

L. Benedetti-Cecchi · F. Bulleri · F. Cinelli

The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean

Received: 22 June 1999 / Accepted: 15 November 1999

Abstract This study examined the interactive effects of grazing by limpets and inclination of the substratum in maintaining differences between mid-shore and low-shore assemblages of algae in the northwest Mediterranean, at different scales of space and through time. Alternative models leading to different predictions about these effects were proposed and tested. Limpets were excluded by fences from areas of the substratum at mid levels on the shore. The response of algal assemblages to this manipulation was compared with control and enclosure plots at the same level, and with unmanipulated plots in the low shore where limpets are less abundant. The effects of limpets were examined at several replicated sites (0.1–4 km apart) for each slope of the substratum (nearly horizontal vs vertical), at different locations (hundreds of kilometres apart) and at different times. Individual taxa responded differently to limpet exclusion. The percentage cover of the coarsely branched and filamentous algae increased significantly in enclosure plots, in some cases reaching values found on the low shore. These patterns, however, varied greatly from shore to shore and significant effects were found both on horizontal and vertical substrata. Multivariate analyses indicated that grazing by limpets accounted for about 20% of the differences between mid-shore and low-shore assemblages. This effect was independent of substratum inclination and was consistent in space and time, suggesting that physical conditions were not as stressful for macroalgae on vertical substrata as initially supposed. Variable recruitment of algae is proposed as a possible explanation for the lack of consistency in the effects of limpets at the scale of the shore. The results of this study emphasize the need for multiple-scale analyses of the interactive effects of physical and biological factors to understand the organization of natural assemblages.

Key words Grazing · Physical factors · Repeated experimentation · Rocky shores · Scales of variability

Introduction

Physical and biological processes interact to generate spatial and temporal patterns in natural assemblages of species. Understanding the interplay of physical and biological processes and the scales at which these interactions take place are major issues in ecology (Menge and Sutherland 1987; Danielson 1991). Spatial and temporal variability are usually large in natural systems, making generalizations of results from studies conducted at particular places and times unreliable (Underwood et al. 1983; Foster 1990; Underwood and Petraitis 1993). As the relative importance of different ecological processes is likely to change with scale, multiscale analyses are necessary to set the spatial and temporal limits within which any relevant ecological process is likely to operate (Wiens et al. 1993; Underwood and Chapman 1996). Understanding the scales of variation in patterns and processes will increase our ability to predict the consequences of natural and anthropogenic disturbances to the environment. These goals can only be achieved by increasing the extent and scope of ecological studies (Schneider 1994; Thrush et al. 1997).

A number of physical and biological processes are known to affect the vertical distribution of algae and animals in intertidal rocky shores. Several studies have inferred, and in part elucidated, the importance of physical forces such as desiccation and exposure to waves (Stephenson and Stephenson 1949; Southward 1958; Lewis 1964), and of biological interactions including the effects of consumers (Paine 1974; Lubchenco 1980; Moreno and Jaramillo 1983) and competition (Connell 1961; Lubchenco 1980; Shonbeck and Norton 1980; Hawkins and Hartnoll 1985) in setting the upper and lower limits of distribution of intertidal populations. This research has enhanced our understanding of the relative importance of different processes in regulating local pat-

L. Benedetti-Cecchi (✉) · F. Bulleri · F. Cinelli
Dipartimento di Scienze dell'Uomo e dell'Ambiente,
via A. Volta 6,
56126 Pisa, Italy
e-mail: bencecc@discat.unipi.it
Tel.: +39-50-500943, Fax: +39-50-49694

terns of distribution. Whether these processes interact or operate additively, and the scales at which these interactions eventually take place, are still open questions. Grazing, for example, is considered a major biological interaction on rocky shores. Invertebrate grazers may affect high intertidal populations of ephemeral algae as well as low-shore foliose or canopy species, and often set the upper limits of distribution of these algae (Lubchenco and Gaines 1981; Sousa et al. 1981; Underwood and Jernakoff 1981; Hawkins and Hartnoll 1983; Cubit 1984). Grazing may also affect patterns of recolonization in disturbed patches of habitat, either by enhancing, inhibiting or deflecting succession (Sousa 1979; Lubchenco 1983; Farrell 1991; Hixon and Brostoff 1996; Benedetti-Cecchi, 2000). Fewer studies have examined whether the effects of grazers can be altered by changes in some physical or biological attributes of the habitat (e.g. Dayton 1971; Underwood 1980; Buschman 1990; Williams 1994; Kaehler and Williams 1998). Very few studies, however, have examined hypotheses about scales of variation in these effects, although some evidence indicates that the ecological importance of grazing may be spatially and temporally variable (Hawkins 1981; Underwood and Jernakoff 1981, 1984; Cubit 1984; Breitburg 1985; Sousa 1985). Most studies have focused on the response of single populations to the impact of grazers, and the potential for this process to affect whole assemblages has been explored less frequently (e.g. Anderson and Underwood 1997).

In the Mediterranean, the most common organisms at mid levels on the shore are filamentous and foliose algae, barnacles and limpets. Different assemblages may occur at lower levels, including areas dominated by turf-forming algae, more complex habitats characterized by canopy species, or mussel beds (Benedetti-Cecchi and Cinelli 1994; Benedetti-Cecchi et al. 1996). Limpets may occur low on the shore in patches of encrusting coralline algae or on bare rock, but they are generally less abundant at this level than at higher elevations. These grazers may exert strong effects on the other organisms. On the mid shore, limpets may promote succession by removing filamentous algae and indirectly facilitating the establishment of foliose algae and barnacles (Benedetti-Cecchi and Cinelli 1993; Benedetti-Cecchi 2000). Low on the shore, limpets have no effects on filamentous and canopy algae though they may affect other algal groups such as the coarsely branched and articulated coralline algae. These effects appeared to be consistent among sites hundreds of metres apart (Benedetti-Cecchi et al. 1996). Whether limpets play a role maintaining differences between assemblages occurring at different levels on the shore is not yet known.

In the present study, limpets were experimentally excluded from areas of substratum of different slope (horizontal or gently sloping vs vertical) at mid levels on the shore. We tested the general model that limpets set the upper limits of distribution of the most representative groups of algae occurring low on the shore, and examined whether this effect changed with slope. We also

tested multivariate hypotheses about the role of limpets in maintaining differences between mid-shore and low-shore assemblages. Multivariate responses generally reflect strong direct effects of grazing on a few groups of algae, indirect effects on other algae and invertebrates, and weak effects on some other components of these assemblages (Menge et al. 1994; Menge 1995; Anderson and Underwood 1997; Benedetti-Cecchi 2000).

Different patterns of interaction between limpets and slope might occur depending on the relative sensitivity of limpets and algae to physical stress (e.g. Menge and Olson 1990). Physical factors might be more important than grazing in regulating the distribution and abundance of algae on vertical substrata in the Mediterranean. This basin is characterized by narrow tides (30–40 cm) and vertical surfaces can experience long periods of aerial exposure under prevailing conditions of calm sea and high atmospheric pressure. In contrast, the retention of water would decrease desiccation on horizontal surfaces providing better conditions for the growth and persistence of macroalgae. This model predicts a larger effect of limpets on horizontal than vertical substrata, consistently in space and time.

Alternatively, physical stress may be more important in regulating the foraging activity of limpets than in limiting the colonization of algae. In this case, a larger effect of limpets can be expected on vertical substrata because these habitats usually provide better physical conditions for limpets, eventually enhancing their foraging efficiency in comparison to horizontal surfaces (e.g. Garrity 1984; Williams and Morritt 1995). This model still predicts an interaction between limpets and slope that should be consistent at different spatial and temporal scales, but in a direction opposite to that predicted by the previous model.

Finally, physical factors may affect both limpets and algae in complex ways, and no clear hierarchy in the sensitivity of these organisms to physical stress may be evident. For example, desiccation might prevent the colonization of algae on vertical substrata at some sites but not at others, due to intrinsic differences among these sites (e.g. orientation). Similarly, physical stress might reduce the foraging efficiency of limpets on horizontal substrata, but only during hot days. This model predicts spatially and temporally variable interactions between limpets and inclination of the substratum.

As a first attempt to distinguish among these models, we repeated experimental exclusions of limpets at different sites for each slope (0.1–4 km apart), at different locations (hundreds of kilometres apart), and at different times.

Materials and methods

This study was conducted at three localities in the northwest Mediterranean: Baratti, about 100 km south of Livorno (43° N, 10°30' E); Capraia, an island offshore from Livorno (43°02' N, 9°50' E), and Punta Bianca, about 70 km north of Livorno (44°05' N, 10° E). Only the western coast of Capraia was used for the experi-

ment, to maintain consistency with the geographical orientation of the locations on the mainland. The three locations provided one of several possible sets of shores that might have been chosen to represent the north-west Mediterranean. The relevant criterion used to select the locations was that they should have qualitatively similar assemblages characterized by limpets, filamentous and erect algae.

On all shores, mid levels (0.2 to 0.4 m above the mean low-water level) were characterized by the presence of the fleshy red alga *Rissoella verruculosa* (Bertolini) J. Agardh, the encrusting brown alga *Ralfsia verrucosa* (Areschoug) J. Agardh, cyanobacteria (*Rivularia* spp.), the barnacles *Chthamalus montagui* Southward and *C. stellatus* (Poli), and the limpets *Patella aspera* Rodding and *P. rustica* Linné. Patches of bare rock were also common at mid levels. These organisms were generally present on all shores, although their relative abundance could vary. Low levels (–0.1 to 0.1 m with respect to the mean low-water level) were characterized by turf-forming algae which comprised several species of filamentous algae, the geniculate coralline alga *Corallina elongata* (Ellis et Solander) and the coarsely branched algae *Laurencia* spp., among others. At Capraia, canopy algae of the genus *Cystoseira* were also common low on the shore, while at Punta Bianca, mussels (*Mytilus galloprovincialis* Lamark) were dominant, although both geniculate corallines and coarsely branched algae were present on the valves of mussels and in patches opened in the mussel matrix.

The experiment was initiated independently three times on each shore, between June 1996 and March 1997. At each time, on each shore, limpets were manipulated in two replicate sites for each of the two slopes of substratum. Thus, there were a total of 12 sites on each shore (2 sites \times 2 inclinations \times 3 times). A site was a 10- to 20-m stretch of coastline where the substratum could be nearly horizontal ($<20^\circ$), or vertical. The 12 sites were interspersed along about 4 km of the coast on each shore, and the 6 sites available for each slope were assigned randomly to the different times.

In each site, nine plots were haphazardly marked at mid levels on the shore, in areas above those colonized by the filamentous or other erect algae but with limpets present. These plots were 17 \times 17 cm in size and were marked at their corners with small pieces of epoxy putty (Subcoat S; Veneziani). Three replicate plots were then randomly assigned to each of the following treatments: (1) controls (open plots that were marked and left undisturbed thereafter), (2) enclosures (plots where limpets were included at natural densities) and (3) exclosures (plots where limpets were excluded). Fences were erected to include/exclude limpets. These devices (17 \times 17 \times 4 cm) were made of plastic mesh reinforced with a mesh of galvanized iron (0.5 \times 0.5 cm mesh size), anchored with stainless steel screws inserted into Rawl-plugs in the rock. Epoxy putty was used to bolt the corners of the fences to the substratum. Enclosures served as a procedural control for artefacts due to the fences (e.g. Anderson and Underwood 1997). Partial fences were also used as procedural controls, but only on horizontal substrata. This type of control did not reveal any artefact in the present experiment, but partial fences may be inadequate to reproduce the sort of changes that a whole fence can impose on a habitat (e.g. Johnson 1992). Given this potential bias, we used the more conservative (see Results) enclosure treatment to control for possible artefacts due to the experimental procedure.

The experimental sites were visited approximately every 2 months. During each visit, damaged fences were replaced by new ones and the efficacy of the treatments was checked. Limpet densities in enclosures were adjusted to match those found in controls. When necessary, limpets were added by collecting individuals from nearby areas and placing them into the appropriate plots. Water was dripped over them for some minutes until they had re-attached to the rock. The size of these limpets was similar to that of the animals present in the controls. Some limpets invaded the enclosure plots and/or recruited into them (see Results). These were generally small individuals that were removed by hand.

The experimental plots were sampled after 1 year. Three additional replicate plots were sampled randomly in each site in the low-shore habitat for comparison. One year was considered a suf-

ficient period to observe any effect of limpets in these assemblages, given the biology and life histories of the organisms involved (Benedetti-Cecchi and Cinelli 1993; Benedetti-Cecchi et al. 1996). The percentage cover of algae, barnacles and mussels was assessed in areas of 10 \times 10 cm centred in the experimental plots, or in equal areas sampled in the low-shore habitat. Percentage cover estimates were obtained as intersections using a metal frame with a grid of 64 points. Limpet densities were assessed by counting animals in the whole plots and in areas of the same size low on the shore.

Statistical analyses

The predicted outcome of the experiment was that the exclusion of limpets should cause changes in the abundance of single populations of algae and in whole assemblages at mid levels on the shore, increasing the similarity between these assemblages and those in the low-shore habitat. The proposed models (see Introduction) also predicted significant interactions between limpets and slope of the substratum, which might or might not be consistent in space and time. These hypotheses were tested using both univariate and multivariate procedures. The univariate response of the most abundant groups of macroalgae was examined using multifactorial mixed-model ANOVAs. The five factors were: shore (random and orthogonal), time (random, nested within shore), slope (fixed and orthogonal), site [random and nested within each combination of time(shore) \times slope] and treatment (fixed and orthogonal). Treatment had four levels and included the comparison of the three mid-shore treatments with the low-shore habitat. The assumption of homogeneity of variances was checked using Cochran's *C*-test and transformations were used if necessary. When required, SNK tests were used for post hoc comparisons of the means.

Multivariate analyses were used to compare assemblages among the four treatments, including the low-shore habitat, by examining the response of different groups of algae (see above), barnacles and mussels to the manipulation of limpets. A matrix of similarities between each pair of samples was calculated using the Bray-Curtis similarity coefficient (Bray and Curtis 1957) on fourth-root-transformed data (Clarke 1993). Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the rank orders of similarities among samples in the different treatments (Field et al. 1982; Clarke 1993; Underwood and Anderson 1994; Anderson and Underwood 1997).

Analysis of similarities (ANOSIM) is a procedure that enables statistical tests of hypotheses about multivariate responses. This procedure cannot, however, handle designs with more than two factors (Clarke 1993). To test predictions (see above) about the response of whole assemblages to the exclusion of limpets, a different procedure was used. The abundance of the taxa present in the three replicate plots sampled from the low-shore habitat in each site was averaged to produce an 'average' sample. Then the similarity between each of the plots from the mid-shore habitat and the 'average' sample was calculated (see also Underwood and Chapman 1998). This produced, for each site, three replicate estimates of the similarity between each treatment in the mid-shore habitat (control, enclosure and exclosure) and the low-shore habitat. These data were analysed with the same ANOVA model used in the univariate case. This procedure enabled us to test the relevant hypotheses (the treatment \times slope interaction and its consistency in space and time) in a multivariate context (following Anderson and Underwood 1997; Underwood and Chapman 1998).

Results

Limpets

Fences were effective in excluding large limpets, but small individuals were sometimes present in enclosure

Table 1 Analysis of variance on mean densities of limpets in the experimental treatments. Tests of factors involved in higher-order interactions are not interpreted because there are no hypotheses related to them (Underwood 1997). Pooling procedure have been

Source of variation	df	MS	F	P	F-ratio versus
Shore	2	2.251	6.7	<0.05	Time(shore)
Time(shore)	6	0.335	0.7	>0.6	Site[slope×time(shore)]
Slope	1	0.484	0.4	>0.6	Slope×shore
Site[slope×time(shore)]	18	0.463	2.0	<0.01	Residual
Treatment	3	8.440	17.6	<0.003	Treatment×shore
Slope×shore	2	1.331	2.5	>0.15	Slope×time(shore)
Slope×time(shore)	6	0.535	1.2	>0.35	site[slope×time(shore)]
Treatment×slope	3	1.233 ^a	4.3	<0.05	treatment×slope×shore
Treatment×shore	6	0.480	3.1	<0.05	Treatment×time(shore)
Treatment×time(shore)	18	0.153	0.6	>0.9	Treatment×site[slope×time(shore)]
Treatment×site[slope×time(shore)]	54	0.274	1.2	>0.15	Residual
Treatment×slope×shore	6	0.310	1.1	>0.4	Treatment×slope×time(shore)
Treatment×slope×time(shore)	18	0.282	1.0	>0.4	Treatment×site[slope×time(shore)]
Residual	288	0.229			
Total	431				

^a Tested against the pooled term [treatment×slope×shore]+[treatment×slope×time(shore)] (MS=0.289, df=24)

plots. These densities were analysed using ANOVA to determine whether the differences among treatments were consistent in space and time. This analysis detected significant treatment×slope and treatment×shore interactions (Table 1). Inspection of the interaction plots (Fig. 1A), and SNK tests, revealed that the first of these interactions resulted from the greater abundance of limpets on vertical than on horizontal substrata in the controls, while there was no difference between substrata for each of the other treatments. Furthermore, limpets in enclosure plots could not be maintained at the same density as the controls on vertical substrata, although the mean number of limpets in enclosure plots was reduced to match numbers found in the low-shore habitat (Fig. 1A). These patterns resulted in the following ranking of the means for vertical substrata (after SNK test): control>enclosure>exclosure=low shore. In contrast, on horizontal substrata, the following pattern resulted from the SNK test: enclosure=control>low shore=exclosure.

Patterns of differences among treatments in mean densities of limpets were similar at Baratti and Capraia, but these patterns differed from those occurring at Punta Bianca, resulting in a treatment×shore interaction (Fig. 1B). On the first two shores, limpet densities in controls and enclosures were similar and significantly greater than densities in exclosure plots and in the low-shore habitat, which did not differ significantly (SNK tests). Control plots at Punta Bianca had the highest density of limpets among the three shores (Fig. 1B). Limpets in enclosure plots could not be maintained at the same density as the controls on this shore, although numbers were similar across the three shores for this particular treatment. The SNK test produced the following ranking of the mean limpet density at Punta Bianca: control>enclosure=exclosure>low shore. There were large and significant differences in mean density of limpets from site to site (Table 1).

used according to Winer et al. (1991) and Underwood (1997). Probabilities that are relevant for the interpretation of the results are indicated in *italics* [Cochran's $C=0.032$, $P>0.05$; values were $\ln(x+1)$ transformed for analysis]

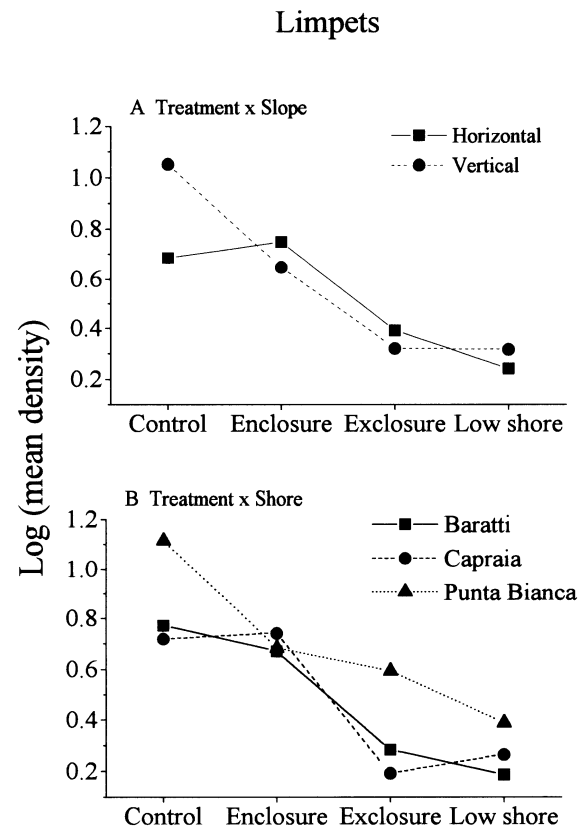


Fig. 1 Diagrams of the treatment×slope (A) and treatment×shore (B) interactions from the analysis of the mean abundance of limpets

These analyses indicated that the mean density of limpets was effectively reduced in exclosure plots and that a similar proportional reduction with respect to controls was achieved on all shores. However, because the efficacy of the exclusion/inclusion procedure was inversely related to

Table 2 Analyses of variance on mean percentage covers of algae. *F*-ratios calculated as in Table 1. Tests of factors involved in higher-order interactions are not interpreted because there are no hypotheses related to them (Underwood 1997). Pooling procedure

Source of variation	df	Articulated coralline algae			Coarsely branched algae			Filamentous algae		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Shore	2	47.65	10.8	<0.05	54.60	2.6	>0.1	15,765	2.3	>0.15
Time(shore)	6	4.39	4.6	<0.006	20.86	3.9	<0.05	7,018	5.1	<0.01
Slope	1	0.84	0.5	>0.5	5.98	3.5	>0.2	7,855	8.7	>0.05
Site[slope×time(shore)]	18	0.96	1.2	>0.25	5.33	5.8	<0.001	1,388	3.9	<0.001
Treatment	3	161.12	123.2	<0.001	31.67	4.9	<0.05	14,499	6.9	<0.05
Slope×shore	2	1.76	0.6	>0.5	1.70	0.3	>0.7	904	0.4	>0.6
Slope×time(shore)	6	3.02	3.1	<0.05	6.48	1.2	>0.3	2,160	1.6	>0.2
Treatment×slope	3	6.64	3.3	>0.05	4.58	2.2	>0.15	1,105	0.9	>0.4
Treatment×shore	6	1.31	0.7	>0.6	6.51	7.6	<0.001	2,108	3.5	<0.05
Treatment×time(shore)	18	1.94	2.2	<0.05	0.86	0.7	>0.8	595	1.2	>0.25
Treatment×site[slope×time(shore)]	54	0.88	1.1	>0.3	1.25	1.4	>0.05	499	1.4	<0.05
Treatment×slope×shore	6	2.00 ^a	2.2	<0.05	2.08	3.1	<0.05	1,211 ^a	2.4	<0.05
Treatment×slope×time(shore)	18	0.93	1.1	>0.4	0.67	0.5	>0.9	512	1.2	>0.4
Residual	288	0.81			0.93			358		
Total	431									
Cochran's <i>C</i>		C=0.058, <i>P</i> >0.05			C=0.043, <i>P</i> >0.05			C=0.051, <i>P</i> >0.05		
Transformation		ln(x+1)			ln(x+1)			None		

^a Tested against the pooled term [treatment×slope×time(shore)]+[treatment×site(slope×time(shore))]. Articulated coralline algae: MS=64.2; filamentous algae: MS=502; *df*=72 in both cases

the ambient density of animals, enclosures did not provide an appropriate control for artefacts at Punta Bianca and enclosures on this shore were not directly comparable to the corresponding treatment on the other shores.

Algae

There were three main groups of algae characterizing the low-shore habitat whose patterns of distribution could be affected by the interaction of limpets and aspect of the substratum: the articulated coralline algae, the coarsely branched algae and the filamentous algae. All groups responded to some extent to the removal of limpets and in all cases there were significant treatment×slope×shore interactions (Table 2), but the pattern of differences among treatments and the meaning of these interactions varied from group to group.

In general, limpets had little effect on the articulated coralline algae on any shores (Fig. 2). The exclusion of limpets caused only a slight increase in the abundance of these algae (about 10% on average) in enclosure plots at Capraia at time 1 and time 2 on horizontal and vertical substrata, respectively, and at Punta Bianca on horizontal substrata at time 2 and vertical substrata at time 3 (Fig. 2). When averaged over the three times, however, the abundance of the articulated coralline algae was significantly greater in the low-shore habitat than in any of the other treatments on all shores. That is, the treatment×slope×shore interaction resulted from changes in the magnitude of differences between the low-shore habitat and the other treatments and not because of significant increases in the abundance of these algae in exclo-

have been used according to Winer et al. (1991) and Underwood (1997). Probabilities that are relevant for the interpretation of the results are indicated in *italics*

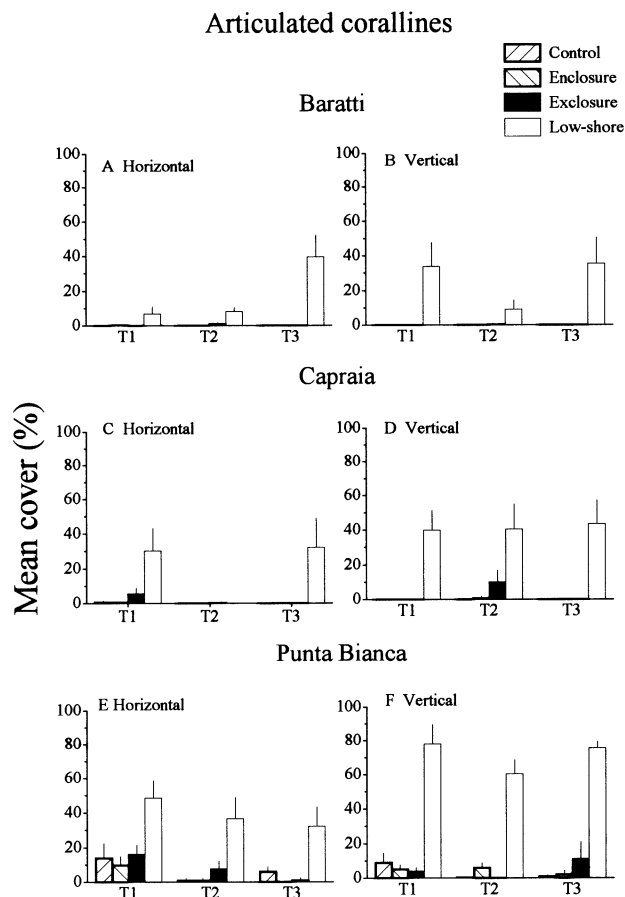


Fig. 2A–F Mean (+SE, *n*=6) percentage cover of articulate coralline algae in experimental plots for three independent repeats of the experiment on each shore

Coarsely branched algae

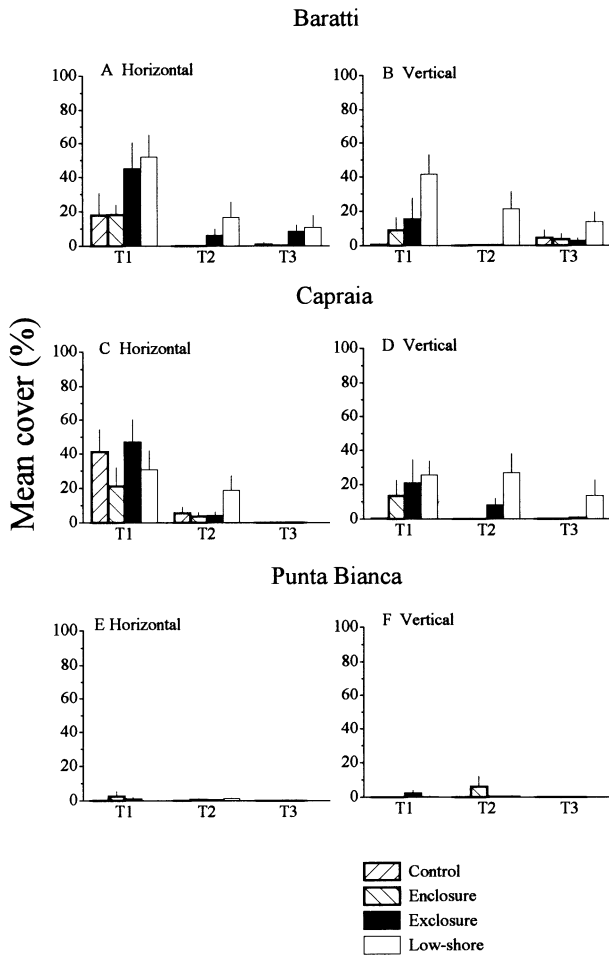


Fig. 3A–F Mean (+SE, $n=6$) percentage cover of coarsely branched algae in experimental plots for three independent repeats of the experiment on each shore

sure plots on some shores (SNK tests within each combination of slope and shore). Similarly, the treatment \times time(shore) interaction resulted from natural temporal fluctuations in the abundance of the articulated coralline algae in the low-shore habitat and not from significant increases in algal coverage on exclosure plots (Fig. 2). The SNK tests repeated at each time within each shore indicated that when averaged over substrata, the abundance of the articulated coralline algae was significantly greater in the low-shore habitat than in any of the other treatments in all the comparisons, while the three treatments at mid levels on the shore were never significantly different. Finally, inclination of the substratum had little effect on the mean cover of the articulated coralline algae, although at Capraia at time 2, these algae were more abundant on vertical than horizontal substrata, resulting in a significant slope \times time(shore) interaction in the analysis (Table 2).

The coarsely branched algae were abundant in the low-shore habitat both at Baratti and Capraia, while they

Filamentous algae

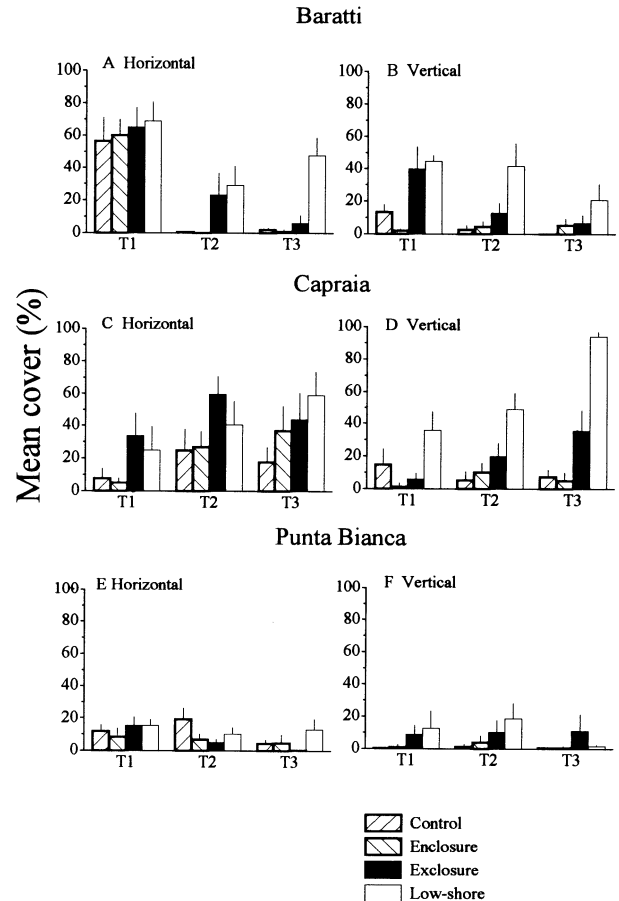


Fig. 4A–F Mean (+SE, $n=6$) percentage cover of filamentous algae in experimental plots for three independent repeats of the experiment on each shore

were nearly absent at Punta Bianca (Fig. 3). These algae were also abundant in control plots at time 1 in Capraia (Fig. 3C), indicating that episodic recruitment in the mid-shore habitat could eventually eliminate differences in the abundance of these plants across heights on the shore. Contrary to the observation with the articulated coralline algae, in this case, the treatment \times slope \times shore interaction indicated a significant effect of limpets (Fig. 3, Table 2). The SNK tests comparing treatment means within each combination of slope \times shore revealed a strong effect of limpets on horizontal substrata at Baratti (Fig. 3A). In this case, the exclusion of grazers resulted in an increase in the abundance of the coarsely branched algae at mid levels on the shore, where percentage cover reached values found in the low-shore habitat (Fig. 3). Treatments were ranked by the SNK test as follows: low shore=exclosure>enclosure=control. In contrast, there was no effect of limpets on vertical substrata at Baratti (SNK test: low shore>exclosure=enclosure=control). There were no relevant differences among treatments on horizontal sub-

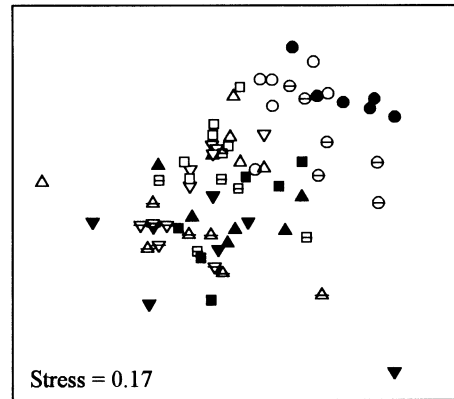
strata at Capraia (the only significant difference detected by the SNK test was that between the low-shore habitat and enclosure plots), while the exclusion of limpets on vertical substrata resulted in a significant increase in the abundance of the coarsely branched algae with treatments ranked by SNK test as: low-shore>enclosure>enclosure=control. Thus, limpets accounted for some of the differences in the abundance of the coarsely branched algae between mid-shore and low-shore habitats on vertical substrata at Capraia. In contrast, there was no significant effect of limpets on these algae at Punta Bianca, on either horizontal or vertical substrata (Fig. 3E,F). The percentage cover of the coarsely branched algae was, however, very variable both in space and time, as indicated by the significant main effects of site[slope×time(shore)] and time (Table 2).

Limpets also had important, but variable, effects on filamentous algae, resulting in significant treatment×slope×shore and treatment×site[slope×time(shore)] interactions (Fig. 4, Table 2). Similar to the observations for the coarsely branched algae, the filamentous algae could recruit heavily at mid levels on the shore irrespective of the presence of grazers. This occurred at time 1 on horizontal substrata at Baratti (Fig. 4A). On this shore, there were significantly more filamentous algae in the low-shore habitat than in the other treatments, which did not differ significantly, either on horizontal or vertical substrata (SNK tests within each combination of shore×slope). The treatment×slope×shore interaction resulted from significant effects of limpets at Capraia on horizontal substrata (Fig. 4C). Treatments within this particular combination of shore×slope were ranked as follows (by SNK test): enclosure=low shore>enclosure=control. In contrast, limpets had minor effects on vertical substrata at Capraia and the differences among treatments were similar to those described for Baratti (low shore>enclosure=enclosure=control). The abundance of filamentous algae was generally low at Punta Bianca and treatments did not differ significantly either on horizontal or vertical substrata (Fig. 4E,F). There was also small-scale spatial variation in the effects of limpets irrespective of the inclination of the substratum, as indicated by the treatment×site[slope×time(shore)] interaction. The SNK tests comparing treatment means within each site (for a total of 36 sites) indicated that exclusion of limpets could enhance the abundance of filamentous algae both on horizontal and vertical substrata, but that these effects occurred only occasionally (significant effects of limpets were observed on one vertical and two horizontal sites at Capraia, and on one vertical site at Baratti). There were large and significant temporal fluctuations in the abundance of the filamentous algae during the study period that were independent of grazing (Table 2).

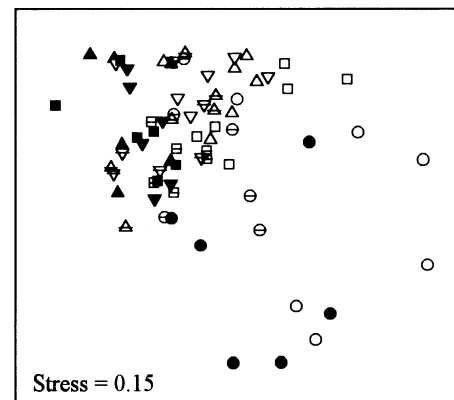
Multivariate analyses

The nMDS ordinations comparing plots of different treatments on each shore independently for horizontal

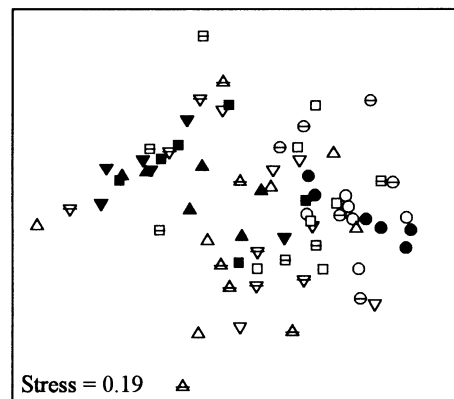
A Baratti



B Capraia



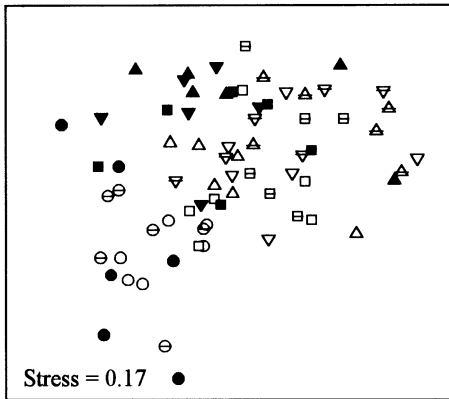
C Punta Bianca



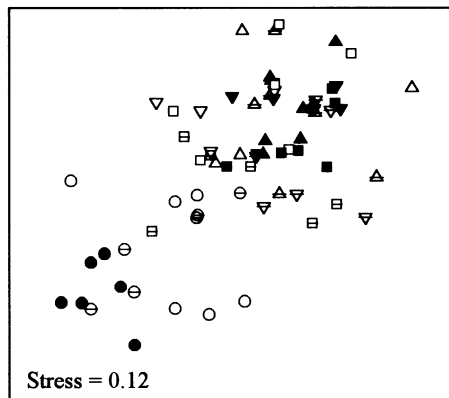
Up triangle = Control Hollow = T1
 Down triangle = +Limpets Bar = T2
 Square = -Limpets Filled = T3
 Circle = Low shore

Fig. 5A–C Two-factor nMDS plots comparing assemblages in different treatments at different times on horizontal substrata for each shore separately

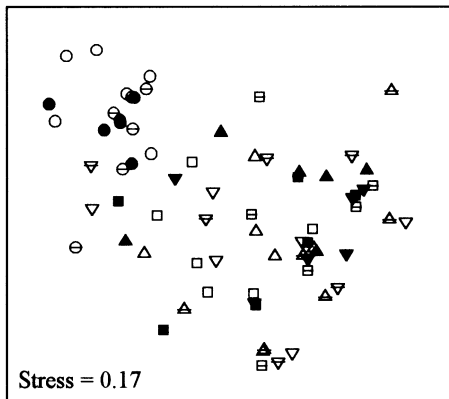
A Baratti



B Capraia



C Punta Bianca



Up triangle = Control
Down triangle = +Limpets
Square = -Limpets
Circle = Low shore

Hollow = T1
Bar = T2
Filled = T3

Fig. 6A–C Two-factor nMDS plots comparing assemblages in different treatments at different times on vertical substrata for each shore separately

Baratti

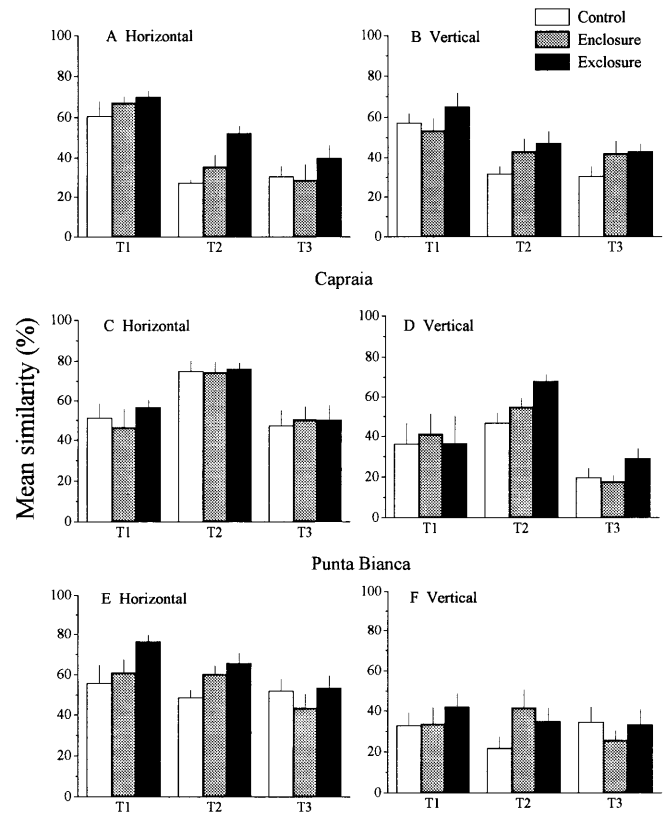


Fig. 7A–F Mean similarity (+SE, $n=6$) between each of the mid-shore treatments and assemblages in the low-shore habitat for three independent repeats of the experiment on each shore

(Fig. 5) and vertical (Fig. 6) substrata separated assemblages in the low-shore habitat from those at mid levels. These patterns were clearer at Baratti and Capraia and less evident at Punta Bianca. There was no evidence for enclosure plots to segregate with those of the low-shore habitat in any comparison. Stress values were always less than 0.2, which is considered the threshold value for an interpretable nMDS (Field et al. 1982; Clarke 1993). Thus, these analyses suggested that limpets did not play an important role in maintaining differences between mid-shore and low-shore assemblages. This hypothesis was further tested by comparing the mean similarity between the ‘average’ sample in the low-shore habitat of each site and each of the treatments at mid levels on the shore, using ANOVA. On average, the similarity between mid-shore and low-shore habitats was about 50% (Fig. 7). The exclusion of limpets increased the similarity between these assemblages by about 10% and the ANOVA detected a significant main effect of limpets (Table 3). Treatments were ranked by the SNK test as follows: exclusion>enclosure=control. Thus, when considering the multivariate response of assemblages, the exclusion of limpets was found to increase the similarity between mid-shore and low-shore assemblages independently of the slope of the substratum and consistently in space and time. These changes were significant but ac-

Table 3 Analysis of variance on multivariate differences in mean similarity between each treatment and the low-shore habitat. *F*-ratios calculated as in Table 1 (with limpets replacing treatment). Tests of factors involved in higher-order interactions are not interpreted because there are no hypotheses related to them (Underwood 1997). Probabilities that are relevant for the interpretation of the results are indicated in *italics* (Cochran's $C=0.054$, $P>0.05$; values were not transformed)

Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Shore	2	372.5	0.1	>0.9
Time(shore)	6	5,606.8	4.1	<0.01
Slope	1	17,076.7	3.8	>0.1
Site[slope×time(shore)]	18	1,362.0	7.1	<0.001
Limpets	2	2,758.4	28.3	<0.005
Slope×shore	2	4,479.7	13.0	<0.007
Slope×time(shore)	6	344.8	0.3	>0.9
Limpets×slope	2	73.4	0.7	>0.5
Limpets×shore	4	97.5	0.4	>0.7
Limpets×time(shore)	12	238.8	1.8	>0.05
Limpets×site[slope×time(shore)]	36	132.8	0.7	>0.9
Limpets×slope×shore	4	108.3	0.7	>0.5
Limpets×slope×time(shore)	12	148.1	1.1	>0.3
Residual	216	192.4		
Total	323			

counted for only about 20% of the differences between habitats (10% over 50% of dissimilarity). The analysis also revealed a significant slope×shore interaction, indicating that substratum slope affected the similarity between mid-shore and low-shore assemblages but that these effects were not consistent from shore to shore. SNK tests comparing differences between slopes for each shore separately indicated that there was no effect of slope at Baratti, while at Capraia and Punta Bianca the similarity between mid-shore and low-shore assemblages was greater on horizontal than vertical substrata. Finally, there were large fluctuations in mean similarity between these assemblages in space and time, as indicated by the significant effects of site[slope×time(shore)] and time(shore) (Table 3).

Discussion

No general conclusion can be drawn from the results of this study about the interactive effects of grazing and aspect of the substratum in maintaining differences between mid-shore and low-shore habitats in the north-west Mediterranean. A significant treatment×slope×shore interaction was found for all the taxa examined, leading to the rejection of any model predicting consistent spatial and temporal interactions between limpets and substratum slope. Patterns recorded depended entirely on which group of algae and which shore were considered. The exclusion of limpets increased the abundance of coarsely branched algae at Baratti and filamentous algae at Capraia on horizontal substrata. The opposite pattern was observed on vertical substrata, with filamentous algae increasing in abundance in enclosure plots at Baratti and coarsely branched algae colonizing enclosure

plots at Capraia. No response of algae to the manipulation of limpets was observed at Punta Bianca. The multivariate analyses indicated that grazing accounted for some of the differences between mid-shore and low-shore assemblages and that this process did not depend on the inclination of the substratum. Thus, there was no clear hierarchy in the sensitivity of limpets and macroalgae to physical stress. Rather, there was abundant evidence to suggest that physical and biological processes interacted in complex ways in this assemblage.

Other studies in rocky intertidal habitats have addressed the issue of the interplay between physical and biological factors (reviewed in Underwood 1985). Manipulative field experiments have mainly been used to investigate the interactions between desiccation and grazing on rocky shores (Underwood 1980; Underwood and Jernakoff 1981, 1984; Buschmann 1990; Williams 1994; Kaehler and Williams 1998). Collectively, these studies have shown that physical factors may influence patterns of distribution and abundance of intertidal populations both directly, by imposing physiological constraints on growth, and indirectly, by mediating the foraging activity of consumers. In some cases, physical and biological factors may operate additively rather than in interaction (Buschmann 1990). In addition, physical factors may have indirect effects on consumers. This may occur, for example, in low-shore habitats where benign physical conditions increase proliferation of algae that monopolize the substratum at the expense of limpets (Underwood and Jernakoff 1981). These interactions may account for the lack of a consistent effect of limpets in areas of the shore where colonization of algae is plentiful.

To date, there has been no way to assess whether the results of previous studies on interactions between physical and biological factors reflect local processes or can be assumed as general explanations for the structure of assemblages on rocky shores. The present study suggests that these interactions are context dependent in the Mediterranean, although this basin, with its particular physical conditions and narrow tides, is not directly comparable to macrotidal systems. There is no clear explanation for the lack of a consistent treatment×slope interaction on these shores. The relative importance of grazing and slope of the substratum might have changed in relation to other physical and/or biological processes that contributed to the maintenance of differences between mid-shore and low-shore assemblages. It is clear that physical conditions for macroalgae on vertical surfaces were not as stressful as initially supposed. Possibly, increased stress due to fast drainage of sea water was compensated by diminished solar radiation on vertical substrata. Studies on tropical rocky shores have shown that the temperature of the substratum and the rate of evaporation are higher on horizontal than vertical surfaces, and these differences can explain variability in patterns of distribution and abundance of organisms in relation to the inclination of the shore (Garrity 1984; Williams and Morritt 1995). The higher density of lim-

pets on vertical than horizontal surfaces is in agreement with this view, although the alternative model of a larger effect of limpets on vertical substrata was not supported by the results.

The reasons why there were differences between Baratti and Capraia in the groups of algae that responded to the manipulation of limpets on vertical substrata, and why limpets affected different algae on substrata of different slope on each of these shores are not clear. This variability suggested that the foraging efficiency of limpets could change in relation to stochastic processes such as the timing and intensity of algal recruitment. Coarsely branched algae, for example, proliferated massively on horizontal substrata at Capraia at time 1 and a similar pattern occurred for the filamentous algae at Baratti, independently of the grazing activity of limpets. Limpets might have been incapable of removing and controlling algae that recruited extensively, as has been proposed in some of the studies mentioned above. These events also indicated that the upper limits of algal distribution could change after periods of intense recruitment. Thus, differences among shores in patterns of algal recruitment might explain some of the variation found in this study. Although the implications of variable recruitment for the structure of marine benthic assemblages have been examined in some detail (Grosberg 1982; Connell 1985; Gaines and Roughgarden 1985; Sutherland 1990), the interactions between this and other processes, including grazing, on rocky shores are still poorly understood.

Variability in recruitment, and particularly lack of recruitment, may explain why the articulate coralline algae were nearly absent at mid levels on the shore, independently of whether limpets were excluded or not. This result is very similar to the findings of Kaehler and Williams (1998) on a tropical rocky shore in Hong Kong. These authors manipulated both physical stress (by wetting patches of substratum) and herbivory at two tidal heights. Articulated coralline algae (*Corallina* spp.) became established in all treatments in the low-shore habitat, but never colonized the high-shore habitat during the experiment, irrespective of whether herbivores were removed or physical conditions were ameliorated by wetting. These patterns were interpreted in terms of limited dispersal capabilities of *Corallina* from the main source of propagules in the shallow subtidal zone. Physiological stress, however, cannot be eliminated as a possible explanation for the lack of articulate coralline algae at mid levels on the shore, because we did not manipulate physical conditions directly in this experiment.

Limited recruitment could also explain the lack of a significant effect of limpets at Punta Bianca, although these grazers were present at high densities on this particular shore. The coarsely branched algae, however, were rare both in the mid-shore and the low-shore habitats, so there was no relevant source of algal colonists to replenish enclosure plots with propagules. Furthermore, filamentous algae were scarce at Punta Bianca and no recruitment event comparable to that observed at the other localities occurred on this shore. Although possible, the

small limpets (<7 mm) that invaded the enclosure plots are unlikely to have buffered large inputs of filamentous algae propagules, had these events of intense recruitment really occurred. Circumstantial observations also indicated that small limpets had minor effects on algae (L. Benedetti-Cecchi, unpublished data).

Substantial evidence indicates that the effects of invertebrate grazers on rocky shores are temporally variable, often as a result of variability in periods of reproduction and recruitment of algae (reviewed in Sousa 1985). In contrast, no temporal variation in the effects of limpets and their interactions with slope of the substratum was found in the present study. Most of the temporal variation present in the data reflected overall temporal changes in the abundance of algae. This is surprising, because several of the results of the present study are best interpreted in terms of variability in (or lack of) recruitment of algae and the consequences of these changes on the foraging efficiency of limpets, as discussed above. This apparent contradiction is explained by the similar proportional changes from time to time in the abundance of algae for the different treatments and slopes, so that no interaction among these factors could emerge from the analyses.

Most studies on grazing in marine habitats have explored the response of single taxa to the exclusion/removal of herbivores (but see Farrell 1989; Anderson and Underwood 1997). In general, these studies have documented strong effects of herbivores but on a limited number of taxa. In addition to these effects, grazers may also induce more subtle and diffuse effects in assemblages through direct as well as indirect interactions (Wootton 1992; Menge 1995; Anderson and Underwood 1997; Benedetti-Cecchi 2000). These patterns are not easily detected by univariate analyses, but they may be considered collectively by analysing the response of whole assemblages to the manipulation of grazers. In the present study, the exclusion of limpets from mid-shore areas increased the similarity between assemblages at this level and those in the low shore from 50% to 60%. Thus, limpets alone accounted for about 20% of differences between mid-shore and low-shore assemblages and this effect was consistent across scales in space and time. This result is important for a number of reasons. First, it provides a quantitative estimate of the effect size of limpets and their importance in maintaining spatial patterns along the vertical gradient of the shore. Second, it shows that although the effects of limpets may be locally important on some particular groups of algae, about 80% of differences between mid-shore and low-shore assemblages are due to other processes (as discussed above; see also Benedetti-Cecchi et al., 1999). Finally, as a general result for the north-west Mediterranean, this reveals a pattern that occurs both on horizontal and vertical substrata and is consistent at small and large spatial scales and through time. This suggests that multivariate measures like mean similarity are less variable than univariate quantities, and as such can offer more predictive power. Thus, ecological models allowing for predictions about patterns described by multivariate measures may be more precise and accurate than

those focusing on univariate measures, although interpreting these patterns can be more difficult. Predictions from the latter models are often frustrated by the large variability intrinsic to most natural systems.

Few studies have tested hypotheses about interactions among different ecological processes and examined whether these interactions change across scales in space and time (e.g. Lively et al. 1993). Studies of this sort are extremely important if we are to understand how biological assemblages are organized and predict the effects of environmental changes on these systems. Increasing evidence suggests that most of the ecological processes commonly invoked as major determinants of the structure of natural assemblages are context and scale dependent (e.g. Dayton and Tegner 1984; Levin 1992; Schneider 1994; Underwood and Chapman 1996). Experimental studies embracing a range of spatial and temporal scales are necessary to estimate this variability, to identify the context in which a particular process or interaction among processes can be expected to be relevant, and to relate patterns and processes with scale (Kotliar and Wiens 1990; Wu and Loucks 1995; Underwood and Chapman 1996; Thrush et al. 1997). Combining the results of several independently executed experiments through a meta-analysis (e.g. Gurevitch and Collins 1994) offers a way to address these issues. These procedures are useful (and usually are the only alternative) for comparisons at very large spatial scales, or to contrast different systems (e.g. aquatic vs terrestrial). Experiments executed by different ecologists with different techniques and different allocation of resources may, however, not always be comparable. When possible, the alternative of replicating experiments within a single logical framework seems a better option for a meta-analysis of patterns and processes.

Acknowledgements We sincerely thank G. Williams for helpful comments on the manuscript. This work was supported by the EU under Contract MAS3-CT95-0012, and by a 60% project from the University of Pisa.

References

- Anderson MJ, Underwood AJ (1997) Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: a multivariate and univariate approach. *Oecologia* 109:442–453
- Benedetti-Cecchi L (2000) Predicting direct and indirect interactions during succession in a midlittoral rocky shore assemblage. *Ecol Monogr* 70:45–72
- Benedetti-Cecchi L, Cinelli F (1993) Early patterns of algal succession in a midlittoral community of the Mediterranean sea: a multifactorial experiment. *J Exp Mar Biol Ecol* 169:15–31
- Benedetti-Cecchi L, Cinelli F (1994) Recovery of patches in an assemblage of geniculate coralline algae: variability at different successional stages. *Mar Ecol Prog Ser* 110:9–18
- Benedetti-Cecchi L, Nuti S, Cinelli F (1996) Analysis of spatial and temporal variability in interactions among algae, limpets and mussels in low-shore habitats on the west coast of Italy. *Mar Ecol Prog Ser* 144:87–96
- Benedetti-Cecchi L, Menconi M, Cinelli F (1999) Preemption of the substratum and the maintenance of spatial pattern on a rocky shore in the northwest Mediterranean. *Mar Ecol Prog Ser* 181:13–23
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Breitburg DL (1985) Development of a subtidal epibenthic community: factors affecting species composition and the mechanisms of succession. *Oecologia* 65:173–184
- Buschmann AH (1990) The role of herbivory and desiccation on early successional patterns of intertidal macroalgae in southern Chile. *J Exp Mar Biol Ecol* 139:221–230
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J Exp Mar Biol Ecol* 93:11–45
- Cubit JD (1984) Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65:1904–1917
- Danielson BJ (1991) Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. *Am Nat* 138:1105–1120
- Dayton PK (1971) Competition, disturbance, and community organizations: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 41:351–389
- Dayton PK, Tegner MJ (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodchikoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. Wiley, New York, pp 457–483
- Farrell TM (1989) Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *J Exp Mar Biol Ecol* 128:57–73
- Farrell TM (1991) Models and mechanisms of succession: an example from a rocky intertidal community. *Ecol Monogr* 61:95–113
- Field JC, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Foster MS (1990) Organization of macroalgal assemblages in the northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* 192:21–33
- Gaines SD, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc Natl Acad Sci USA* 82:3707–3711
- Garrity SD (1984) Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65:559–574
- Grosberg RK (1982) Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology* 63:894–899
- Gurevitch J, Collins SL (1994) Experimental manipulation of natural plant communities. *Trends Ecol Evol* 9:94–98
- Hawkins SJ (1981) The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *J Mar Biol Assoc UK* 61:1–15
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanogr Mar Biol Annu Rev* 21:195–282
- Hawkins SJ, Hartnoll RG (1985) Factors determining the upper limits of intertidal canopy forming algae. *Mar Ecol Prog Ser* 20:265–271
- Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol Monogr* 66:67–90
- Johnson LE (1992) Potential and peril of field experimentation: the use of copper to manipulate molluscan herbivores. *J Exp Mar Biol Ecol* 160:251–262
- Kaehler S, Williams GA (1998) Early development of algal assemblages under different regimes of physical and biotic factors on a seasonal tropical rocky shore. *Mar Ecol Prog Ser* 172:61–71
- Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260

- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Lewis JR (1964) The ecology of rocky shores. English University Press, London
- Lively CM, Raimondi PT, Delph LF (1993) Intertidal community structure: space-time interactions in the northern Gulf of California. *Ecology* 74:162–173
- Lubchenco J (1980) Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344
- Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:1116–1123
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu Rev Ecol Syst* 12:405–437
- Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol Monogr* 65:21–74
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* 5:52–57
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to gradients of environmental stress and recruitment. *Am Nat* 130:730–757
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol Monogr* 64:249–286
- Moreno CA, Jaramillo E (1983) The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. *Oikos* 41:73–76
- Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120
- Schneider DC (1994) Quantitative ecology: spatial and temporal scaling. Academic Press, San Diego
- Schonbeck MW, Norton TA (1980) Factors controlling the lower limits of fucoid algae on the shore. *J Exp Mar Biol Ecol* 43:131–150
- Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal community. *Ecol Monogr* 49:227–254
- Sousa WP (1985) Disturbance and patch dynamics on rocky intertidal shores. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, pp 101–124
- Sousa WP, Schroeter SC, Gaines SD (1981) Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia* 48:297–307
- Southward AJ (1958) The zonation of plants and animals on rocky sea shores. *Biol Rev* 33:137–177
- Stephenson TA, Stephenson A (1949) The universal feature of zonation between tide-marks on rocky coasts. *J Ecol* 37:289–305
- Sutherland JP (1990) Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71:955–972
- Thrush SF, Schneider C, Legendre P, Whitlatch RB, Dayton PK, Hewitt JE, Hines AH, Cummings VJ, Lawrie SM, Grant J, Pridmore RD, Turner SJ, McArdle BH (1997) Scaling-up from experiments to complex ecological systems: where to next? *J Exp Mar Biol Ecol* 216:243–254
- Underwood AJ (1980) The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal algae. *Oecologia* 46:201–213
- Underwood AJ (1985) Physical factors and biological interactions: the necessity and nature of ecological experiments. In: Moore PG, Seed R (eds) The ecology of rocky coasts. Hodder Stoughton, London, pp 372–390
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK
- Underwood AJ, Anderson MJ (1994) Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *J Mar Biol Assoc UK* 74:563–584
- Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- Underwood AJ, Chapman MG (1998) A method for analysing spatial scales of variation in composition of assemblages. *Oecologia* 117:570–578
- Underwood AJ, Jernakoff P (1981) Effects of interactions between algae and grazing gastropods on the structure of a low shore intertidal algal community. *Oecologia* 48:221–223
- Underwood AJ, Jernakoff P (1984) The effects of tidal height, wave exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. *J Exp Mar Biol Ecol* 75:71–96
- Underwood AJ, Petraitis PS (1993) Structure of intertidal assemblages in different locations: how can local processes be compared? In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 38–51
- Underwood AJ, Denley EJ, Moran MJ (1983) Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56:202–219
- Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66:369–380
- Williams GA (1994) The relationship between shade and molluscan grazing in structuring communities on a moderately-exposed tropical rocky shore. *J Exp Mar Biol Ecol* 178:79–95
- Williams GA, Morritt D (1995) Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Mar Ecol Prog Ser* 124:89–103
- Winer BJ, Brown DR, Michelis KM (1991) Statistical principles in experimental design, 3rd edn. McGraw-Hill, New York
- Wootton JT (1992) Indirect effects, prey susceptibility and habitat selection: impacts of birds on limpets and algae. *Ecology* 73:981–991
- Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q Rev Biol* 70:439–466