

Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean

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Abstract

Marine protected areas (MPAs) are increasingly used as a management tool to preserve species and habitats. Testing hypotheses about the effectiveness of MPAs is important for their implementation and to identify informative criteria to support management decisions. This study tested the general proposition that MPAs affected assemblages of algae and invertebrates between 0.0 and 0.5 m above the mean low water level of rocky coasts on two islands in the Tuscan Archipelago (northwest Mediterranean). Protection was concentrated mainly on the west coasts of the islands, raising the possibility that neither the full range of assemblages nor the relevant scales of variation were properly represented within MPAs. This motivated the comparison of assemblages on opposite sides of islands (habitats). The effects of MPAs and habitat were assessed with a multifactorial sampling design; hypotheses were tested about differences in structure of assemblages, in mean abundance of common taxa and in univariate and multivariate measures of spatial variation. The design consisted of three replicate shores for each condition of protected and reference areas on the west side of each island and three unprotected shores on the eastern side. Assemblages were sampled independently four times on each island between June 1999 and January 2001. At each time of sampling two sites were selected randomly at each of two tidal heights to represent midshore and lowshore assemblages on each shore. Estimates of abundance were obtained using non-destructive sampling methods from five replicate 20×20 cm quadrats at each site. Results

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indicated differences among habitats in structure of assemblages, in mean abundance of common taxa and in univariate and multivariate measures of spatial variation at the scale of shores. Most of these patterns were inconsistent with the predicted effect of management through MPAs. The data suggest that designation of MPAs in the Tuscan Archipelago should proceed through management of multiple shores and types of habitat selected to guarantee protection to a representative sample of assemblages and to the processes responsible for maintenance of spatial patchiness at different scales. This study also shows that considerations of spatial heterogeneity are important to underpin management decisions about the number, size and location of MPAs.

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1. Introduction

The wide range of anthropogenic disturbances impinging on marine coastal assemblages is of increasing concern to ecologists, managers and the general public (Schmitt & Osenberg, 1996; Underwood, 1995). Effective management procedures are necessary in order to guarantee sustainable development and to ensure conservation of species and habitats in the face of human impacts (Goodland, 1995; Sherman, 1994). Designation of marine protected areas (MPAs) is becoming a widespread management option aimed at achieving these goals (Agardy, 1994; Allison, Lubchenco, & Carr, 1998; Botsford, Castilla, & Peterson, 1997). The primary purposes of MPAs include the conservation or enhancement of stocks of exploited species, the preservation of biological diversity, the conservation of habitats and the protection of species of particular interest for their rarity, cultural value or emotional appeal (Palumbi, 2001).

A vast amount of literature is accumulating on the effects of declaring MPAs on populations and assemblages. Most of these studies focus on fish stocks and report an increase in density and/or size of exploited species in MPAs compared with non-protected areas (Babcock, Kelly, Shears, Walker, & Willis, 1999; García-Charton & Pérez Ruzafa, 1999; Paddock & Estes, 2000; Rakitin & Kramer, 1996). Aside from the direct influence of MPAs on some species, a wide range of indirect effects, including trophic cascades, have been postulated and partially supported by field studies (Lindberg, Estes, & Warheit, 1998; Pinnegar et al., 2000; Sala, Boudour-esque, & Harmelin-Vivien, 1998; Steneck 1998). Theoretical and empirical analyses suggested that MPAs can have regional effects by exporting larvae and post-larval stages to nearby areas, thereby replenishing fished stocks (Hastings & Botsford, 1999; McClanahan & Mangi, 2000). The magnitude of these effects is a complex function of the size of the reserve, the dispersal of larvae and the mobility of adults, and more empirical studies are needed to test hypotheses about likely interactions among these processes (Palumbi, 2001).

Protection from anthropogenic influences can also have important effects on intertidal assemblages of rocky shores. Humans intrude upon intertidal habitats in several ways, including chronic removal of predatory gastropods, grazers and algae

to support commercial activities (Castilla, 1999; Castilla & Bustamante, 1989; Castilla & Duran, 1985; Hockey & Bosman, 1986; Lasiak, 1998, 1999; Moreno, Sutherland, & Jara, 1984), harvesting of species for bait by recreational fishermen (Kingsford, Underwood, & Kennelly, 1991), collection of shells for aesthetic purposes (Underwood, 1993) and trampling (Brosnan & Crumrine, 1994; Keough & Quinn, 1998). Few studies have examined the effects of MPAs on intertidal invertebrates and algae compared with those on fishes in subtidal habitats. Nevertheless, results indicated that harvesting top predators can also have profound effects on webs of interactions in intertidal habitats, promoting major changes in patterns of distribution and dominance of organisms on the shore (Castilla, 1999). Other studies, in contrast, have shown negligible effects of MPAs on algae and invertebrates in intertidal and subtidal environments (Edgar & Barrett, 1999; Lasiak, 1998).

Evaluating the effectiveness of MPAs is an important component of management procedures. The general approach is to compare estimates of the mean abundance of populations between managed and reference areas. This procedure provides a powerful tool, but is sensitive to natural fluctuations in density of populations in space and time (Dayton, Tegner, Edwards, & Riser, 1998; García-Charton et al., 2000). There is, in fact, considerable variability in patterns of distribution and abundance of populations over a range of spatial and temporal scales (Levin, 1992; Schneider, 1994; Underwood & Chapman, 1996; Wiens, Stenseth, Van Horne, & Ims, 1993; Wu & Loucks, 1995). This heterogeneity has important implications in any analysis of hypotheses about protection. First, adequate sampling designs are necessary to separate the effects of management from other sources of variation. The logic developed in the context of environmental sampling for the analysis of impacts, including considerations of power and optimal allocation of resources, applies here (Benedetti-Cecchi, 2001a; Bernstein & Zalinski, 1983; Eberhardt & Thomas, 1991; Green, 1979; Mapstone, 1995; Osenberg, Schmitt, Holbrook, Abu-Saba, & Flegal, 1994; Stewart-Oaten, Bence, & Osenberg, 1992; Underwood, 1992, 1994). These issues are increasingly recognised in the literature (e.g. Fraschetti, Bianchi, Terlizzi, Fanelli, Morri, & Boero, 2001; García-Charton & Pérez Ruzafa, 1999; García-Charton et al., 2000).

Second, and much less appreciated, are the implications of scale-dependent changes in spatial and temporal patterns of distribution, abundance and diversity of species for the design, monitoring and implementation of MPAs. Effective management should ensure protection of a representative sample of species and assemblages characteristic of a particular locality or region. Decisions on the number, size and location of MPAs should therefore be based also on considerations of the spatial and temporal heterogeneity in patterns of distribution of species (Schwartz, 1999). Protection also requires that the ecological processes relevant to populations and assemblages are maintained within MPAs. There is increasing evidence indicating that different ecological processes are likely to generate patterns at different scales (Benedetti-Cecchi, 2001b; Benedetti-Cecchi, Bulleri, Acunto, & Cinelli, 2001; Benedetti-Cecchi, Bulleri, & Cinelli, 2000; Holling, 1992; Horne & Schneider, 1995; Thrush, Hewitt, Cummings, Green, Funnell, & Wilkinson, 2000; Underwood & Chapman, 1996). Effective management should, therefore, guarantee that the relevant scales of

spatial and temporal patterns of populations and assemblages are properly represented within MPAs. Addressing these issues requires comparison of patterns in spatial and temporal variance of populations and assemblages within MPAs with those of reference areas at a hierarchy of scales. To date, no study evaluating the effectiveness of MPAs has incorporated such a comparison.

The present study investigated the general proposition that MPAs affected populations and assemblages between 0.0 and 0.5 m above the mean low water level of rocky coasts on the islands of Capraia and Giannutri in the Tuscan Archipelago (northwest Mediterranean). This was compared with the alternative, but not mutually exclusive model, that assemblages changed in response to the characteristics of the habitat rather than management. In fact, most of the protected shores are on the western side of the islands, raising the possibility that neither the full range of assemblages nor the relevant scales of variation are properly represented within protected shores. Effects of MPAs (presence vs. absence) and habitat (western side protected, western side reference and eastern side unprotected) were investigated using a multifactorial sampling design consisting of three replicate shores for each protected and reference condition on the west side of each island, and three replicate shores on the east side. Hypotheses were tested about differences in structure of assemblages, in mean abundance of common taxa and in measures of spatial variance in abundance of these taxa. Effects were evaluated over a hierarchy of spatial scales, ranging from 10s of cm (variance among replicate quadrats) up to 100s of km (variation between islands). Temporal variance was estimated by sampling the same shores four times over a period of 20 months using new sets of sites on each shore at each sampling occasion, to provide measures of space×time interactions at the scales of the shore, the habitat and the island.

Specific hypotheses on the direct and indirect effects of protection on mean abundance could be specified a priori for some taxa. In particular, under effective protection, one would expect larger densities of those species that are negatively influenced by humans. An increase in abundance of gastropod grazers, barnacles and canopy algae was therefore expected as a consequence of reducing human pressure (either by exploitation or through trampling) in MPAs. Furthermore, low cover of filamentous algae was expected in MPAs as a consequence of the expected increase in number of limpets (e.g. Benedetti-Cecchi, 2000). In contrast, no a priori hypotheses on changes in spatial and temporal variance in abundance were possible for these or other taxa.

2. Materials and methods

2.1. The study system

The National Park of the Tuscan Archipelago was established in July 1996 with the primary aims of preserving natural habitats and promoting eco-tourism. It is the largest system of MPAs in the Mediterranean, consisting of seven islands that are managed according to different regimes of protection. Public access was prohibited

before 1996 on some islands because of the presence of prisons (Gorgona and Pianosa), or because the locality was already a natural reserve (Montecristo). Other islands are intensively exploited by tourism and only a small fraction of their coasts are protected (Elba and Giglio). Finally, two islands (Capraia and Giannutri) provide extensive areas where human activities are totally banned and areas where recreational activities are allowed (Fig. 1). Tourists are usually present during the summer on several shores outside MPAs, and potential sources of disturbance to mid-shore and low-shore assemblages include all sorts of anthropogenic influences as discussed above (see Section 1). Only a few tourists have been observed on shores inside MPAs during the summer months (personal observation), so that trampling and bait collection are likely to be strongly reduced in these areas compared to unprotected areas. Nevertheless, poaching cannot be dismissed despite active protection by patrols.

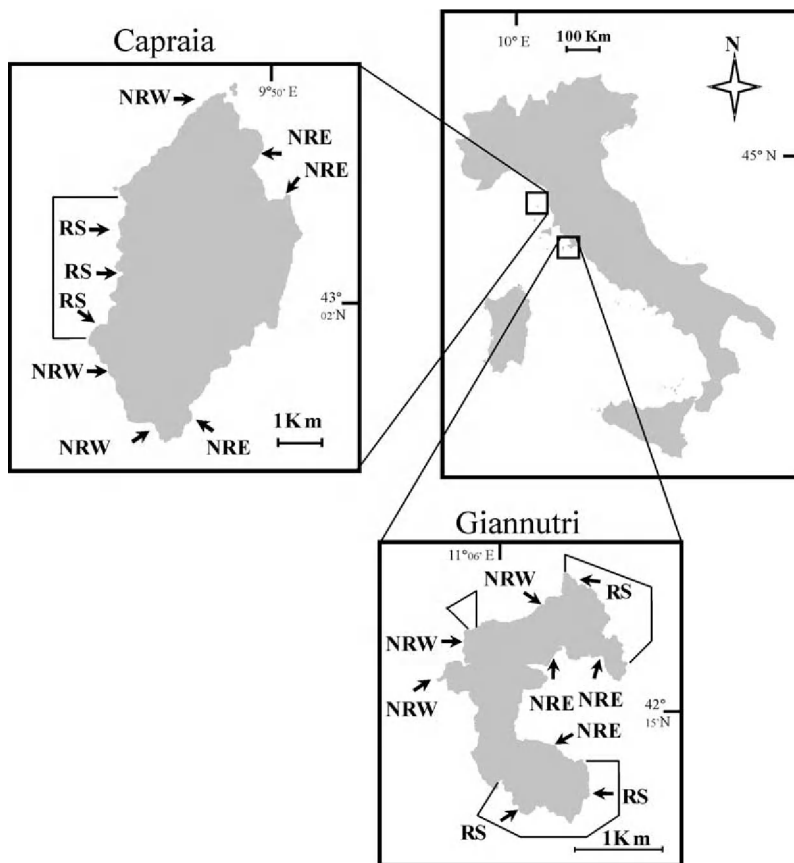


Fig. 1. Map of the study locations. Delimited sectors along the coastline identify the fully protected areas. RS: reserve; NRW: reference—west; NRE: reference—east.

Midshore and lowshore assemblages of rocky coasts have been described several times in this geographical region (Benedetti-Cecchi, 2001b; Benedetti-Cecchi et al., 2001; Menconi, Benedetti-Cecchi, & Cinelli 1999). Briefly, the most common organisms in midshore assemblages were filamentous algae such as *Polysiphonia sertularioides* (Grateloup) and *Chaetomorpha aerea* (Dillwyn) Kützinger, encrusting corallines, the encrusting brown alga *Ralfsia verrucosa* (Aresoug) J. Agardh, the fleshy alga *Rissoella verruculosa* (Bertolini) J. Agardh and cyanobacteria (*Rivularia* spp.). Invertebrates included the barnacle *Chthamalus stellatus* (Poli), the limpets *Patella rustica* L. and *Patella aspera* (Röding) and the topshell *Osilinus turbinatus* (Von Born). Lowshore assemblages included those dominated by canopy algae such as *Cystoseira amentacea* Bory var. *stricta* Montagne and sessile invertebrates (mainly sponges, hydrozoans, bryozoans and actinians), and those dominated by turf-forming algae. The latter were dominated by geniculate coralline algae such as *Corallina elongata* Ellis et Solander and *Haliptilon virgatum* (Zanardini) Garbary and Johansen, coarsely branched algae like *Laurencia* spp., *Chondria* spp. and *Gastroclonium clavatum* (Roth) Ardissonne and several species of filamentous algae. Grazers such as limpets and sea urchins were rare low on the shore at the study sites.

2.2. Sampling design and collection of data

Midshore and lowshore assemblages, 0.2–0.4 and 0.0–0.1 m above mean low water level (MLWL), respectively, were sampled between June 1999 and January 2001 on the islands of Capraia and Giannutri. The sampling design consisted of three shores (stretches of rocky coast of 30–50 m and 100s–1000s of m apart) selected randomly within each of three habitats on each island: reserve (RS), no reserve, but with the same geographical orientation of protected shores—mainly west—(NRW), and no reserve on the east coast (NRE). Contrasts between RS and NRW allowed hypotheses about effects of MPAs to be tested. Contrasts between NRE and NRW provided tests of hypotheses about effects of habitat associated with geographical orientation.

Each shore was sampled four times on a particular island, but the two islands were sampled at different times that were interspersed across the study period (times of sampling will be referred to as T1–T4 throughout the paper; Giannutri: T1 = June 1999, T2 = December 1999, T3 = October 2000, T4 = January 2001; Capraia: T1 = September 1999, T2 = February 2000, T3 = October 2000, T4 = December 2000). Midshore and lowshore assemblages were sampled independently using two replicate sites (stretches of coastline 3–5 m in length and 10s of m apart) on a particular shore at each time; new sites were established at different times at each height on the shore. Five replicate quadrats (20×20 cm) were sampled randomly within each site. Data consisted of estimates of percent cover for sessile organisms (algae and invertebrates) and number of individuals per quadrat for mobile animals (limpets). Percent cover estimates were obtained visually, by dividing each quadrat into 25 sub-quadrats of 4×4 cm and assigning to each of them a score from 0 (absence of a particular taxon) to 4 (the sub-quadrat was totally covered by a particular taxon)

and adding up the 25 estimates (Benedetti-Cecchi, Airoldi, Abbiati, & Cinelli, 1996; Dethier, Graham, Cohen, & Tear, 1993).

2.3. Analysis of data

Multivariate and univariate procedures were used to test hypotheses about differences among habitats in the structure of assemblages, in measures of spatial variance in abundance at different scales and in patterns of mean abundance of common taxa. Multivariate analyses were used to compare assemblages among habitats for each island and time of sampling separately, using shores as a nested factor and sites as replicates (an 'average' sample was calculated for each site and used in the analyses). A matrix of similarities between each pair of samples was calculated using the Bray–Curtis similarity coefficient (Bray & Curtis, 1957), and a two-way nested ANOSIM (Clarke, 1993) was performed to test for differences among habitats and shores. Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the rank orders of similarities in the different habitats (Anderson & Underwood, 1997; Clarke, 1993; Field, Clarke, & Warwick, 1982; Underwood & Anderson, 1994). The 'average' sample for each shore was plotted in these analyses.

Patterns of spatial variation in assemblages were compared across habitats using measures of dissimilarity among pairs of samples, obtained from the Bray–Curtis index of similarity. The null hypothesis that patchiness in assemblages at the smallest spatial scale (among quadrats) was comparable across habitats was tested using ANOVAs on the mean dissimilarity among every pair of quadrats in each site. These analyses were done for each island separately and consisted of the following factors: Time (four levels, random), Habitat (three levels, fixed and orthogonal to Time) and Shore (three levels, random and nested within Habitat), with sites providing replicate measures of average dissimilarity. Among-site variation was examined with two-factor ANOVAs on measures of dissimilarity between the 'centroids' of the two sites available on each shore at each time of sampling, and using shores as replicates. Time (four levels, random) and Habitat (three levels, fixed and orthogonal to Time) were the factors in these analyses. Finally, the centroid for each shore was used to calculate the average dissimilarity among shores within each habitat. The mean and standard error of these measures over the four times of sampling were then compared across habitats graphically.

Analysis of variance (ANOVA) was used on data from each island separately to test for the effects of Time (random, four levels), Habitat (fixed, three levels and orthogonal to Time), Shore (random, nested within Habitat and orthogonal to Time), and Site (random, two levels and nested within the Time×Shore interaction) on mean abundances.

A similar analysis was used to investigate patterns in spatial variance at the scale of the quadrat; in this case the two sites sampled at each time on each shore provided replicate estimates of spatial variance among quadrats and factor Site was removed from the analysis. Patterns in spatial variance at the scale of the site and the shore were compared graphically across habitats.

In many of the analyses presented here it was not possible to test for the effect of Habitat unless other terms could be eliminated or pooled from the linear model, following the logic described in Winer, Brown, and Michelis (1991) and in Underwood (1997). In general, the effect of Habitat was tested over the Shore(Habitat) mean square if the Time×Habitat interaction was not significant at $P>0.25$; alternatively, Time×Habitat was used as denominator if the Shore(Habitat) term was not significant at $P>0.25$; other tests are described in the text.

Cochran’s *C* test was used throughout to test the assumption of homogeneity of variances before ANOVAs. When necessary, transformations were applied to raw data to remove heterogeneity. Variances were always log-transformed prior to analysis. SNK tests were used for a posteriori comparisons of the means when appropriate. In multivariate analyses, the fourth-root transformation was used to reduce differences in scale among variables.

3. Results

3.1. Midshore assemblages

Analysis of similarity (ANOSIM) revealed significant differences among shores for the first three times of sampling at Giannutri, with similar assemblages occurring in the different habitats (Table 1). A relatively large value of *R* resulted from the contrast between RS and NRW on the last sampling occasion, when differences among shores were not significant. Differences among habitats were evident at Capraia at Time 2, with assemblages in RS differing from those in NRW and NRE. Variability

Table 1
R values from two-way nested analysis of similarity (ANOSIM) comparing midshore assemblages across habitats and among shores within habitats

	Time 1	Time 2	Time 3	Time 4
<i>Giannutri</i>				
Among habitats				
RS vs. NRW	−0.15	0.00	0.15	0.35 (0.1)
RS vs. NRE	−0.33	0.07	0.00	0.19
NRW vs. NRE	0.04	0.06	0.20	0.37
Among shores	0.69 (0.001)	0.57 (0.001)	0.35 (0.038)	0.22
<i>Capraia</i>				
Among habitats				
RS vs. NRW	−0.33	0.48 (0.1)	−0.19	0.19
RS vs. NRE	0.07	0.78 (0.1)	0.00	0.15
NRW vs. NRE	0.11	0.00	−0.15	0.04
Among shores	0.65 (0.004)	0.29 (0.001)	0.65 (0.002)	0.5 (0.002)

Exact probabilities are given in parentheses for significant *R* values. Because only 10 permutations are possible for pairwise comparisons of habitats, a significance level of 10% is considered as indicative of differences among habitats in these analyses. RS: reserve; NRW: reference west; NRE: reference east.

among shores was always large and significant in these analyses (Table 1). Examples of these patterns are illustrated with nMDS plots using data from Time 1 and Time 4 for Giannutri, and Time 1 and Time 2 for Capraia. Plots of the ‘centroids’ of each replicate shore indicated no clear separation among habitats at Time 1, both at Giannutri and Capraia, but large variability among shores (Fig. 2). Differences among habitats were largely driven by the occurrence of distinct assemblages on two shores in NRE at Giannutri on the last sampling occasion. In contrast, data from Capraia at Time 2 revealed differences among habitats, despite large variation among shores in NRW and NRE (Fig. 2).

There were significant differences among habitats in small-scale patchiness of assemblages at Giannutri, as measured by the average dissimilarity among plots (Fig. 3A). Analysis of variance and the SNK test revealed more dissimilarity in NRE compared to NRW and RS, which did not differ significantly (ANOVA: $MS_{\text{HABITAT}} = 301.964$, $MS_{\text{POOLED}} = 63.371$, $F_{2,30} = 4.8$, $P < 0.02$; the denominator for this test was constructed by pooling $MS_{\text{SHORE(HABITAT)}}$ and $MS_{\text{HABITAT} \times \text{TIME}}$, which were not

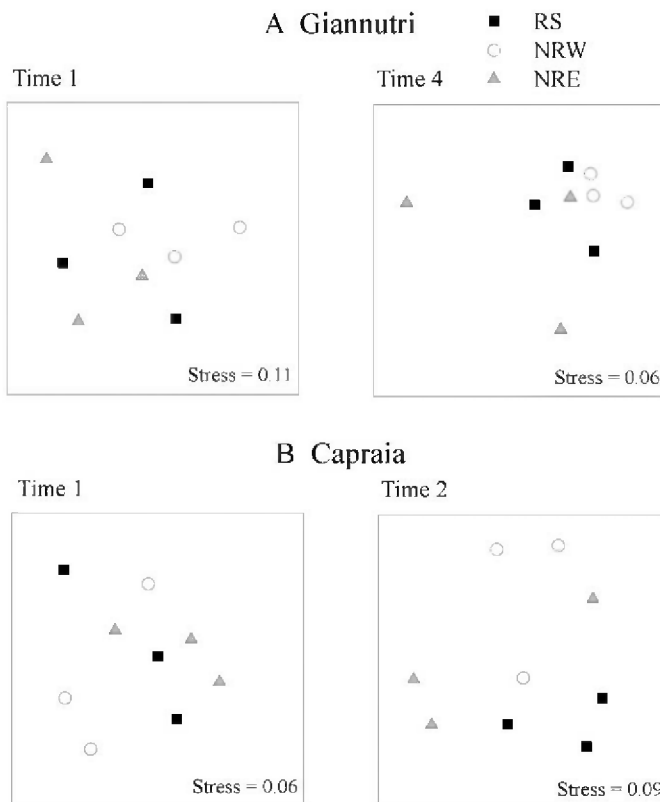


Fig. 2. nMDS plots comparing midshore assemblages in MPAs (RS) with those of reference shores on the west side of the islands (NRW) and those of east side (NRE) at different times. Each symbol is the ‘average sample’ of a shore.

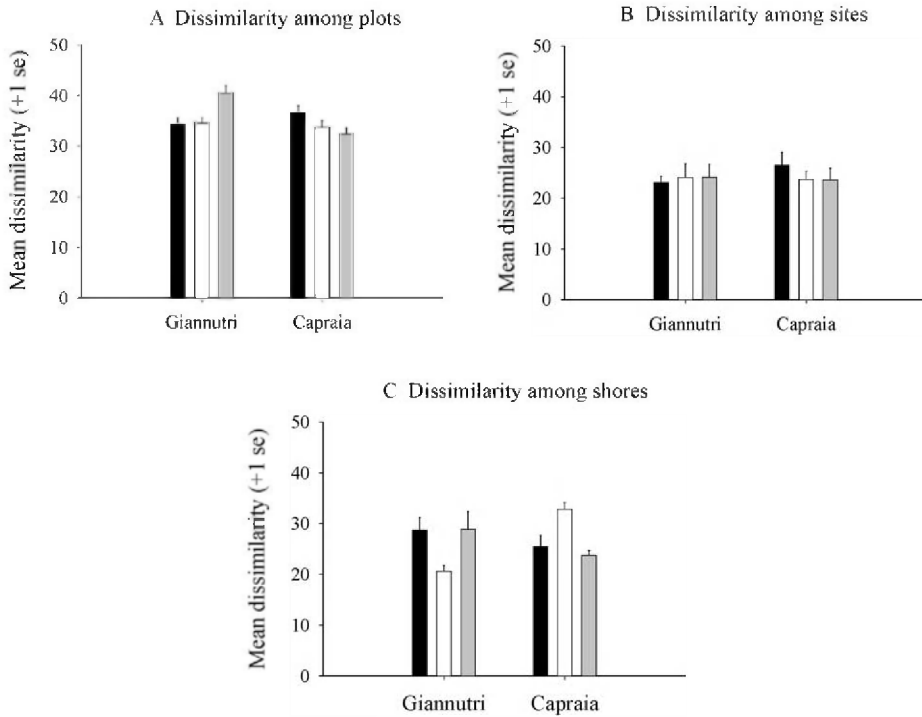


Fig. 3. Mean percentage dissimilarity (+1 SE) measuring patchiness in midshore assemblages at the scale of (A) plot ($n=24$), (B) site ($n=12$) and (C) shore ($n=4$). (■) RS, (□) NRW and (■) NRE. Abbreviations as in Fig. 2.

significant at $P>0.25$, with $MS_{\text{TIME} \times \text{SHORE}(\text{HABITAT})}$; measures of dissimilarity were not transformed in this and the following analyses). In contrast, patchiness did not differ significantly among habitats at Capraia ($MS_{\text{HABITAT}}=110.662$, $MS_{\text{SHORE}(\text{HABITAT})}=91.947$, $F_{2,6}=1.2$, $P>0.6$; test constructed after the elimination of the $MS_{\text{HABITAT} \times \text{TIME}}$ term which was not significant at $P>0.25$), whereas significant differences occurred among shores ($MS_{\text{SHORE}(\text{HABITAT})}=91.947$, $MS_{\text{TIME} \times \text{SHORE}(\text{HABITAT})}=25.385$, $F_{6,18}=3.6$, $P<0.02$).

Patchiness did not differ significantly among habitats when measured at the scale of sites, both at Giannutri and Capraia (Fig. 3B). ANOVAs revealed neither a significant $\text{Habitat} \times \text{Time}$ interaction nor a main effect of Habitat (Giannutri: $MS_{\text{HABITAT} \times \text{TIME}}=18.030$, $MS_{\text{RESIDUAL}}=68.663$, $F_{6,24}=0.3$, $P>0.9$; $MS_{\text{HABITAT}}=4.483$, $F_{2,6}=0.3$, $P>0.7$. Capraia: $MS_{\text{HABITAT} \times \text{TIME}}=44.227$, $MS_{\text{RESIDUAL}}=66.700$, $F_{6,24}=0.7$, $P>0.6$; $MS_{\text{HABITAT}}=32.241$, $F_{2,6}=0.7$, $P>0.5$).

Habitats differed in the degree of patchiness measured at the scale of shores: there was less variation among shores in NRW compared to the other habitats at Giannutri, whereas the opposite pattern occurred at Capraia (Fig. 3C).

Analyses on the mean abundance of the most common taxa indicated few consistent differences among habitats. A detailed example of analysis of variance on

these data is given for cyanobacteria at Capraia (Table 2), whereas a summary of significant effects is reported in the other cases (Table 3). Most of these analyses revealed significant spatial and temporal variation in mean abundance of algae and invertebrates that was unrelated to any effect of habitat. Patterns in abundance of encrusting coralline (Fig. 4A) and filamentous algae (Fig. 4B) at Capraia were exceptions to this general trend: the percentage cover of encrusting corallines was significantly larger in NRE compared with NRW and RS, which did not differ significantly (Table 3, SNK test), whereas no logical alternative to the null hypothesis was detected by the SNK test on mean percentage cover of filamentous algae, despite a significant effect of habitat in the ANOVA (Table 3).

Patterns in spatial variance at the three scales examined (among plots, among sites and among shores), generally reflected those on mean abundances and indicated large spatial and temporal variation with only minor differences among habitats. Taxa for which an effect of habitat was detected included the encrusting coralline alga *Lithophyllum lichenoides* and the barnacle *Chthamalus stellatus* (Fig. 5). Spatial variance in percentage cover of *L. lichenoides* was significantly larger in NRW and RS than in NRE at the scales of the plot and the shore, but only on the island of Giannutri (among plots: $MS_{\text{HABITAT}} = 20.055$, $MS_{\text{TIME} \times \text{SHORE}(\text{HABITAT})} = 3.078$, $F_{2,18} = 6.5$, $P < 0.008$ and SNK test; among-shore variability is compared across habitats graphically, see Fig. 6A). In contrast, differences in spatial variance at the scale of sites and shores were more evident at Capraia than Giannutri for the barnacle *C. stellatus* (Fig. 5B). Variance among sites was significantly larger in RS and NRW than NRE at Capraia ($MS_{\text{HABITAT}} = 20.334$, $MS_{\text{HABITAT} \times \text{TIME}} = 1.451$, $F_{2,6} = 14.0$, $P < 0.006$, SNK test), whereas a trend toward greater variability in RS compared to the other habitats was observed at Giannutri, although this effect was not significant (Fig. 5B). Habitats also differed in patterns of among-shore spatial variance, particularly at Capraia where variation was maximal in NRW, intermediate in RS and minimal in NRE (Fig. 5B).

Table 2

Example of an analysis of variance on mean percentage cover of cyanobacteria at Capraia

Source of variation	d.f.	MS	F	P	Denominator for F
Habitat = H	2	1444.9	1.2	>0.35	Shore(H)
Time = T	3	5304.5	8.2	<0.002	T×Shore(H)
H×T	6	604.9	0.9	>0.4	T×Shore(H)
Shore(H)	6	1238.8	1.9	>0.1	T×Shore(H)
T×Shore(H)	18	650.2	1.8	>0.05	Site(T×Shore(H))
Site(T×Shore(H))	36	363.7	1.9	<0.003	Residual
Residual	288	194.5			
Cochran's test	C = 0.06, P > 0.05				
Transformation	None				

The effect of Habitat was tested over the Shore(H) mean square after elimination of the H×T term that was not significant as $P > 0.25$.

Table 3
Summary of significant results from analyses of variance on mean abundance of common algae and invertebrates from midshore assemblages

Taxa	Island	Test	MS _{NUM}	MS _{DEN}	d.f.	F	Transformation
<i>Algae</i>							
Cyanobacteria	Giannutri	Shore(H)/T×Shore(H)	16.415	5.450	6,18	3.0*	Square root
		Site(T×Shore(H))/Residual	5.956	2.479	36,288	2.4***	
	Capraia	See Table 1					None
Encrusting corallines	Giannutri	No significant result					None
	Capraia	H/T×Shore(H)	5005.208	1016.519	2,18	4.9*	None
		T×Shore(H)/Site(T×Shore(H))	1016.520	498.211	18,36	2.0*	
		Site(T×Shore(H))/Residual	498.211	272.965	36,288	1.8***	
Filamentous algae	Giannutri	T/T×Shore(H)	929.752	119.733	3,18	7.8**	None
	Capraia	H/T×Shore(H)	1926.282	521.797	2,18	3.7*	Arcsine
		T×Shore(H)/Site(T×Shore(H))	521.797	227.947	18,36	2.3*	
		Site(T×Shore(H))/Residual	227.947	87.055	36,288	2.6***	
<i>Litophyllum lichenoides</i>	Giannutri	T×Shore(H)/Site(T×Shore(H))	327.842	162.297	18,36	2.0*	Arcsine
		Site(T×Shore(H))/Residual	162.297	77.246	36,288	2.1***	
	Capraia	Shore(H)/T×Shore(H)	155.953	55.390	6,18	2.8*	None ^a
		Site(T×Shore(H))/Residual	49.692	15.094	36,288	3.3***	
<i>Invertebrates</i>							
<i>Chthamalus stellatus</i>	Giannutri	T/T×Shore(H)	13.501	1.847	3,18	7.3**	Log
		Shore(H)/T×Shore(H)	15.857	1.847	6,18	8.6***	
		Site(T×Shore(H))/Residual	1.824	0.434	36,288	4.2***	
	Capraia	T×Shore(H)/Site(T×Shore(H))	750.107	380.408	18,36	2.0*	None ^a
		Site(T×Shore(H))/Residual	380.408	87.090	36,288	4.4***	
<i>Patella aspera/caerulea</i>	Giannutri	T/T×Shore(H)	6.406	0.612	3,18	10.5***	Log
	Capraia	T×Shore(H)/Site(T×Shore(H))	5.927	2.803	18,36	2.1*	None
<i>Patella rustica</i>	Giannutri	Shore(H)/T×Shore(H)	3.412	0.827	6,18	4.1**	Log
	Capraia	Site(T×Shore(H))/Residual	0.598	0.351	36,288	1.7**	Log

^a Variances were heterogeneous (after Cochran's C test) and could not be stabilised by transformations.

* P<0.05.

** P<0.01.

*** P<0.001.

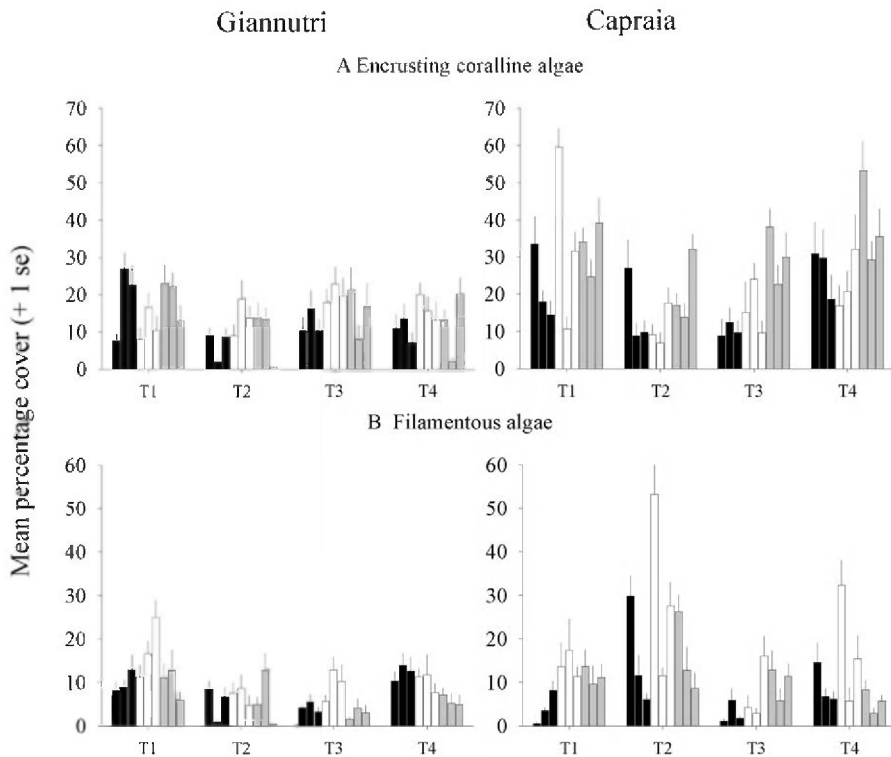


Fig. 4. Mean percentage cover (± 1 SE, $n=10$) of algae in midshore assemblages. Data are shown for each of three replicate shores in (■) RS, (□) NRW and (■) NRE. Abbreviations as in Fig. 2.

3.2. Lowshore assemblages

ANOSIM indicated consistent differences among habitats in the structure of low-shore assemblages on the island of Giannutri. Assemblages in RS were similar to those in NRW and both differed from those in NRE in all sampling occasions, as indicated by the large R values obtained from the analysis (Table 4). Variability among shores was large and significant in the first three times of sampling. In contrast, assemblages at Capraia varied considerably from shore to shore, but differences among habitats were less evident (Table 4). Illustrative examples of these patterns are given with nMDS plots of the 'centroids' of shores sampled at Time 1 and Time 2 at Giannutri, and at Time 1 and Time 3 at Capraia (Fig. 6). Data from Giannutri clearly indicated that the 'centroids' of shores in NRE segregated from those in RS and NRW on both sampling occasions; variability among shores was large in NRE and RS at Time 1 and in NRE at Time 2. Differences among habitats were temporally variable at Capraia (Fig. 6). Assemblages were fairly similar across habitats at Time 1, whereas differences occurred at Time 3 with the 'centroids' of shores in RS separating from those of the other habitats. Variability among shores was larger in NRW and NRE compared to RS at Time 3 (Fig. 6).

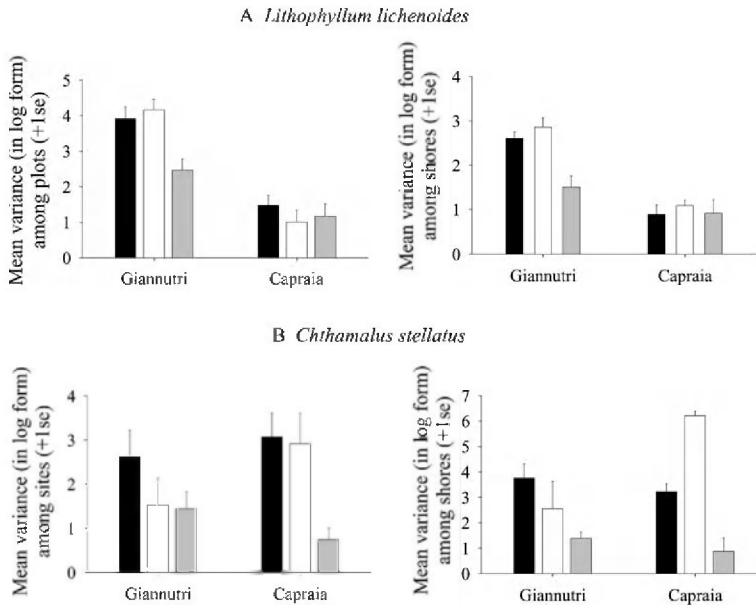


Fig. 5. Mean variance (in log form) in abundance of two species from midshore assemblages at different spatial scales (among plots: $n = 24$; among sites: $n = 12$; among shores: $n = 4$). (■) RS, (□) NRW, (■) NRE. Abbreviations as in Fig. 2.

Small-scale patchiness (dissimilarity among plots) did not differ significantly among habitats, either at Giannutri or Capraia (Fig. 7A). Among-shore variation was large and significant at Giannutri ($MS_{SHORE(HABITAT)} = 191.062$, $MS_{TIME \times SHORE(HABITAT)} = 55.781$, $F_{6,18} = 3.4$, $P < 0.02$; data were not transformed in this and the following analyses on dissimilarity), possibly masking a trend of lower dissimilarity among plots in RS compared with NRW and NRE (Fig. 7A).

There were no differences among habitats in patterns of among-site variation in structure of assemblages (Fig. 7B). ANOVAs revealed neither a significant Habitat \times Time interaction nor a main effect of Habitat (Giannutri: $MS_{HABITAT \times TIME} = 26.041$, $MS_{RESIDUAL} = 114.971$, $F_{6,24} = 0.2$, $P > 0.9$; $MS_{HABITAT} = 62.685$, $F_{2,6} = 2.4$, $P > 0.1$. Capraia: $MS_{HABITAT \times TIME} = 70.521$, $MS_{RESIDUAL} = 45.187$, $F_{6,24} = 1.5$, $P > 0.2$; $MS_{HABITAT} = 43.549$, $F_{2,6} = 0.6$, $P > 0.5$).

The three habitats showed different patterns of among-shore dissimilarity at Giannutri, with less variation occurring in NRW compared with RS and NRE, whereas differences among shores were similar across habitats at Capraia (Fig. 7C).

There was considerable spatial and temporal variability in patterns of mean abundance of common algae and invertebrates both at Giannutri and Capraia (Table 5). In contrast, differences among habitats occurred only at Giannutri and were always in interaction with time (Table 5). The canopy alga *Cystoseira amentacea* var. *stricta* was dominant in RS and was absent in NRE (Fig. 8A), but the ranking of habitats was temporally variable as indicated by SNK tests (Time 1 and Time 3: RS = NRW > NRE; Time 2 and Time 4: RS > NRW > NRE). Filamentous

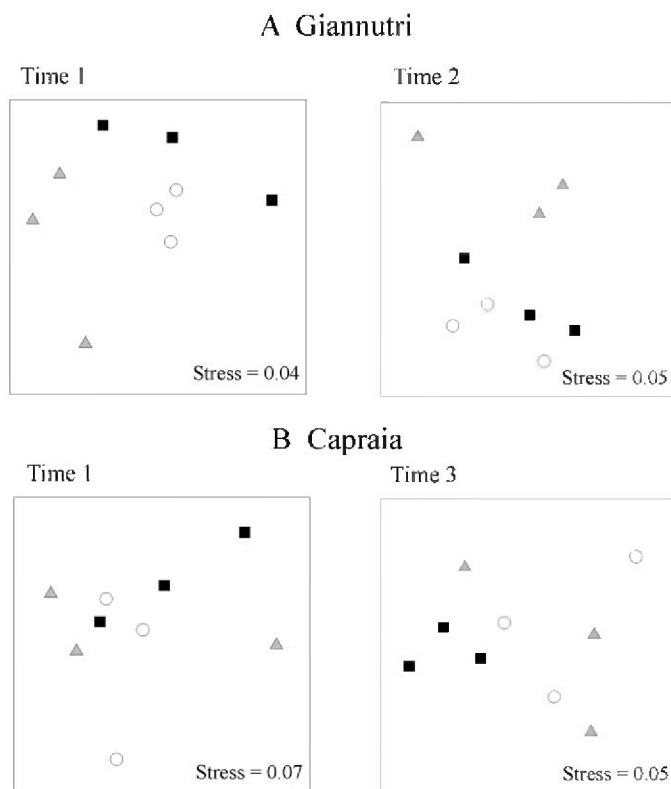


Fig. 6. nMDS plots comparing lowshore assemblages in MPAs (RS) with those of reference shores on the west side of the islands (NRW) and those of east side (NRE) at different times. Each symbol is the 'average sample' of a shore.

algae (Fig. 8B) were more abundant in NRE compared to the other habitats on 2 sampling occasions, as indicated by ANOVA and SNK tests (Time 2: $NRE > NRW = RS$; Time 4: $NRE = NRW > RS$). Despite a significant Habitat \times Time interaction, the green alga *Valonia utricularis* did not show any consistent pattern of differences among habitats (Table 5), whereas hydrozoans were significantly more abundant in NRW and RS compared to NRE at Time 4 (Fig. 8C, Table 5 and SNK tests).

Patterns of spatial variance at the scale of the plot reflected those in mean abundance for *C. amentacea* var. *stricta* (Fig. 9A), with no variation occurring in NRE because the alga was absent in this habitat. A significant main effect of habitat was detected by ANOVAs on coarsely branched algae both at Giannutri and Capraia (Giannutri: $MS_{HABITAT} = 16.960$, $MS_{TIME \times SHORE(HABITAT)} = 3.275$, $F_{2,18} = 5.2$, $P < 0.02$, after elimination of the Shore(Habitat) and Habitat \times Time interactions that were not significant at $P > 0.25$; Capraia: $MS_{HABITAT} = 7.226$, $MS_{POOLED} = 1.751$, $F_{2,30} = 4.1$, $P < 0.03$; the denominator for this test was constructed by pooling MS_{SHORE}

Table 4
R values from two-way nested analysis of similarity (ANOSIM) comparing lowshore assemblages across habitats and among shores within habitats

	Time 1	Time 2	Time 3	Time 4
<i>Giannutri</i>				
Among habitats				
RS vs. NRW	−0.19	0.04	−0.04	0.11
RS vs. NRE	0.61 (0.1)	0.70 (0.1)	0.52 (0.1)	0.57 (0.1)
NRW vs. NRE	0.74 (0.1)	0.81 (0.1)	0.82 (0.1)	0.70 (0.1)
Among shores	0.59 (0.002)	0.69 (0.005)	0.48 (0.006)	0.28
<i>Capraia</i>				
Among habitats				
RS vs. NRW	0.00	0.00	0.22 (0.1)	−0.04
RS vs. NRE	−0.04	0.32	0.41 (0.1)	0.20
NRW vs. NRE	−0.11	0.07	−0.07	−0.19
Among shores	0.20	0.56 (0.001)	0.74 (0.001)	0.44 (0.032)

Exact probabilities are given in parentheses for significant *R* values. Because only 10 permutations are possible for pairwise comparisons of habitats, a significance level of 10% is considered as indicative of differences among habitats in these analyses. RS: reserve; NRW: reference west; NRE: reference east.

(HABITAT) and $MS_{HABITAT \times TIME}$, which were not significant at $P > 0.25$, with $MS_{TIME \times SHORE(HABITAT)}$). Whereas the SNK test could not detect unambiguous differences among habitats at Giannutri, it provided the following ranking of the means at Capraia: $NRE > RS = NRW$ (see also Fig. 9B). Similarly, there was no consistent effect of habitat in small-scale patchiness for articulated coralline algae at Giannutri, whereas a trend toward larger variation in RS compared with the other habitats was evident at Capraia (Fig. 9C). In this case analysis of variance indicated a significant $Habitat \times Time$ interaction ($MS_{HABITAT \times TIME} = 6.361$, $MS_{SHORE(HABITAT) \times TIME} = 2.097$, $F_{6,18} = 3.0$, $P < 0.04$), and SNK tests detected differences among habitats on two sampling occasions (Time 2: $RS > NRE = NRW$; Time 3: $RS = NRE > NRW$). Finally, changes in among-plot variance across habitats also occurred for filamentous algae (Fig. 9D), with greater patchiness in RS compared to NRE and NRW at Capraia ($MS_{HABITAT} = 12.848$, $MS_{SHORE(HABITAT)} = 1.34$, $F_{2,6} = 9.6$, $P < 0.02$, after elimination of the $Shore(Habitat) \times Time$ interaction, and SNK test), and a trend toward greater variation in NRE at Giannutri. This pattern was, however, temporally variable at Giannutri, as indicated by analysis of variance and SNK tests ($MS_{HABITAT \times TIME} = 6.957$, $MS_{SHORE(HABITAT) \times TIME} = 2.118$, $F_{6,18} = 3.3$, $P < 0.03$; Time 1: $NRE > RS = NRW$, Time 4: $NRW = NRE > RS$, no difference among habitat occurred at the other times).

Patterns in spatial variance of *C. amentacea* var. *stricta* at the scale of the site differed among habitats both at Giannutri and Capraia (Fig. 10A). Patterns at Giannutri were still driven by the lack of canopy algae in NRE, whereas variation at Capraia was less important in RS than in the other habitats that did not differ significantly ($MS_{HABITAT} = 15.501$, $MS_{HABITAT \times TIME} = 1.136$, $F_{2,6} = 13.6$, $P < 0.006$,

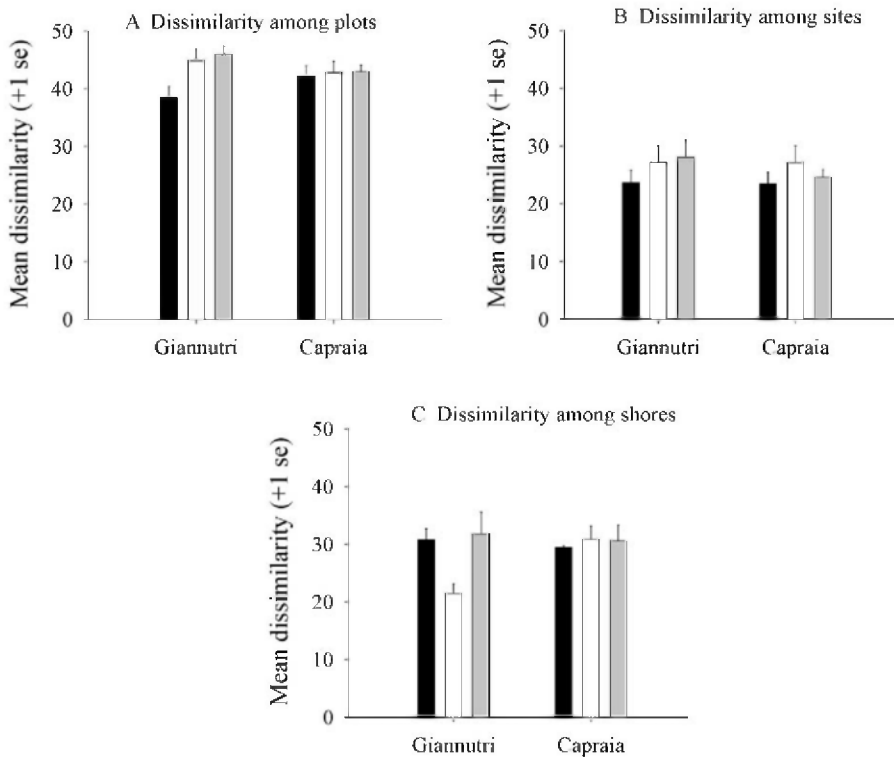


Fig. 7. Mean percentage dissimilarity (+1 SE) measuring patchiness in lowshore assemblages at the scale of the (A) plot ($n=24$), (B) site ($n=12$) and (C) shore ($n=4$). (■) RS, (□) NRW, (■) NRE. Abbreviations as in Fig. 2.

SNK test). Variance among sites was significantly larger in NRE compared to the other habitats for filamentous algae at Giannutri ($MS_{\text{HABITAT}}=5.867$, $MS_{\text{HABITAT} \times \text{TIME}}=0.933$, $F_{2,6}=6.3$, $P<0.04$, SNK test), whereas no difference among habitats was observed at Capraia (Fig. 10B). Finally, among-site variance of sheet-like algae was significantly lower in RS compared to NRW and NRE at Capraia ($MS_{\text{HABITAT}}=12.582$, $MS_{\text{HABITAT} \times \text{TIME}}=1.251$, $F_{2,6}=10.1$, $P<0.02$, SNK test); no difference among habitats occurred at Giannutri, either in interaction with time or as a main effect.

Spatial variance at the scale of the shore differed among habitats for a number of taxa, but patterns were not consistent between the 2 islands (Fig. 11). Articulated coralline, coarsely branched and filamentous algae were less variable in NRW than RS or NRE at Giannutri but not at Capraia (Fig. 11B–D). In contrast, a trend toward larger among-shore variance in NRW compared to the other habitats was evident at Capraia for hydrozoans and sponges (Fig. 11F,G). On this island, sheet-like algae, sponges and *Vermetus* sp. had lower among-shore variance in RS than NRW and NRE (Fig. 11E,G,H).

Table 5

Summary of significant results from analyses of variance on mean abundance of common algae and invertebrates from lowshore assemblages

Taxa	Island	Test	MS _{NUM}	MS _{DEN}	d.f.	F	Transformation
<i>Algae</i>							
Articulated corallines	Giannutri	Shore(H)/T×Shore(H)	8.370	1.387	6,18	6.0**	Log
	Capraia	T/T×Shore(H)	2125.585	576.883	3,18	3.7*	Arcsine
		Shore(H)/T×Shore(H)	3585.648	576.883	6,18	6.2**	
		Site(T×Shore(H))/Residual	732.426	171.071	36,288	4.3***	
<i>Cystosiera amentacea</i> var. <i>stricta</i>	Giannutri	H×T/T×Shore(H)	3156.114	537.659	6,18	5.9**	None ^a
		Shore(H)/T×Shore(H)	15372.220	537.659	6,18	28.6***	
		Site(T×Shore(H))/Residual	1990.681	445.078	36,288	4.5***	
		Capraia	Shore(H)/T×Shore(H)	9617.222	2551.030	6,18	3.8*
	Site(T×Shore(H))/Residual	1910.353	670.243	36,288	2.9***		
Coarsely branched algae	Giannutri	H/Shore(H)	887.233	162.022	2,6	5.5*	Arcsine
	Capraia	T×Shore(H)/Site(T×Shore(H))	406.988	210.413	18,36	1.9*	None
		Site(T×Shore(H))/Residual	251.800	142.804	36,288	1.8**	
<i>Cystoseira compressa</i>	Giannutri	Shore(H)/T×Shore(H)	9.272	0.828	6,18	11.2***	Log
	Capraia	Shore(H)/T×Shore(H)	16.284	3.114	6,18	6.7***	Log
		Site(T×Shore(H))/Residual	3.114	0.762	36,288	4.1***	
Filamentous algae	Giannutri	H×T/T×Shore(H)	5.835	1.266	6,18	4.6**	Log
		Shore(H)/T×Shore(H)	6.501	1.266	6,18	5.1**	
		Site(T×Shore(H))/Residual	1.762	1.090	36,288	1.6*	
		Capraia	T/T×Shore(H)	2499.160	319.386	3,18	7.8**
	Site(T×Shore(H))/Residual	228.292	100.088	36,288	2.3***		
Sheet-like algae	Giannutri	T×Shore(H)/Residual	86948	46.372	18,288	1.9*	None ^a
	Capraia	Shore(H)/T×Shore(H)	616.588	181.235	6,18	3.4*	Arcsine
		Site(T×Shore(H))/Residual	199.719	68.942	36,288	2.9***	
<i>Valonia utricularis</i>	Giannutri	H×T/T×Shore(H) + Site(T×Shore(H))	972.195	421.463	6,54	2.3*	None
		Shore(H)/T×Shore(H)	2149.500	494.989	6,18	4.3**	
		Site(T×Shore(H))/Residual	384.700	236.817	36,288	1.6*	
		Capraia	T×Shore(H)/Site(T×Shore(H))	160.694	46.317	18,36	3.5***
	<i>Invertebrates</i>						
Hydrozoans	Giannutri	H×T/T×Shore(H)	6.567	1.581	6,18	4.2**	Log
	Capraia	Shore(H)/T×Shore(H)	5.968	1.581	6,18	3.8*	None ^a

(continued on next page)

Table 5 (continued)

Taxa	Island	Test	MS _{NUM}	MS _{DEN}	d.f.	F	Transformation
		Site(T×Shore(H))/Residual	1.447	0.543	36,288	2.7***	
		T×Shore(H)/Site(T×Shore(H))	69.534	22.444	18,36	3.1**	
Sponges	Giannutri	T×Shore(H)/Site(T×Shore(H))	103.900	45.419	18,36	2.3*	None ^a
	Capraia	Shore(H)/T×Shore(H)	121.758	24.025	6,18	5.1**	None ^a
<i>Vermetus</i> spp.	Giannutri	Shore(H)/Site(T×Shore(H))	2.858	0.869	6,36	3.3*	Log
		Site(T×Shore(H))/Residual	0.869	0.443	36,288	2.0**	
	Capraia	Shore(H)/Site(T×Shore(H))	116.908	52.814	6,36	2.9*	Angular
		Site(T×Shore(H))/Residual	52.814	32.916	36,288	1.6*	

^a Variances were heterogeneous (after Cochran's *C* test) and could not be stabilised by transformations.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

4. Discussion

Results showed considerable differences among habitats in structure of assemblages, in mean abundance of taxa and in univariate and multivariate measures of spatial variation. Most of these patterns were inconsistent with the predicted effect of management of populations and assemblages through MPAs (Table 6). The model that MPAs affected populations and assemblages predicted differences between RS and NRW (i.e. between protected and adjacent unprotected shores with similar orientation of the coastline). In contrast, the alternative model that habitat was more important than management predicted differences between NRE and NRW (i.e. between shores on different sides of the islands). Simultaneous effects of MPAs and habitat would have been detected by differences between RS and NRW and any concomitant difference between NRE and NRW.

Patterns consistent with an effect of MPAs were identified at Capraia for the structure of midshore and lowshore assemblages on two of the four sampling dates, T2 and T3 respectively, and for measures of spatial variance in abundance at several scales for a number of taxa in lowshore assemblages. In contrast, a priori hypotheses on the influence of MPAs on the mean abundance of taxa were not supported by the results. Patterns in spatial variance occurred mostly at Capraia, with the exception of filamentous algae at Giannutri for T2. Concomitant effects ascribed to management and habitat were identified only for measures of spatial variance in abundance of barnacles at the scale of shores at Capraia. The importance of habitat was revealed both by multivariate and univariate analyses of midshore and lowshore assemblages, regardless of time of sampling and spatial scale.

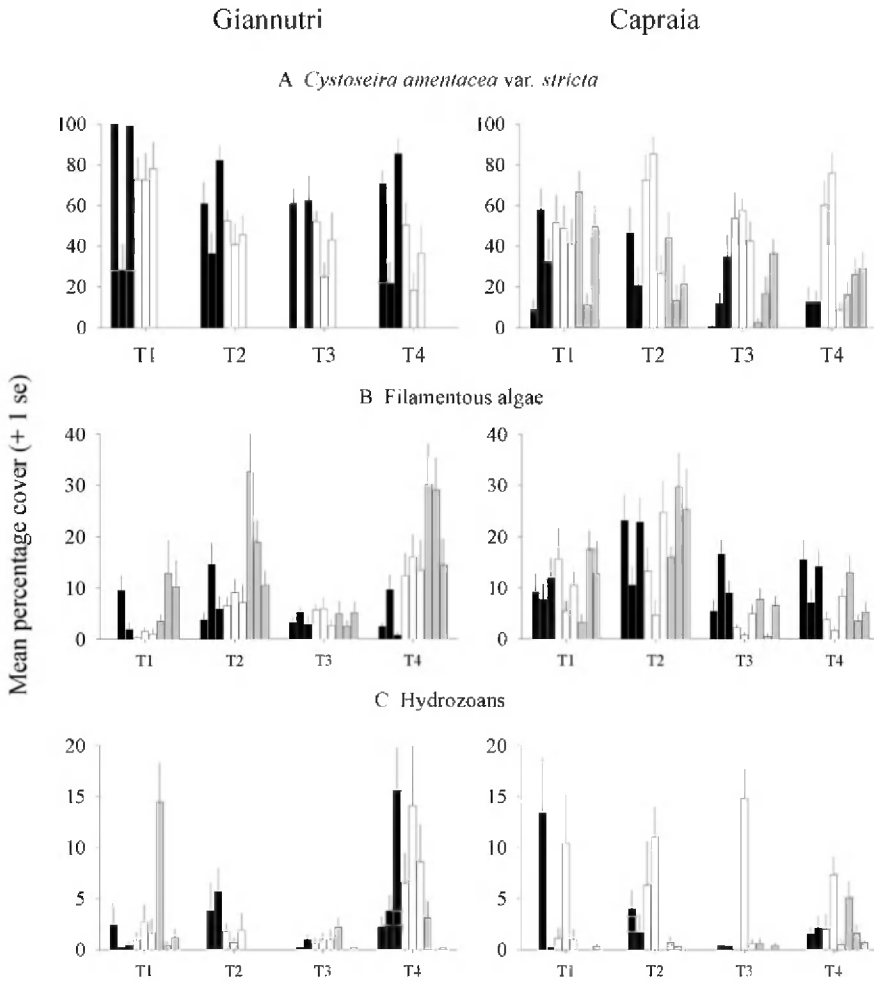


Fig. 8. Mean percentage cover (± 1 SE, $n = 10$) of algae and invertebrates in lowshore assemblages. Data are shown for each of three replicate shores in (■) RS, (□) NRW and (■) NRE. Abbreviations as in

Our results raise important questions about the design and management of MPAs in this region that, we suspect, identify general problems in this type of managerial activity. Specifically, does the number, size and location of MPAs guarantee (1) protection of a sample of species and assemblages that are representative of the biota of the region or at least of the location, (2) inclusion of the relevant patterns of variation in structure and composition of assemblages, and (3) proper representation of the relevant ecological processes that naturally operate over different spatial and temporal scales in the system? Below we discuss plausible explanations for the lack of relevant effects of MPAs on assemblages and on mean abundance of common taxa and the apparent effect of management on measures of spatial variance in abundance. Then we will focus on differences between NRW and NRE to address

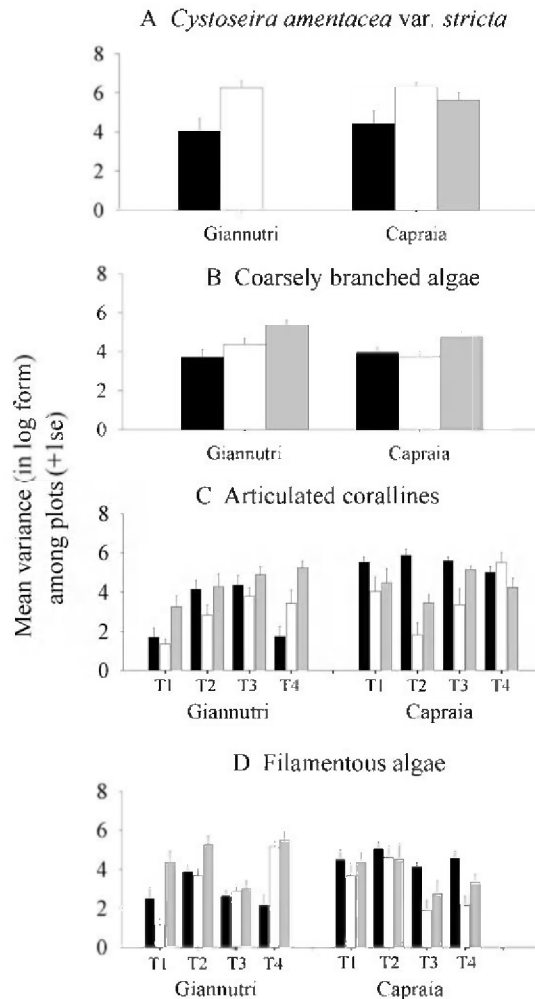


Fig. 9. Mean variance (+1 SE, $n=24$, data log-transformed) in abundance among plots for several taxa in lowshore assemblages. (■) RS, (□) NRW, (■) NRE. Abbreviations as in Fig. 2.

the questions raised above concerning the design of MPAs. Finally, we will discuss the implications of spatial heterogeneity for the design and implementation of MPAs.

4.1. Effects of MPAs (contrasts between RS and NRW)

There are at least three explanations for the lack of important effects of MPAs on assemblages and on mean abundances of common taxa reported in this study. First, anthropogenic disturbance might not have been effectively reduced in RS compared with NRW. Second, there is the possibility that RS and NRW were intrinsically

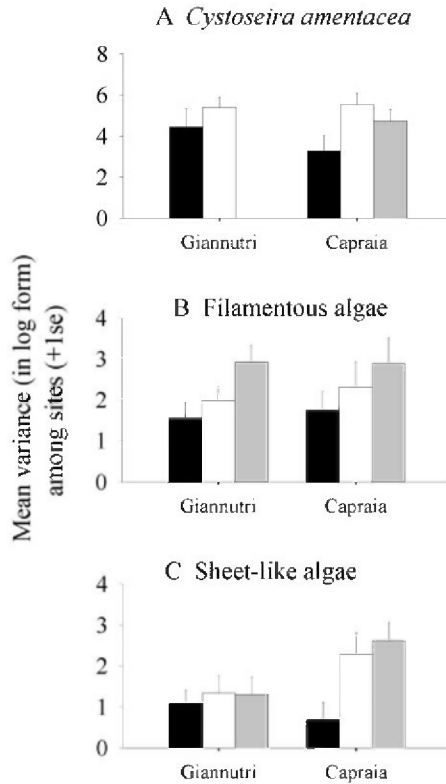


Fig. 10. Mean variance (± 1 SE, $n = 12$, data log-transformed) in abundance among sites for several taxa in lowshore assemblages. (■) RS, (□) NRW, (■) NRE. Abbreviations as in Fig. 2.

different before the establishment of MPAs and that the processes responsible for such differences became ineffective under protection. Third, it is possible that people visiting these shores did not have ecologically detectable impacts on the biota.

The first alternative seems very unlikely. Although we do not have any quantitative data on number of people visiting the shores, observations repeated over 5 years of research on the island of Capraia revealed the presence of people in RS only occasionally, whereas many tourists reached NRW and NRE by boat or from land. Fewer observations were available at Giannutri. The overall number of tourists visiting the shores appeared to be lower at Giannutri compared with Capraia, but a difference between RS and NRW was still appreciable, though on a subjective basis.

The possibility that RS and NRW provided different types of habitat with different original assemblages and that the establishment of MPAs counteracted any processes responsible for such differences, seems unlikely. There is no macroscopic feature of the habitat that could account for any difference in composition and structure of assemblages. At Giannutri, replicate shores in RS and NRW were interspersed and apparently sampled a comparable range of habitats. At Capraia, however, only the central part of the west coast was protected, so that shores in

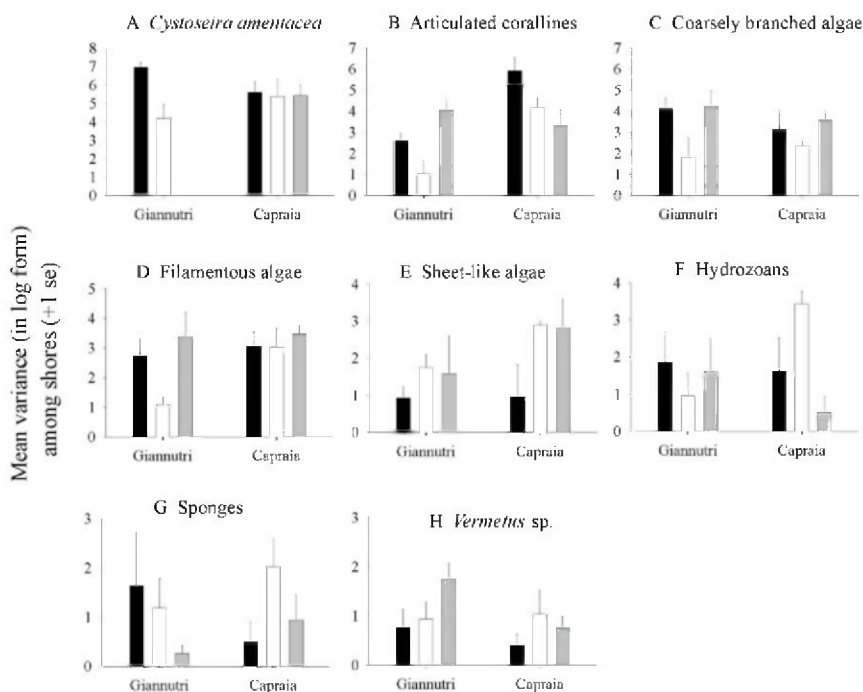


Fig. 11. Mean variance (± 1 SE, $n=4$, data log-transformed) in abundance among shores for several taxa in lowshore assemblages. (■) RS, (□) NRW, (■) NRE. Abbreviations as in Fig. 2.

NRW were located north and south of those in RS. It is also difficult to imagine what processes protection might affect in order to remove initial differences in assemblages between RS and NRW. We recognise, however, that these are inductive arguments and because establishment of MPAs is not a random process, there is no logical basis to conclude that RS and NRW differed only in terms of management (Stewart-Oaten & Bence, 2001). This remains an open question that can be addressed only with baseline data describing the structure and composition of assemblages over a range of spatial and temporal scales *before* establishment of MPAs.

The third alternative, lack of relevant effects of humans on our shores, is at odds with the findings of other studies reporting large effects of people on plants and animals of rocky shores (e.g. Kingsford et al., 1991). Trampling and collection of animals for bait and food are among the most common activities (Keough & Quinn, 1998; Moreno et al., 1984). This is widespread also in the northwest Mediterranean, at least on the mainland (Benedetti-Cecchi personal observation). Possibly, people visiting islands are more concerned about environmental issues and are educated in the conservation of natural habitats. In fact, eco-tourism is a common slogan to attract tourists to these areas. It is surprising that one of the most visited shores of Capraia (Cala Cote) is also one of the shores with the largest density of the topshell *Osilinus turbinatus*, a gastropod that is extensively harvested and nearly driven to extinction in other places (Benedetti-Cecchi et al., unpublished data). Eco-tourism,

Table 6
Summary of relevant results of the study

Type of analysis	Response variable(s)	Result	Island	Time	Spatial scale
<i>Midshore</i>					
Multivariate (structure)	Species composition and abundance	RS≠Others ^a	Capraia	T2	
Multivariate	Dissimilarity (patchiness)	NRE>Others	Giannutri	All	Plot
		NRW<Others	Giannutri	All	Shore
		NRW>Others	Capraia	All	Shore
Mean abundance	Encrusting corallines	NRE>Others	Capraia	All	
Spatial variance in abundance	<i>L. lichenoides</i>	NRE<Others	Giannutri	All	Plot
		NRE<Others	Giannutri	All	Shore
	<i>C. stellatus</i>	NRE<Others	Capraia	All	Site
		NRW>RS>NRE ^a	Capraia	All	Shore
<i>Lowshore</i>					
Multivariate (structure)	Species composition and abundance	NRE≠Others	Giannutri	All	
		RS≠Others ^a	Capraia	T3	
Multivariate (patchiness)	Dissimilarity	NRW<Others	Giannutri	All	Shore
Mean abundance	<i>C. amentacea</i> var. <i>stricta</i>	NRW<Others	Giannutri	All	
	Filamentous algae	NRE>Others	Giannutri	T2 and T4	
	Hydrozoans	NRE<Others	Giannutri	T4	
Spatial variance in abundance	<i>C. amentacea</i> var. <i>stricta</i>	NRE<Others	Giannutri	All	Site
		NRE<Others	Giannutri	All	Shore
		RS>Others ^a	Capraia	All	Site
	Articulated corallines	NRW<Others	Giannutri	All	Shore
		RS>Others ^a	Capraia	T2	Plot
		NRE>Others	Capraia	T3	Plot
	Coarsely branched algae	NRW<Others	Giannutri	All	Shore
		NRE>Others	Capraia	All	Plot
	Filamentous algae	NRE>Others	Giannutri	T1	Plot
		RS>Others ^a	Giannutri	T2	Plot
		NRE>Others	Giannutri	All	Site
		NRW<Others	Giannutri	All	Shore
		RS>Others ^a	Capraia	All	Plot
	Sheet-like algae	RS<Others ^a	Capraia	All	Site
		RS<Others ^a	Capraia	All	Shore
	Hydrozoans	NRW>Others	Capraia	All	Shore
	Sponges	NRW>Others	Capraia	All	Shore
	<i>Vermetus</i> sp.	RS<Others ^a	Capraia	All	Shore

^a Indicates results that are consistent with a reserve effect.

however, can affect assemblages of rocky shores through trampling. Experimental studies have shown that trampling must be in the form of a press disturbance to have appreciable effects (Keough & Quinn, 1998). Possibly, concentration of tourism during the summer season was not sufficient to trigger relevant changes in

assemblages or, alternatively, visitors elicited pulse responses (in the sense of Glasby & Underwood, 1996) that the temporal resolution of this study could not detect. Comparisons of protected and reference shores before and after the summer season would provide appropriate tests of hypotheses about pulse effects in these assemblages.

Several taxa of lowshore assemblages showed differences in patterns of spatial variance in abundance between RS and NRW at a range of spatial scales. These results were consistent with an effect of management that would have affected spatial heterogeneity rather than mean abundance of organisms. The most common effects of MPAs documented by empirical studies are, however, on mean abundances of populations (in addition to effects on species' diversity and body size) rather than on spatial (or temporal) variation. It is therefore difficult to put our results in the context of the current literature. More studies are needed where comparisons between MPAs and reference areas involve tests of univariate and multivariate hypotheses on spatial and temporal heterogeneity in addition to the traditional tests on mean abundance of common taxa. If management of natural environments has the potential to affect spatial patchiness and temporal changes in populations and assemblages, as our data indicated, then estimates of these effects should provide an additional criterion for evaluating the effectiveness of MPAs.

The difficulty when dealing with spatial or temporal variability is identifying the direction of those effects that would be indicative of the success of management. If an increase in abundance of a commercial, a dominant or a charismatic species can be considered a positive response to protection, the value of increasing or decreasing spatial and temporal heterogeneity is more difficult to assess. Ultimately, the objective would be to preserve or to restore the patterns of variation that would occur in the absence of human impacts. Criteria need to be established in order to define appropriate references for these patterns in a continuously changing world (Dayton et al., 1998). These issues are discussed in more detail below (see Section 4.3).

4.2. Effects of habitat (contrasts between NRW and NRE)

There is a vast amount of literature documenting differences in biota between contrasting habitats (Ceccherelli & Cinelli, 1998; Jacobi & Langevin, 1996; McClanahan & Arthur, 2001). It is therefore not surprising to find differences between NRW and NRE which contrast two opposite sides of the islands. Many processes can differ between NRW and NRE, including intensity and frequency of storms (Underwood, 1999), local oceanography that can affect delivery of larvae and recruitment of organisms to the shore (Gaines & Bertness, 1992; Roughgarden, Gaines, & Possingham, 1988) and hence the intensity of density-dependent biological interactions (Berlow, Navarrete, Briggs, Power, & Menge, 1999). These processes can also account for differences between NRW and NRE in patterns of spatial variation in abundance. The relevant question here is what are the consequences of these differences for management of MPAs?

This study provides strong support to the view that MPAs at Giannutri and Capraia do not include a representative sample of assemblages characteristic of these islands. For example, at Giannutri the canopy alga *C. amentacea* var. *stricta*

was common on the west coast whereas on the eastern side of the island this alga was absent. Canopy algae provide complex habitats allowing persistence of diversified assemblages of understory algae and invertebrates that differ markedly from those developing in the absence of a canopy (Benedetti-Cecchi et al., 2001). In fact, lowshore assemblages in NRE were dominated by turf-forming algae and these assemblages were not properly represented in the MPA. Patterns were different at Capraia where canopy algae were present on all sides of the island. As a consequence, lowshore assemblages did not differ greatly between habitats at Capraia. There, however, midshore assemblages in NRE had significantly more encrusting coralline algae than those in NRW, a pattern that was not observed at Giannutri. These findings highlight another important issue: differences between habitats were inconsistent at the regional scale. The implication is that evaluations of management decisions associated with MPAs do not yield general results and must be conducted on a systematic basis even in the presence of apparently similar environmental conditions.

4.3. Implications of spatial heterogeneity for management of MPAs

Univariate and multivariate measures of spatial heterogeneity revealed two relevant scales of variability: the scale of the plot and the scale of the shore. This has important implications for establishment and management of MPAs. Due to the possibility that different shores supported distinct assemblages, selection of sites for establishment of MPAs in this region should proceed on a per-shore basis in order to ensure that a representative sample of assemblages is included in the managed area. A single large MPA, like the one at Capraia, may not be sufficient to achieve this goal (see also Simberloff, 1988 for a discussion on the relative merits of single large vs. several small reserves).

Furthermore, there were differences between RS and NRW and between NRW and NRE in patterns of spatial heterogeneity of assemblages, particularly at the scale of shores. That is, the managed areas did not encompass the full range of patterns of variation in structure of assemblages present at the study locations. If spatial heterogeneity is indicative of qualitative and/or quantitative changes in fundamental ecological processes (Bell et al., 1993; Fairweather, 1988; Hay, 1985; Underwood & Chapman, 1996; Wiens et al., 1993), our results suggest that the relevant processes generating structure in assemblages were not properly represented within the investigated MPAs. Once again, analyses at the scale of shores were critical to assess whether or not the relevant patterns of spatial heterogeneity and, indirectly, the range of variation in underlying ecological processes were properly managed.

According to the earlier results, designation of MPAs in the Tuscan Archipelago should proceed through careful selection of shores and habitats, so that protection can be directed to a representative set of assemblages and possibly to the relevant processes maintaining their spatial patterns at these relatively large scales. Following these criteria, proper representation of spatial heterogeneity at the scales of the plot and the site should be guaranteed automatically in managed areas. This follows from the consistency of small-scale spatial pattern (i.e. variability among plots and

sites) across shores and habitats documented in the present study. Of course, this applies only to processes that operate at the scale of the MPA, whereas the influence of large-scale processes such as climate change, oceanographic patterns and delivery of long-lived larvae would be largely unaffected by managerial decisions (Allison et al., 1998).

More generally, our results ascribe a value to spatial heterogeneity as an additional informative criterion to use in the design and implementation of MPAs. This, along with considerations of reproductive output, dispersal, mobility and size of the organisms to be protected (Dayton, Sala, Tegner, & Thrush, 2000; Edgar & Barrett, 1999; Hastings & Botsford, 1999; McNeill, 1993; McNeill & Fairweather, 1993) and connectivity in meta-populations (Palumbi, 2001 and references therein), should provide the scientific basis to underpin management decisions concerning the number, size and location of MPAs. Although such decisions usually involve little scientific justification (Allison et al., 1998), identifying meaningful ecological variables and appropriate sampling designs to test hypotheses of the effectiveness of established MPAs should make ecology more successful in solving environmental problems, including conservation of assemblages and relevant processes.

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