Mitigating human disturbance: can protection influence trajectories of recovery in benthic assemblages?

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Summary

1. Understanding whether Marine Protected Areas (MPAs) can be considered as a suitable tool for restoring the structure and function of populations and assemblages is urgently needed to achieve an effective policy of mitigation of human impact in coastal management. However, to date, the role played by MPAs in enhancing ecosystems resilience has been more advocated than unambiguously documented.

2. This study was designed to test whether full protection in marine reserves facilitates recovery of benthos impacted by the date mussel *Lithophaga lithophaga* fishery, one of the most harmful human activities affecting subtidal rocky habitats in the Mediterranean Sea.

3. The effects of this destructive fishery were reproduced at one fully protected location (*P*) and at two unprotected control locations (*Cs*) in the SW Mediterranean Sea. At each location, three plots (4 m^2) of rocky surface at 4–6 m depth were disturbed experimentally, while another three plots served as reference. In each plot, the species composition and relative cover of the sessile benthic assemblages were sampled photographically on each of five occasions during a period of 20 months.

4. Over and above variation in habitat features among locations, multivariate and univariate analyses revealed significant differences between *P*-vs.-*Cs* in patterns of assemblage recovery and showed that, at the fully protected location, recovery was faster than at the unprotected control locations.

5. Our results suggest that MPAs have the potential to change the trajectories of recovery of disturbed assemblages by accelerating the processes of recolonization and call for further investigation to identify the specific mechanisms underlying increased resilience.

Key-words: coastal management, *Lithophaga lithophaga*, Marine Protected Areas, resilience, subtidal rocky reefs.

Introduction

The increasing and widespread process of degradation of marine biota (Bryant *et al*. 1996; Hixon *et al*. 2001; Burbridge & Humphrey 2003) has the negative potential to threaten biodiversity (Roberts & Hawkins 1999), to reduce habitat availability for species (Tilman *et al*. 1994) and to alter ecosystems structure and functioning (Worm & Duffy 2003; Gessner *et al*. 2004).

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In this fast-degenerating scenario, the need to preserve pristine systems (Allison, Lubchenco & Carr 1998), but also to restore degraded systems (Edwards 1998; Epstein *et al*. 2005), calls for more effective approaches in order to implement programmes and tools focused upon supporting systems' resilience (Hughes *et al*. 2005). Marine Protected Areas (MPAs) are recognized widely as a powerful tool for marine conservation and resources management (Lubchenco *et al*. 2003; Fraschetti *et al*. 2005) and can provide privileged areas where experimental works on natural processes under conditions of limited human disturbances can be carried out. MPAs could boost temporal

trajectories of recovery, triggering processes of recruitment (Planes *et al*. 2000), the reproductive potential of populations (Gerber *et al*. 2003) and trophic cascades (Pinnegar *et al*. 2000), possibly enhancing systems' resilience and avoiding the establishment of an irreversible chronic status of degradation (Bellwood *et al*. 2004). However, empirical studies of whether full protection enhances ecosystems resilience are largely lacking, and this role has been more advocated than documented unambiguously (Hughes *et al*. 2005). Most studies on MPAs have focused upon the restoration of fished stocks of commercial interest (e.g. Micheli *et al*. 2004a), but in general a single-species regulation does not include critical ecological linkages among species and between species and their environment. These relationships all play a crucial role in determining assemblage structure and functioning (Benedetti-Cecchi, Bulleri & Cinelli 2000; Connell 2005) and, thus, are fundamentally important for effective management (Micheli *et al*. 2004b). Human activities have the potential to affect the whole system even when acting on single components, due to complex interactions and feedbacks. In view of this, ecosystems properties such as the ability to recover after disturbance are likely to be different when human activities are excluded. Within marine reserves boundaries, for instance, the increased abundance and size of large predators has widely documented the indirect effects on benthic assemblages, reversing, through regulation processes such as top-down control (Shears & Babcock 2002), the transition from macroalgal-dominated assemblages to coralline barrens driven by high densities of herbivores. Outside MPAs, as well as the direct and indirect consequences of fishing on target stocks, strong human impact is likely to exert a negative influence on recovery dynamics through the degradation and fragmentation of habitats (Watling & Norse 1998).

In temperate coastal systems, shallow rocky reefs are among the most productive and diverse habitats. Rocky reefs supply food resources, nurseries and shelters to a variety of organisms and sustain high levels of biodiversity due to their heterogeneity and three-dimensional complexity (Turner *et al*. 1999). The degradation of these systems, which are affected intensively by a wide range of human impacts, could have a negative resonance for the whole coastal biota and strong socio-economical implications (Steneck & Carlton 2001; Witman & Dayton 2001). In the Mediterranean Sea, shallow rocky calcareous habitats are heavily threatened due to the destructive fishery of the European date mussel *Lithophaga lithophaga* (L.) (hereafter simply date-mussel fishery, DMF), which leads to the desertification of tens of kilometres of rocky coast each year (Fanelli *et al*. 1994). As in a type of extreme by-catch, this completely illegal fishery involves the removal of the benthic assemblages because, to extract and collect these boring bivalves from rocky reefs, scuba divers scrape and break the carbonate rocks with special sledgehammers, with a detrimental effect on the organisms living

on the surface and within the substrate (Fanelli *et al*. 1994). These bivalves are a very slowly renewable resource, leading fishermen to exploit increasingly larger patches of rocky substrates due to their extraordinarily low growth rate (18–36 years to reach the commercial size) (Galinou-Mitsoudi & Sinis 1995). The extending clearing action of DMF is causing a phase shift from multilayered macrobenthic assemblages to coralline barrens in large areas of subtidal reefs in the Mediterranean Sea (Fanelli *et al*. 1994; Fraschetti *et al*. 2001; Guidetti *et al*. 2003), representing one of the most harmful human activities affecting temperate shallow rocky habitats (Dayton *et al*. 1995). The impact of DMF has also been found to affect patterns of distribution of sea urchins, which show higher densities and biomass in impacted areas (Guidetti *et al*. 2003). Thus, patches created by DMF may remain in a bare state for a long time because the increased grazing pressure may be detrimental for recolonization processes (McClanahan *et al*. 1996).

This study investigated the effects of full protection in MPAs on the recovery dynamics of benthic sessile assemblages affected by strong human impact in order to explore the potential role of MPAs in mitigating the consequences of anthropogenic disturbance. Specifically, we carried out a manipulative experiment designed to reproduce the impact of DMF within a no-take, no-access MPA and in two unprotected control locations to test the null hypothesis that full protection has no effect on patterns of recovery of disturbed assemblages. As herbivore grazing may affect recolonization in disturbed patches, we also tested for differences in density of dominant grazers (i.e. the sea urchins *Paracentrotus lividus* Lamarck and *Arbacia lixula* L.) between the protected and unprotected locations.

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

The experiment was set up in April 2003, at Punta Campanella, Campania (40°34′ N, 14°23′ E, SW Italy). The MPA of Punta Campanella was established in 1997 and covers approximately 1200 ha. One of the three study locations was situated inside a no-take, no-access MPA (hereafter indicated as *P*). The other two were unprotected locations, which served as controls (Fig. 1). Controls (hereafter indicated as *Cs*), were selected randomly from a set of possible locations identified in preliminary surveys as characterized by comparable environmental conditions to *P* in terms of nature and slope of the substrate, exposure to waves and dominant currents and type of assemblage. Locations were separated by approximately 3 km. At each location, six square plots of rocky surface (each approx. 4 m²) were selected randomly on subvertical walls at 4–6 m depth and marked permanently at the four corners with epoxy putty to facilitate their localization. Three of the six plots were selected randomly to be disturbed
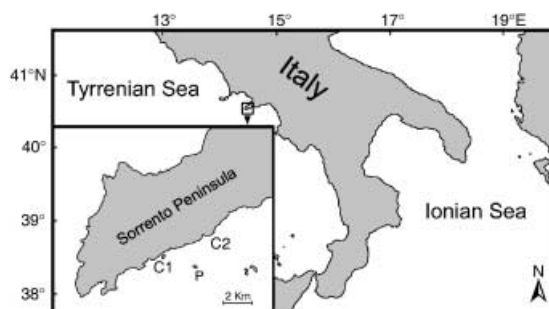
Fig. 1. Study area and position of protected (*P*) and control (*C1*, *C2*) locations.

experimentally and the other three were not manipulated and served as reference conditions. The experimental treatment fully reproduced DMF and consisted of scraping organisms from substrate and breaking rocks using picks and sledgehammers to collect *L. lithophaga* specimens from their holes. Plots were sampled five times, separated by at least 3 months (i.e. April and July 2003, January, May and November 2004). Although the timing of the disturbance could affect the recovery of benthic assemblages significantly (Airoldi 1998; Benedetti-Cecchi 2000), suggesting additional treatments to test for the effect of DMF, ethical considerations due to the destructive nature of the experimental manipulation led us to not repeat the experiment multiple times. The need to reconcile a rigorously designed experiment with the need to limit its impact also guided our choice to keep the number of experimental sites low. In contrast, we chose a plot size that was representative of the patch sizes and heterogeneity associated with the DMF damage (e.g. Fanelli *et al.* 1994; Fraschetti *et al.* 2001), which allowed the collection of independent units of observation through time.

SAMPLING OF SESSILE ASSEMBLAGES

Plots were monitored using a non-destructive, photographic sampling method (Roberts, Fritzhenry & Kennelly 1994). The photographic equipment consisted of a Nikonos V underwater camera, 28 mm focal length, close-up macro system and two SB105-Nikon strobes. On each sampling occasion, five randomly located replicate quadrats of 16×23 cm were photographed in each plot for a total of 450 replicate units. The slides were analysed under a binocular microscope by superimposing a transparent grid of 24 equally sized squares to help the quantification of taxa. Abundances of sessile macrobenthic organisms were estimated by visual percentage cover estimation (Meese & Tomich 1992; Dethier *et al.* 1993). Mobile organisms (e.g. gastropods, polychaetes and ophiuroids) were not included in the analyses. When organisms could not be identified, they were collected and brought back to the laboratory for taxonomic identification. Thirty-nine of 72 taxa

detected could be identified to the species level. The remaining taxa were identified to the genus (17), family (three), order (one) and class (two) level, or were assigned to morphological groups (10) (see Appendix S1 for full taxonomic details).

SAMPLING OF SEA-URCHIN DENSITY

Sea-urchin densities were estimated on three sampling occasions (January, May and November 2004). On each sampling date, underwater identification and counts of sea urchins within 20 replicate 1 m^2 quadrats were performed at each location for a total of 180 quadrats. Counts were made at approximately 3–8 m depth during the daylight. Care was taken to search for urchins in crevices.

STATISTICAL ANALYSES

Two separate distance-based permutational multivariate analyses of variance (PERMANOVA; Anderson 2001a; McArdle & Anderson 2001) were performed to test different hypotheses regarding the effects of protection. The first analysis did not consider data from manipulated plots and tested the null hypotheses of no differences between *P* and *Cs* in the structure of undisturbed assemblages. The second analysis was performed on the full data set (450 samples and 72 variables) and possible differences were examined between *P* and *Cs* in patterns of recovery of disturbed assemblages. Both analyses were based on Bray–Curtis dissimilarities (Bray & Curtis 1957) on untransformed data, and each term in the analysis was tested by 4999 random permutations of appropriate units (Anderson 2001b; Anderson & ter Braak 2003). For the first analysis, the experimental design comprised three factors: time (Ti, five levels, random), location (Lo, three levels, random, crossed with Ti) and plot (Pl, three levels, random, nested in Lo), with five replicate observations per combination of factors. For the second analysis the experimental design consisted of four factors: time (Ti, five levels, fixed), treatment (Tr, two levels fixed, crossed to Ti), location (Lo, three levels, random, crossed with Ti and Tr) and plot (Pl, three levels, random, nested in Tr × Lo interaction), with five replicates. In both cases, the design was asymmetrical (Underwood 1994) due to the presence of a single protected location. Therefore, for the analyses, the location term was partitioned into two portions: the 1 d.f. contrast of *P*-vs.-*Cs* and the variability between *Cs*. The same partitioning was performed for all terms involving the location term (e.g. the Ti × Tr × Lo term was partitioned into Ti × Tr × *Cs* and Ti × Tr × *P*-vs.-*Cs*). Finally, the residual variation was divided into two parts: the residual variability for observations within *P* (Res *P*) and the residual variability for observations within *Cs* (Res *Cs*). Appropriate denominators for *F* ratios were identified from expected mean squares (Winer, Brown & Michels 1991) and tests were constructed following the logic of asymmetrical

design (see particularly Underwood 1992 and Glasby 1997). Tests of terms that involved sources of variation specific for *P* or *Cs*, however, were constructed using the natural denominator for that term, not the pooled one. For example, the $Ti \times Tr \times Cs$ interaction was tested over the $Ti \times Pl(Tr \times Cs)$ term, rather than the overall effect of $Ti \times Pl(Tr \times Lo)$. Full details for the choice of appropriate *F* denominators in asymmetrical designs are reported elsewhere (Terlizzi *et al.* 2005). The analysis was performed using the computer programs DISTLM.exe and PERMANOVA.exe (Anderson 2004, 2005). Multivariate patterns of differences between disturbed and undisturbed plots across locations were visualized for each of the five times of sampling by non-metric multidimensional scaling (nMDS) (Kruskal & Wish 1978) of plot centroids. Centroids and distances between them in Bray–Curtis space were obtained using the computer program PCO.exe (Anderson 2003); nMDS plots of distance matrices between centroids were then generated with PRIMER 6 software (Clarke & Gorley 2001). As significant differences between *P*-vs.-*Cs* were detected in temporal patterns of recovery of disturbed assemblages (see Results), a single canonical analysis of principal coordinates (CAP, Anderson & Robinson 2003; Anderson & Willis 2003) was performed for the factor location using data from the fifth time of sampling (i.e. 20 months after the experimental disturbance) and calculating the distance matrix among sampling units in disturbed plots. Distinctness among locations was assessed using leave-one-out allocation success (Lachenbruch & Mickey 1968; Anderson & Robinson 2003). Individual taxa that might be responsible for any group differences seen in the CAP plot were investigated by calculating product–moment correlations of original variables (taxa) with canonical axes (e.g. Anderson & Willis 2003). These correlations of individual variables with the two canonical axes (r_1 and r_2) were then represented as lines in a projection biplot. Taxa were included in the biplot only if exceeding an arbitrarily chosen value of correlation (i.e. $\sqrt{r_1^2 + r_2^2} \geq 0{\cdot}35$). Asymmetrical analysis of variance (ANOVA) was employed to test, for single response variables, the same hypotheses described above for the whole assemblages. Overdispersion prevented the use of univariate analyses on most taxa. Therefore, for the analyses, single taxa variables were collapsed into morphological groups (Steneck & Dethier 1994) and identified as encrusting algae, turf-forming algae, erect algae, sponges, hydrozoans and bryozoans (see Appendix S1 for details). In addition, univariate analyses were used to analyse the total number of taxa and the total cover per observation unit. Asymmetrical ANOVAS were also employed to test for differences between *P*-vs.-*Cs* in density of sea urchins. Prior to analyses, the assumption of homogeneity of variances was checked using Cochran's *C*-test and data were appropriately transformed, if required. The analyses were performed using GMAV version 5 software (University of Sydney, Australia).

Results

PERMANOVA on the multivariate data set of the undisturbed plots showed non-significance of the interaction terms $Ti \times Cs$ and $Ti \times P$-vs.-*Cs*, indicating that variation between control locations (*Cs*) and between protected vs. control locations (*P*-vs.-*Cs*) did not differ through time (Table 1). There were no appropriate *F* denominators for testing the main effects of *Cs* and of *P*-vs.-*Cs*. Tests were possible only by conducting separate PERMANOVAS investigating the full design separately at each of the five times of sampling. These analyses showed that control locations differed significantly from one another for times 1, 2 and 3 but not for times 4 and 5. The main contrast of *P*-vs.-*Cs* was not significant at any of the considered times (Table 1), indicating no apparent effects of protection on the structure of undisturbed assemblages. PERMANOVA on the full multivariate data set revealed (Table 2) the non-significance of the interaction term $Ti \times Tr \times Cs$, suggesting that the temporal pattern of recovery of disturbed assemblages did not differ between *Cs*. The analysis also detected a significant $Ti \times Tr \times P$-vs.-*Cs* interaction, indicating that temporal changes of disturbed assemblages at *P* were distinct from those occurring, on average, at *Cs* and suggesting a significant effect of protection in modifying the temporal trajectory of the response of assemblages to disturbance. Such patterns were portrayed clearly by nMDS ordinations of the plots' centroids (Fig. 2). At the beginning of the experiment (Fig. 2a) manipulated plots were, as expected, all well separated from the unmanipulated ones. From time 2 (3 months after the experimental disturbance), however, symbols corresponding to the manipulated plots of the protected location (Fig. 2b–e) moved towards the right-hand side of the diagrams (i.e. that characterized by the assemblages in the undisturbed plots). Manipulated plots from *Cs*, regardless of the time of sampling, were all located on the left-hand side of the diagrams, indicating that the level of dissimilarity between disturbed and undisturbed assemblages at *Cs* did not change greatly through time (Fig. 2). The canonical analysis of principal coordinates for the term location at time 5 achieved the highest allocation success (91·1%) using $m = 10$ principle coordinate (PCO) axes, which explained 99·5% of variation in the original dissimilarity matrix. The two canonical axes had very high canonical correlations with the multivariate assemblages (δ^2, Fig. 3). Plots of disturbed assemblages from *P* were fairly distinct from those of the *Cs* which, in turn, clustered together on the right-hand side of the graph (Fig. 3a). Several individual taxa were highly correlated with the canonical axes (Fig. 3b). This correlation indicated that 20 months after the experimental disturbance (time 5) the assemblages at *P* were characterized mainly by taxonomic groups of turf-forming [dark filamentous algae (DFA)] and erect [*Corallina elongata* (Cor), *Caulerpa racemosa* (Cau), *Laurencia* complex (Lau)] algae. Encrusting algae of the genus *Peyssonnelia* (Pey)

Table 1. PERMANOVA analyses investigating differences between undisturbed assemblages in protected versus control locations based on Bray–Curtis dissimilarities (no transformation) of multivariate data (72 taxa). Each test was performed using 4999 permutations of appropriate units. *P*-values given in italics were obtained using 4999 Monte Carlo samples from the asymptotic permutation distribution. The term used for the denominator mean square in each case is given in column MS$_{DEN}$. As there were no appropriate *F* denominators to test the main effects of *Cs* and *P*-vs.-*Cs*, five PERMANOVA analyses were also performed separating data for each time of sampling

Source of variation	d.f.	SS	MS	F	P	MS$_{DEN}$	Permutable units
Time = Ti	4	111 265·25	27 816·31				
Location = Lo	2	61 682·85	30 841·42				
Controls = Cs	1	29 968·65	29 968·65	nt			
P-vs.-Cs	1	31 714·20	31 714·20	nt			
Plot (Lo) = Pl(Lo)	6	16 466·62	2 744·44				
Pl(Cs)	4	11 746·00	2 936·50	1·512	0·086	Ti × Pl(Cs)	30 Ti × Pl(Cs) cells
Pl(P)	2	4 720·62	2 360·31				
Ti × Lo	8	28 713·64	3 589·21	1·900	0·002	Ti × Pl(Lo)	45 Ti × Pl(Lo) cells
Ti × Cs	4	11 891·57	2 972·89	1·531	0·078	Ti × Pl(Cs)	30 Ti × Pl(Cs) cells
Ti × P-vs.-Cs	4	16 822·08	4 205·52	1·414	*0·179*	Ti × Cs	10 Ti × Cs cells
Ti × Pl(Lo)	24	45 330·86	1 888·79	2·832	0·000	Residual	180 raw data units
Ti × Pl(Cs)	16	31 066·20	1 941·64	2·676	0·000	Res Cs	120 raw data units
Ti × Pl(P)	8	14 264·66	1 783·08	3·244	0·004	Res P	60 raw data units
Residual	180	120 033·84	666·85				
Res Cs	120	87 056·64	725·47				
Res P	60	32 977·20	549·62				

Source of variation	d.f.	Time 1 MS	F	P	Time 2 MS	F	P	Time 3 MS	F	P	Time 4 MS	F	P	Time 5 MS	F	P
Location = Lo	2	5407·25	2·592	0·004	5954·14	1·629	0·010	6300·48	2·106	0·014	4598·60	1·173	0·306	5545·28	1·337	0·082
Cs	1	5139·30	2·404	*0·030*	7335·25	2·007	*0·043*	8088·47	2·703	*0·004*	4730·84	1·207	*0·299*	5458·55	1·316	*0·218*
P-vs.-Cs	1	5675·19	1·104	*0·444*	4573·03	0·623	*0·779*	4512·48	0·558	*0·848*	4466·37	1·140	*0·331*	5631·01	1·358	*0·202*
Plot(Lo) = Pl(Lo)	6	2137·90	0·881	0·701	3655·73	1·471	0·007	2992·31	1·160	0·155	3919·17	1·625	0·009	4148·16	1·446	0·009
Res	36	2427·34			2484·99			2580·80			2411·69			2868·84		

nt = no test.

Table 2. PERMANOVA analyses investigating differences in patterns of recovery between protected versus control locations based on Bray–Curtis dissimilarities (no transformation) of the full multivariate data set (72 taxa × 450 samples). Each test was performed using 4999 permutations of appropriate units. The term used for the denominator mean square in each case is given in column MS$_{DEN}$. Terms already involved in significant higher-order interactions were not analysed

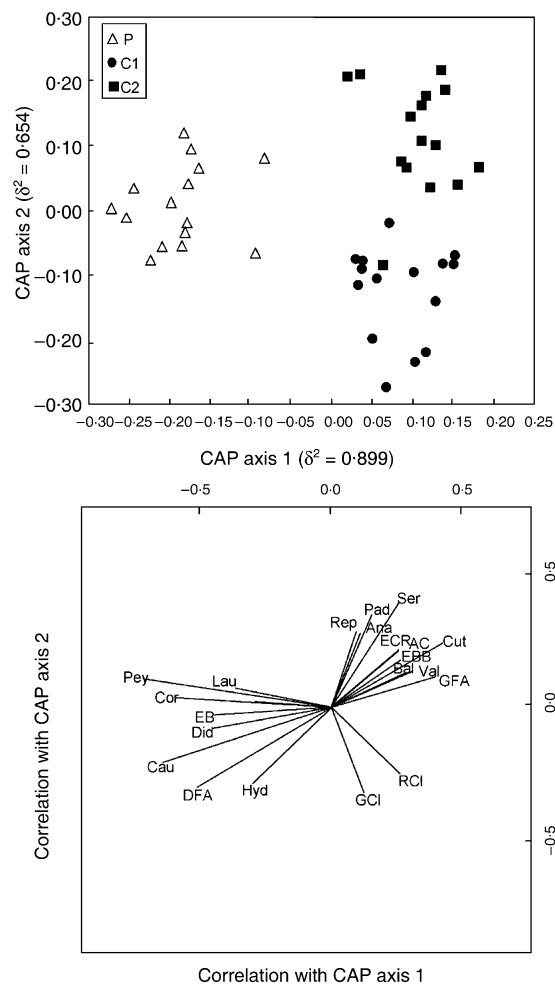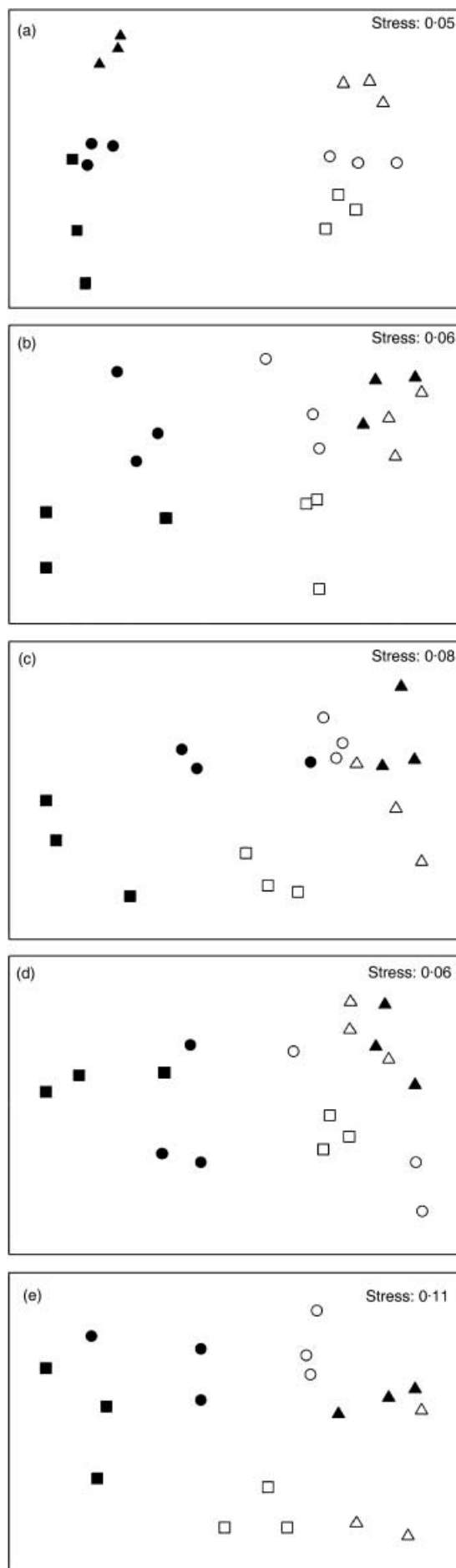| Source of variation	d.f.	SS	MS	F	P	MS$_{DEN}$	Permutable units
Time = Ti	4	175 591·76	43 897·94				
Treatment = Tr	1	95 626·45	95 626·45				
Location = Lo	2	136 681·45	68 340·72				
Controls = Cs	1	34 076·71	34 076·71				
P-vs.-Cs	1	102 604·74	102 604·74				
Plot (Tr × Lo) = Pl(Tr × Lo)	12	39 450·54	3 287·54				
Pl(Tr × Cs)	8	29 385·24	3 673·15				
Pl(Tr × P-vs.-Cs)	4	10 065·30	2 516·32				
Ti × Tr	4	45 865·46	11 466·37				
Ti × Lo	8	66 100·24	8 262·53				
Ti × Cs	4	22 294·06	5 573·51				
Ti × P-v-Cs	4	43 806·19	10 951·55				
Ti × Pl(Tr × Lo)	48	93 114·17	1 939·88				
Ti × Pl(Tr × Cs)	32	67 888·82	2 121·53				
Ti × Pl(Tr × P-vs.-Cs)	16	25 225·35	1 576·58				
Tr × Lo	2	36 975·33	18 487·66				
Tr × Cs	1	13 280·05	13 280·05				
Tr × P-v-Cs	1	23 695·27	23 695·27				
Ti × Tr × Lo	8	26 139·12	3 267·39				
Ti × Tr × Cs	4	8 329·49	2 082·37	0·982	0·465	Ti × Pl(Tr × Cs)	60 Ti × Pl(Tr × Cs) cells
Ti × Tr × P-vs.-Cs	4	17 809·62	4 452·41	2·295	0·003	Ti × Pl(Tr × Lo)	90 Ti × Pl(Tr × Lo) cells
Residual	360	298 683·75	829·68				
Res Cs	240	231 961·82	966·51				
Res P	120	66 721·94	556·02				

Fig. 3. Canonical analysis of principal coordinates (CAP) for the factor Location based on the distance matrix among sampling units in disturbed plots at the fifth time of sampling. White triangles = protected location (*P*); black circles = control location 1 (*C1*); black squares = control location 2 (*C2*).

and a few taxa of invertebrates [hydroids (Hyd), erect bryozoans (EB), *Didemnum* spp. (Did)] also characterized the assemblages at *P*. The assemblages at *Cs* were characterized by invertebrate taxa such as boring sponges [green Clionidae (GCl), red Clionidae (RCl)], encrusting bryozoans [encrusting brown bryozoans (EBB), *Reptadeonella violacea* (Rep)], serpulids [Serpulidae (Ser)] and barnacles [*Balanus perforatus* (Bal)]. With respect to algae, encrusting [encrusting calcified rhodophytes (ECR), Cutleriales (Cut)],

Fig. 2. Non-metric multidimensional scaling ordinations (nMDS) on the basis of the Bray–Curtis dissimilarity measure of plots' centroids of each location at (a) the first, (b) the second, (c) the third, (d) the fourth and (e) the fifth time of sampling. Centroids were calculated using principal coordinates (see text for further details). Triangles = protected location (*P*); circles = control location 1 (*C1*); squares = control location 2 (*C2*). Black symbols = disturbed plots; white symbols = undisturbed plots.
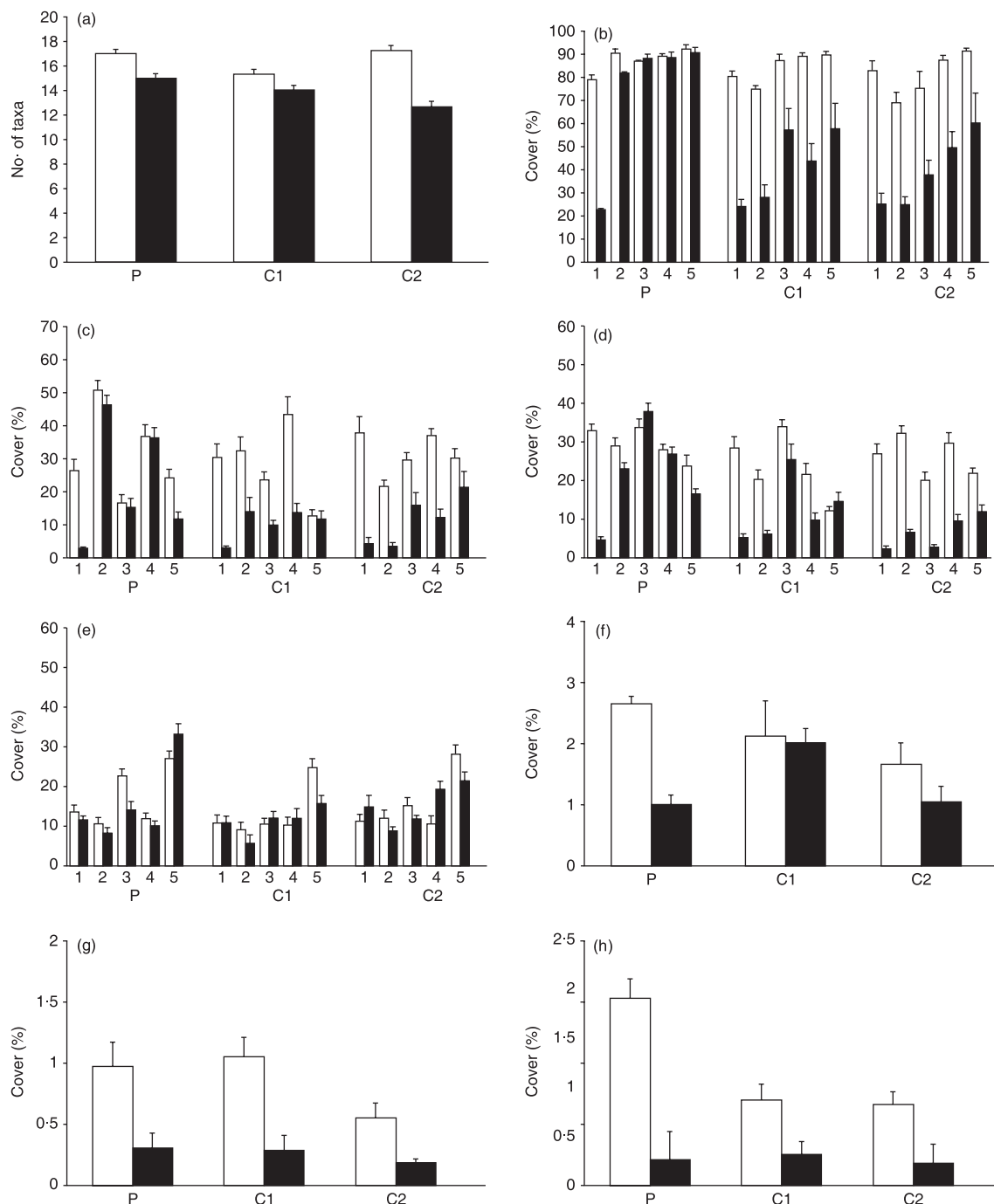
Fig. 4. Mean (± SE, *n* = 75) total number of taxa (a) at *P* and *Cs* (*C1* and *C2*) across time. Mean (± SE, *n* = 15) % cover of the whole assemblage (b), erect algae (c), turf-forming algae (d) and encrusting algae (e) at *P* and *Cs* (*C1* and *C2*) at each time of sampling (1, 2, 3, 4, 5). Mean (± SE, *n* = 75) % cover of sponges (f), hydrozoans (g) and bryozoans (h) at *P* and *Cs* (*C1* and *C2*) across time. Black bars = manipulated plots; white bars = not manipulated plots.

cryptic [*Valonia macrophysa* (Val), *Anadyomene stellata* (Ana)] and a few erect [*Padina pavonica* (Pad)] and turf-forming [articulated corallines (AC), green filamentous algae (GFA)] taxa also distinguished the assemblages at *Cs*. Asymmetrical ANOVA on mean number of taxa revealed the non-significance of the Ti × Tr × *Cs* and Ti × Tr × *P*-vs.-*Cs* interaction terms, indicating that differences among manipulated and unmanipulated plots across protected and unprotected locations did not vary through time (Table 3). *Post-hoc* comparisons

of the significant Tr × Lo term (Fig. 4a) revealed that the mean number of taxa across locations was always reduced in manipulated plots. A similar pattern was observed when examining invertebrates. The abundance of sponges, hydrozoans and bryozoans were lower in manipulated than in unmanipulated plots. However, although this effect varied in its magnitude across locations, it did not change through time (Table 3, Fig. 4f,g,h). Analyses of mean total cover, turf-forming algae, encrusting algae and erect algae highlighted a

Table 3. Summary of asymmetrical ANOVAs testing differences between protected and control locations in patterns of recovery of the mean number of taxa, mean total cover and mean cover percentage of morphological groups. Only tests relevant to hypotheses are reported. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS = not significant

	$Ti \times Tr \times Cs$		$Ti \times Tr \times P\text{-vs.-}Cs$	
	F	P	F	P
Number of taxa	0·186	NS	2·074	NS
Total cover	0·231	NS	12·416	***
Erect algae	0·426	NS	3·531	*
Turf-forming algae	1·526	NS	4·971	***
Encrusting algae	0·720	NS	4·000	**
Sponges	0·986	NS	1·537	NS
Hydrozoans	3·538	NS	0·171	NS
Bryozoans	1·178	NS	0·144	NS

Fig. 5. Mean ($\pm$ SE, $n = 60$) total number of sea urchins at P (white bar) and Cs ($C1$ and $C2$, black bars).

significant effect of protection in influencing differences among manipulated and unmanipulated plots through time. In all cases (Table 3, Fig. 4b,d,e) the increase of mean values in the manipulated plots was more rapid at P than Cs, indicative of faster recovery at the protected location. ANOVA also detected significant differences between P-vs.-Cs in sea-urchin densities, showing that sea urchins were significantly less abundant, on average, in the protected location than in controls. This pattern was consistent through time, as indicated by the non-significance of the $Ti \times Lo$ interaction term (Table 4, Fig. 5).

Discussion

Despite the widespread occurrence of DMF in the Mediterranean Sea (about two-thirds of the shallow calcareous subtidal rocky shore is affected along the Italian coasts; Fanelli *et al.* 1994) and its large and significant impact on coastal biota (Guidetti *et al.* 2003; Guidetti & Boero 2004), patterns of recovery of benthic assemblages from this disturbance are poorly understood. The impact of DMF on rocky assemblages has been explored through mensurative studies (Fraschetti *et al.* 2001), but no attempt has been made to quantify its effect experimentally. This study has
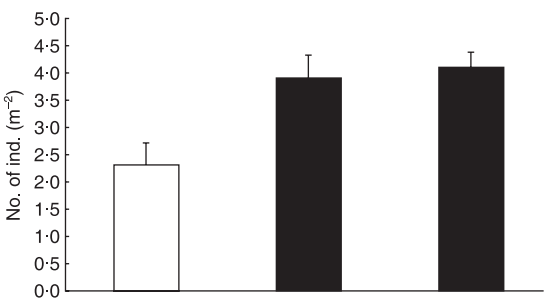
demonstrated that the DMF significantly reduces the mean number of taxa, resulting in the complete disappearance of several algal and invertebrate species (e.g. *Codium bursa*, *Tricleocarpa fragilis*, *Chondrosia reniformis*, *Hemimycale columella*, *Ircinia variabilis*, *Petrosia ficiformis*, *Serpulorbis* sp., *Ciona intestinalis*). Such a pattern, although variable in its magnitude, was observed at both P and Cs. The negative effects of DMF on mean total cover acted mainly on algal turf, erect algae and large invertebrates. This affected the three-dimensional structure of assemblages that switched from high-cover, multilayered systems to sparse and mono-layered ones. Consequently, the loss of biodiversity could be more severe than that quantified in the present study. By dismantling the whole endo- and epibenthic assemblages, DMF compromises the primary and secondary production of shallow rocky reefs. As a consequence, DMF could affect also vagile invertebrates and fish due to reduced habitat complexity and depletion of food resources (Fanelli *et al.* 1999; Chemello & Milazzo 2002; Guidetti *et al.* 2004). Sessile assemblages in the unmanipulated plots were composed of taxa encompassing a wide range of life cycles, dispersal and reproductive strategies. Different ecological processes such as pre- and post-settlement mortality (Hunt & Scheibling 1997; Fraschetti *et al.* 2003), variation in recruitment (Grantham, Eckert & Shanks 2003) and vegetative regrowth potential of taxa (Airoldi 2000a) are likely to contribute to driving the ecological secondary succession observed in manipulated plots

Table 4. Asymmetrical ANOVA testing differences in sea urchins' density between protected versus control locations. ***$P < 0.001$; NS = not significant

Source of variation	d.f.	SS	MS	F	F versus
Time = Ti	2	0·08	0·04		
Location = Lo	2	14·02	7·01		
Controls = Cs	1	0·85	0·85	0·988 NS	$Ti \times Cs$
P-vs.-Cs	1	13·17	13·17	22·706***	Residual
$Ti \times Lo$	4	2·33	0·58	1·289 NS	Residual
$Ti \times Cs$	2	1·71	0·86	2·263 NS	Res Cs
$Ti \times P$-vs.-Cs	2	0·62	0·31	0·689 NS	Residual
Residual	171	76·97	0·45		
Res Cs	114	43·49	0·38		
Res P	57	33·48	0·59		

(Connell & Slayter 1977; Breitburg 1985). In this study, the experimental disturbance produced medium-sized 'embedded patches' (*sensu* Holt, Robinson & Gaines 1995) that were characterized by a species' legacy from original assemblages, involving fragments and small colonies that had escaped complete desertification. Under such circumstances, local sources of recolonization by lateral growth and sexual propagules from neighbours and vegetative propagation from fragments are likely to have greater importance than external larval supply in shaping the structure of assemblages following disturbance (Connell & Keough 1985). Results indicated that recovery from DMF disturbance, although varying interactively with protection, was driven mainly by encrusting and turf-forming algae which, in turn, largely characterized the nearby undisturbed assemblages. These algal groups are known to gain space very rapidly after disturbance, regardless of the temporal and spatial variability of it's occurrence (Airoldi 2000b). Sessile invertebrates probably need much more time to exhibit evidence of recovery due to their complex life cycles (Vance 1973) or slow rates of growth and recruitment (Watling & Norse 1998). For instance, long-living filter-feeders heavily affected by DMF disturbance, such as large sponges, may return at a later stage in disturbed patches. Thus, even though the recovery of some structural properties of assemblages impacted by DMF (e.g. cover) may occur quickly through rapid vegetative regrowth of macroalgal species and short-living invertebrates, long-lasting periods may be needed for the recovery of assemblage functioning, especially when important functional groups of organisms are characterized by long life cycles, planktonic larval recruitment and low growth rates.

Variations in patterns of recovery could have reflected differences in the composition of natural assemblages between *P* and *Cs*. In fact MPAs, regardless of their size and with few exceptions, are known to increase density, biomass, individual size and diversity in all functional groups (Halpern 2003; Micheli *et al.* 2004a). Therefore, variations in recovery trajectories of disturbed assemblages between *P* and *Cs* could be attributable to differences in existing surrounding assemblages (Allison 2004). Interestingly, there were no significant differences in undisturbed assemblages between *P*-vs.-*Cs*. The significant variations in patterns of recovery between *P* and *Cs* were thus likely to depend on factors other than differences in assemblage structure and composition. These findings underscore the fact that even when protection has not, or has still not had, direct effects on benthic assemblages, it may affect resilience through indirect effects on ecological recolonization processes arising after the occurrence of disturbance. Sea urchins, for instance, with effects varying with their natural fluctuations in abundance and/or disrupted trophic cascades, can mediate the trade-off between recolonization strategies and competitive abilities of turfing, erect and encrusting algae, influencing spatial dominance

relationships among different algal groups (e.g. Paine & Vadas 1969; Hagen 1983; Himmelman 1986; Hart & Schiebling 1988; Estes, Duggins & Rathbun 1989; Bulleri, Benedetti-Cecchi & Cinelli 1999). Their unselective grazing on new settlers could play a crucial role in the maintenance of the bare state in disturbed patches (McClanahan *et al.* 1996), especially when the disturbance results in a topographic homogenization of the substrate. Our experiment was not designed to test the interactive role of grazing and protection on recovery dynamics. Densities of sea urchins, however, were significantly lower in *P* than in *Cs*. As observed in other studies (e.g. Sala & Zabala 1996; McClanahan 2000; Shears & Babcock 2002), decreased fishing pressure on large fish predators inside MPAs could trigger trophic cascades resulting in a decrease of sea-urchin populations and, consequently, in reduced rates of grazing on sessile assemblages. Preliminary results of a research programme carried out in the same area (G. F. Russo, unpublished data) did not detect a significant effect of protection on either abundance or size of predatory fish (i.e. sparids), suggesting care in invoking classical trophic cascades as a potential mechanism to explain patterns of sea-urchin distributions at *P*-vs.-*Cs*. Even though low sea-urchin densities can exert a significant control on macroalgal stands (Palacín *et al.* 1998; Guillou, Grall & Connan 2002), differences between *P* and *Cs* in sea urchin density are likely to be too small to produce significant changes in undisturbed assemblages (Kitching & Thain 1983; Palacín *et al.* 1998). On the other hand, these differences could be large enough to affect the recolonization of taxa vulnerable to grazing, thus possibly explaining the lack of differences in undisturbed assemblages between *P* and *Cs* coupled with different recovery trajectories of disturbed assemblages. Sea-urchin grazing typically involves a significant effect on turfing and erect algae, whereas encrusting algae and invertebrates are less affected (e.g. Andrew & Underwood 1993; Benedetti-Cecchi, Bulleri & Cinelli 1998). Accordingly, most taxa characterizing the manipulated plots in *Cs* at the end of the study (e.g. encrusting algae and invertebrates, endolithic sponges, calcareous tube worms, barnacles) had biological and ecological traits that could confer higher resistance to grazing than erect and turf algae which, instead, were the dominant taxa in manipulated plots at *P* at the end of the study. Besides changes in biological processes arising inside MPAs, alternative explanations of different patterns of assemblage recovery between *P* and *Cs* could be invoked considering possible differences in physical traits, such as in the supply of nutrients, or in interactive effects among biological and physical factors. Indeed, bottom-up and top-down controls may coparticipate, from the early stages, in shaping macroalgal assemblage structure (Lotze, Worm & Sommer 2001). Grazing and nutrients load, for instance, may interact in determining dominance relationships among algal groups in temperate coastal systems (Russell & Connell 2005). In our case,

however, the lack of evident sources of organic pollution in the entire experimental area led us to consider the supply of nutrients as homogeneous across locations. The insular nature of the protected location, moreover, could have affected assemblages structure patterns (Brown & Lomolino 2000; Benedetti-Cecchi *et al*. 2003). With the inclusion of an island (*CI*) as a control location, the natural variability in the study area was estimated to also include these possible differences and their effects on patterns of recovery. The recovery of disturbed assemblages was significantly different between *P* and *Cs*, suggesting a significant effect of protection on recovery patterns, over and above any differences between islands and the mainland. This finding confirms the need for the careful selection of multiple control locations to avoid the possible confusions between the 'reserve effect' and habitat features when comparing protected and unprotected locations (García-Charton & Pérez-Ruzafa 1999; Fraschetti et al. 2005). The dramatic effect of DMF on benthic assemblages exemplifies the outcome of a wide range of human impacts involving strong mechanical disturbance (such as coral mining, trawling, dredging, anchoring), which lead to extensive habitat destruction and open patches in subtidal systems (Peterson & Estes 2001). Sea-urchin grazing may affect post-settlement events, compromising systems' resilience and maintaining the secondary successions in disturbed patches at early stages (Nyström, Folke & Moberg 1998; Bulleri, Bertocci & Micheli 2002). In such cases recovery after disturbance may take a long time, both for structural components and processes, depending on the length of reproductive cycles and the complexity of interspecific relationships in highly structured marine systems (Roberts *et al*. 2003).

One of the hypothesized benefits of protection in MPAs consists of maintaining or rebuilding ecosystem resilience, and thus the system's ability to recover from catastrophic natural or anthropogenic disturbances (e.g. Bellwood *et al*. 2004). However, a substantial lack of studies have tested this hypothesis directly in the field. Here, we provide evidence that benthic assemblages within a no-take, no-access Mediterranean marine reserve exhibit faster recovery from disturbance than assemblages at unprotected locations, with the recolonization of dominant taxonomic groups. The protection effect seems to accelerate recolonization processes with no apparent change in the direction of recovery trajectories toward different assemblage structures. Thus, even though large-scale processes (e.g. external larval supply) could be fundamental in the recolonization of disturbed patches, outcomes are likely to be influenced strongly by local factors (Micheli *et al*. 2005) and protection may affect the dynamics of recovery through its influence on such small-scale processes (e.g. competitive trade-offs, herbivory) (Hixon & Brostoff 1996). Processes and dynamics underlying recovery of disturbed assemblages, however, are likely to show substantial variations in response to habitat features and can also depend on the

organisms involved. This calls for replicated, long-term experimental inspections aiming at assessing whether the increased systems' resilience could be a general consequence of protection. In this framework, the use of MPAs as natural laboratories for experimental ecology may provide powerful tools in exploring the response of different assemblages to a wide range of human disturbance (Castilla 1999, 2000). If protection has the potential to enhance assemblage resilience, then MPAs, in addition to protecting the structure of natural systems, may contribute to conserve their dynamic properties (Dayton *et al*. 2000). Understanding this potential role in insuring the long-term persistence of assemblages is strongly needed to define valuable strategies for the mitigation of human disturbance and to improve the management of coastal systems.

Acknowledgements

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Supplementary material

The following supplementary material is available for download as part of the full-text version of this article from http://www.blackwell-synergy.com.

Appendix S1. Taxonomic list of the species (or species groups) recorded.