfaces at our study sites.

The same mechanisms invoked for encrusting algae could explain the larger abundance of *Rivularia* spp. on vertical than horizontal substrata in the lower mid-shore habitat during the first year of recovery. In particular, reduced interaction with erect algae (e.g. *Chaetomorpha aerea*), possibly mediated by limpets (Espinosa et al. 2007, Bulleri et al. 2000), explains the initially large abundance of cyanobacteria in quadrats cleared on vertical substrata.

Despite differences in composition and abundance of taxa, assemblages on vertical and horizontal sub-

Table 8. ANOVA examining the effects of slope of substratum and treatment on individual taxa in the lower mid-shore habitat. Sl: Slope; Si: Site; Tr: Treatment. *p < 005; **p < 0.01; ***p < 0.001; NS: p > 0.05

Source of variability	df	Sep 2004 MS	Sep 2004 *F*	Jul 2005 MS	Jul 2005 *F*	Oct 2006 MS	Oct 2006 *F*
Encrusting corallines							
Sl 16.61**	1	29627.01	27.02**	8510.06	5.55	25560.02	
Si(Sl)	6	1096.51	2.53*	1534.11	2.44*	1539.08	2.44*
Tr 18.68**	1	2104.51	2.32	3782.25	4.70	1969.14	
Sl × Tr	1	165.76	0.18	1040.06	1.29	594.14	5.64
Tr × Si(Sl)	6	905.47	2.09	805.36	1.28	105.43	0.17
Residual	48	433.36	629.63	631.48			
Cochran's test		*C* = 0.141, NS		*C* = 0.224, NS		*C* = 0.202, NS	
Transformation		None		None		None	
***Rivularia* spp.**							
Sl	1	1650.39	2.90	0.02	0.08	3.90	1.76
Si(Sl)	6	569.32	1.07	0.27	0.26	2.21	3.16*
Tr	1	25082.64	36.99***	10.54	12.34*	0.16	0.14
Sl × Tr	1	1000.14	13.44*	1.02	1.20	0.46	0.41
Tr × Si(Sl)	6	74.43	0.14	0.85	0.79	1.13	1.62
Residual	48	532.51	1.08	0.70			
Cochran's test		*C* = 0.164, NS		*C* = 0.252, NS		*C* = 0.208, NS	
Transformation		None		Ln(*x* + 1)		Ln(*x* + 1)	
Chaetomorpha aerea							
Sl	1	26.58	13.53*	9.44	35.26***	1278.06	7.93*
Si(Sl)	6	1.96	1.57	0.26	0.22	161.19	1.28
Tr	1	0.04	0.04	0.12	0.60	400.00	3.96
Sl × Tr	1	0.04	0.04	0.09	0.47	400.00	3.96
Tr × Si(Sl)	6	0.92	0.74	0.20	0.17	101.04	0.80
Residual	48	1.24	1.19	126.26			
Cochran's test		*C* = 0.194, NS		*C* = 0.207, NS		*C* = 0.420, p < 0.01	
Transformation		Ln(*x* +1)		Ln(*x* +1)		None	
Chthamalus stellatus							
Sl	1	1.69	1.51	236.39	0.41	8.90	4.32
Si(Sl)	6	1.12	1.01	575.43	1.61	2.06	2.07
Tr	1	15.05	7.38	178.89	0.57	0.91	2.73
Sl × Tr	1	5.78	2.84	1048.14	3.32	1.43	4.25
Tr × Si(Sl)	6	2.03	1.84	315.59	0.88	0.34	0.34
Residual	48	1.10	357.65	1.00			
Cochran's test		*C* = 0.173, NS		*C* = 0.262, NS		*C* = 0.164, NS	
Transformation		Ln(*x* + 1)		None		Ln(*x* + 1)	

strata displayed similar capabilities to recover after disturbance. None of the Slope × Treatment interactions were significant in the multivariate analyses, indicating that differences between cleared and unmanipulated quadrats were similar for vertical and horizontal substrata. Thus, although differences in the structure of assemblages between the 2 slopes were detected and changes in species richness and composition are known to affect the ability of assemblages to resist to and to recover from disturbance (Allison 2004), our findings lead us to the prediction that sea level rise should not have drastic effects on the stability properties of assemblages of rocky shores at Calafuria.

The present study illustrates clear and persistent differences between assemblages of vertical and horizontal substrata at Calafuria. These differences were maintained by a combination of recruitment and post-recruitment processes that appeared to operate in similar ways at different heights of the shore. However, it is worth noting that the differences in assemblages revealed by the sampling programme were not always consistent with those observed in the control plots of the experiment. For instance, observational data showed larger abundances of *Chthamalus stellatus* on horizontal than on vertical substrata, while this pattern was either much less evident or completely absent from control quadrats in the upper and lower mid-shore habitat, respectively. Encrusting coralline algae were more abundant on vertical substrata in the sampling programme, but the opposite pattern was detected during the experiment in control quadrats of the upper mid-shore habitat.

Two explanations (that are not mutually exclusive) may be invoked to interpret such inconsistencies:

(1) it has been suggested that differences in intensity and quality of biotic processes, such as recruitment and competition, and/or small-scale variation in abiotic conditions may determine different patterns of distribution and abundance of dominant taxa between the upper and lower margins of the mid-shore habitat (Benedetti-Cecchi et al. 2005). While the experimental quadrats were established at the margins (and therefore represented extreme conditions for most of the organisms living in the mid-shore habitat), the sampling programme examined patterns of abundance in the middle of this habitat, thereby sampling average conditions for many organisms. This is particularly evident for *Chthamalus stellatus*; the sampling programme yielded percentage cover values of 15.53 ± 1.88 and 31.41 ± 4.89 (mean ± SE, n = 4) for this species on vertical and horizontal substrata, respectively. These values were intermedi-

ate between those obtained from the unmanipulated experimental plots, which consisted of data coming from both the upper and lower mid-shore levels. In this case the vertical substrata yielded cover values of 37.37 ± 2.58 and 12.35 ± 0.94 (n = 7) for the upper and lower mid-shore levels, respectively, whilst barnacle cover on horizontal substrata ranged from 43.04 ± 2.59 and 12.13 ± 1.18 at the upper and lower heights, respectively. Hence, the different outcomes of the sampling and experimental programme may be the result of the different positioning of quadrats across the vertical gradient of the shore.

(2) The descriptive and experimental components of the present study were undertaken at different times, so differences in environmental conditions between periods may explain some of the variability in outcomes. In fact, previous studies have shown that in this system the magnitude of important processes influencing the structure of assemblages on vertical and horizontal substrata, like grazing, can change over temporal scales analogous to those encompassed by the present studies (Benedetti-Cecchi et al. 2000a).

Our findings indicate that vertical substrata should become increasingly common at the expense of horizontal surfaces with sea level rise. These physical changes are expected to drive major shifts in assemblages, leading to contractions in the populations of those species that occur mostly on horizontal substrata, like the currently dominant barnacle *Chthamalus stellatus* and turf-forming (filamentous and coarsely branched) algae, and to the expansion of assemblages dominated by encrusting coralline algae and grazing gastropods, which are more common on vertical substrata. We conclude that sea level rise has a great potential to alter the structure of assemblages of rocky shores, and should be added to the list of the major anthropogenic impacts affecting marine coastal biodiversity.

Acknowledgements. We are grateful to F. Bulleri and L. Tamburello for helpful comments on an early version of the manuscript. This work is part of a PhD dissertation by S.V. at the University of Pisa. This study was supported by grants from the University of Pisa, the Census of Marine Life Programme NaGISA and the MARBEF (Marine Biodiversity and Ecosystem Functioning) Network of Excellence funded in the Community's Sixth Framework Programme. This is contribution No. 8046 of MARBEF.

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Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: January 30, 2008; Accepted: June 26, 2008
Proofs received from author(s): September 4, 2008