

## CASCADING HUMAN IMPACTS, MARINE PROTECTED AREAS, AND THE STRUCTURE OF MEDITERRANEAN REEF ASSEMBLAGES

FIORENZA MICHELI,<sup>1,6</sup> LISANDRO BENEDETTI-CECCHI,<sup>2</sup> SILVIA GAMBACCINI,<sup>3</sup> IACOPO BERTOCCHI,<sup>2</sup>  
COSTANZA BORSINI,<sup>4</sup> GIACOMO CHATO OSIO,<sup>5</sup> AND FEDERICO ROMANO<sup>2</sup>

<sup>1</sup>Hopkins Marine Station, Stanford University, Pacific Grove, California 93950 USA

<sup>2</sup>Dipartimento di Scienze dell'Uomo e dell'Ambiente, Università di Pisa, 56126 Pisa, Italy

<sup>3</sup>Centro Interuniversitario di Biologia Marina e Ecologia Applicata, Livorno, Italy

<sup>4</sup>Dipartimento di Biologia Animale e Genetica, Università di Firenze, 50124 Florence, Italy

<sup>5</sup>WWF Mediterranean Programme Office, Marine Unit, 00198 Rome, Italy

**Abstract.** Coastal marine assemblages are shaped by interactions between physical factors, biological interactions, and almost ubiquitously, human impacts. Large-scale manipulations of human access replicated over a range of physical and biological conditions can generate insights over the processes shaping marine assemblages. We examined the relative roles of human impacts and hydrographic conditions on assemblages of shallow (3–10 m depth) rocky reefs by comparing no-take reserves with fishing areas occurring in gradients of exposure of the coastline to dominant winds and waves around two Mediterranean islands, Capraia and Giannutri, Italy. We hypothesized that fishing influences assemblages directly by reducing populations of target fish species, and indirectly by reducing predation on sea urchins, intensifying herbivory, and causing “barrens” of encrusting coralline algae. We examined how the possible effects of fishing varied with physical exposure of the coastline.

The composition of fish assemblages differed significantly between sites within no-take reserves and fished reference sites. Abundances and sizes of predatory fishes targeted by local fisheries were greater in no-take reserves than in fished areas. Sea urchin densities, the extent of coralline barrens, and the structure of the algal and invertebrate benthic assemblages showed clear variation associated with exposure of the coastline to dominant winds and waves, but weak effects of protection from human use. Densities of the black sea urchin *Arbacia lixula* were significantly greater along the windward than along the leeward sides of the islands, and were positively correlated with the extent of coralline barrens. In contrast, the purple sea urchin *Paracentrotus lividus* was more abundant along the leeward sides of islands and showed indirect responses to protection at Giannutri, where purple sea urchins tended to have greater densities at fished than at protected sites. Protection from fishing influenced fish assemblages directly, and benthic assemblages indirectly, but the latter effect was observed only at sites with lower physical exposure. Indirect effects of fishing and recovery of assemblages within marine protected areas through cascading trophic interactions are likely to vary depending on local physical conditions and on the characteristics of species that are locally dominant.

**Key words:** coralline barrens; fishing impacts; human impacts; marine protected areas; Mediterranean Sea; no-take marine reserves; recovery; temperate rocky reefs; trophic cascades; Tuscan Archipelago.

### INTRODUCTION

Major questions in ecology regard the interactions of abiotic and biotic processes and the role of indirect effects, in which the interaction between two species has positive or negative effects on a third species, in structuring natural assemblages. In the marine environment, extensive research has examined the relative importance and joint effects of oceanographic processes and local biotic interactions (Roughgarden et al. 1988, Bustamante et al. 1995, Bertness et al. 2001),

the variation in intensity and in the consequences of biotic interactions along gradients of physical stress, disturbance, and recruitment intensity (Sousa 1979, Menge and Sutherland 1987, Menge and Farrel 1989, Connolly and Roughgarden 1999), and the frequency and importance of indirect interactions such as keystone predation (Paine 1966, Menge et al. 1994, Power et al. 1996) and trophic cascades (Menge 1995, Estes et al. 1998, Sala et al. 1998a).

In recent years, it has become clear that humans are crucially important forces shaping marine assemblages, both modifying the physical environment where organisms live and directly and indirectly impacting populations and assemblages (Botsford et al. 1997, Vitou-

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<sup>6</sup> E-mail: micheli@stanford.edu

sek et al. 1997). Globally, nearly 70% of fish and invertebrate stocks are depleted or heavily exploited (Botsford et al. 1997, FAO 1997). In addition, fishing impacts nontarget species and habitat (Dayton et al. 1995, Watling and Norse 1998), and alters food web structure and interactions (Fogarty and Murawski 1998, Pauly et al. 1998, Micheli et al. 2001), causing major changes to marine systems worldwide over historical times (Jackson et al. 2001, Myers and Worm 2003, Pandolfi et al. 2003). Thus, humans and human activities in the marine environment must be included as important interactors, directly influencing species dynamics, and triggering indirect effects and change in the structure of whole assemblages. Most importantly, human impacts alter, combine, and interact with natural forces and processes shaping marine ecosystems. Studies of the consequences of human interventions on natural systems should explicitly account for and integrate natural variability in physical conditions and assemblages.

Restrictions on human uses of marine resources within marine protected areas (MPAs) provide large-scale manipulations of human activities, and allow for investigations of human impacts on individual populations and whole assemblages. Comparisons between no-take marine reserves and adjacent fished areas, or prior and following the establishment of marine reserves (e.g., Halpern 2003), or among fishing grounds with varying fishing intensity (Jennings and Polunin 1996) have shown that protection from fishing generally leads to greater abundances, biomasses, sizes, and diversity in coastal marine assemblages. Effects vary depending on the species life histories and degree of exploitation. In particular, meta-analyses of studies of reserve effects on fish assemblages found that species that are targeted by fisheries, reach large sizes, or are at top trophic levels show the strongest responses (Mosquera et al. 2000, Micheli et al. 2004b). To date, most information about effects of reserves is available for single species and for fish populations; much less is known about how protection influences benthic taxa, whole assemblages, and ecological interactions (Palumbi 2001). In addition, most existing studies are limited in their temporal and spatial replication. For example, Russ (2002) found that only six out of 25 studies of effects of marine reserves included spatial replication of reference sites, and only four included data prior to reserve establishment.

In addition to direct effects on survivorship and reproduction of target species, protection in no-take reserves can cause indirect changes to assemblages, through cascading trophic interactions (Steneck 1998, Pinnegar et al. 2000). In the Las Cruces marine reserve, central Chile, the predatory gastropod *Concholepas concholepas* increased in abundance within the reserve compared to adjacent areas where it was harvested. Increased predation by *Concholepas* on its prey, particularly mussels, led to the almost complete elimi-

nation of mussel beds, which were replaced by barnacles and algae (Castilla 1999). Similar cascading effects of predators increasing within marine reserves have been documented both in intertidal (Hockey and Branch 1984, Lindberg et al. 1998) and subtidal (Sala and Zabala 1996, Babcock et al. 1999, McClanahan et al. 1999, Shears and Babcock 2002) reefs.

Oceanographic conditions, recruitment variability, food subsidies, substrate topography and the availability of shelters, and the composition of the consumers and prey guild interact in shaping marine assemblages and can determine the occurrence and outcome of cascading trophic interactions in coastal marine assemblages (Harrold and Reed 1985, Foster and Schiel 1988, Watanabe and Harrold 1991, Estes and Duggins 1995, Sala et al. 1998a). Thus, trophic interactions are variable in space and time due to environmental variation and fluctuations in numbers of interacting organisms, as illustrated by studies on interactions among fishes, sea urchins, and algae within and outside reserves in the Mediterranean (Sala and Zabala 1996, Sala et al. 1998b). Although cascading effects of fishing and, conversely, recovery in marine reserves have been documented in a suite of locations and ecosystems types (e.g., Pinnegar et al. 2000), the question remains of how their intensity varies along physical gradients and with species characteristics (e.g., Micheli et al. 2001). Studies examining variation along physical gradients and responses of multiple species are needed.

We used four no-take, no-access marine reserves established in 1989 within the Tuscan Archipelago, in the northwestern Mediterranean Sea, to test hypotheses about possible effects of protection, to quantify variation in fish and benthic rocky reef assemblages, and to examine possible correlates of the extent and distribution of sea urchin barrens. The existence of multiple no-take reserves, located on different islands and with varying exposure to dominant winds and waves, allowed for a test of the generality of possible effects of fishing on rocky reef assemblages through trophic interactions, as well as of the alternative hypothesis that variation in hydrodynamic conditions may underlie the distribution and extent of sea urchin barrens (see Plate 1) and the overall structure of the reef assemblages.

We quantified spatial and temporal variation in the structure of the fish and benthic assemblages around the islands of Giannutri and Capraia, contrasting shores that differed in protection regime (no-take, no-access reserves vs. areas with partial or no protection) and exposure to seasonally dominant winds. We used this extensive data set to examine effects of protection in no-take, no-access marine reserves on benthic and fish assemblages of shallow rocky reefs, and the distribution and extent of sea urchin barrens in relation to variation in human fishing pressure and hydrodynamic conditions (i.e., physical exposure of the coastline). Specifically, the following set of conditional hypoth-

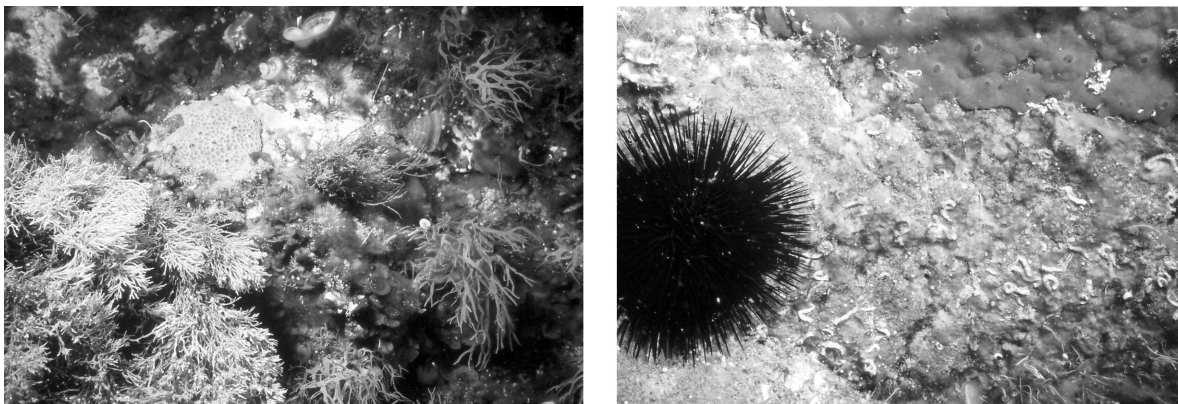


PLATE 1. Benthic algal and invertebrate communities in 16 × 24-cm plots (left) outside and (right) within sea urchin barrens near Giannutri Island, Italy. The black sea urchin, *Arbacia lixula*, is seen in the right-hand photo. Photo credits: F. Micheli and C. Borsini.

eses originated from existing theory on cascading trophic interactions in marine protected areas (MPAs) were examined: (1) species of fishes that are fished by recreational and artisanal fisheries should be more abundant in no-take, no-access reserves compared to reference, fished sites; (2) because targeted species of fishes include predators of sea urchins, we would predict that the abundance of these invertebrates is lower in reserves compared to reference sites; and (3) benthic assemblages in reserves would be different from those outside reserves, the latter having larger extent of sea urchin barrens and lower diversity. Furthermore, we also tested whether expected differences between reserves and fished sites changed in relation to physical exposure of the coastline.

#### METHODS

##### *Study area and marine protected area zoning*

Field surveys were conducted around the islands of Capraia and Giannutri, two of the seven islands of the Tuscan Archipelago, off the northwestern coast of Italy (Fig. 1). The coastal marine environment around these islands is protected through the establishment of marine zones varying in the degree of restriction of human activities (Fig. 1). All fishing and recreational activities, including boating, anchoring, swimming, snorkeling, and walking on the shore are prohibited in Zone 1, which extends 1 km from the shoreline. Recreational activities are allowed in Zone 2, as well as fishing by residents of these islands and by nonresidents to whom the administration of the National Park of the Tuscan Archipelago has granted fishing permits. Thus, angling and fishing with long lines, gill nets, and traps are carried out year-round within Zone 2, which extends three nautical miles (5.56 km) from the shoreline. Finally, no additional restrictions of human activities are in place outside of Zones 1 and 2 (i.e., Zone 3), except for fishery regulations enforced along all Italian coastlines (e.g., trawling is not allowed at depths shallower

than 50 m). Both islands have limited human development, and alteration of the coastline and pollution are not likely to have significant impacts on coastal marine assemblages.

Marine protected areas (MPAs) were established in Capraia and Giannutri in July 1989, but no agency was officially charged with the mandate to manage the MPAs and enforce restrictions within Zones 1 and 2 until 1996, when the National Park of the Tuscan Archipelago was established and the Coast and the Forestry Guards assigned personnel for surveillance around the islands. Three separate no-take, no-access zones (Zone 1) were established at Giannutri, protecting ~40% of the 11 km Giannutri coastline (Fig. 1). A single no-take, no-access zone was established on Capraia (Fig. 1), comprising ~20% of the 27 km coastline of Capraia.

Unfortunately, no data on conditions prior to the establishment of the reserves exist for these islands. The problem of a lack of prior data is common to most marine reserves (e.g., Fraschetti et al. 2002, Russ 2002), and prevents the application of BACI (before–after/control–impact; e.g., Green 1979, Stewart-Oaten et al. 1986, Schmitt and Osenberg 1996) or beyond-BACI (Underwood 1992) designs for a rigorous evaluation of the effects of protection on populations and assemblages. Lack of “before data,” however, should not prevent us from conducting post impact studies (e.g., Glasby 1997) or, as it is done in the present analysis, from examining whether assemblages within reserves differed from those in fished areas. The existence of multiple reserves, established simultaneously on both islands, provided a unique opportunity to examine effects of protection with adequate spatial and temporal replication. By means of a multifactorial sampling design, we were able to take into account natural variation at several nested spatial scales and through time. Though the study remains correlative in nature, accounting for spatial and temporal variation increased

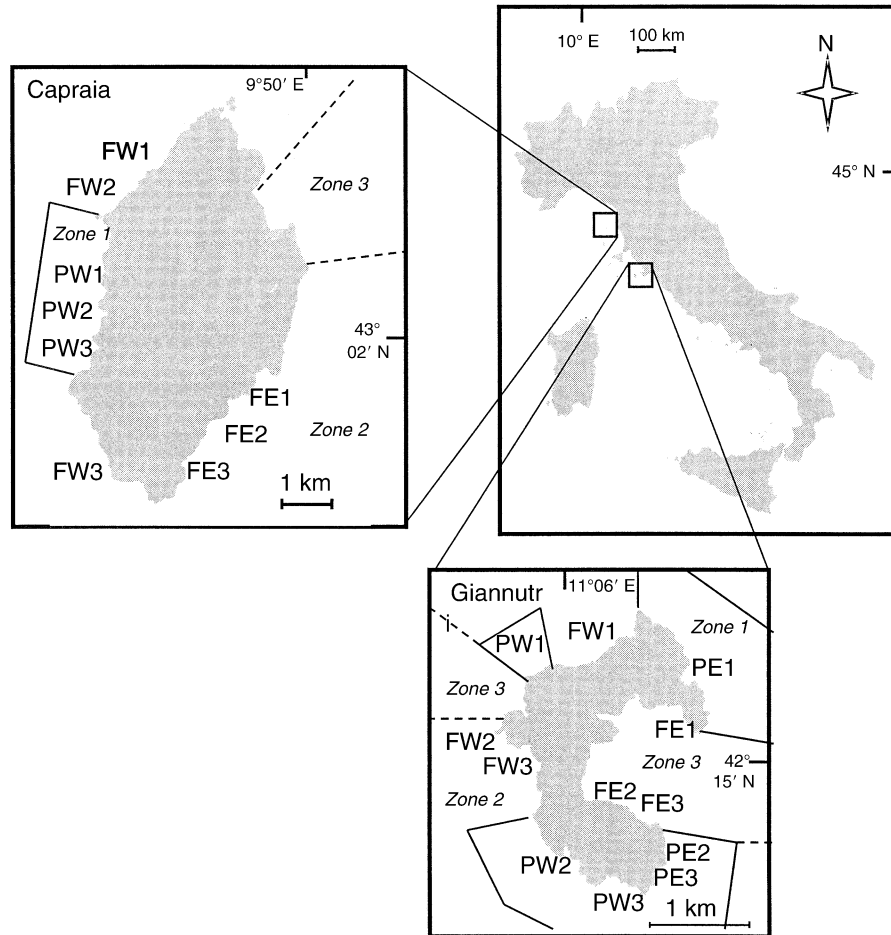


FIG. 1. Map of the study areas, showing the location of the no-take, no-access reserves (delimited by solid lines) on the islands of Capraia and Giannutri, and location of the 21 shores where fish and benthic surveys were conducted. Dotted lines represent the boundaries of Zones 2, where recreational activities and fishing are allowed. Shores were assigned to one of the following categories: protected shores located on the western side of the island (PW); fished shores located on the western side of the island (FW); protected shores located on the eastern side of the island (PE); fished shores located on the eastern side of the island (FE). Protected eastern shores were not present at Capraia.

our ability to tease apart possible effects of protection from other factors. Protection from human disturbances would still remain the most plausible explanation for any observed difference between protected and fished areas on these islands.

We assumed that fishing occurs year-round throughout Zones 2 and 3, whereas no fishing occurs in Zone 1, the no-take, no-access reserves. Most fishing is conducted by island residents and by day visitors from the mainland, particularly for Giannutri (F. Micheli, *personal observations*). Because local recreational and artisanal fishing is essentially unreported, it is difficult to quantify actual spatial distribution and intensity of fishing activities around these islands. Our assumption that the establishment of no-take zones has resulted in distinct spatial variation in fishing intensity around these islands is based on the following observations. First, during the hundreds of hours we spent in the field, we frequently observed fishing occurring in

Zones 2 and 3, primarily with long lines and gill nets, but found long lines within Zone 1 only once, at Giannutri (fishing gear was immediately removed by the local guards). Interviews that we conducted with local diving operators at Giannutri and Capraia confirmed our observations that fishing commonly occurs in Zones 2 and 3, but not in Zone 1. Second, whereas the majority of reserves examined in the ecological literature allow for nonextractive uses, these reserves are unique in that all human uses are prohibited within Zone 1. This restriction greatly decreases the likelihood that illegal take by visitors to the reserve may occur. Finally, onsite personnel have been assigned to the enforcement of fishing and access restrictions in both islands. Given the small size of these islands, the presence of onsite personnel further decreases the likelihood that fishing occurs within the no-take reserves. Thus, while poaching within the no-take reserves cannot be ruled out, our observations and the unique fea-



tures of these reserves (no-access status and local enforcement) indicate that clear differences in fishing intensity between no-take reserves and surrounding areas must exist.

In addition to variation in the types and intensity of human activities associated with MPA zoning, there are distinct patterns of variation over scales of kilometers in physical conditions associated with exposure of the coastline to winds and waves and in the extent and distribution of different habitat types. The western sides of the islands are affected by major winter storms from the west and southwest. The eastern side is affected by strong winds from northeast and southeast, particularly in fall and winter. However, the exposure to storms also varies between the two islands, in that the eastern side of Giannutri is relatively protected from easterly winds because of its proximity to the mainland (12 km), whereas easterlies have a larger fetch at Capraia, which is located 64 km away from the mainland. In contrast, westerlies blow virtually unobstructed by landmasses at Giannutri but have a shorter fetch at Capraia, which is located 25 km away from the island of Corsica.

To determine how the distribution of different habitat types varied around the islands, we quantified the relative proportion of different habitats using published benthic maps available for all islands of the Tuscan Archipelago (*available online*).<sup>7</sup> Maps had been developed with Side Scan Sonar followed by ground truthing by scuba divers. The distribution of types of habitat around the two islands is reported in Appendix A.

#### *Surveys of fish and benthic assemblages*

To determine whether abundances of sea urchins, their fish predators, and the structure of the whole fish and benthic assemblages varied with human use and physical characteristics of the coastal marine environment, we conducted extensive field surveys around the islands of Capraia and Giannutri. We quantified spatial variation in focal species abundances and in the composition of shallow (between 3 m and 10 m in depth) fish and benthic assemblages along multiple 100–150 m stretches of the rocky coastline (“shores”) of each island.

We sampled 21 shores, 12 in Giannutri and 9 in Capraia (Fig. 1). At Giannutri, three shores were selected randomly within the following combinations of protection regime and coastline exposure: (1) three shores within no-take, no-access reserves on the protected western side of the island (PW1, Villa Romana; PW2, Cala Brigantina; and PW3, Grottoni); (2) three shores within no-take, no-access reserves on the protected eastern side of the island (PE1, Cala dello Scoglio; PE2, Cala Scirocco; and PE3, Punta Capel Rosso); (3) three shores within fished areas on the western side of the island (FW1, Punta Secca; FW2, Punta Pennello;

and FW3, Cala Ischiaiola); and (4) three shores within fished areas on the eastern side of the island (FE1, Punta San Francesco; FE2, Cala Volo di Notte; and FE3, La Scaletta). At Capraia, the only no-take reserve is located on the western side of the island (Fig. 1), resulting in three types of shores: (1) three shores within no-take, no-access reserves on the western side of the island (PW1, Punta Nord di Cala del Fondo; PW2, Punta Sud di Cala del Fondo; and PW3, Cala del Vetriolo); (2) three shores within fished areas on the western side of the island (FW1, Strisce Gialle; FW2, Punta della Seccatoia; and FW3, Punta delle Linguelle); and (4) three shores within fished areas on the eastern side of the island (FE1, Punta del Patello; FE2, Punta del Capo; and FE3, Punta del Turco).

Because this study was conducted within marine protected areas, we used nondestructive, visual sampling methods for both the fish and benthic surveys. Fish abundances, size structure, and species composition were quantified by conducting eight replicate visual censuses along each of the 21 shores, using a modification of the stationary point count method of Bohnsack and Bannerot (1986). Stationary point counts were selected over other visual census methods (e.g., belt transects) to allow for high replication within the relatively small and heterogeneous field sites. A recent comparison between belt transects and stationary points conducted in another Italian MPA (Miramare, in the northern Adriatic Sea) found no significant differences in total fish abundances estimated through the two methods, although there were trends for greater abundances in belt transects for several species (P. Guidetti, *unpublished data*).

To ensure consistency of sampling methods and taxonomic resolution, two of us (S. Gambaccini and F. Romano) conducted all point counts. Point counts were conducted at 10-m depths by counting and identifying all fish within a 5-m radius cylinder of the water column while slowly rotating the observer’s field of view 360° from a fixed point over a 5-min period. Individuals were assigned to one of three size classes (small, medium, and large). The small, medium, and large size classes corresponded to the lower, intermediate, and upper 30% range of sizes reported in the literature for each species. Prior to this study, observers had trained in estimating sizes of different fish species in the field using outlines drawn on PVC slates. At the end of each 5-min count, an additional minute was spent searching for benthic fish species, such as Gobiidae and Blenniidae, on the sea floor within a 5-m radius from the observation point. Following each point count, divers moved to a new location, tens of meters away from the previous point count, by performing a randomly drawn number of fin kicks. To avoid confounding effects of day–night variation in fish assemblages, point counts were always conducted between 09:00 and 14:00 hours. Fish surveys were repeated, following an identical pro-

<sup>7</sup> (<http://gis.cnuce.cnr.it/posid/html/arcip.html>)

TABLE 1. ANOVA on total abundance of fish, number of fish species, cumulative abundance of sea urchin predators (i.e., *Diplodus sargus*, *D. vulgaris*, *Coris julis*, and *Thalassoma pavo*), and cumulative abundance of sea urchin predators in the largest size class at Capraia, Italy.

Source	df	Total abundance		No. species	
		MS	F	MS	F
Shore type = ST	2	0.9	0.25	170.7	32.0**
Shore(ST) = sh(ST)	6	3.7	1.37	5.3	0.45
Date = DA	2	5.5	2.02	121.5	10.1**
ST × DA	4	1.0	0.37	8.0	0.67
DA × sh(ST)	12	2.7	8.69***	12.0	2.4**
Residual	189	0.3		5.0	
Transformation		log(x + 1)		...‡	
Cochran's test		C = 0.15*		C = 0.08 NS	

Notes: For each variable, MS, F ratios, and significance level are reported. The effect of shore type (i.e., shores protected in no-take, no-access marine reserves along the west side of the island, fished shores along the west side, and fished shores along the east side) was tested over the shore(ST; i.e., shore nested within shore type, with three replicate shores for each shore type), mean square after elimination of the ST × DA term when this term was not significant at  $P > 0.25$ . NS = not significant. See *Methods: Surveys of fish and benthic assemblages*.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

† No F test was done.

‡ No transformation was done.

to col, in May, October, and December 2000, for a total of 504 point counts.

Benthic assemblages were surveyed along the same shores using two different methods, photographic sampling and quadrat sampling. Benthic assemblage composition was quantified using photographic sampling. Photographs were taken using a Nikonos-V 35 mm underwater camera, equipped with a 28 mm objective and macro lens, and a metal distancer and framer ensuring that each photograph covered the same surface of the rocky substrate (a  $16 \times 24$  cm rectangle). All sampling was conducted using Fuji Sensia 100 A slide film. Slides were projected onto a grid of twenty-five  $10 \times 10$  cm subquadrats and percent cover of each species or species group was estimated visually within each subquadrat using a score of 0 (absence of that species or species group) to four (when the species occupied the entire subquadrat). Scores were then summed over the 25 subquadrats to obtain estimates of percent cover (Dethier et al. 1993, Benedetti-Cecchi et al. 1996).

Invertebrates and algae were identified to species whenever possible (following Riedl 1991). When organisms could not be confidently identified to species, they were assigned to broader taxonomic or morphological categories. Taxonomic groups included sponges, hydrozoans, anemones, ascidians, gastropods, bryozoans, vermetid gastropods, and serpulid, sabellid, and terebellid polychaetes. Morphological algal groups were based on the categories proposed by Littler and Arnold (1982), and included articulated coralline algae, encrusting coralline algae, encrusting fleshy algae, coarsely branched algae, thin tubular and sheet-like algae, and filamentous algae. Three additional categories were used to describe the substrate characteristics (i.e., bare rock, sediment, and crevice).

Abundances and size structure of the two dominant sea urchin species in this area, the purple sea urchin, *Paracentrotus lividus* (Lamarck) and the black sea urchin, *Arbacia lixula* (Linné; see Plate 1), were quantified by counting all individuals of each species within  $0.5\text{-m}^2$  quadrats. Quadrats were divided into 25 subquadrats by a nylon twine grid. To quantify the extent of the barren habitat at each site, percent cover of bare rock (i.e., exposed substrate without macroscopic algae or invertebrates) and of encrusting coralline algae were visually estimated as described for the photoquadrats.

Urchin abundances and benthic assemblage composition were quantified using a partly nested sampling design. Three shores were selected randomly within each of three (at Capraia: PW, FW, and FE) or four (at Giannutri: PW, FW, PE, and FE) shore types (i.e., combinations of protection regime and exposure of the coastline). Each shore was sampled three times on each island, in May, October, and December 2000, at the same time when the fish censuses were conducted. On each sampling date, 10 replicate  $0.5\text{-m}^2$  quadrats (for sea urchin counts) and 10 replicate  $384\text{-cm}^2$  photographs (for estimates of abundances and percent cover of benthic taxa) were sampled randomly at each of two depths (3–5 m and 8–10 m) at each shore. In December, photographic samples could not be taken at shore FW3 in Capraia (Fig. 1). Thus, data on the composition of the benthic assemblage are not available for this shore on the December date.

#### Statistical analyses

Analysis of variance (ANOVA) was used to examine variation in total fish abundances, fish and benthic taxon richness (i.e., the total number of fish and benthic species or species groups identified in point counts and benthic photoquadrats), percent cover of coralline bar-

TABLE 1. Extended.

Urchin predators		Large urchin predators	
MS	F	MS	F
2.7	...†	4.2	5.54*
1.1	2.66	0.7	1.35
11.9	27.16***	2.4	4.29*
1.4	3.39*	0.2	0.46
0.4	2.14*	0.6	2.67**
0.2		0.2	
log(x + 1) C = 0.09 NS		log(x + 1) C = 0.09 NS	

rens (i.e., percent cover of bare rock and encrusting coralline algae; Lawrence 1975, Sala et al. 1998a), abundance of sea urchins, and abundance of the main sea urchin predators in Mediterranean rocky reefs, the sparid fishes *Diplodus sargus* and *D. vulgaris*, and the labrid fishes *Coris julis* and *Thalassoma pavo* (Sala 1997, Sala et al. 1998a). Diet studies conducted with time-lapse photography, stomach content analyses, and direct observations indicated that other reported predators of sea urchins, including spiny lobster, sea stars, and crabs cause minor mortality of sea urchins in shallow rocky reefs of the northwestern Mediterranean (Sala et al. 1998a; F. Micheli, *personal observations*). Because different combinations of protection regime and exposure exist on the two islands (see *Methods: Study area and marine protected area zoning*), separate ANOVAs were conducted for each island.

For fishes, we used partly nested ANOVA models with the following factors. At Capraia, factors comprised shore type (fixed, three levels: PW, FW, and FE), shore (random, three levels and nested within shore type), and time (random, three levels: May, October, and December 2000, crossed both with shore type and shore). At Giannutri, all combinations of protection regime and coastline exposure were available, allowing for a test of the separate and combined effects of these two factors. Thus, at Giannutri factors comprised protection (fixed, two levels: no-take, no-access reserves and fished areas); exposure (fixed, two levels: western and eastern shores, crossed to protection); shore (random, three levels: nested within the protection  $\times$  exposure interaction); and time (random, three levels: crossed with all other factors). For benthos, the same factors were used in the ANOVA models, with the addition of depth (fixed, two levels: crossed with all other factors). Cochran's *C* test was used throughout to test the assumption of homogeneity of variances before ANOVAs and data were transformed using the arcsine transformation for percent cover data or the  $\log(x + 1)$  transformation for counts when necessary. When interactions containing random factors were not significant, using the conservative nominal value of  $P = 0.25$ , these terms were pooled to increase the degrees of free-

dom available for tests of *F* ratios (Underwood 1997). Student-Newman-Keuls (SNK) tests were used for post hoc comparisons of means (at  $P = 0.05$ ). ANOVAs were performed using the statistical package GMAV5 (coded by A. J. Underwood and M. G. Chapman, University of Sydney, Australia).

The structure of the fish and benthic assemblages was compared among shores with variable exposure and protection regime using multivariate ordination and randomization tests. A matrix of similarities between each pair of samples was calculated using the Bray-Curtis similarity coefficient (Bray and Curtis 1957), after the raw data were transformed using the fourth-root transformation to decrease the influence of the most abundant species (Clarke and Warwick 1994). Nonmetric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the rank orders of similarities among the different shores (Clarke 1993).

For both fish and benthic assemblages, analyses of similarity (ANOSIM) randomization tests were used to compare differences among shore types (Clarke and Warwick 1994). One-way ANOSIM comparing similarity in the fish and benthic assemblages among shore types were conducted with data from Capraia. Pairwise comparisons between western shores within protected and fished areas, and between unprotected shores along the western and eastern sides of this island were performed to examine variation in composition of assemblages associated with fishing and human access, and coastline exposure, respectively. Because all combinations of protection regime and coastline exposure exist at Giannutri, two-way crossed ANOSIM comparing shores with different protection (no-take, no-access reserves vs. fished areas) and with different exposure (eastern vs. western sides of islands) were conducted.

The contributions of different species and species groups to the observed patterns of dissimilarity among shores subject to different exposures and protection regimes were quantified using analyses of dissimilarity (SIMPER; Clarke and Warwick 1994). First, SIMPER was used to determine what taxa accounted for 50% of observed dissimilarity in the fish and benthic assemblages. Second, the best discriminating taxa were identified by selecting taxa with ratios of mean Bray-Curtis dissimilarity over the standard deviation of dissimilarity greater or equal to 1. High values of these ratios indicate that differences in the abundance of a particular taxon between groups of shores were relatively consistent among samples (Clarke and Warwick 1994).

Separate multivariate analyses were conducted for the fish and benthic assemblages. Separate analyses were also performed for each island, each sampling date, and, for the benthic assemblage, at each depth. In all cases, abundances and percent cover data were averaged across the eight replicate point counts and 10 replicate photoquadrats sampled on each date at each

TABLE 2. ANOVA on total abundance of fish, number of fish species, cumulative abundance of sea urchin predators (i.e., *Diplodus sargus*, *D. vulgaris*, *Coris julis*, and *Thalassoma pavo*), and cumulative abundance of sea urchin predators in the largest size class at Giannutri, Italy.

Source	df	Total abundance		No. species	
		MS	F	MS	F
Exposure = E	1	0.19	2.95	6.12	0.40
Protection = P	1	0.05	0.04	45.12	2.95
Shore(E × P) = sh(EP)	8	0.99	0.71	10.77	0.60
Date = DA	2	6.47	4.65	87.39	4.89*
E × P	1	0.51	0.42	6.12	0.00
E × DA	2	0.06	0.05	15.17	0.85
P × DA	2	1.22	0.88	15.29	0.85
DA × sh(ST)	16	1.39	6.95***	17.89	3.86***
E × P × DA	2	0.96	0.69	42.12	2.35
Residual	252	0.20		4.63	
Transformation		log(x + 1)		...†	
Cochran's test		C = 0.09 NS		C = 0.08 NS	

Notes: For each variable, MS, F ratios, and significance level are reported. The effects of exposure and of protection were tested over the E × DA and P × DA mean square, respectively, after elimination of the E × P × DA and the sh(EP) terms when these terms were not significant at  $P > 0.25$ . NS = not significant. See *Methods: Surveys of fish and benthic assemblages*.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

† No transformation was done.

shore. All multivariate analyses were conducted using the software package PRIMER, Version 5 (PRIMER-E, Plymouth, UK; Clarke and Warwick 1994).

We examined correlation between the densities of sea urchins, their fish predators, and the extent of coralline barrens (measured as percent cover) using Pearson correlation between variables averaged within each shore and sampling date combination (i.e., across the eight replicate fish point counts and 10 replicate quadrats for sea urchin counts and estimates of percent coralline barren). Correlations were conducted using the statistical package SAS, Version 6.12 (SAS Institute, Cary, North Carolina, USA).

## RESULTS

### Fish assemblages

Forty-one fish taxa were censused at Capraia and 46 taxa were censused at Giannutri over the three sampling dates (see Appendix A for a complete list). For both islands, total fish abundances, summed across all species and size classes, varied significantly across combinations of dates and shores, with no overall effect of protection in no-take, no-access reserves or exposure to the dominant directions of seasonal winds (Tables 1 and 2). Fish total densities ranged from 0.3/m<sup>2</sup> to 20.6/m<sup>2</sup> (mean = 2.6/m<sup>2</sup>, SE = 0.17,  $N = 216$  point counts) at Capraia, and from 0.3/m<sup>2</sup> to 9.1/m<sup>2</sup> (mean = 2.4/m<sup>2</sup>, SE = 0.09,  $N = 288$ ) at Giannutri (fish abundance data are reported in Appendix B). Similarly, fish species richness varied significantly across combinations of dates and shores, but there was no significant effect of protection from fishing (Tables 1 and 2). At Capraia, fish species richness did not vary significantly between the protected and fished western shores, but mean species richness was significantly greater at eastern than at western shores (SNK test; Fig. 2A). At Giannutri,

species richness did not vary with protection from fishing or exposure of the coastline (Table 2, Fig. 2B).

In contrast to the lack of a protection effect on total fish abundances and species richness, the composition of the fish assemblage varied both with protection and exposure of the coastline (Fig. 3). Analyses of similarity (ANOSIM) randomization tests indicated that the composition of the fish assemblage varied significantly between no-take, no-access reserves and fished areas on two of the three sampling dates at Giannutri, and on one date at Capraia (Table 3). In addition, fish assemblages differed between eastern and western shores in the fall and winter sampling dates at both islands (Table 3).

At Capraia, 10 species accounted for 50% of overall dissimilarity between protected and fished shores, seven of these consistently across shores (i.e., with relatively high ratios between mean dissimilarity among shores and variability in dissimilarity values). Results are reported in Appendix C. Four of the seven species had greater abundances within no-take reserves than in fished areas: the sparids *Oblada melanura* and *Diplodus sargus*, both major targets of local recreational and artisanal fisheries; the labrid *Thalassoma pavo*; and the small planktivorous pomacentrid *Chromis chromis*. One additional target species, the centrarchid *Spicara flexuosa*, exhibited greater abundances in fished areas than in no-take reserves. At Giannutri, 13 species accounted for 50% of overall dissimilarity between protected and fished shores, 11 of these consistently across shores (results reported in Appendix C). Four species targeted by fishing (*S. flexuosa*, *O. melanura*, *D. sargus*, and *D. vulgaris*) and one nontarget species (*C. chromis*) exhibited greater abundances within no-take reserves. In contrast, one target species, the piscivorous gadid *Phycis phycis*, and four nontarget species (the



TABLE 2. Extended.

Urchin predators		Large urchin predators	
MS	F	MS	F
1250.0	1.8	0.02	0.08
22969	6.1*	5.90	22.93*
1484.2	1.3	1.15	0.41
111.4	0.1	3.39	1.21
58.7	0.05	0.01	0.00
687.5	0.6	0.20	0.07
409.4	0.3	0.26	0.09
1164.7	6.3***	2.79	6.83***
1015.0	0.9	0.19	0.07
183.3		0.41	

...†	log(x + 1)
C = 0.09 NS	C = 0.07 NS

herbivorous sparid *Sarpa salpa*, the gobiid *Gobius luteus*, the labrid *Symphodus rostratus*, and the apogonid *Apogon imberbis*) were more abundant in fished areas.

At Capraia, the same species discriminating between fish assemblages within no-take and fished areas also explained differences between eastern and western shores, with the addition of the labrids *S. mediterraneus* and *T. pavo*, both most abundant at eastern shores. Similarly, at Giannutri the species that best characterized eastern and western shores coincided with those separating no-take from fished areas, with the exception of *S. rostratus* and *A. imberbis*, which did not contribute significantly to dissimilarity between eastern and western shores.

The benthic invertebrate feeders *Diplodus sargus*, *D. vulgaris*, *Coris julis*, and *Thalassoma pavo*, the main

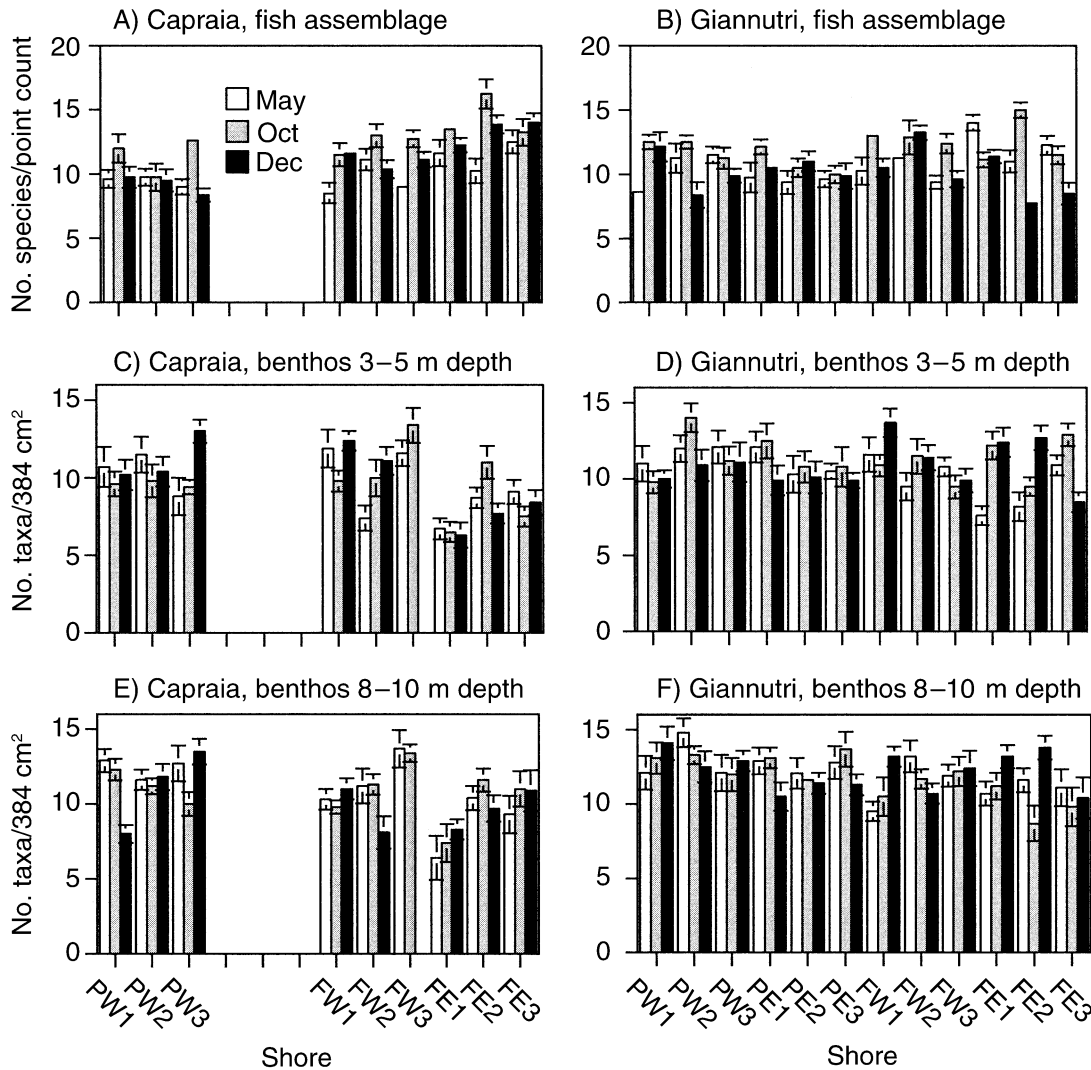


FIG. 2. (A, B) Fish species richness (number of fish species identified in point counts), and (C–F) benthos taxon richness (number of benthic taxa identified from photoquadrats) at Capraia and Giannutri, Italy. Bars are means  $\pm$  1 SE of data from eight replicate point counts or 10 replicate photoquadrats surveyed at each of two depths, 3–5 m (C, D) and 8–10 m (A, B, E, F), at each shore (see Fig. 1 for shore codes) on each of three sampling dates (May, October, and December 2000).

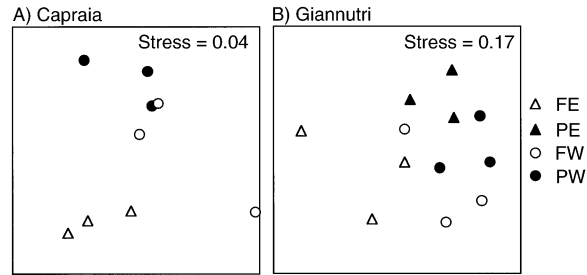


FIG. 3. Ordination plots (nMDS, nonmetric multidimensional scaling) of relative similarities in fish assemblages among shores at (A) Capraia and (B) Giannutri. Before calculating the similarity matrices, abundances of individual species were averaged across the 24 point counts surveyed at each shore on the three sampling dates (May, October, and December 2000). Category abbreviations are as in Fig. 1: P, protected; F, fished; W, western side; E, eastern side. The stress value is a measure of the distortion between the similarity rankings between samples and the corresponding distance rankings in the ordination plot. Stress <0.2 corresponds to a useful ordination.

predators of sea urchins on Mediterranean rocky reefs (Sala and Zabala 1996, Sala 1997, Sala et al. 1998a), tended to be more abundant within no-take reserves than in fished areas in both islands, but predator abundances were greater and effects of protection stronger at Giannutri than at Capraia (Table 2, Fig. 4). At Gian-

nutri, total abundances of sea urchin predators were significantly greater in no-take reserves (mean = 0.53/m<sup>2</sup>, SE = 0.02, *N* = 144 point counts) than fished areas (mean = 0.30/m<sup>2</sup>, SE = 0.01, *N* = 144), regardless of shore exposure and sampling date (Table 2, Fig. 4B). At Capraia, there was a significant interaction between shore type and date (Table 1), and effects of protection were significant for the October and December sampling but not for May (SNK tests; Fig. 4A). At Capraia, densities of sea urchin predators averaged 0.24/m<sup>2</sup> (SE = 0.02, *N* = 72) within the no-take reserves, and 0.18/m<sup>2</sup> (SE = 0.01, *N* = 144) within the fished areas.

Similar results were obtained at Giannutri when only large individuals (in the upper third of the reported size range of each species) were included in the analyses (Fig. 4D, Table 2). At Giannutri, abundances of large urchin predators, capable of killing and consuming adult urchins (Sala and Zabala 1996, Sala 1997, Sala et al. 1998a), were significantly greater in no-take reserves (mean = 0.08/m<sup>2</sup>, SE = 0.01, *N* = 144 point counts) than in fished areas (mean = 0.05/m<sup>2</sup>, SE = 0.004, *N* = 144; SNK test; Fig. 4D). In contrast, abundances of large predators of sea urchins were significantly greater at eastern than western shores at Capraia, with no significant difference between protected and fished areas (SNK test; Fig. 4C).

TABLE 3. *R* values and significance levels of analyses of similarity (ANOSIM) comparing fish and benthic assemblages among shores within the islands of Capraia and Giannutri, on each of three sampling dates in May, October, and December 2000.

Comparison	Fish assemblage		Benthic assemblage			
	<i>R</i>	<i>P</i>	3–5 m depth		8–10 m depth	
			<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
<b>Capraia</b>						
May						
PW vs. FW	–0.14	0.80	<b>0.31</b>	<b>0.03</b>	0.11	0.29
FW vs. FE	–0.19	0.80	0.15	0.40	0.01	0.60
October	0.07	0.40	0.37	0.20	0.18	0.40
PW vs. FW	<b>0.52</b>	<b>0.004</b>	0.16	0.22	–0.04	0.61
FW vs. FE	<b>0.22</b>	<b>0.10</b>	0.01	0.50	0.07	0.40
December	<b>0.85</b>	<b>0.10</b>	<b>0.48</b>	<b>0.10</b>	–0.11	0.90
PW vs. FW	<b>0.56</b>	<b>0.004</b>	<b>0.67</b>	<b>0.01</b>	<b>0.73</b>	<b>0.01</b>
FW vs. FE	0.30	0.20	0.33	0.30	0.01	0.40
	<b>0.59</b>	<b>0.10</b>	<b>0.99</b>	<b>0.10</b>	<b>0.99</b>	<b>0.10</b>
<b>Giannutri</b>						
May						
Protected vs. fished	0.22	0.19	0.07	0.33	0.09	0.37
West vs. east	0.19	0.18	<b>0.46</b>	<b>0.02</b>	0.06	0.41
October						
Protected vs. fished	<b>0.44</b>	<b>0.02</b>	0.02	0.53	–0.04	0.58
West vs. east	<b>0.48</b>	<b>0.02</b>	<b>0.33</b>	<b>0.08</b>	0.11	0.32
December						
Protected vs. fished	<b>0.37</b>	<b>0.06</b>	0.13	0.27	<b>0.31</b>	<b>0.07</b>
West vs. east	<b>0.41</b>	<b>0.07</b>	<b>0.52</b>	<b>0.03</b>	<b>0.46</b>	<b>0.07</b>

Notes: Because only 10 permutations are possible for the pairwise comparisons of shore types, a significance level of 0.10 (shown in boldface type) is chosen for these analyses. At Capraia, the factors in the analyses were shore type (i.e., protected shore on the west side of the island, PW; fished shore on the west side, FW; and fished shore on the east side, FE). At Giannutri, protection (protected vs. fished shores) and side (west vs. east side) were the factors used. No-take reserves are not present on the eastern side of Capraia, making it impossible to examine interactions between protection and side.

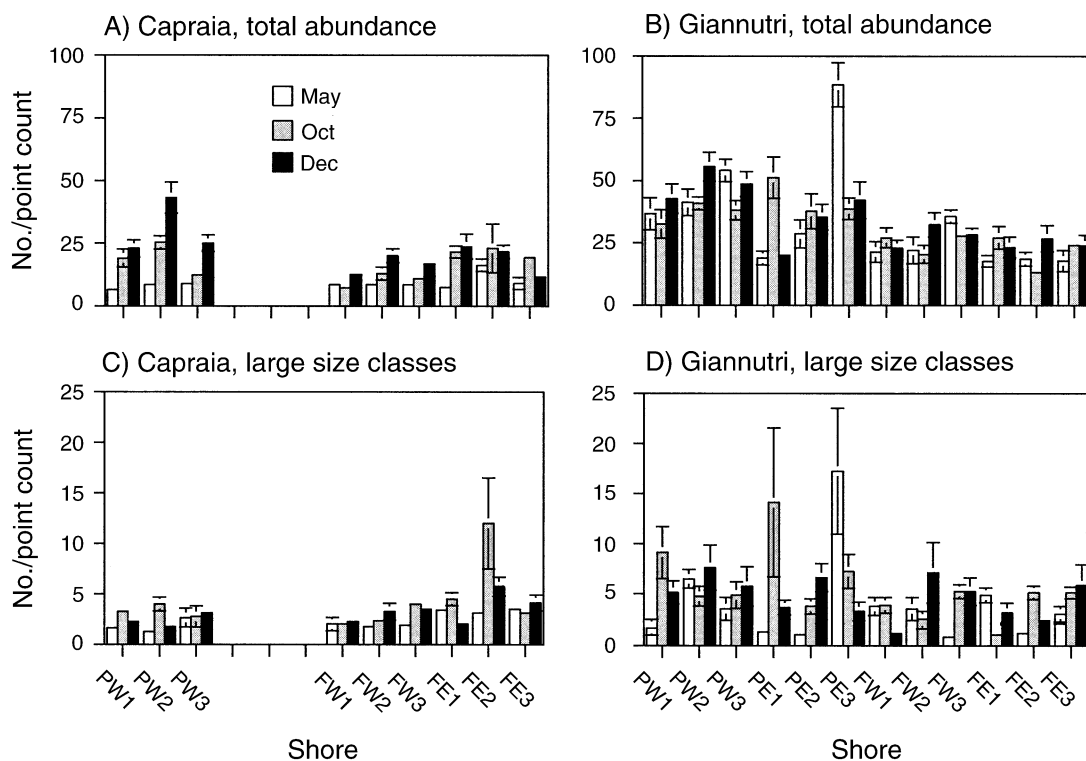


FIG. 4. Abundances (i.e., total number of individuals per point count) of fish species reported as major predators of sea urchins in Mediterranean rocky reefs (see *Methods: Surveys of fish and benthic assemblages*). (A, B) Total abundances and (C, D) abundances of large individuals (i.e., those in the upper third of the size range reported for each species) are presented separately for Capraia (A, C) and Giannutri (B, D). Bars are means  $\pm 1$  SE of data from eight replicate point counts conducted at each shore (see Fig. 1 for shore codes) on each of three sampling dates (May, October, and December 2000).

#### Benthic assemblages

Percent cover (for algae and sessile invertebrates) or abundances (for mobile species such as small gastropods and sea urchins) were quantified for a total of 116 taxa (i.e., species or species groups): 50 algal taxa, 65 invertebrate taxa, and the seagrass *Posidonia oceanica* (see Appendix A). The diversity and structure of benthic assemblages were significantly influenced by the physical exposure of the coastline, but not by protection within no-take, no-access reserves.

Benthic taxon richness (i.e., the number of invertebrate and algal taxa identified within each photoquadrat) varied significantly among shores at Capraia (Table 4, Fig. 2C, E), and with depth and the shore  $\times$  date interaction at Giannutri (Table 5, Fig. 2D, F). At Capraia, taxon richness was significantly greater at the western than eastern shores both in the May and October sampling in SNK tests, coinciding with the greater extent of coralline barrens at eastern shores. Differences in taxon richness in the December sampling could not be tested statistically because the sampling design was unbalanced on this date. At Giannutri, taxon richness did not show any clear trend of variation among shores with different protection regime or exposure to dominant winds (Table 5, Fig. 2D, F).

Differences between benthic assemblage composition in no-take reserves and fished areas were detected only for the deep benthic assemblages at Giannutri (Table 3, Fig. 5). At 8–10 m depths, protected and fished benthic assemblages separated into two distinct groups along the eastern, but not along the western, side of Giannutri (Fig. 5D). Moreover, these differences were statistically significant only for the December samples (Table 3). Anemones, hydrozoans, the erect brown algae *Cystoseira* spp. and *Dyctiota* spp., and the coarsely branched and foliose algal groups had greater abundance within protected than fished shores, whereas the algae *Peyssonellia squamaria* and *Padina pavonica*, both with short and thick thalli, showed the opposite trend (see results of SIMPER analyses reported in Appendix C).

In both islands, benthic assemblage composition at the shallower depths (3–5 m) differed between western and eastern shores (Fig. 5A, B). This difference was significant in ANOSIM randomization tests in all cases except for the May sampling date at Capraia (Table 3). At the deeper sampling locations (8–10 m), differences in the benthic assemblage composition between eastern and western shores were less apparent than at the shallower depths (Fig. 5), and significant differences were

TABLE 4. ANOVA on numbers of benthic taxa, percent cover of coralline barren, and densities of purple (*Paracentrotus lividus*) and black (*Arbacia lixula*) sea urchins at Capraia.

Source	No. taxa			Barren (%)		
	df	MS	F	df	MS	F
Shore type = ST	2	198.1	...†	2	4789.8	...†
Shore(ST) = sh(ST)	6	87.4	9.5**	6	562.2	1.6
Date = DA	1	0.00	0.0	2	399.1	1.1
Depth = DE	1	148.2	...†	1	10 513	...†
ST × DA	2	23.6	2.6	4	897.8	2.6
ST × DE	2	6.6	...†	2	1081.1	...†
DA × sh(ST)	6	9.2	1.0	12	351.3	4.5***
DE × sh(ST)	6	14.3	1.1	6	207.9	0.6
DA × DE	1	0.3	0.0	2	330.5	0.9
ST × DA × DE	2	9.3	0.7	4	1378.8	3.8*
DA × DE × sh(ST)	6	13.3	1.5	12	363.1	4.6***
Residual	324	8.9		486	78.5	
Transformation		...‡			arcsine	
Cochran's test		C = 0.07			C = 0.23**	

Notes: Because the sampling design for the number of benthic taxa was unbalanced during the December sampling, only the first two dates were included in this analysis. For each variable, MS, F ratios, and significance level are reported. The effect of shore type was tested over the shore(ST) mean square after elimination of the ST × DA × DE term when this term was not significant at  $P = 0.25$ . NS = not significant.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

† No F test was done.

‡ No transformation was done.

detected only in the December samples for both islands (Table 3).

The clear and consistent separation of shallow (3–5 m depth) benthic assemblages between the western and eastern shores (Table 3, Fig. 5A, B) was driven by variation in a suite of algae and benthic invertebrates (a complete list of the species driving these differences is included in Appendix D). At Capraia, 18 taxa accounted for 50% of dissimilarity between western and eastern shores. Eleven algal species and species groups explained a cumulative 34% of dissimilarity, followed by the encrusting sponge *Crambe crambe*, ascidians, hydrozoans, and serpulid polychaetes. Among the 11 algal species and species groups discriminating the two assemblages, erect algae were more abundant at the western shores of Capraia, whereas encrusting corallines dominated at the eastern shores. Similarly, ascidians and hydrozoans were more abundant on the western shores, whereas encrusting sponges and bryozoans dominated the eastern shores. At Giannutri, 21 taxa accounted for 50% of dissimilarity of the shallow benthic assemblages between western and eastern shores. A suite of erect brown and green algae, the anemone *Parazoanthus axinellae*, hydrozoans, and the sponge *Crambe crambe* were more abundant along eastern than western shores, whereas encrusting corallines, the red alga *Peyssonellia squamaria* and *Laurencia* spp., the brown *Dyctiota* spp., and the green *Valonia macrophysa* showed the opposite trend.

#### Coralline barrens, sea urchins, and sea urchin predators

The extent of coralline barrens, quantified as the percent cover of bare rock substrate and encrusting cor-

allines in 0.5-m<sup>2</sup> quadrats, showed considerable variation among shores, depths, and sampling dates in both islands, ranging, on average, from 8% to 71% of the substrate at Giannutri and from 3% to 79% at Capraia (Fig. 6). High variability in percent barren resulted in significant interactions between the factors shore type (i.e., PW, FW, and FE shores), depth (3–5 m vs. 8–10 m depth), and date (May, October, and December 2000) at Capraia (Table 4), and between exposure of the coastline (western vs. eastern shores), protection (protected vs. fished shores), depth, and date at Giannutri (Table 5). However, general trends in the distribution and extent of coralline barrens were apparent (Fig. 6). In both islands, variation in percent barren tended to be associated with physical exposure of the coastline, but not with protection in no-take, no-access reserves (Fig. 6). At Capraia, percent barren tended to be greater at eastern (mean = 30.5%, SE = 2.8,  $N = 90$  quadrats) than western shores (mean = 12.8%, SE = 0.7,  $N = 180$ ) at the 3–5 m depths (Fig. 6A), but this trend was statistically significant only for the May sampling date (SNK tests). Percent barren at the 8–10 m depth range was generally lower than at the shallow depth (mean = 8.5%, SE = 0.5,  $N = 270$ ), and did not vary with exposure of the coastline or protection regime (SNK tests; Fig. 6C).

Similarly, at Giannutri, percent barren at the 3–5 m depth was generally greater at western, windward (mean = 41.6%, SE = 1.7,  $N = 180$  quadrats) than eastern, leeward shores (mean = 36.1%, SE = 1.5,  $N = 180$ ; Fig. 6B). In contrast with Capraia, percent barren was high at the deep locations as well (varying between 8% and 48%, on average, across shores), and showed trends towards greater values at western (mean



TABLE 4. Extended.

<i>P. lividus</i>		<i>A. lixula</i>	
MS	F	MS	F
6.5	2.4	4.7	...†
2.8	3.5*	0.9	2.3
0.6	0.8	1.2	2.9
4.2	...†	12.5	35.2*
0.6	0.7	0.3	0.6
0.2	0.6	3.2	25.1***
0.8	4.7***	0.4	3.3***
0.7	2.8	0.1	0.8
0.6	2.4	0.3	4.1*
0.3	1.4	0.1	0.6
0.2	1.5	0.1	0.7
log(x + 1) C = 0.08**		log(x + 1) C = 0.07 NS	

= 26.3%, SE = 1.4, N = 180) than at eastern shores (mean = 17.4%, SE = 1.0, N = 180; Fig. 6D). Percent barren was significantly greater at western than eastern shores for five of the 12 combinations of protection regime, date, and depth in this data set, whereas this trend was not significant for the remaining seven combinations of factor levels (SNK tests). The direction of differences in percent barren between protected and fished shores did not show any consistent trends (SNK tests; Fig. 6B, D).

Densities of the purple and black sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, showed significant variation among shores and sampling dates in both islands (Tables 4 and 5). At Capraia, there was no significant overall effect of protection on densities of *P. lividus* (Table 4). However, densities tended to be greater at western protected shores (mean = 2.3/m<sup>2</sup>, SE = 0.4, N = 180 quadrats) than at western and eastern fished shores (mean = 0.5/m<sup>2</sup>, SE = 0.1, N = 360; Fig. 7A, C). For *A. lixula*, differences among shore types varied between the shallow and deep sampling locations, with no overall effect of protection in reserves (Table 4). At shallow depths, eastern shores had the greatest densities (mean = 2.7/m<sup>2</sup>, SE = 0.3, N = 90), western fished shores the lowest (mean = 0.5/m<sup>2</sup>, SE = 0.1, N = 90), and western protected shores were intermediate (mean = 1.3/m<sup>2</sup>, SE = 0.2, N = 90; SNK tests; Fig. 8A). *Arbacia lixula* densities were low and not significantly different among shore types at the deep sampling locations (mean = 0.3/m<sup>2</sup>, SE = 0.05, N = 270; SNK tests; Fig. 8C).

At Giannutri, *P. lividus* densities tended to be greater at fished (mean = 2.5/m<sup>2</sup>, SE = 0.2, N = 360 quadrats) than at protected shores (mean = 1.8/m<sup>2</sup>, SE = 0.2, N = 360), but the magnitude and statistical significance of difference between protected and fished shores varied depending on date and depth (Table 5). Densities of *P. lividus* were significantly greater at fished than at protected shores in two of the six combinations of

protection regime, date, and depth, and not significantly different in all other cases (SNK tests; Fig. 7B, D). *Paracentrotus lividus* densities also exhibited a trend towards greater densities at eastern (mean = 2.8/m<sup>2</sup>, SE = 0.2, N = 360) than at western shores (mean = 1.5/m<sup>2</sup>, SE = 0.2, N = 360), though this trend was not statistically significant (Table 5). Densities of *A. lixula* were generally high at Giannutri (up to 32 individuals/m<sup>2</sup>), and tended to be greater at western (mean = 3.8/m<sup>2</sup>, SE = 0.2, N = 360) than at eastern shores (mean = 1.8/m<sup>2</sup>, SE = 0.2, N = 360), though densities varied depending on combinations of all four main factors (exposure × protection × date × depth interaction; Table 5). *Arbacia lixula* densities were significantly greater at western than at eastern shores in eight of the 12 combinations of protection regime, date, and depth, and not significantly different in the remaining four combinations (SNK tests; Fig. 8B, D).

The percent cover of coralline barrens was positively and significantly correlated with densities of black sea urchins both at Capraia (Pearson correlation coefficient  $r = 0.73$ ,  $P < 0.001$ ,  $N = 27$ ) and at Giannutri ( $r = 0.68$ ,  $P < 0.001$ ,  $N = 36$ ). In contrast, there was no significant correlation between percent barren and densities of purple sea urchins (Capraia:  $r = 0.04$ ,  $P \geq 0.8$ ,  $N = 27$ ; Giannutri:  $r = 0.21$ ,  $P > 0.2$ ,  $N = 36$ ). In both islands, combined densities of the main sea urchin predators in these fish assemblages, the sparids *Diplodus sargus* and *D. vulgaris* and the labrids *Coris julis* and *Thalassoma pavo*, were not significantly correlated with densities of black sea urchins (Capraia:  $r = 0.22$ ,  $P > 0.25$ ,  $N = 27$ ; Giannutri:  $r = 0.31$ ,  $P > 0.05$ ,  $N = 36$ ) or purple sea urchins (Capraia:  $r = 0.15$ ,  $P > 0.45$ ,  $N = 27$ ; Giannutri:  $r = -0.12$ ,  $P > 0.45$ ,  $N = 36$ ). Similar results were obtained when only sea urchin predators in the largest size class were included in the analyses. For both islands, there was no significant correlation between large urchin predators and purple sea urchin densities (Capraia:  $r = -0.07$ ,  $P > 0.7$ ,  $N = 27$ ; Giannutri:  $r = -0.09$ ,  $P > 0.5$ ,  $N = 36$ ). At Capraia, there was a positive significant correlation between large predator abundances and black sea urchin densities ( $r = 0.40$ ,  $P < 0.05$ ,  $N = 27$ ) but no significant correlation at Giannutri ( $r = 0.04$ ,  $P > 0.8$ ,  $N = 36$ ).

## DISCUSSION

Protection from fishing in no-take, no-access reserves resulted in enhanced abundance and sizes of predatory fishes and influenced the structure of the whole fish assemblage. Fishing has played a crucial role in shaping Mediterranean food webs both historically and in present times (Sala 2004). Our results indicate that fish assemblages respond to cessation of fishing over relatively short time frames, with significant effects after five years of protection. However, effects of protection were highly variable among species, and in time and space, and consisted in differences

TABLE 5. ANOVA on numbers of benthic taxa, percent cover of coralline barren, and densities of purple (*Paracentrotus lividus*) and black (*Arbacia lixula*) sea urchins at Giannutri.

Source	df	No. taxa		Barren (%)	
		MS	F	MS	F
Exposure = E	1	63.7	5.7*	9302.4	...†
Protection = P	1	92.3	8.3*	66.0	...†
Shore(E × P) = sh(EP)	8	11.1	0.4	2829	3.1*
Date = DA	2	3.9	0.1	7148.1	7.9**
Depth = DE	1	215.3	11.8***	52 088	...†
E × P	1	2.2	0.2	594.1	...†
E × DA	2	5.7	0.2	8945.4	9.9**
E × DE	1	1.4	0.0	533.9	...†
P × DA	2	83.8	3.1	500.3	0.5
P × DE	1	32.0	1.7	48.0	...†
DA × sh(EP)	16	27.1	3.1***	907.4	3.6***
DE × sh(EP)	8	18.3	1.9	863.0	1.5
DA × DE	2	19.7	2.1	1882.6	3.3
E × P × DA	2	14.6	0.5	4504.7	5.0*
E × P × DE	1	0.3	0.0	281.2	...†
E × DA × DE	2	13.8	1.5	579.0	1.0
P × DA × DE	2	12.1	1.3	356.0	0.6
DE × DA × sh(EP)	16	9.5	1.1	575.2	2.3**
E × P × DA × DE	2	25.5	2.9*	2943.6	5.1*
Residual	648	8.9		249.1	
Transformation			...†		...†
Cochran's test			C = 0.03 NS		C = 0.05 NS

Notes: For each variable, MS, *F* ratios, and significance level are reported. For the number of benthic taxa, the effects of exposure and protection were tested over the shore(E × P) mean square after elimination of the DE × DA × sh(EP) term, which was not significant at  $P > 0.25$ . For the density of *P. lividus*, the effects of exposure and protection were tested over the shore(EP) mean square after elimination of the E × P × DA × DE term, which was not significant at  $P > 0.25$ . NS = not significant.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

† No *F* test was done.

‡ No transformation was done.

in the composition of the fish assemblages (e.g., Micheli et al. 2004b) rather than in greater overall abundance and species richness in protected compared to fished areas, as observed in other studies of marine reserves (e.g., Halpern 2003).

The main predators of sea urchins in Mediterranean shallow reefs, the sea breams *Diplodus sargus* and *D. vulgaris* and the wrasses *Coris julis* and *Thalassoma pavo*, were more abundant and tended to be larger in no-take reserves compared to fished sites. Although we did not quantify predation intensity at different sites directly, extensive observations and tethering experiments conducted in the Medes Islands marine reserves, Spain, established clear links between the abundances of these predatory fishes and predation rates on sea urchins (Sala 1997). Cascading effects of predator enhancement in reserves on benthic species and assemblages were overall weak and were detected only in one island. At Giannutri, the purple sea urchin *Paracentrotus lividus*, the dominant sea urchin species along the leeward side of the islands, tended to have greater densities in fished than in protected areas, and the structure of the deeper benthic assemblages differed between protected and fished areas, though significantly so only for one of the three sampling dates. The result that significant differences in the structure of benthic assemblages were observed only at the deeper locations

(between 8 m and 10 m depth) and were more evident for eastern than western shores (Fig. 5D), in both cases coinciding with the habitats where purple sea urchins tended to be more abundant (Fig. 7), suggests that these differences may have arisen through indirect effects on purple sea urchins. In contrast, no indirect effects of protection were observed for the black sea urchin *Arbacia lixula*, the most abundant sea urchin species along the windward sides of the islands.

Our results indicate that these two common sea urchin species, *P. lividus* and *A. lixula*, may show contrasting responses to predation and variation in abiotic conditions, and likely play different ecological roles in controlling algal cover and structuring benthic assemblages. Thus, the persistence, extent, and temporal dynamics of sea urchin barrens may vary depending on the dominant urchin species at a particular site. Fish feeding preferences may partly explain the different responses to protection between the two sea urchin species. Purple sea urchins may suffer greater mortality from fish predation than black sea urchins, with greater potential for both direct and indirect effects of predation on this species. Comparisons of predation rates on these two urchin species support the hypothesis that sea breams and wrasses prefer purple to black sea urchins (E. Sala, unpublished data). Elucidation of the processes influencing the extent and dynamics of cor-

TABLE 5. Extended.

<i>P. lividus</i>		<i>A. lixula</i>	
MS	F	MS	F
11.1	3.3	24.0	...†
1.0	0.3	1.3	...†
3.4	2.0	2.4	5.7**
1.2	0.7	4.6	10.9**
6.2	4.3	69.9	...†
0.7	0.2	4.2	...†
0.3	0.2	0.1	0.2
2.1	0.2	0.1	...†
0.3	0.2	0.5	1.1
0.9	0.6	0.7	†
1.7	6.2***	0.4	1.6
1.4	1.9	1.0	2.6*
1.6	2.1	1.6	4.2*
1.6	1.0	0.0	0.1
0.5	1.0	1.7	...†
1.6	2.1	0.5	1.4
4.5	5.9*	0.0	0.0
0.7	2.7***	0.4	1.5
0.3	0.5	1.6	4.4*
0.3		0.2	

$\log(x + 1)$	$\log(x + 1)$
$C = 0.04$ NS	$C = 0.05$ NS

alline barrens in temperate reefs will require a better understanding of the behaviors and population dynamics of different grazers and their predators.

The presence of extensive coralline barrens, where up to an average 80% of the substrate was devoid of erect macroalgae, was clearly associated with high densities of sea urchins, particularly the black sea urchin *A. lixula*. In turn, coralline barrens were associated with lower diversity of the benthic assemblage. In particular, a significantly lower mean number of benthic taxa was found along eastern shores at Capraia, coinciding with a significantly greater extent of coralline barrens, and at both islands mean number of benthic taxa was negatively correlated with mean percent cover of coralline barren, though significantly so only at Giannutri (Capraia:  $r = -0.23$ ,  $P = 0.10$ ,  $N = 52$ ; Giannutri:  $r = -0.28$ ,  $P = 0.02$ ,  $N = 72$ ). The composition of the benthic assemblage also exhibited clear separation between eastern and western shores at both islands, coinciding with significant differences in the extent of barrens on the two sides of both islands.

In contrast with the significant effects of protection in no-take marine reserves on fish assemblages, most of the variation in the abundances of invertebrate grazers (e.g., sea urchins), the extent of coralline barrens, and the structure and diversity of the benthic assemblage was associated with variation in the physical exposure of the coastline. Variation in hydrographic conditions at scales of kilometers to tens of kilometers likely influences assemblages through the temporal variability and intensity of disturbance associated with waves and storms, the delivery of propagules from the water column, and the direction and strength of biotic

interactions. Similar patterns emerged in a parallel study of variation in the composition of rocky intertidal assemblages within our study area (Benedetti-Cecchi et al. 2003). Intertidal algal and invertebrate assemblages showed significant differences in their structure between western and eastern sides of the two islands. These results suggest that physical forcing of biological processes, including recruitment and species interactions, via hydrographic processes and benthic topography may result in relatively predictable patterns in coastal marine assemblages over spatial scales of tens of kilometers.

The effects of physical exposure of the shores on the patterns of abundance and distribution of the two sea urchin species, and on the composition of the whole assemblage around the island could be both direct and indirect. Greater attachment strength of black than purple sea urchins (F. Micheli, *personal observations*) may result in a greater ability of black sea urchins to withstand waves and strong currents associated with storms, explaining both its horizontal distribution along the shore and its dominance at shallow depths. Alternatively, the extent of different benthic habitats around the islands may indirectly affect the composition of both fish and benthic assemblages on rocky reefs. In particular, seagrass beds were more extensive on the western than eastern side of Capraia, and along the

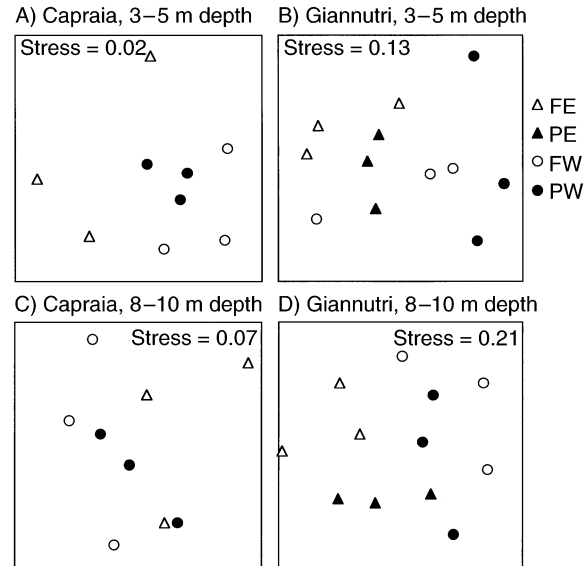


FIG. 5. Ordination plots (nMDS) of relative similarities in benthic assemblage composition from photoquadrats surveyed at (A, B) 3–5 m and (C, D) 8–10 m depths at Capraia (A, C) and Giannutri (B, D). Percent cover (for sessile organisms) and numbers of individuals per photoquadrat (for mobile species) were averaged over the 30 photoquadrats taken at each shore on the three sampling dates before calculating the similarity matrices. The stress value is a measure of the distortion between the similarity rankings between samples and the corresponding distance rankings in the ordination plot. Stress <0.2 corresponds to a useful ordination.

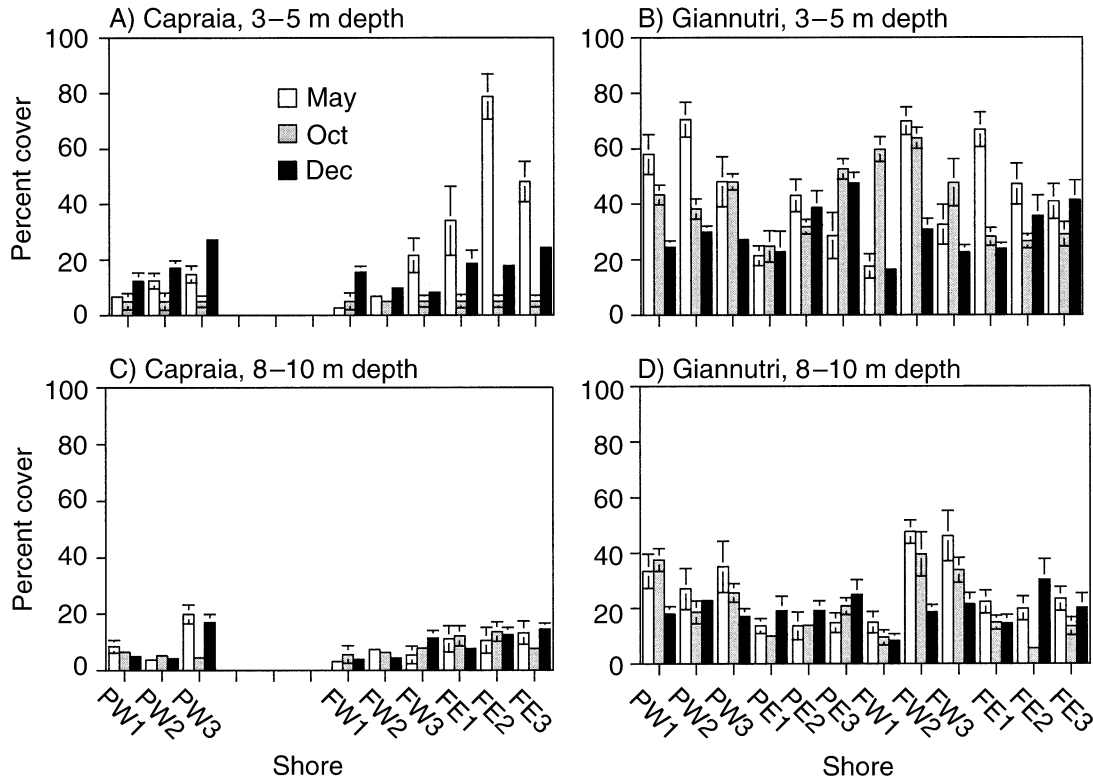


FIG. 6. Percent cover of coralline barrens (i.e., bare rocky substrate and encrusting coralline algae) at (A, C) Capraia and (B, D) Giannutri. Bars are means  $\pm$  1 SE of data from 10 replicate 0.5-m<sup>2</sup> quadrats surveyed at each of two depths, 3–5 m (A, B) and 8–10 m (C, D), at each shore (see Fig. 1 for shore codes), on each of three sampling dates (May, October, and December 2000).

eastern than western side of Giannutri. Seagrasses may act as sources of food and refuge for some fish species, indirectly influencing the composition of the fish assemblage in nearby habitats (e.g., Heck and Orth 1980, Beck et al. 2001).

Causal linkages between the patterns of abundance and distribution of fish, invertebrate, and algal taxa observed in our surveys are likely complex and cannot be teased apart in our study. Sea urchin grazing can play a key role in structuring benthic assemblages in this (Benedetti-Cecchi and Cinelli 1995, Benedetti-Cecchi et al. 1998, Bulleri et al. 1999) and other systems (Paine and Vadas 1969, Lawrence 1975, Andrew 1993, Hagen 1995). Thus, spatial variation in sea urchin densities around these islands likely underlies variation in algal cover and in the overall composition of the algal assemblage over similar spatial scales. However, the result that significant differences in the assemblage structure between eastern and western shores were also observed in the fish and invertebrate assemblages suggests that part of this variation may be caused by direct responses of individual taxa and species interactions other than herbivory (e.g., competition for space among sessile invertebrates and algae and facilitation between canopy-forming algae and invertebrates) to differences in hydrographic conditions as-

sociated with exposure of the coastline, or to differences in other features of the habitat.

The result of a greater predictability of structure of assemblages at intermediate spatial scales (i.e., kilometers to tens of kilometers) may be widely applicable to both tropical and temperate reef assemblages. In a comparison of coral reef assemblages over a range of spatial scales and ecological to geological time frames, Pandolfi (2002) found that reef assemblages exhibited greater degrees of order at scales ranging from kilometers to tens of kilometers compared to smaller (meters to kilometers) and larger (from hundreds to thousands of kilometers) scales. Such predictable structure of reef assemblages over intermediate spatial scales is remarkably persistent over a 125 000-yr period from a Pleistocene fossil reef terrace in Curaçao (Pandolfi and Jackson 2001). Large-scale spatial surveys of benthic and fish assemblages on the Great Barrier Reef showed predictable patterns of variation associated with gradients in exposure (e.g., Harriott and Banks 2002, Mundy 2002, Ninio and Meekan 2002). In southern Australia, spatial variability in benthic assemblages declines with increasing spatial scales of sampling in intertidal (Underwood and Chapman 1996) and subtidal (Fowler-Walker and Connell 2002) reefs.



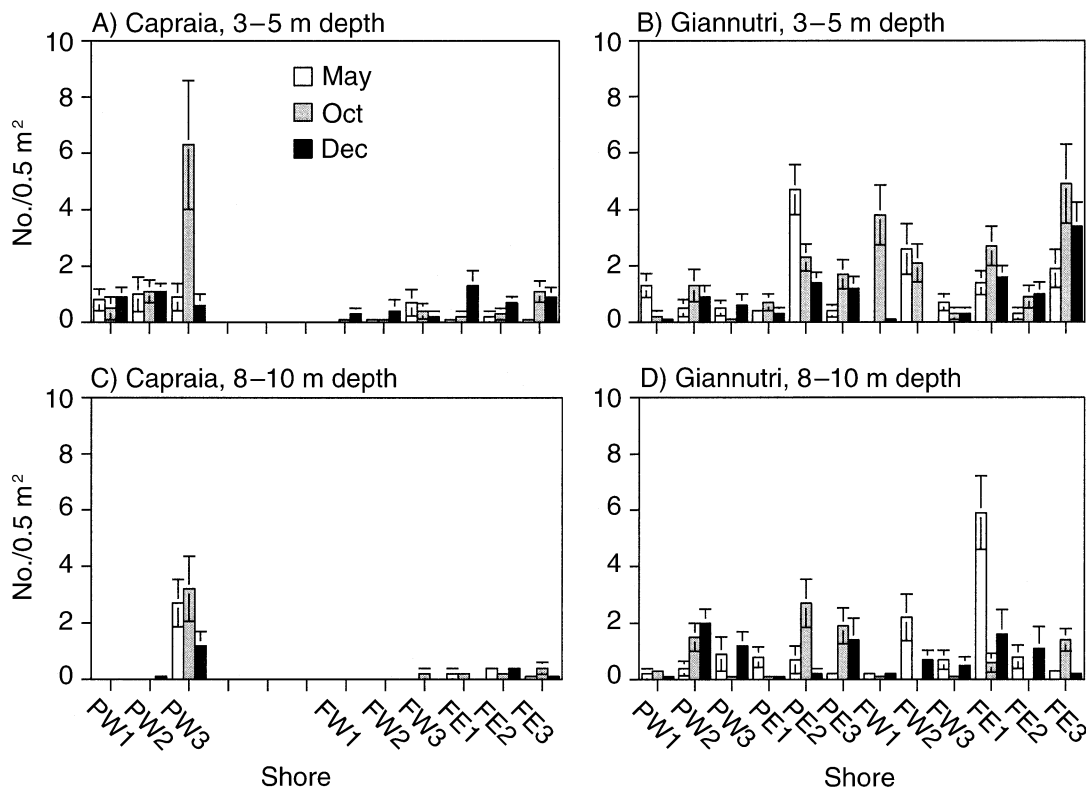


FIG. 7. Densities of the purple sea urchin, *Paracentrotus lividus*, at (A, C) Capraia and (B, D) Giannutri. Bars are means  $\pm 1$  SE of counts from 10 replicate 0.5-m<sup>2</sup> quadrats surveyed at each of two depths, 3–5 m (A, B) and 8–10 m (C, D), at each shore (see Fig. 1 for shore codes), on each of three sampling dates (May, October, and December 2000).

The presence of multiple no-take marine reserves, established in different geographic locations and hydrographic conditions provided the unique opportunity to test hypotheses about the separate and combined effects of physical setting and fishing on whole coastal assemblages. While large-scale studies focusing on multispecies assemblages leave many questions about mechanistic linkages between system components unanswered, they constitute the only possible approach to identifying relevant scales of processes shaping whole assemblages and to determining the extent to which generalizations about the structure of assemblages can be made under specific environmental settings.

Interestingly, in our study, effects of protection varied across the physical gradients of exposure shaping assemblages over scales from kilometers to tens of kilometers. Indirect effects of enhanced predator biomass on sea urchins and possibly on benthic assemblages were detected only for one sea urchin species, whose distribution was in turn associated with wave exposure. Studies of marine reserves from other systems also showed that effects of protection combine with natural environmental gradients in shaping marine assemblages. For example, Friedlander et al. (2003) found that marine reserves located at sites with moderate wave

exposure and high rugosity of the substrate had the highest levels of fish species richness in large-scale surveys of the main Hawaiian Islands. Long-term studies of reserve effects on rocky intertidal communities in Chile indicated that recovery of herbivorous gastropods targeted by artisanal fisheries had different indirect effects on algal communities at wave-exposed and sheltered sites. Recovery of limpets in reserves led to decreased cover of palatable algae (e.g., *Mazzaella laminarioides* and *Ulva* sp.) in the mid-intertidal zone within a few years from reserve establishment. However, after eight years of protection, the low-intertidal unpalatable alga *Durvillaea antarctica* invaded the mid-intertidal at wave-exposed sites (e.g., Moreno 2001). In rocky reefs of northeastern New Zealand, cascading effects of protection of predatory fishes on sea urchins and macroalgae were apparent only at sites with intermediate wave exposure. At the most exposed and most sheltered locations, sea urchins occurred at low densities and did not overgraze macroalgae (R. Babcock and N. Shears, *personal communications*).

Despite clear responses to protection in no-take reserves of some of the variables considered, others revealed weak and variable effects of protection. This result may be due to insufficient power of the sampling design, to a lack of strict protection enforcement within

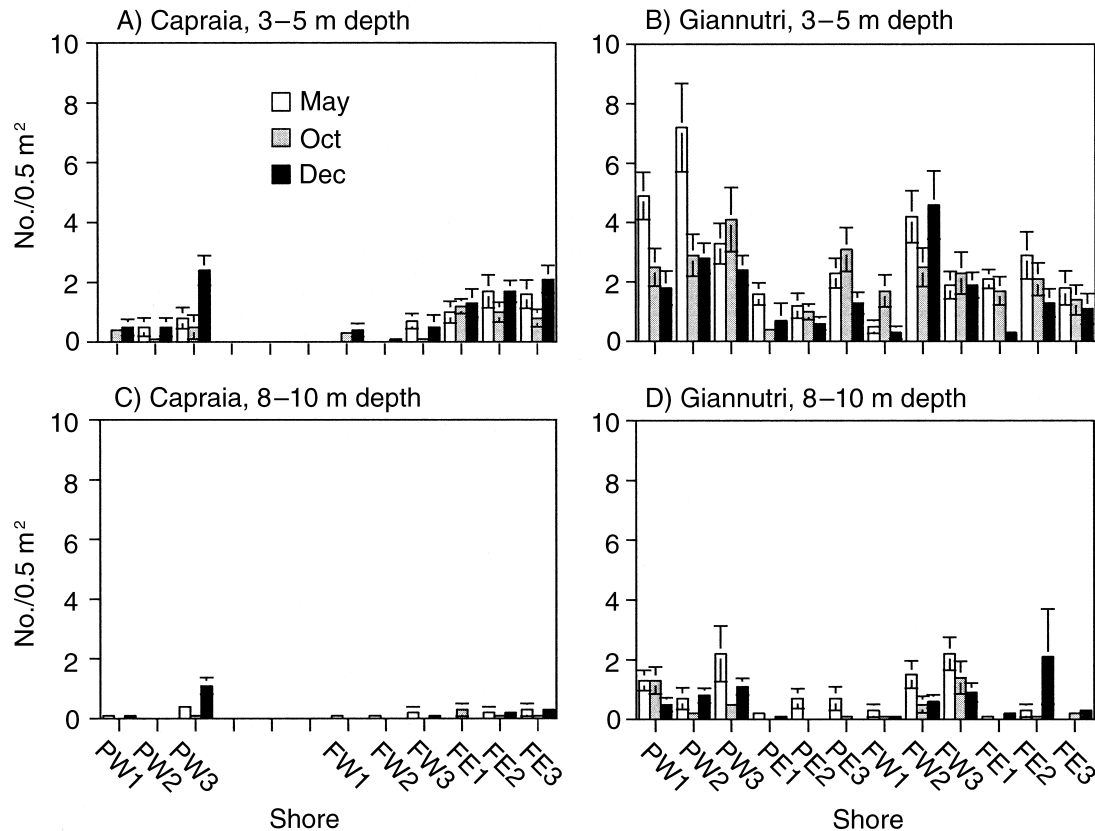


FIG. 8. Densities of the black sea urchin, *Arbacia lixula*, at (A, C) Capraia and (B, D) Giannutri. Bars are means  $\pm$  1 SE of counts from 10 replicate 0.5-m<sup>2</sup> quadrats surveyed at each of two depths, 3–5 m (A, B) and 8–10 m (C, D), at each shore (see Fig. 1 for shore codes), on each of three sampling dates (May, October, and December 2000).

no-take zones, to the short duration of time of protection, to the small size of reserves, or to intense fishing pressure in areas surrounding these small no-take zones. Insufficient power seems unlikely given the high level of replication in this study. In contrast with many previous studies of effects of marine reserves (reviewed by Russ 2002, Halpern 2003, Micheli et al. 2004b), multiple no-take reserves and fished areas were sampled. In addition, there was no evidence of the occurrence of consistently large, not significant  $F$  values in our analyses, even though tests of protection (as a main effect or in interaction with other factors) were not done on the residual mean square, and other terms involving less degrees of freedom than those associated with the error term were used as the denominators. Thus, when statistical tests failed to detect significant differences between protected and fished shores, this was likely due to the lack of significant effects, rather than lack of statistical power.

Lack of data on actual compliance with fishing restrictions at these sites makes it impossible to determine whether any fishing occurs within the no-take reserves. However, the no-take, no-access status of these reserves, the presence of onsite personnel charged with enforcing the fishing and access restrictions within

the core no-take zones of both islands, and our personal observations of fishing commonly occurring in Zones 2 and 3 but not within the core no-take zones, support our assumptions that differences in fishing intensity must exist between the no-take reserves and our reference, fished sites (see *Methods: Study area and marine protected area zoning*). Lack of data on variation in fishing intensity within and around marine protected areas (MPAs) is common to most studies of MPAs (e.g., Russ 2002). It is critically important that future studies include this information.

Recovery of populations and whole assemblages may occur with lags of decades, particularly for long-lived species with sporadic recruitment (McClanahan 2000, Russ 2002, Micheli et al. 2004b). In addition, intense fishing pressure in areas surrounding the reserve can cause high mortality of mobile species, slowing down or preventing their recovery, and possibly, in the case of top predators, reducing their impacts on lower trophic levels and on food web structure (Micheli et al. 2004a). The weak and variable negative effects of predatory fishes on sea urchins in our study may be due to the generally low densities of predators at our field sites.

Abundances of fish species reported to prey upon, and in some cases control, populations of sea urchins (Sala and Zabala 1996, Sala et al. 1998a) tended to be greater within no-take reserves than in fished areas but were generally low even within protected areas. A meta-analysis of data from Mediterranean MPAs revealed that negative correlations between densities of the main sea urchin predators in Mediterranean rocky reefs, the sparid fishes *Diplodus sargus* and *D. vulgaris*, and sea urchin densities exist only when *Diplodus* combined densities exceed 10–15 individuals/100 m<sup>2</sup> (P. Guidetti and E. Sala, unpublished data). At lower *Diplodus* densities, sea urchin densities were highly variable and ranged up to 30 urchins/m<sup>2</sup> (P. Guidetti and E. Sala, unpublished data). After we converted our data from number of individuals per point count (i.e., per 78.5 m<sup>2</sup>) to numbers per 100 m<sup>2</sup>, our combined densities for *D. sargus* and *D. vulgaris* ranged from 0 to 12.7/100 m<sup>2</sup> (mean = 3.0 ± 0.5 SE, *N* = 288 point counts) at Giannutri and from 0 to 8.1/100 m<sup>2</sup> (mean = 3.6 ± 0.5 SE, *N* = 216) at Capraia, in all cases below the threshold for a strong negative impact of these predators on sea urchin densities.

Thus, effects of protection are likely to become more obvious through time unless the size of these reserves is not sufficient to fully protect these populations and assemblages (e.g., Botsford et al. 2003). Based on existing studies for other systems, both within the Mediterranean and elsewhere (e.g., Halpern 2003, Micheli et al. 2004b), positive effects of protection on the relatively sedentary species dominating these reef assemblages should occur. For example, clear effects of protection on Mediterranean reef assemblages were documented for the reserves of Scandola (Francour 1991), Carry-le-Rouet (Harmelin et al. 1995), and Islas Medes (Garcia-Rubies and Zabala 1990, Sala and Zabala 1996), all smaller than the no-take reserves of the Tuscan Archipelago (Micheli et al. 2004b).

Results from this study have important implications for our understanding and conservation of coastal marine environments. Effective networks of marine reserves should protect representative assemblages and habitat types (e.g., Possingham et al. 2000). Our result that distinct assemblages occur along Mediterranean shores with different levels of physical exposure indicates that physical gradients should be a crucial consideration in the design of future MPAs. In addition, physical gradients and spatial variation of habitats and assemblages should be explicitly included in monitoring and evaluation of marine reserve efficacy. Studies of marine reserves should stratify sampling by existing physical gradients, and identify natural variation at different spatial scales through hierarchical sampling designs in order to separate such underlying variation from effects of protection. In addition, expectations about reserve effects may depend on the physical exposure and other environmental characteristics of sites. In particular, cascading effects of fishing in rocky reef

assemblages may be more likely to occur at wave-protected than at wave-exposed locations.

Because data describing assemblages of islands before no-take reserves were established are not available, it is not possible to exclude that the variation in fish and benthic assemblages between levels of protection we observed may be preexisting and not linked to the protection itself. However, our results are robust across multiple no-take reserves, making the possibility of preexisting differences unlikely. Continued monitoring of MPAs in this and other systems is essential for understanding temporal dynamics and recovery trajectories of coastal marine assemblages severely impacted by fishing. Long-term data from marine reserves, particularly including data prior the reserve establishment, are available for a very limited number of systems (e.g., Micheli et al. 2004b). This type of data is essential for establishing effects of protection on marine ecosystems. Based on our results, we propose the following predictions concerning future temporal dynamics of these coastal assemblages within MPAs. Further buildup of the abundances and biomass of predatory fishes within no-take reserves may lead to decreased abundances of purple sea urchins, *P. lividus*, within reserves and possibly around them through spillover of predators. Purple sea urchin declines within reserves may enhance the structural differences among different shores. Increased macroalgal cover may also enhance variation in the structure of the fish assemblage through “bottom-up” effects of habitat characteristics on the fish assemblage. Thus, we expect that both the fish and benthic assemblage should diverge through time between protected and fished areas, possibly to different degrees along windward and leeward shores. If black sea urchin, *A. lixula*, densities are indeed controlled primarily by physical factors, we would expect long-term cycles in their population sizes associated with recruitment pulses (Ebert et al. 1993, Sala et al. 1998b), extreme weather events, or disease outbreaks, but an uncoupling of their patterns of distribution and abundance from gradients in fishing pressure.

Temperate rocky reef assemblages are highly variable and dynamic systems. However, consistent patterns of variation in assemblage composition were observed at similar spatial scales both for fish and benthic assemblages and on two different islands. Effects of protection from fishing in no-take marine reserves on the structure of the fish assemblage, in the abundances of the sea urchin *P. lividus*, and in the structure of benthic assemblages were overlain on variation associated with physical exposure of the coastline. Future dynamics and trajectories of recovery from human disturbances may vary depending on the different hydrographic context of locations. Large-scale “manipulations” of human use of the coastal marine environments (e.g., MPAs) encompassing a range of different abiotic conditions and types of biological assemblages can provide crucial insights into the processes struc-

turing marine assemblages, on the relevant scales for investigating such processes, and for applying this understanding to marine conservation.

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#### APPENDIX A

Quantification of habitat extent, fish, and benthic taxa at Capraia and Giannutri, Italy, is available in ESA’s Electronic Data Archive: *Ecological Archives* M075-003-A1.

#### APPENDIX B

A table giving total fish abundances at Capraia and Giannutri in May, October, and December 2000 is available in ESA’s Electronic Data Archive: *Ecological Archives* M075-003-A2.

#### APPENDIX C

A table with results of similarity percentage (SIMPER) analyses showing major species characterizing fish assemblages at locations with different regimes of protection and exposure of the coastline at Capraia and Giannutri, Italy, is available in ESA’s Electronic Data Archive: *Ecological Archives* M075-003-A3.

#### APPENDIX D

A table giving major species discriminating benthic assemblages sampled at 3–5 m and 8–10 m depths at locations with different exposure of the coastline at Capraia and Giannutri, Italy, is available in ESA’s Electronic Data Archive: *Ecological Archives* M075-003-A4.