

Scales of variation in the effects of limpets on rocky shores in the northwest Mediterranean

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ABSTRACT: Grazing is an important determinant of the spatial and temporal patterns of distribution of intertidal organisms on rocky shores. This process is likely to interact with other environmental factors at different scales in space and time. Understanding these interactions is important before generalizations about the ecological role of grazing can be advanced. In the present study, the ecological significance of grazing was evaluated by excluding limpets from mid-shore levels on rocky coasts in the northwest Mediterranean. Alternative models were evaluated leading to different predictions about the interactive effects of limpets, slope of the substratum and season. These models were distinguished on the basis of spatial and temporal consistency in these interactions. The null hypothesis of consistent effects of limpets was examined at relatively small (0.1 to 5 km) and large (100s of km) spatial scales, between seasons (summer vs winter), between dates within seasons, and in relation to slope of the substratum (horizontal vs vertical substrata). Univariate and multivariate analyses indicated inconsistencies in the effects of limpets at different spatial and temporal scales. Interactions between grazing, slope of the substratum and season changed from shore to shore, and strong effects of limpets were observed only occasionally. This variability is discussed in relation to differences in productivity and intensity of recruitment of algae among shores.

KEY WORDS: Algae · Limpets · Grazing · Rocky shores · Spatial scale · Temporal scale

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INTRODUCTION

Natural populations fluctuate in abundance at varying scales in space and time. Identifying the scales at which variability occurs, and the processes that generate and maintain ecological heterogeneity, are among the major goals of ecology (Dayton & Tegner 1984, Danielson 1991, Kolasa & Pickett 1991, Wiens et al. 1993). Most of the past ecological research has focused on patterns and processes occurring at spatial scales of metres to hundreds of metres. Natural assemblages may exhibit drastic changes at these scales, both in terrestrial and aquatic systems, due to variability in biological interactions, recruitment and physical attributes of the habitat (e.g. Underwood & Denley 1984,

Menge & Sutherland 1987). These are also the spatial scales amenable to experimentation, and several studies have elucidated the roles of predation, grazing and competition in maintaining differences between or within habitats (Connell 1983, Schoener 1983, Sih et al. 1985, Huntly 1991). These analyses have been successful in explaining patterns of distribution of organisms at particular places and times, and have provided the basis for the development of general ecological concepts. All experiments are, however, scale- and context-dependent, and problems arise from generalizing the results of single experiments. The problem of context dependency is recognized explicitly in the ecological literature, but few studies have investigated variability in ecological processes at several spatial and temporal scales simultaneously so that the peril inherent in scaling-up from the small to the large can be evaluated formally (Underwood & Petraitis 1993).

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Grazing is one of the major biological processes in terrestrial and aquatic systems. In rocky intertidal habitats, invertebrate grazers, such as limpets and snails, may have a profound influence on patterns of abundance and distribution of intertidal organisms through direct as well as indirect effects (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Sousa 1985, Menge 1995, Benedetti-Cecchi 2000). Although inferences about large-scale effects of grazing have been made, including contrasts between different geographical regions (Gaines & Lubchenco 1982, Dethier & Duggins 1988), and sheltered versus exposed shores (Lubchenco & Menge 1978, Hawkins et al. 1992), most experimental analyses focused on small-scale spatial patterns (reviewed in Underwood 1985). This was justified by the fact that the foraging behaviour and patterns of movement of grazing gastropods are themselves influenced by small-scale features of the habitat, such as general aspect of the substratum, presence of predators and availability of refuges, and changes in physical conditions associated with height on the shore (Chapman & Underwood 1992). Thus, experiments investigating the influence of grazing on intertidal assemblages generally require high spatial resolution (*sensu* Schneider 1994).

In addition to responding to local features of the habitat, patterns of activity of grazers on rocky shores are also likely to interact with ecological processes that operate at larger scales. Populations of grazing gastropods are known to change in abundance from place to place and time to time in relation to variability in recruitment and mortality (Underwood 1979, Branch 1981). The impact of grazers on intertidal assemblages is directly related to the size of the grazer populations, but it may also depend on the timing and intensity of recruitment of algae or other organisms, such as barnacles, events that may themselves be spatially and temporally variable (Underwood et al. 1983, Farrell 1991, Benedetti-Cecchi 2000). Therefore, differences in the general physical and biological settings of the habitat, and seasonal or other temporal changes in patterns of foraging of grazers and in the recruitment of the target populations are all likely to influence the relative importance of grazing at varying scales in space and time. These issues can only be addressed by increasing the extent and scope of experimental investigations about grazing.

In this study we investigated the long-term effects of limpets at different spatial and temporal scales on rocky coasts in the northwest Mediterranean. Knowledge of the effects of environmental factors on the foraging activity of limpets and how grazing affects assemblages is limited for these rocky shores, so that specific predictions about these interactions are difficult to make. Some general models can, however, be

proposed on the basis of the evidence obtained from other studies (see above). In a system like the Mediterranean, characterized by narrow tidal ranges (35 to 40 cm), desiccation may limit the growth of algae on vertical substrata compared to flat surfaces, where physical stress is reduced due to the retention of sea water. This model predicts that limpets have a larger effect on algae on horizontal than vertical substrata, while physical factors are more important on vertical surfaces. These patterns are also likely to be more important in the summer, during prolonged periods of calm seas and high temperatures.

Alternatively, the aspect of the substratum might be more important in regulating the behaviour and foraging activity of limpets than in influencing the establishment of algae. For example, vertical substrata usually provide better physical conditions (more shade and lower temperatures) for limpets than horizontal surfaces (Garrity 1984, Williams & Morritt 1995). If this is the case, excluding limpets from vertical substrata should result in larger effects on algae than excluding limpets from flat surfaces. This difference may be less pronounced during the winter, when physical stress on flat substrata should be reduced in comparison to the summer season.

The 2 models above predict interactive effects of limpets, slope of the substratum and season that are consistent in space and time. As a third alternative, these interactions may change from place to place and time to time in relation to other physical and biological processes such as storms or recruitment. To distinguish among these models, we experimentally excluded limpets at sites of different slope (nearly horizontal vs vertical), at 2 different scales in space and time. Two replicate sites for each slope were established in each of 2 different seasons (summer and winter) and on 2 dates within each season on 3 shores. Sites on each shore were 0.1 to 5 km apart, while shores were 100s of km apart.

METHODS

Study sites and organisms. The study was performed at 3 localities in the northwest Mediterranean: Baratti (42° 57' N, 10° 30' E), Capraia (43° 02' N, 9° 50' E), and Punta Bianca (44° 02' N, 9° 58' E). Capraia is an island, while the other localities are on the mainland. Only the rocky coast on the west side of Capraia was used for the experiments, to be consistent with the geographical orientation of the locations on the mainland. These localities represented 1 of several possible sets of shores that might have been chosen to test whether the effects of limpets are general at scales of hundreds of kilometres in the northwest Mediterranean. The

relevant criterion used to select the locations was that they should have qualitatively similar assemblages of barnacles, limpets, encrusting algae and erect algae.

Assemblages at mid-shore levels were represented mainly by the foliose alga *Rissoella verruculosa* (Bertolini) J. Agardh, by filamentous algae such as *Chaetomorpha aerea* (Dillwyn) Kützing and *Polysiphonia* spp., by encrusting red algae (probably the encrusting base of *Corallina elongata* Ellis et Solander) and the brown crust *Ralfsia verrucosa* (Areschoug) J. Agardh, and by the barnacles *Chthamalus montagui* Southward and *C. stellatus* (Poli). The most common grazers were the limpets *Patella aspera* Roding, *P. caerulea* Linné and *P. rustica* Linné. Further descriptions of mid-shore assemblages in the northwest Mediterranean can be found in Benedetti-Cecchi & Cinelli (1993, 1997), Menconi et al. (1999), Benedetti-Cecchi (2000) and Benedetti-Cecchi et al. (2000).

Experimental design. The experiments were initiated independently on each shore on 2 dates during summer 1996 and on 2 dates in winter 1997. Dates were randomly assigned to shores in each particular season. At each date on a particular shore, 2 nearly horizontal (slope $<20^\circ$) and 2 nearly vertical (slope $>60^\circ$) sites were established, where a site was a stretch of coastline of 10 to 20 m. Vertical and horizontal sites were selected randomly at the beginning of the experiment and were interspersed along approximately 5 km on each shore. Thus, there was a total of 48 sites in this experiment (3 shores \times 2 seasons \times 2 dates \times 2 slopes \times 2 sites), which started in June 1996 and lasted until November 1998.

Nine 17×17 cm plots were haphazardly marked with pieces of epoxy-putty (Subcoat S, Veneziani) at mid-shore levels in areas generally occupied by barnacles and limpets and with no or only minor cover ($<10\%$) of erect algae. Three plots with limpets were randomly assigned to each of the following treatments: control plots (marked and not further disturbed); enclosures (plots where limpets were included at natural densities); exclosures (plots from which limpets were removed). Limpets were excluded/included using fences constructed with a plastic mesh reinforced with a mesh of galvanized iron. These devices were $17 \times 17 \times 4$ cm in size (mesh size of 0.5×0.5 cm), and were anchored to the substratum with stainless-steel screws inserted into rawl-plugs in the rock. Although these devices were flexible enough to follow the rugosity of the substratum, epoxy-putty was used to bolt the corners of the fences to the rock and to fill gaps between them and the substratum. Enclosures provided procedural controls for artifacts due to these devices (e.g. Anderson & Underwood 1997). As a further control for artifacts, we also established partial fences, but only on horizontal substrata (3 replicate plots in each site). A

partial fence consisted of 4 angles placed at the corners of the plot, so that a gap about 8 cm wide occurred in the middle of each side of the quadrat. Although we did not control for potential effects of enclosures on the foraging activity of limpets (and possible indirect effects on the rest of the assemblage), enclosures were apparently more effective in detecting artifacts than partial fences (Benedetti-Cecchi et al. unpubl. data), so that only results from enclosures are presented here. The experimental sites were visited approximately every 2 mo during the experiment. At each visit, damaged fences (including those that showed signs of oxidation) were replaced and the density and size of limpets in enclosures were adjusted to match densities and sizes found in the controls. Some limpets re-invaded the enclosure plots. These were generally small individuals that were removed by hand.

Sampling and statistical analyses. Plots were sampled 4 times (every 2 to 3 mo) for the first year of the experiment, and a final sample was collected 1.5 yr after the start. Sampling after 1.5 yr confounded the effects due to time when the experiment was set up with patterns occurring when the plots were monitored (the experiments begun in summer were sampled in winter and the experiments begun in winter were sampled in summer). There was, however, no problem in distinguishing among the models proposed above, since there were no consistent seasonal effects in our study (see 'Results'). We use these data to examine the long-term effects of limpets on this assemblage in relation to the life-histories and biology of the relevant taxa (Benedetti-Cecchi & Cinelli 1993, Menconi et al. 1999, Benedetti-Cecchi 2000). The percentage cover of algae was assessed in areas of 10×10 cm in the middle of the experimental plots. Estimates of percentage cover were obtained as intersections using a metal frame with a grid of 64 points. Densities of limpets were estimated by counting the individuals present in whole plots.

Univariate and multivariate procedures were used to test hypotheses about consistency of the effects of limpets over space and time. A 6-factor mixed-model analysis of variance (ANOVA) was used for univariate tests. The factors were: shore (random and orthogonal), season (fixed and orthogonal), date (random and nested within each combination of shore \times season), slope (fixed and orthogonal), site (random and nested within each combination of slope \times date [shore \times season]), and limpets (fixed and orthogonal). All data were transformed to natural logarithms to homogenize variances (after Cochran's *C*-test). When necessary, Student-Newman-Keuls (SNK) tests were used for post-hoc comparisons of the means estimated by the ANOVA.

Multivariate analyses were carried out to compare assemblages among treatments, separately for each

season, shore and slope of the substratum. A matrix of similarity between each pair of samples was calculated using the Bray-Curtis coefficient (Bray & Curtis 1957) on fourth-root-transformed data (Clarke 1993). This transformation was used to reduce differences in scale among variables, while preserving information about relative abundance of species among samples. Non-metric multidimensional scaling (nMDS) was used to produce 2-dimensional plots of the rank orders of similarities among samples in the different treatments (Field et al. 1982, Clarke 1993, Anderson & Underwood 1997). The variables included in these analyses consisted of several taxa of algae (see Menconi et al. 1999), barnacles and mussels. Invertebrates were also included in these analyses since they might have been affected by the manipulation of limpets directly (e.g. Dayton 1971), and indirectly through changes in the abundance of algae (Petraitis 1990, Anderson & Underwood 1997, Benedetti-Cecchi 2000).

RESULTS

Fences were effective in excluding limpets of medium to large size (10 to 20 mm) during the study period. However, small limpets (<7 mm) tended to re-invade the exclosure plots, particularly by the end of the study, and total exclusion was not achieved. The mean number of limpets found in each treatment (averaged across 5 sampling occasions) was analyzed using ANOVA to test for possible artifacts due to using fences, and to compare patterns of abundance of limpets across scales in space and time. These analyses indicated that there were significantly fewer limpets in exclosures than in each of the other treatments, and that exclosures and controls had similar numbers of limpets on horizontal, but not on vertical substrata, where limpets were particularly abundant (Fig. 1A). These patterns resulted in a significant treatment \times slope interaction (Table 1 and results from SNK tests). There were significantly more limpets on vertical than horizontal substrata in unmanipulated plots, but slope had no effect on the number of limpets present in each of the other treatments (Fig. 1A; SNK tests). Thus, the treatment \times slope interaction resulted from the larger number of limpets in controls on vertical substrata and not from the effectiveness of excluding limpets differing between slopes.

Differences between slopes in the mean number of limpets were not consistent from shore to shore, resulting in a significant shore \times slope interaction (Table 1). Vertical substrata had more limpets than horizontal substrata at Baratti and Punta Bianca, but not at Capraia (Fig. 1B; SNK tests). The analysis also detected a significant shore \times season interaction, with significantly more limpets in plots established in summer than winter at Punta Bianca, and no difference between seasons on the other shores (Fig. 1C, Table 1; and SNK tests). In addition to the large variability at the scale of the shore (in interaction with other factors), the mean number of limpets was also highly variable at small spatial scales, as indicated by the significant differences among sites in the analysis (Table 1).

Limpets decreased the abundance of coarsely branched algae, but this effect was very variable as indicated by the significant limpets \times slope \times date (shore \times season) and limpets \times shore interactions (Table 2). Only at Baratti did limpets influence the abundance of these plants, but effects were variable and changed with inclination of the substratum and among dates (Fig. 2). There was a significant effect of limpets on horizontal but not on vertical substrata for both the summer- and winter-initiated experiments on the first date, while on the second date grazing was significant irrespective of slope in treatments initiated in summer, and only on vertical substrata for those ini-

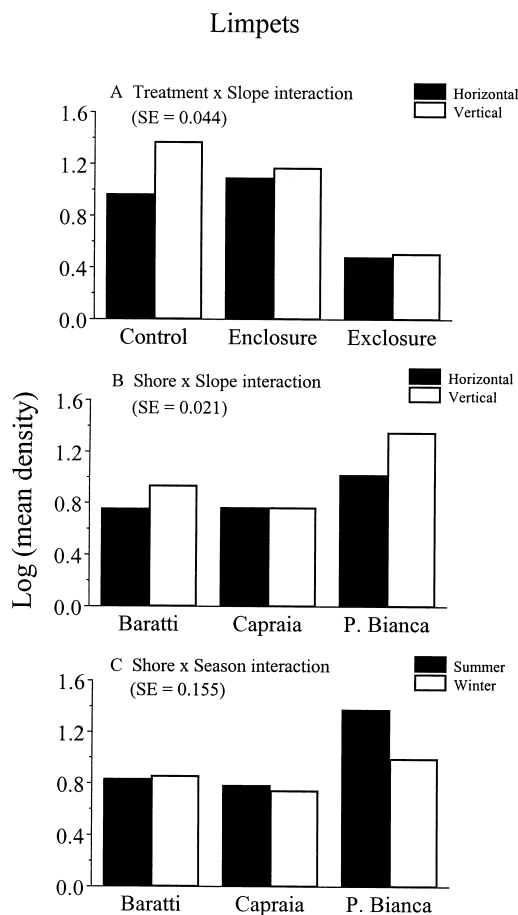


Fig. 1. Interaction plots for (A) treatment \times slope, (B) shore \times slope, and (C) shore \times season effects from the analysis of variance on the mean abundance of limpets. Standard errors for comparisons of the means are given in parentheses in each plot

Table 1. ANOVA on densities of limpets averaged over 5 sampling occasions in each treatment. Tests of factors involved in higher-order interactions are not interpreted because there are no hypotheses related to them (Underwood 1997). Probabilities of relevant tests are indicated in **bold**

Source of variation	df	MS	F	p	F-ratio versus
Shore	2	7.1906	98.4	<0.001	Date (Shore × Season)
Season	1	1.9009	1.1	>0.4	Shore × Season
Shore × Season	2	1.7352	23.7	<0.002	Date (Shore × Season)
Date (Shore × Season)	6	0.0731	0.2	>0.9	Site (Slope × Date [Shore × Season])
Slope	1	3.1288	3.2	>0.2	Shore × Slope
Shore × Slope	2	0.9883	6.1	<0.05	Slope × Date (Shore × Season)
Season × Slope	1	0.7000	14.3	>0.5	Shore × Season × Slope
Shore × Season × Slope	2	0.0491	0.3	>0.7	Slope × Date (Shore × Season)
Slope × Date (Shore × Season)	6	0.1609	0.4	>0.8	Site (Slope × Date [Shore × Season])
Site (Slope × Date [Shore × Season])	24	0.3906	3.0	<0.001	Residual
Treatment	2	20.5913	60.2	<0.002	Treatment × Shore
Treatment × Shore	4	0.3423	2.3	>0.1	Treatment × Date (Shore × Season)
Treatment × Season	2	0.1156	0.5	>0.6	Treatment × Shore × Season
Treatment × Slope	2	1.5140	10.8	<0.05	Treatment × Shore × Slope
Treatment × Shore × Season	4	0.2456	1.7	>0.2	Treatment × Date (Shore × Season)
Treatment × Shore × Slope	4	0.1404	0.9	>0.4	Treatment × Slope × Date (Shore × Season)
Treatment × Season × Slope	2	0.1940	0.5	>0.6	Treatment × Shore × Season × Slope
Treatment × Shore × Season × Slope	4	0.3628	2.3	>0.1	Treatment × Slope × Date (Shore × Season)
Treatment × Date (Shore × Season)	12	0.1464	1.3	>0.2	Treatment × Site (Slope × Date [Shore × Season])
Treatment × Slope × Date (Shore × Season)	12	0.1558	1.4	>0.2	Treatment × Site (Slope × Date [Shore × Season])
Treatment × Site (Slope × Date [Shore × Season])	48	0.1115	0.9	>0.7	Residual
Residual	288	0.1283			
Total	431				

Table 2. ANOVAs on mean percentage cover of algae after 1.5 yr from start of the experiment. *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). Pooling procedures have been used according to Winer et al. (1991) and Underwood (1997). Probabilities of relevant tests are indicated in **bold**

Source of variation	df	Coarsely branched algae			Encrusting algae			Filamentous algae		
		MS	F	p	MS	F	p	MS	F	p
Shore	2	20.29	110.7	<0.001	128.10	15.2	<0.001	38.76	4.4	>0.05
Season	1	35.60	1.8	>0.3	3.58	0.2	>0.65	11.09	0.1	>0.75
Shore × Season	2	19.70	107.5	<0.001	17.69	2.1	>0.2	102.64	11.7	<0.01
Date (Shore × Season)	6	0.18	0.1	>0.9	8.45	2.2	>0.05	8.80	2.2	>0.05
Slope	1	26.61	4.0	>0.15	0.20	0.1	>0.8	78.96	24.6	<0.05
Shore × Slope	2	6.59	3.7	>0.05	3.22	1.9	>0.2	3.21	0.6	>0.5
Season × Slope	1	14.55	2.6	>0.2	0.92	0.2	>0.7	2.19	165.1	<0.01
Shore × Season × Slope	2	5.57	3.3	>0.1	5.33	3.1	>0.1	0.01	0.0	>0.9
Slope × Date (Shore × Season)	6	1.78	1.1	>0.35	1.73	0.4	>0.8	5.34	1.3	>0.25
Site (Slope × Date [Shore × Season])	24	1.62	1.9	<0.01	3.85	2.3	<0.001	4.01	2.0	<0.01
Limpets	2	7.12	3.4	>0.1	3.76	0.5	>0.6	20.91	14.2	<0.05
Limpets × Shore	4	2.10 ^a	2.4	<0.05	7.76	4.5	<0.05	1.48	2.9	>0.05
Limpets × Season	2	1.11	1.3	>0.3	0.09	0.0	>0.9	5.25	1.5	>0.3
Limpets × Slope	2	1.10	1.6	>0.3	5.04	24.1	<0.01	3.85	12.0	<0.05
Limpets × Shore × Season	4	0.83	0.9	>0.4	3.29	1.9	>0.15	3.49	6.9	<0.01
Limpets × Shore × Slope	4	0.69	0.4	>0.7	0.21	0.1	>0.9	0.32	0.3	>0.8
Limpets × Season × Slope	2	0.34	0.8	>0.5	3.28	3.6	>0.5	0.95	1.8	>0.25
Limpets × Shore × Season × Slope	4	0.41	0.3	>0.8	5.29	3.3	<0.05	0.52	0.5	>0.7
Limpets × Date (Shore × Season)	12	0.93	1.1	>0.4	1.71	1.5	>0.15	0.51	0.2	>0.9
Limpets × Slope × Date (Shore × Season)	12	1.58 ^b	1.9	<0.05	1.58	1.3	>0.2	0.99	0.4	>0.9
Limpets × Site (Slope × Date [Shore × Season])	48	0.87	1.0	>0.4	1.18	0.7	>0.9	2.27	1.2	>0.2
Residual	288	0.85	1.68			1.97				
Total	431									

^aTested against the pooled term Limpets × Date (Shore × Season) + Limpets × Site (Slope × Date [Shore × Season]) + Residual (MS = 0.85, 348 df)

^bTested against the pooled term Limpets × Site (Slope × Date [Shore × Season]) + Residual (MS = 0.85, 336 df)

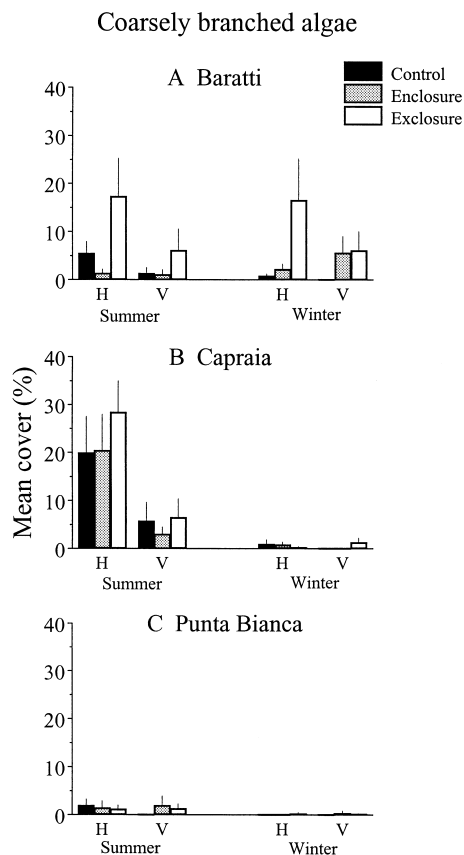


Fig. 2. Effects of limpets on mean percentage cover (+ SE, $n = 12$) of coarsely branched algae in relation to season and slope (H: horizontal; V: vertical) of the substratum on 3 shores. Data pooled across sites and dates

tiated in winter (SNK tests). Coarsely branched algae were more abundant in plots established in summer at Capraia, while no difference between seasons was observed on the other shores, resulting in a significant shore \times season interaction (Table 2; SNK tests). Finally, small-scale spatial variability was large for the coarsely branched algae, as indicated by the significant effect of site (Table 2).

The cover of encrusting coralline algae decreased at Baratti when limpets were excluded from horizontal substrata in the summer, whereas on vertical substrata the lowest cover was observed in enclosures, possibly indicating artifacts due to the fences; artifacts might have occurred in treatments initiated in winter as well at Baratti (Fig. 3). Limpets exerted some negative effects on encrusting coralline algae at Punta Bianca, and no effects at Capraia. These patterns resulted in a significant limpets \times shore \times season \times slope interaction (Table 2), but the SNK test could discriminate among treatments only for the summer start at Punta Bianca on vertical substrata, producing the following ranking of the means: enclosure > enclosure = control. Exclud-

ing limpets had no effects on horizontal substrata. Small-scale spatial variation was important also for the encrusting coralline algae, as indicated by the significant effect of site in the analysis (Table 2).

The effects of limpets on filamentous algae were spatially and temporally variable, and also changed with slope of the substratum, as indicated by the significant limpets \times shore \times season and limpets \times slope interactions (Fig. 4, Table 2). SNK tests within each combination of shore and season indicated that enclosure plots had significantly more filamentous algae than the other treatments at Baratti and Capraia for treatments initiated in winter (enclosure > enclosure > control on both shores), but not in summer, when treatments did not differ significantly; there was no significant effect of grazing at Punta Bianca. The exclusion of limpets increased the percentage cover of the filamentous algae on both horizontal and vertical substrata. The following ranking of the means resulted from the SNK test on horizontal surfaces: enclosure > control > enclosure. The ranking on vertical substrata was: enclosure > enclosure > control, indicating that fences increased the abundance of the filamentous algae in

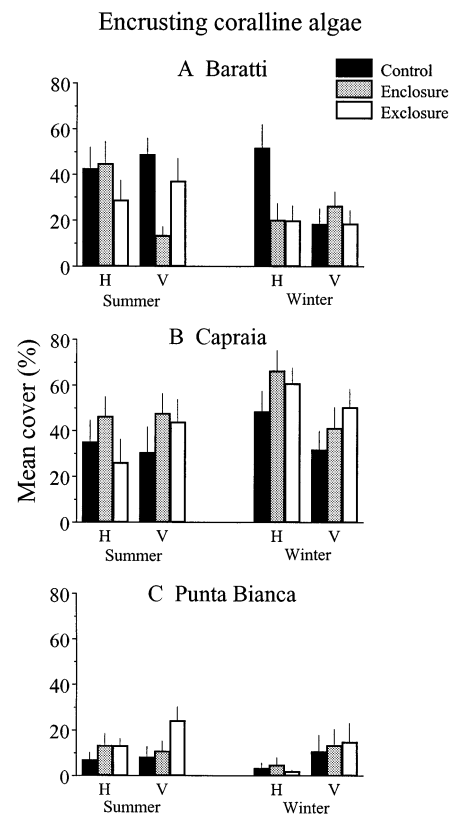


Fig. 3. Effects of limpets on mean percentage cover (+ SE, $n = 12$) of encrusting coralline algae in relation to season and slope of the substratum on 3 shores. Data pooled across sites and dates

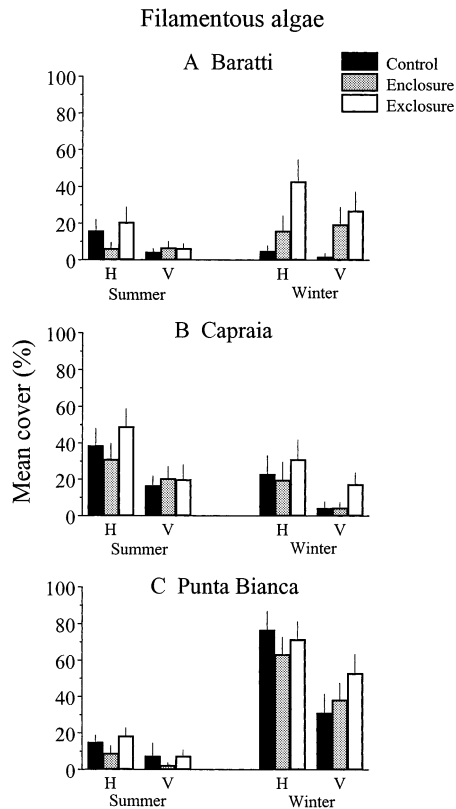


Fig. 4. Effects of limpets on mean percentage cover (+ SE, $n = 12$) of filamentous algae in relation to season and slope of the substratum on 3 shores. Data pooled across sites and dates

this habitat. Although percentage cover was significantly larger on horizontal surfaces irrespective of the treatment considered (from SNK tests comparing slopes in each treatment), limpets accounted for about 38% of the differences between vertical and horizontal substrata when only fenced plots were compared. There were also differences between seasons and slopes that were independent of any effect of limpets. There were consistently more filamentous algae on horizontal than vertical substrata and in plots initiated in winter than in those initiated during the summer, but differences between seasons were larger on vertical substrata, resulting in a significant season \times slope interaction (Table 2, Fig. 4). Finally, there were large and significant differences among sites (Table 2).

Only the nMDS ordinations comparing treatments initiated in winter, independently for each shore and slope of the substratum, are presented and interpreted here (Fig. 5). Those relative to the summer starts had stress values >0.2 , which is considered a threshold value for an interpretable nMDS (Field et al. 1982, Clarke 1993). The ordination separated most of the exclosure plots from the other treatments on vertical substrata of Baratti and Capraia, although there was

considerable variation among plots within any treatment (Fig. 5A,B). Separation of some exclosure plots also occurred on horizontal surfaces at Baratti, while no effect of limpets was evident at Punta Bianca (Fig. 5C). The large stress values of these analyses suggest caution in the interpretation of the results.

DISCUSSION

There was considerable variation in the effects of limpets on rocky shores in the northwest Mediterranean. None of the models predicting consistent interactions among limpets, slope of the substratum and season were supported by the data. The importance of grazing changed in relation to the inclination of the substratum, but these effects were spatially and temporally variable. Most of the variability occurred at large spatial scales (i.e. from shore to shore). The relationship between grazing and slope of the substratum

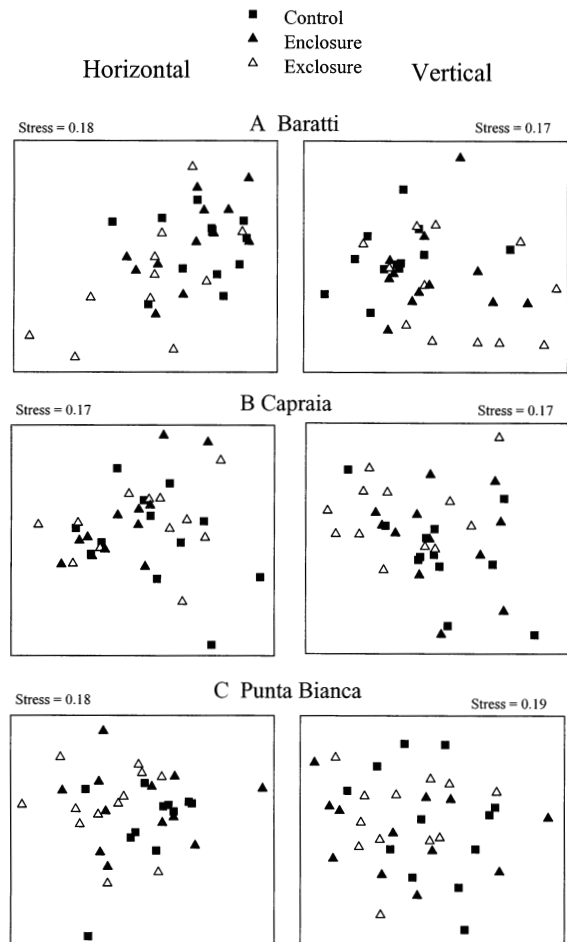


Fig. 5. nMDS ordination plots comparing assemblages in treatments initiated in winter on horizontal and vertical substrata for each shore separately

depended on the particular shore and date or season considered. Similarly, the relationship between grazing and season was not consistent across shores. Despite this variability, significant effects of limpets were observed more frequently at Baratti and less frequently at Punta Bianca, with *Capraia* intermediate between the two. It is known from previous studies that small limpets have no effects on these assemblages (Benedetti-Cecchi 2000), so it is unlikely that reinvasion of some enclosure plots by limpets <7 mm in length can explain the large amount of variation in grazing documented here.

Several factors may account for the patterns of interaction at large spatial scales observed in this study, including variability in recruitment of algae (Benedetti-Cecchi et al. unpubl. data), variability in patterns of distribution and abundance of limpets and differences in other environmental factors. In particular, the effects of limpets at Punta Bianca might have been counteracted by events of intense recruitment of algae. It is well known that under benign physical conditions macroalgae may proliferate and usurp space from grazing invertebrates such as limpets, so that the relationship between these organisms shifts from a trophic interaction to a competitive one (Underwood & Jernakoff 1981). These processes can be expected to occur in areas with high availability of nutrients, where the growth of algae is not limited by physical factors such as desiccation or other types of stress, and where grazers are small in size. Bottom-up effects (Menge 1992, Power 1992, Carpenter et al. 1995) were probably important at Punta Bianca, where physical conditions could differ from those occurring on the other shores. Punta Bianca is located in the Ligurian Sea, one of the most productive areas of the Mediterranean, with high concentrations of nutrients and low temperatures of surface waters (Cruzado 1985, Estrada et al. 1985). Punta Bianca is also close to a relatively small estuary that may have increased the local concentration of nutrients and decreased the temperature of the sea water. These conditions might account for the events of intense recruitment of filamentous algae observed on this shore.

High productivity in this area might also explain the large number of limpets observed at Punta Bianca (see Fig. 1B,C). Supply of food is important for the maintenance of spatial differences in the abundance of grazers. Availability of food in the form of drift algae, for example, is known to maintain high densities of limpets on rocky shores in South Africa (Bustamante et al. 1995). In contrast, the proliferation of filamentous algae might have been responsible for the reduction in the density of limpets observed in winter at Punta Bianca (see Fig. 1C). This discrepancy might have occurred because of the different size and mode of

feeding of limpets on these shores. In South Africa, limpets are large and can forage on stands of adult plants (Bustamante et al. 1995). In contrast, in the northwest Mediterranean limpets are generally small (15 mm on average), and they apparently forage on the microbial film and on propagules of macroalgae, but not on the adult thalli of these plants. This suggests that while limpets at Punta Bianca benefited from being in a productive area, strong bottom-up effects were not necessarily positive events for these organisms, since they were apparently unable to exploit large supplies of resources when these occurred in the form of intense recruitment of macroalgae. Further experimental investigations are necessary to test alternative models about bottom-up effects and trophic interactions on these shores on the basis of these observations. Experiments should also address whether the different species of *Patella* spp. can have different effects on these assemblages (e.g. Della Santina et al. 1993).

Limpets were numerically more abundant on vertical than horizontal substrata at Baratti and Punta Bianca, supporting the model that vertical substrata provide a better habitat for these grazers than flat surfaces (Garity 1984, Williams & Morritt 1995). In contrast, the reverse was often observed for the filamentous algae. Limpets accounted for about 38% of the differences between substrata, indicating that grazing was important in maintaining variable patterns of distribution of the filamentous algae among sites of different slope.

The effects of grazing gastropods on rocky shores are known to vary seasonally in relation to variation in recruitment of algae and/or in the foraging activity of herbivores (Hawkins 1981, Cubitt 1984, Breitburg 1985). Here, although differences between seasons changed from shore to shore and in relation to slope of the substratum, there was a trend for a larger effect of limpets in treatments initiated in winter, as indicated by the response of the filamentous algae. However, because plots were monitored after 1.5 yr, those treatments initiated in winter were sampled during the summer months and the results indicated that the filamentous algae were abundant in this season. This suggested that physical stress was not as intense as initially supposed during the summer. Thus, excluding limpets in summer or winter probably made no difference in terms of long-lasting effects on assemblages. Rather, specific patterns of abundance of organisms at the time of sampling might have originated from the interactions between grazing and season observed here. This is consistent with the results of a companion study, where the effects of limpets were monitored over shorter periods (Benedetti-Cecchi et al. unpubl. data).

Whether grazers have negative or positive effects on encrusting algae is not clear. Some evidence indicates

that by removing erect plants, herbivores indirectly enhance the survival and growth of encrusting algae which are morphologically adapted to withstand the effects of grazing (Lubchenco & Cubitt 1980, Steneck & Dethier 1994). Other evidence suggests that herbivory may be detrimental to algal crusts, as observed for erect plants (e.g. Levings & Garrity 1984). In the present study, there was a trend for encrusting coralline algae to be more abundant in the presence of limpets on horizontal substrata at Baratti. This might have resulted from the overgrowth of these plants by erect algae in plots from which limpets were excluded. However, the only significant effect of limpets on encrusting coralline algae was observed at Punta Bianca, and this was a negative effect. These results did not help in clarifying patterns of interactions between limpets and encrusting algae, but suggested that these interactions cannot be generalized and must be interpreted within the specific spatial and temporal context in which they occur. Again, the possibility that the 3 species of limpets present on these shores can have distinct effects on macroalgae (Della Santina et al. 1993) might explain some of this variability.

The effect of limpets on whole assemblages was generally weak and changed over space and time with no clear pattern; there was also considerable variation among replicates within any treatment. These patterns contrasted to those found in a companion study on the role of limpets in maintaining differences between mid- and low-shore assemblages in the northwest Mediterranean (Benedetti-Cecchi et al. 2000). In that study, limpets were found to account for about 20% of the differences between habitats, and this effect was consistent over space and time.

Some studies have shown that interactions between different processes occur at small scales in space and time (e.g. Kennelly & Underwood 1993, Lively et al. 1993, Chapman & Underwood 1998). It has been suggested that small-scale variability results from experiments with high resolution, and this is viewed as an impediment to the detection of large-scale processes (Root & Schneider 1995, see discussion in Hewitt et al. 1998). High resolution occurs when experimental units of small size are used, a condition that may be dictated by logistical constraints. More often, however, the size of the experimental unit is chosen as a function of the particular processes being investigated and in relation to the natural history of the system. Thus, for example, the size of the experimental units used to investigate models about physical disturbance and its interactions with biological processes is usually chosen to match the size of naturally disturbed patches (Sousa 1984, Chapman & Underwood 1998, Benedetti-Cecchi 2000). Similarly, experimental analyses on the effects of limpets on rocky shores require high resolution be-

cause limpets respond to fine-scale features of the habitat. As shown in the present investigation, where interactions at relatively large spatial and temporal scales were found, high resolution does not necessarily obscure large-scale events. Increasing the extent of ecological studies while maintaining the resolution consistent with the hypotheses being tested and the biology of the system seems the best approach to investigate and understand scales of variation in ecological processes.

Although multiscale analyses on the spatial and temporal patterns of distribution of natural populations are increasing both in terrestrial and aquatic systems (Schneider 1994), and the need for large-scale experiments has been emphasized (Paine et al. 1985, Reader et al. 1994, Carpenter et al. 1995, Berlow & Navarrete 1997), few experimental investigations have examined multiple scales of variation in ecological processes. Studies of this sort are important for a number of reasons. First, they set limits to ecological generalizations by identifying the spatial and temporal context within which ecological processes operate consistently. Second, by detecting the scale(s) at which the magnitude of ecological processes change, they increase our understanding of the causes of spatial and temporal variations in abundance of natural populations. Third, the detection of these changes is useful to identify profitable areas for further research. Studies conducted at multiple scales are therefore important for understanding the circumstances under which ecological processes can be expected to produce predictable patterns in populations and assemblages (Benedetti-Cecchi 2000, and references therein). For example, grazing was consistent across sites on any given shore in the present study, so that knowledge of the effects of limpets at a few sites could be used to predict the consequences of grazing at other sites on a particular shore. In contrast, the large variability among shores prevented scaling-up from the shore to the regional scale when examining hypotheses about the effects of limpets in the northwest Mediterranean. Although this variability poses limits to generalizations, identifying the underlying causes would provide a basis for predicting the effects of limpets on other shores. Understanding the processes that prevent generalizations can result in useful, albeit rather specific, ecological models (Benedetti-Cecchi 2000). This may be a starting point to addressing the issue of how we can move beyond the fatalistic view that natural variability makes general ecological models inaccurate and imprecise.

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