MARINE RESERVES REESTABLISH LOST PREDATORY INTERACTIONS AND CAUSE COMMUNITY CHANGES IN ROCKY REEFS

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Abstract. In the last decades, marine reserves have dramatically increased in number worldwide. Here I examined the potential of no-take marine reserves to reestablish lost predatory interactions and, in turn, cause community-wide changes in Mediterranean rocky reefs. Protected locations supported higher density and size of the most effective fish preying on sea urchins (the sea breams *Diplodus sargus* and *D. vulgaris*) than unprotected locations. Density of sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) was lower at protected than at unprotected locations. Size structure of *P. lividus* was bimodal (a symptom of predation on medium-sized urchins) only at the protected locations. Coralline barrens were less extended at protected than at unprotected locations, whereas turf-forming and erect-branched algae showed an opposite pattern. Erect-unbranched and erect-calcified algae and conspicuous zoobenthic organisms did not show any pattern related to protection. Tethering experiments showed that predation impact on urchins was (1) higher at protected than at unprotected locations, (2) higher on *P. lividus* than on *A. lixula*, and (3) higher on medium-sized (2–3.5 cm test diameter) than large-sized (>3.5 cm) urchins. Sea urchins preyed on by fish in natural conditions were smaller at unprotected than at protected locations. The analysis of sea urchin remains found in *Diplodus* fish stomachs revealed that medium-sized *P. lividus* were the most frequently preyed upon urchins and that size range of consumed sea urchins expanded with increasing size of *Diplodus* fish. These results suggest that (1) depletion and size reduction of predatory fish caused by fishing alter patterns of predation on sea urchins, and that (2) fishing bans (e.g., within no-take marine reserves) may reestablish lost interactions among strongly interactive species in temperate rocky reefs with potential community-wide effects.

Key words: Arbacia lixula; community changes; Diplodus sargus; Diplodus vulgaris; fishing impacts; marine reserves; Mediterranean Sea; Paracentrous lividus; species interactions; sublittoral rocky reefs; top-down control; trophic cascades.

INTRODUCTION

Predation is one of the key processes governing structure of natural communities (Hairston et al. 1960, Duffy 2002). Besides direct effects on prey, predators may indirectly influence the entire community through so-called trophic cascades (Paine 1980, Witman and Dayton 2001). Only in recent years, however, has the threat of human activities affecting populations of large predators in natural ecosystems been fully recognized. Special attention has been paid to fishing, which has been demonstrated to severely impact target species, in most cases represented by high trophic level predators. The impact has consequent top-down perturbations (e.g., through trophic cascades) of marine community structure and ecosystem functions (Pauly et al. 1998, Sala et al. 1998, Steneck 1998, Tegner and Dayton 2000, Jackson et al. 2001, Myers and Worm 2003).

In temperate, subtidal rocky reefs, trophic cascades often imply strong interactions among at least three

trophic levels (Estes and Duggins 1995, Sala et al. 1998, Pinnegar et al. 2000, Tegner and Dayton 2000, Shears and Babcock 2003): (1) predators (e.g., fish, lobsters, otters), (2) grazers (e.g., sea urchins), and (3) macroalgal assemblages (e.g., kelp forests) (Sala et al. 1998, Pinnegar et al. 2000). The trophic cascade model predicts flourishing macroalgal beds in the presence of abundant predators along with low densities of sea urchins (the most important grazers in temperate reefs; [Lawrence 1975, Tegner and Dayton 1981, Sala et al. 1998]). Conversely, when released from predation because of predator removal, sea urchins increase in density and overconsume erect macroalgae causing formation of barrens (i.e., bare rocks with encrusting algae) (Estes and Duggins 1995, Shears and Babcock 2003).

Benthic communities in Mediterranean rocky reefs range between two alternative states: macroalgal beds and coralline barrens (Sala et al. 1998; see Plate 1). Sea urchins (i.e., *Paracentrotus lividus* and *Arbacia lixula*), especially when at high density, may cause the transition from macroalgal beds to barrens (Verlaque 1987, Sala et al. 1998, see also Bulleri et al. 2002), which involves dramatic changes in community structure and ecosystem functioning (Sala et al. 1998, Sala 2004). Recent studies
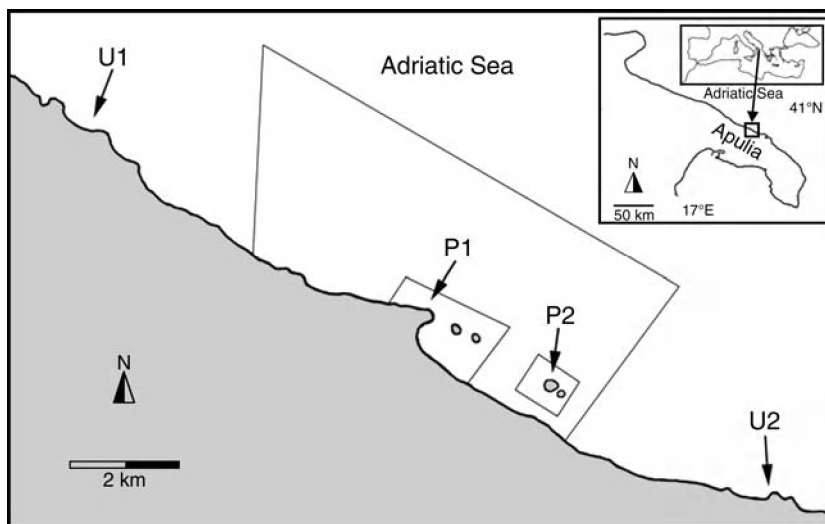
FIG. 1. Study area and map of sampling locations (U1 and U2, unprotected locations; P1 and P2, protected locations). Boundary lines delimit the Torre Guaceto marine reserve and the two no-take zones.

showed that many species can potentially eat sea urchins (e.g., lobsters, crabs, gastropods, starfishes), but only a few species of fish prey upon sea urchins with adequate intensity to influence population density in Mediterranean rocky reefs (Sala 1997, Sala et al. 1998, Guidetti 2004*a*, Hereu et al. 2005): the sea breams *Diplodus sargus* and *D. vulgaris* (preying on juvenile and adult urchins) and large-sized individuals of the wrasses *Coris julis* and *Thalassoma pavo* (preying upon sea urchins <1 cm in test diameter). Sea breams are targeted by many kinds of fishery, while wrasses have a lower commercial value and are impacted (mostly as by-catch) in areas where angling and traps are used intensely (Harmelin et al. 1995, Coll et al. 2004). All the above issues suggest that fishing, by removing fish predators of sea urchins, may have community-wide effects in Mediterranean rocky reefs.

No-take marine reserves represent an opportunity to test for cascading effects of predator removal at meaningful spatial and temporal scales (Sala et al. 1998, Shears and Babcock 2002). In the Mediterranean Sea, assessments of community-wide changes following protection from fishing provided contradictory results. In one case, no cascading effects were found on prey in spite of significant differences in predatory fish abundance and size (Guidetti et al. 2005). Another study showed recovery of fish within reserves, but indirect effects on benthic assemblages were only evident at sites with low physical exposure (Micheli et al. 2005). Finally, Sala et al. (1998) stated that patterns were only partially consistent in time with the trophic cascade model. These results stress the need for further research aimed at understanding the mechanisms underlying the realization of trophic cascades in temperate rocky reefs.

This study is aimed at assessing possible differences between protected and unprotected rocky reefs in (1)

distribution patterns of predatory fish, sea urchins, barrens, and conspicuous benthic organisms (especially macroalgae), (2) levels of fish predation upon sea urchins evaluated by tethering experiments, and (3) size–frequency distributions of sea urchins preyed on by fish in natural conditions. The relationship between predatory fish size and sea urchin size was also examined.

MATERIALS AND METHODS

Study area

The study area is located in southeastern Italy (Adriatic Sea) and is characterized by a rocky plateau with a gentle to medium slope, declining from the water surface to a depth of ~10 m over coarse sand. Distribution patterns of fish, sea urchins, and benthos were assessed at two protected and two unprotected locations (Fig. 1). Sampling was repeated four times (May–June and September–October in 2002 and 2003) to assess whether the response to protection was coherent in time. The two protected locations (hereafter P1 and P2) were represented by the two no-take zones of the Torre Guaceto Marine Reserve (TGMR; the whole reserve covers ~2220 ha and was established in 1992), where enforcement is successful. The two unprotected locations were off similar stretches of coast (in terms of slope and wave exposure) northward (U1) and southward (U2) of the TGMR (Fig. 1), far enough to exclude any possible spillover of adult fish from the reserve (Vierucci 2005). The TGMR was chosen for this study as it is actually protected (it is not a "paper park" where protection is only formal). It is big enough to allow for recovery of *Diplodus* fish populations and it has been protected long enough to encompass the life span of *Diplodus* species.

TABLE 1. ANOVA of fish predation levels on sea urchins between two levels of protection, at the spatial scales of locations and sites, between two sea urchin species, and between two size classes.

Source of variation	df	MS	F	P
Protection	1	13760.32	25.51	0.03
Location (protection)	2	539.31	2.58	0.19
Site (location (protection))	4	209.26	2.72	0.04
Species	1	5509.61	37.44	0.02
Size	1	2722.58	5.47	0.14
Protection × species	1	2293.04	15.58	0.07
Protection × size	1	667.56	1.34	0.37
Species × location (protection)	2	147.17	2.63	0.19
Size × location (protection)	2	497.43	19.59	<0.01
Species × site (location (protection))	4	55.86	0.73	0.58
Size × site (location (protection))	4	25.39	0.33	0.85
Species × size	1	2715.81	19.4*	0.04
Protection × species × size	1	2.48	0.02	0.91
Size × species × location (protection)	2	140.00	1.93	0.26
Size × species × site (location (protection))	4	72.38	0.94	0.44
Residual	64	76.98		

Note: Levels of protection are present vs. absent; the two sea urchin species are *Paracentrotus lividus* and *Arbacia lixula*, and the two size classes are medium (2–3.5 cm) and large (>3.5 cm).

Fish predators of sea urchins

Density of predator fish (i.e., *D. sargus, D. vulgaris,* and *Coris julis*) was estimated by visual census at a depth of 4–7 m along 25 × 5 m transects (Harmelin-Vivien et al. 1985). Detected individuals of *D. sargus, D. vulgaris,* and *C. julis* were assigned to one of the three size categories (small, medium, or large) on the basis of the maximum size achieved by each species (Fischer et al. 1987).

Censuses were done at two random sites (located hundreds of meters apart from each other) within each of the four locations, with four replicates at each site and sampling time, for a total of 128 fish counts. Replicates were done at a minimum distance of 50 m from each other to avoid spatial dependence in the density estimates of fish. Juvenile stages (i.e., settlers and recruits) were excluded from fish assessments as their numerical contribution may strongly influence average densities at the local level, while having no predatory effect on sea urchins.

Sea urchins

Density of sea urchins was assessed using quadrats of 1 m² at a depth of 4–7 m. *Paracentrotus lividus* and *Arbacia lixula* were counted in different series of quadrats to avoid dependence of data. Three sites (located from tens to hundreds of meters apart from each other) were sampled within each of the four locations, with 20 random quadrats at each site per each sampling time, for a total of 960 counts. The size of each individual >1 cm (test diameter without spines) was measured by means of a caliper (±0.1 mm). This method is suitable for assessing the adult fraction of sea urchin populations (i.e., individuals >1 cm). Care was taken to examine cryptic spaces, like undersurfaces of boulders and crevices. Sea urchins, finally, were grouped into size classes of 1 cm to examine frequency distributions (Sala and Zabala 1996).

Benthic cover

Cover of barrens, sediment, and benthic organisms was evaluated by analyzing 20 images (sampling area of ~1 m²) taken from three sites within each of the four locations at each sampling time (for a total of 960 images). Images were extracted randomly from underwater video footage taken by a digital video camera held orthogonally downward at a standard distance from the bottom (~1 m, maintained by use of a plumb line). Footage was downloaded to a computer and sampled for the image which were then analyzed by superimposing a grid of 25 squares (each representing 4% of the total area). Cover of barren, sediment, and benthic organisms was quantified by ranking each square from 0 to 4 (0 for absence, 1 for a cover of about one-quarter of a square, 2 for about one-half of a square, 3 for about three-quarters of a square, and 4 for the whole square). Whenever <25% (i.e., less than one-quarter of a square) of the substrate within each square was filled by barren or some benthic category, an arbitrary value of 0.5 was assigned. Scores were then added up for all the 25 smaller squares, and final values were expressed as percentage (Guidetti et al. 2003 and references therein).

Conspicuous benthic organisms were assessed according to morpho-functional categories (as modified by Steneck and Dethier 1994, Airoldi 2000, Williams and Polunin 2001): (a) algal turf (mixed assemblage of diminutive algae with canopy height <1 cm); (b) branched-erect macroalgae (upright and anatomically complex algae with frond extension >1 cm; e.g., Dictyotales, *Cystoseira* spp.); (c) unbranched-erect macroalgae (upright algae with low anatomical complexity and frond extension >1 cm; e.g., *Padina pavonica, Flabellia petiolata*); (d) calcified-erect macroalgae (upright algae with frond extension >1 cm and high calcification; e.g., *Halimeda tuna*); (e) sponges; (f) anthozoans; (g) other sessile invertebrates.

Fish predation levels upon sea urchins

Predation levels upon sea urchins were assessed at protected and unprotected locations in early autumn 2003 using tethering experiments (McClanahan and Muthiga 1989, Sala and Zabala 1996, Shears and Babcock 2002). Sea urchins were collected outside the TGMR far away from the studied locations. Tethering involves inserting thin nylon filaments ~50 cm long, by means of a needle, through the dorsal and ventral surface of each sea urchin test, as far away from the oral–aboral axis as possible. Each experimental unit (EU) was composed of 10 sea urchins tied by the thin filaments to a main 8–10 m long, thick nylon monofila-
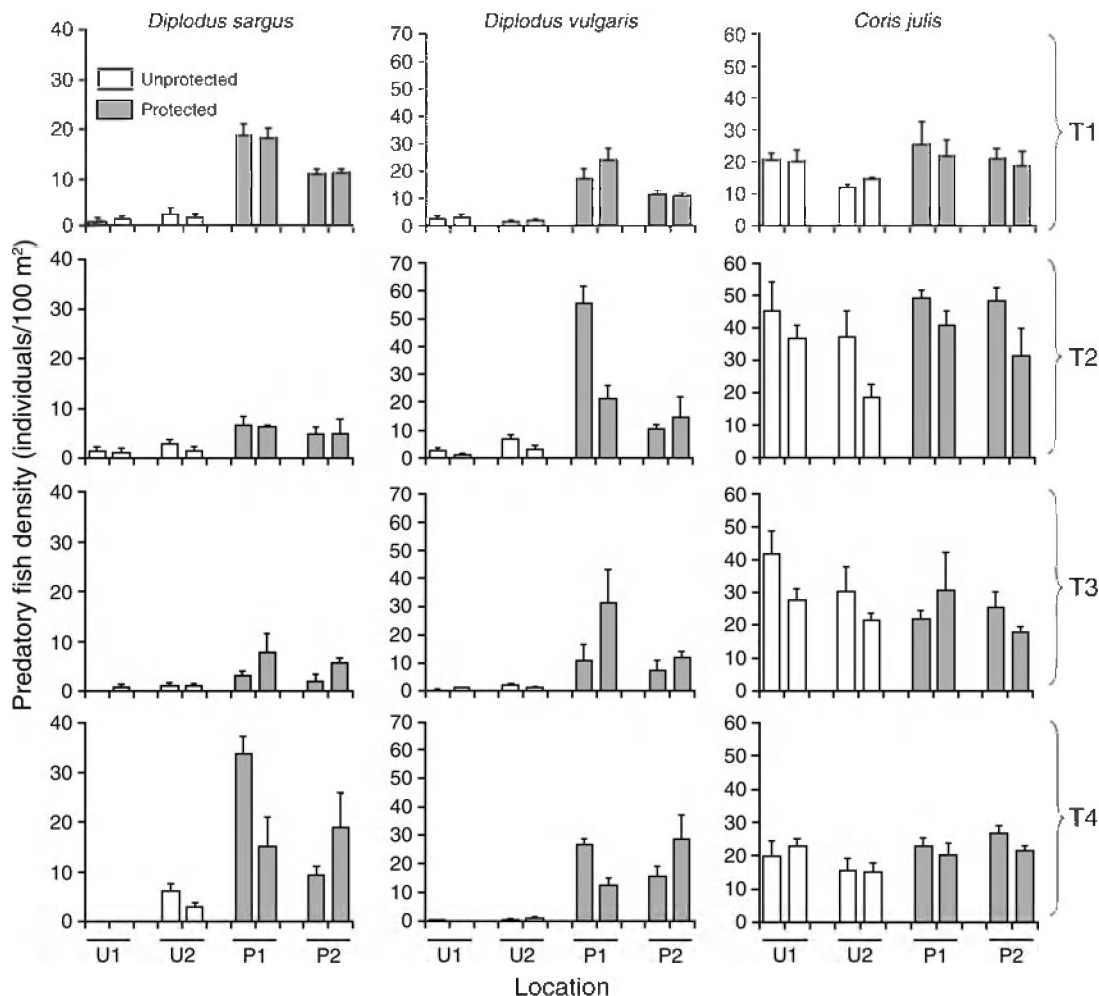
FIG. 2. Density (number of individuals/100 m²; mean + SE) of predatory fish at the unprotected (U1, U2; two sites sampled at each location) and protected locations (P1, P2; two sites sampled at each location), in each of the four sampling times (T1–T4). Unprotected locations are represented by open bars, and protected locations by solid bars.

ment. Separate EUs were made for each of the two species of urchin (*Paracentrotus lividus* and *Arbacia lixula*), and for each of the two size classes (medium, 2–3.5 cm; large, >3.5 cm). Laboratory trials revealed low mortality due to tethering (see also Shears and Babcock 2002), except for sea urchins <2 cm in test diameter (P. Guidetti, *personal observation*), which were thus not included in the experiment. Replicate EUs (*n* = 3) therefore consisted of 10 tethered urchins of a single species and size class positioned at two sites within each of the two protected and two unprotected locations, for a total of 96 EUs. The percentage of urchin tests missing (but remains were often close to the EUs) or opened in the latero-ventral area (typically attacked by *Diplodus* fish) was assessed for each EU five days later.

Sea urchins preyed on in natural conditions and stomach content analysis of Diplodus fish

Size–frequency distributions of sea urchins preyed on by fish in natural conditions were obtained by measuring

the diameter of sea urchins preyed on by fish in rocky reefs during the two-year study at both protected and unprotected locations. For this purpose, I considered only sea urchins with latero-ventral opened tests (typically attacked by *Diplodus* fish), and with spines and pedicels still moving, indicating a recent predatory attack.

Thirty-one stomachs of *Diplodus* fish containing sea urchins were analyzed: 23 *D. sargus* between 15 and 44 cm total length (TL) and 8 *D. vulgaris* between 16 and 39 cm TL. Determination of species and size of urchins from the stomach remains was done following Guidetti (2006). The relationship between prey size (sea urchins) and predator size (*Diplodus* fish) was also examined.

Statistical treatment of data

Analysis of variance was performed using the GMAV5 software package (coded by A. J. Underwood and M. G. Chapman, University of Sydney, Australia) was employed to test for differences in predatory fish
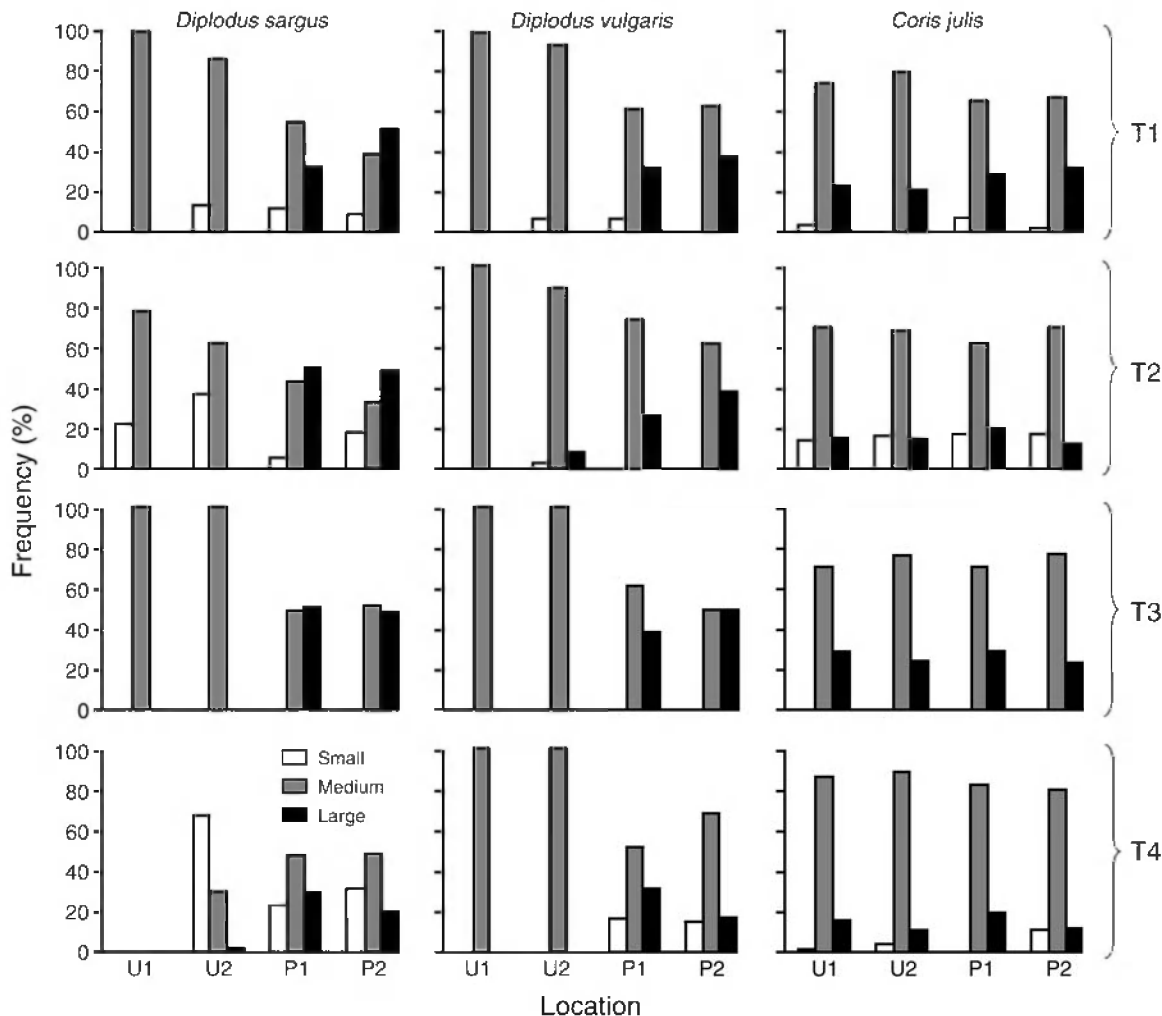
Fig. 3. Size–frequency distribution of the three size classes of fish predators of sea urchins at the unprotected (U1, U2) and protected (P1, P2) locations at four sampling times, T1–T4.

and sea urchin density and cover of barrens and of conspicuous benthic organisms in relation to "protection" (Pro; fixed factor, two levels: present vs. absent), "between locations" within each level of "protection" (L; nested factor), and "among sites" (S; random and nested within "location") (Table 1). Due to the potential for spatial overlap among replicates at each sampling site, independent tests were done for each time of sampling. ANOVA was also used to analyze predation levels upon sea urchins (measured by tethering) and to test for possible differences in relation to "protection" between locations, between sites within location, between the two species of sea urchin (Sp; fixed, two levels: *Paracentrotus lividus* vs. *Arbacia lixula*), and between the two size classes of urchins (Sz; fixed, two levels: medium vs. large). Prior to analysis, the homogeneity of variance was tested by Cochran's test, and whenever necessary, data were appropriately transformed. If transformations did not produce homogeneous variances, ANOVA was used on nontransformed data after setting $\alpha = 0.01$ in

order to compensate for the increased likelihood of Type I error (Underwood 1997). Pooling procedures were used to increase the power of the test for the factor "Protection"; a posteriori SNK tests were run to compare different means, when appropriate (Underwood 1997).

RESULTS

Predator fish density and size distribution

Density of *Diplodus sargus* was significantly higher at the protected than at the unprotected locations (except in T4), with a significant variability at the spatial scales of locations and/or sites in some sampling times (Fig. 2 and Appendix, Table A1). Although it was not possible to formally test for temporal variability, inspection of the graph in Fig. 2 shows that density of *D. sargus* was remarkably variable over time. Percentage distribution of the three size classes showed that large-sized individuals accounted for ~20–50% of the total number
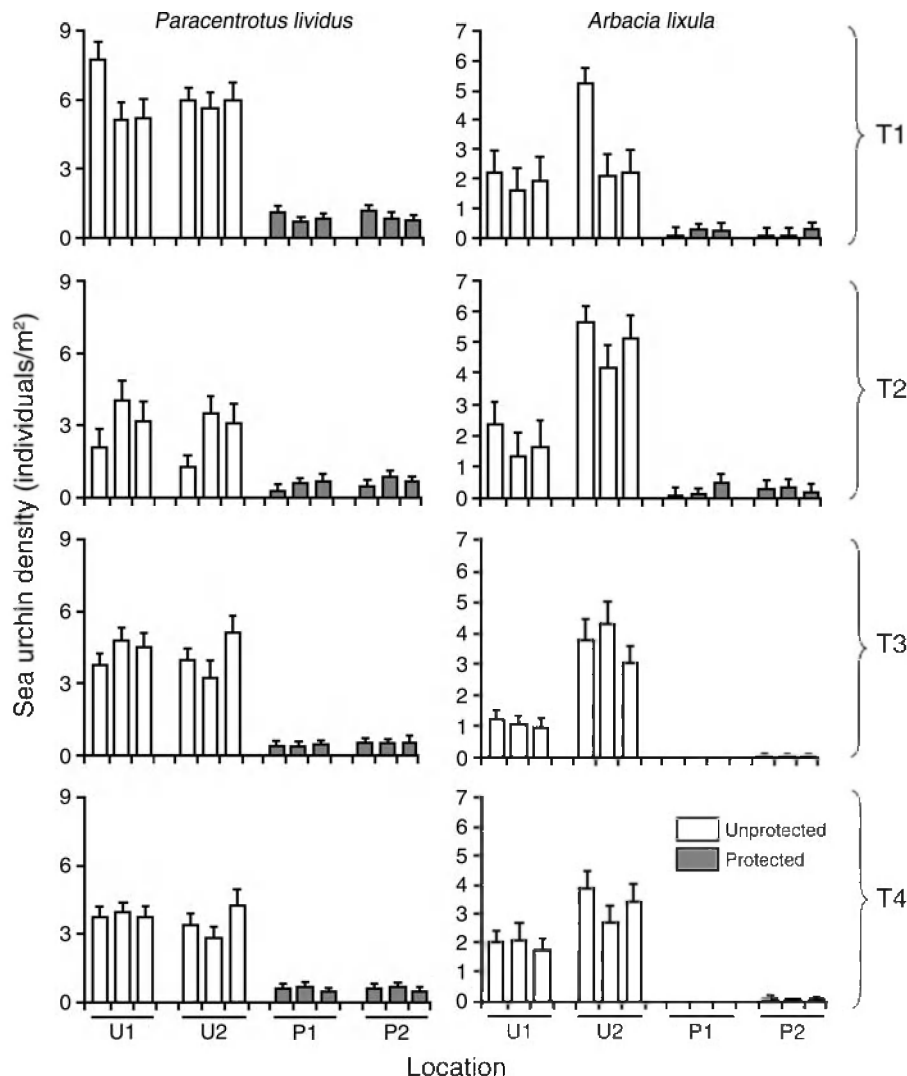
FIG. 4. Density (mean + SE) of sea urchins at the unprotected (U1, U2; three sites sampled at each location) and protected (P1, P2; three sites sampled at each location) locations, in each of the four sampling times (T1–T4). Unprotected locations are represented by open bars, and protected locations by solid bars.

of *D. sargus* recorded at the protected locations. Large individuals, instead, were almost absent at the unprotected locations, where medium-sized specimens dominated (Fig. 3).

Density of *D. vulgaris* was significantly higher at the protected than at the unprotected locations (except in T2), with significant variability detected among locations and/or sites at some sampling times (Fig. 2 and Appendix, Table A2). With regard to size, at the protected locations, large individuals accounted for ~15–50% of the recorded *D. vulgaris*, while at the unprotected locations, medium-sized individuals dominated (Fig. 3).

Density and size distribution of *Coris julis* did not change between protected and unprotected locations (Figs. 2 and 3 and Appendix, Table A3).

Sea urchin density and size–frequency distribution

Density of *Paracentrotus lividus* was significantly higher at the unprotected than at the protected locations at all sampling times, with a significant variability among sites detected in T2 (Fig. 4 and Appendix, Table A4). Size–frequency distribution of *P. lividus* was unimodal with the mode represented by individuals of 3–4 cm in size (followed by urchins of 2–3 cm) at the unprotected locations. At the protected locations, instead, the distribution was bimodal, with the first mode represented by small individuals (1–2 cm) and the second mode formed by urchins of 4–5 cm (Fig. 5).

Density of *Arbacia lixula* was significantly higher at the unprotected than at the protected locations (except in T2 and T3), and displayed a significant variability at the scales of locations and/or sites in some sampling
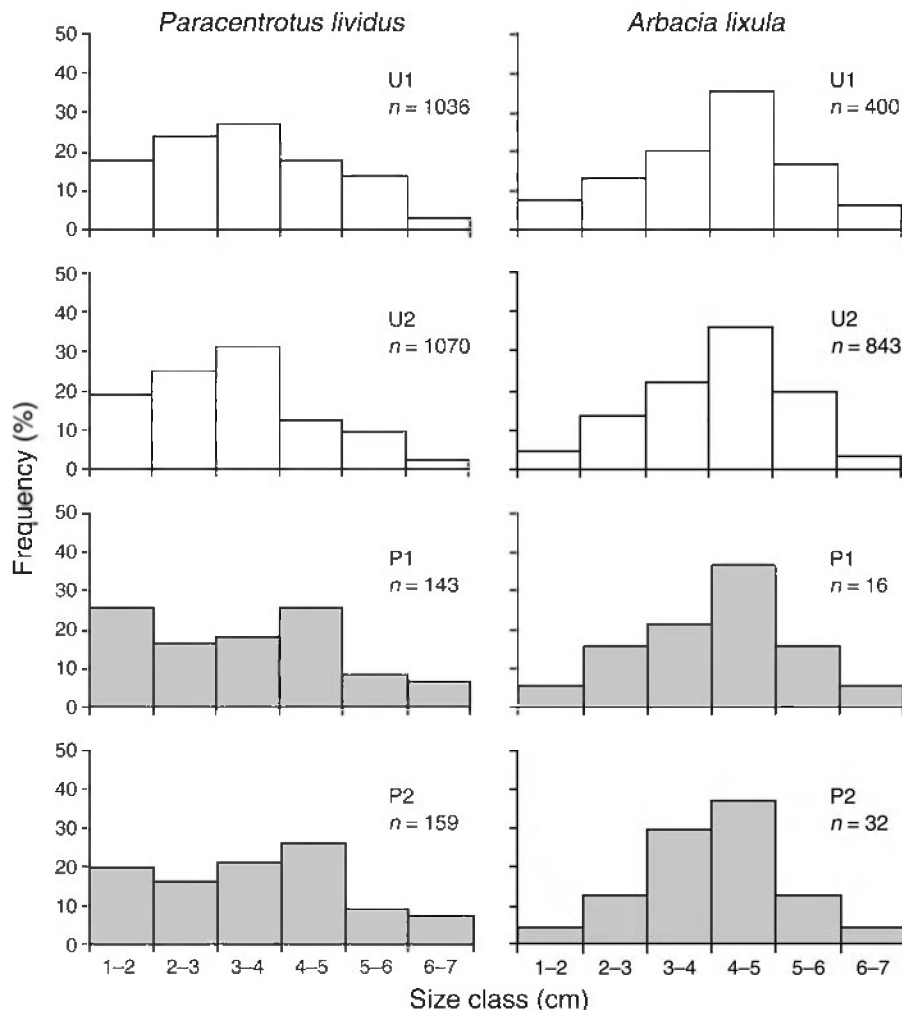
Fig. 5. Size–frequency distributions of sea urchins (test diameter without spines) at the unprotected (U1, U2) and protected locations (P1, P2). Unprotected locations are represented by open bars, and protected locations by solid bars.

times (Fig. 4 and Appendix, Table A5). Size–frequency distribution of this urchin did not show any difference between protected and unprotected locations. Notwithstanding the level of protection, the distribution was unimodal with the modal class formed by *A. lixula* of 4–5 cm (Fig. 5).

Cover of barrens and conspicuous benthic categories

Cover of barrens was higher at the unprotected than at the protected locations in all four sampling times (Fig. 6), with significant variability at both spatial scales of locations and sites (Appendix, Table A6). Although it was not possible to formally test for the temporal variability, barren cover was considerably variable at the unprotected locations among the four sampling times, while it was more stable at the protected locations (Fig. 6). Sediment cover (Fig. 6) did not show any significant difference between protected and unprotected locations (Appendix, Table A7). Algal turf showed a significantly higher cover at the protected than at the unprotected

locations in T1 and T3 (Fig. 6), and a variability at the scale of locations in T1, T2, and T4 (Appendix, Table A8). In spite of the marked variability at the scale of locations and sites, cover of branched-erect algae was significantly higher at the protected than at the unprotected locations, except in T3 (Appendix, Table A9), and it dramatically varied over time (Fig. 6). Cover of unbranched-erect macroalgae, calcified-erect macroalgae, sponges, anthozoans, and other sessile invertebrates did not change between protected and unprotected locations (Fig. 6 and Appendix, Tables A10–A14).

Predation levels by fish upon sea urchins

Predation levels upon sea urchins were significantly higher at the protected than at the unprotected locations (Fig. 7, Table 1). ANOVA also revealed the significant interactions $Sz \times L(Pro)$ (which means that predation levels differed at the scale of locations in relation to the size class considered) and $Sp \times Sz$ (i.e., *P. lividus* and *A.*
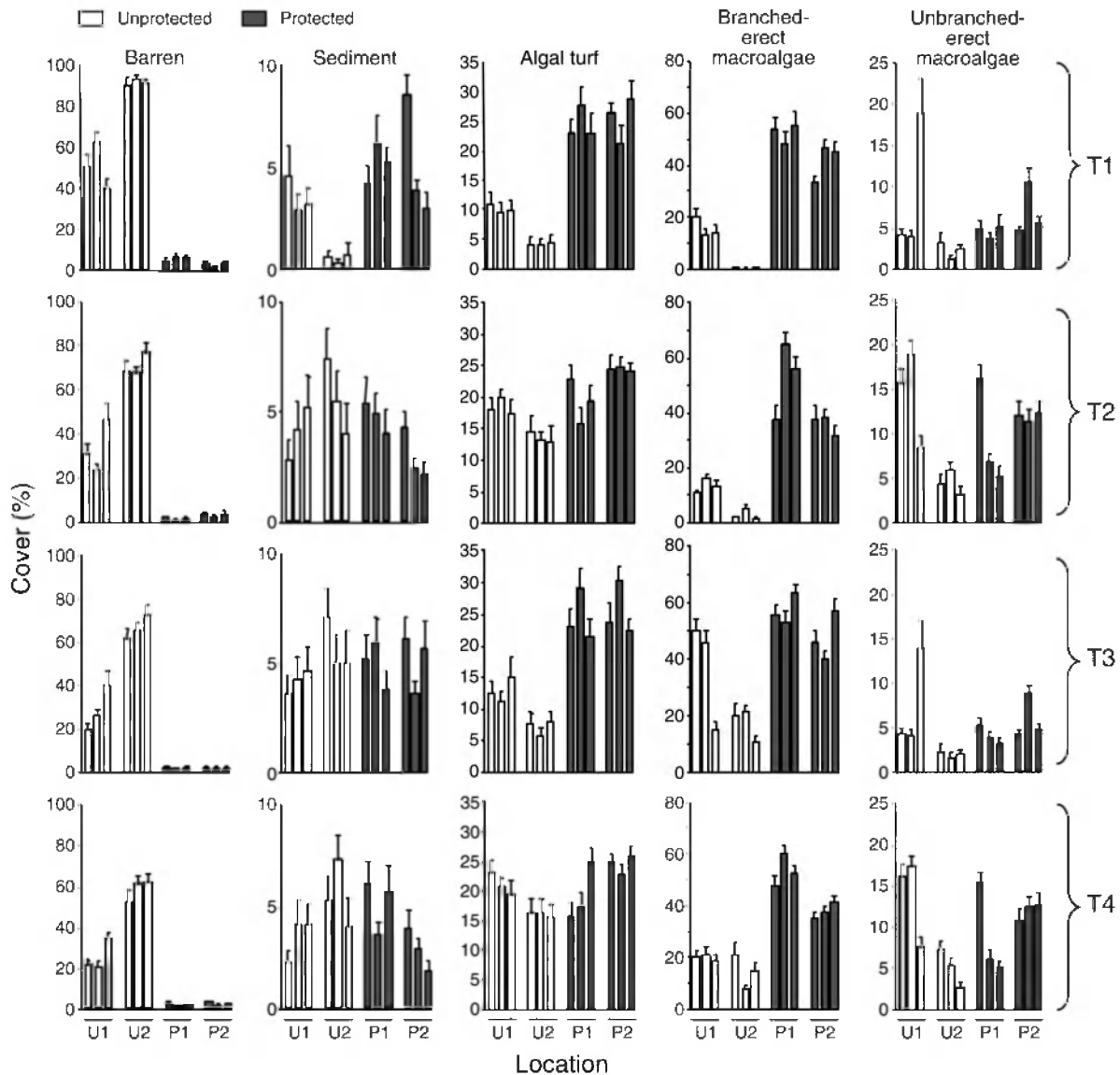
FIG. 6. Percent cover (mean + SE) of barrens, sediment, and conspicuous benthic categories (see *Methods*) at the unprotected (U1, U2; three sites sampled at each location) and protected (P1, P2; three sites sampled at each location) locations, in each of the four sampling times (T1–T4). Unprotected locations are represented by open bars, and protected locations by solid bars.

lixula are subject to different predation levels and such a difference is not the same between the two size classes considered). From this perspective, SNK tests revealed that medium-sized *P. lividus* were much more preyed on than large specimens, as for *A. lixula*, but the magnitude of the difference between the two size classes was greater for *P. lividus* than for *A. lixula* (Fig. 7).

Sea urchins preyed on in natural conditions and stomach content analysis of Diplodus *fish*

At the studied rocky reefs, I found the remains of 39 *P. lividus* and 5 *A. lixula* preyed on by fish. Tests were opened on the latero-ventral side and empty, with spines and pedicels still moving. About 80% of such *P. lividus*

was represented by individuals between 2 and 4 cm in size. Size–frequency distribution of preyed on *P. lividus* showed a modal class of urchins of 2–3 and 3–4 cm at the unprotected and protected locations, respectively (Fig. 8). The four *A. lixula* found at the protected locations showed a size range between 2.8 and 3.2 cm, while the single specimen at the unprotected locations was 2.7 cm in size.

In total, 57 sea urchins (54 *P. lividus* and 3 *A. lixula*) were found in the 31 *Diplodus* examined, which means that more than one sea urchin was found in some stomachs. The largest *Diplodus* fed on urchins from <1 cm to >4 cm in size, whereas the smallest *Diplodus* considered here preyed upon urchins of a maximum size
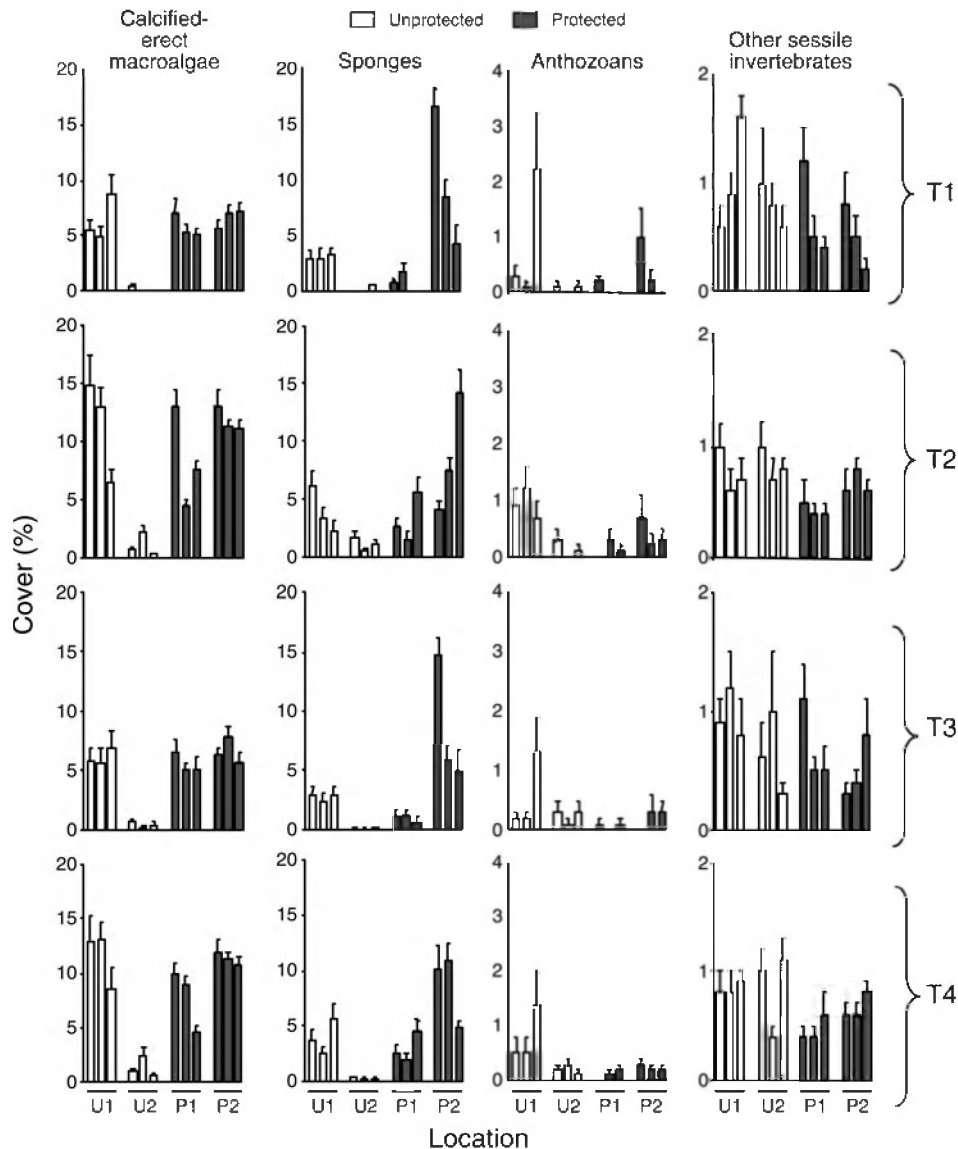
FIG. 6. Continued.

of ~1 cm. The size range of sea urchins found in the fish stomachs expanded with increasing size of *Diplodus* fish (Fig. 9). Sea urchin tests <1 cm were often found intact in the *Diplodus* stomachs (especially for large fish), suggesting that predators can ingest small urchins whole. Larger sea urchins, instead, were found as broken tests and spines and pieces of the Aristotle's lantern. More than 80% of *P. lividus* extracted from the *Diplodus* stomachs were 1–3 cm in size. The three *A. lixula* found in the stomachs of *D. sargus* ranged in size between 1.6 and 3.6 cm.

DISCUSSION

The present study shows that protected rocky reefs at the TGMR supported greater density and size of

Diplodus predatory fish (*D. sargus* and *D. vulgaris*) of sea urchins than unprotected reefs. No differences were observed for *Coris julis*, which could be related to the infrequent use by local fishermen of the fishing techniques (e.g., angling and traps) that have a high impact on wrasses. Moreover, results show that sea urchin density and the cover of barrens were higher at the unprotected locations, while the cover of turf-forming and erect-branched macroalgae were higher at the protected locations.

Even though the use of marine reserves for management purposes is still a matter of debate, worldwide, such practices have been demonstrated to have the potential of increasing density and size of fish inside the reserve boundaries, especially of species targeted by
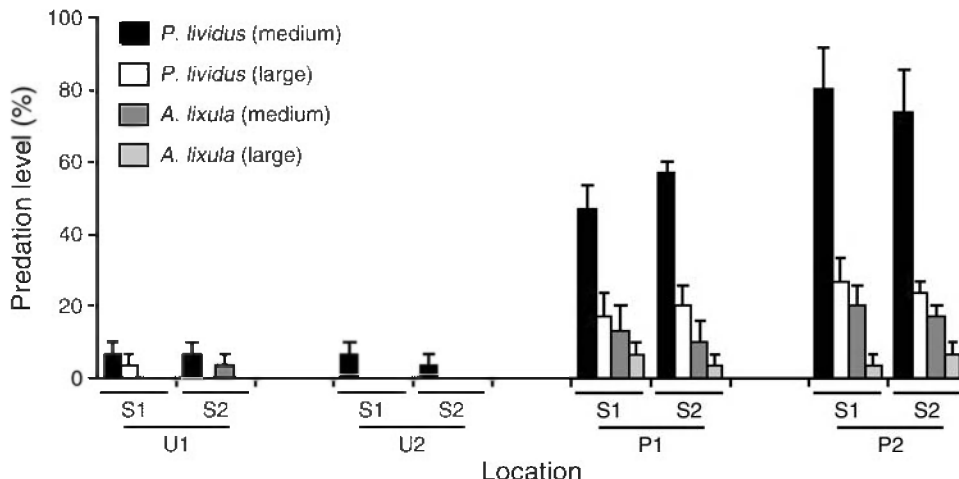
FIG. 7. Predation levels (mean + SE) on *Paracentrotus lividus* and *Arbacia lixula* of different sizes (medium and large; see *Methods*) at the unprotected (U1, U2; two sites sampled at each location: S1 and S2) and protected (P1, P2; two sites sampled at each location: S1 and S2) locations.

fishing (Harmelin et al. 1995, Mosquera et al. 2000, Halpern and Warner 2002, Halpern 2003, Willis et al. 2003, Micheli et al. 2004, Russ and Alcala 2004). Establishing a marine reserve, however, does not guarantee, per se, the recovery of predatory fish and

FIG. 8. Size–frequency distribution of *Paracentrotus lividus* (diameter without spines) preyed upon by fish in natural conditions (see *Methods*; data were pooled for each pair of unprotected and protected locations due to the relatively low number of observations). Unprotected locations are represented by open bars, and protected locations by solid bars.

related community-wide changes unless the protected area has the proper physical and biological characteristics to trigger changes at population and/or community levels. From this perspective, the TGMR is successfully enforced: it includes the appropriate habitat for *Diplodus* fish (for both adult and juvenile stages); it is large enough to harbor large *Diplodus* populations; and it has been protected long enough to encompass the life span of *Diplodus* species. The recovery of *Diplodus* populations at the TGMR also appeared to reestablish their predatory control upon sea urchins, similar to what is observed in other temperate regions (Shears and Babcock 2002). This was reflected in significantly different benthic assemblages (chiefly in the cover of some macroalgal categories) between unprotected and protected locations as a response to the different grazing intensity of sea urchins. Other factors potentially affecting the distribution of algae in rocky reefs, such as herbivory of fish (i.e., *Sarpa salpa*) and sediment scouring (Boudouresque and Verlaque 2001, Airoldi 2003), are unlikely to have had remarkable effects. In fact, density and size of herbivorous fish (Guidetti 2004*b*) or the amount of sediment did not differ between protected and unprotected locations. The algal categories that showed lower cover at unprotected locations (i.e., turf and erect-branched macroalgae) include algae that are highly palatable to Mediterranean sea urchins, such as *Bryopsis* spp., *Cystoseira* spp., *Stypocaulon scoparium*, and Dictyotales (Boudouresque and Verlaque 2001; see Plate 1). Their cover, although not formally tested, dramatically changed in time. This suggests that macroalgal cover probably depends on both local grazing intensity and seasonal recruitment (Airoldi 1998), and that recolonization of barrens by macroalgae could occur in a relatively short time provided that sea urchin grazing is not too intense. Erect-calcified and unbranched macroalgae, instead, did
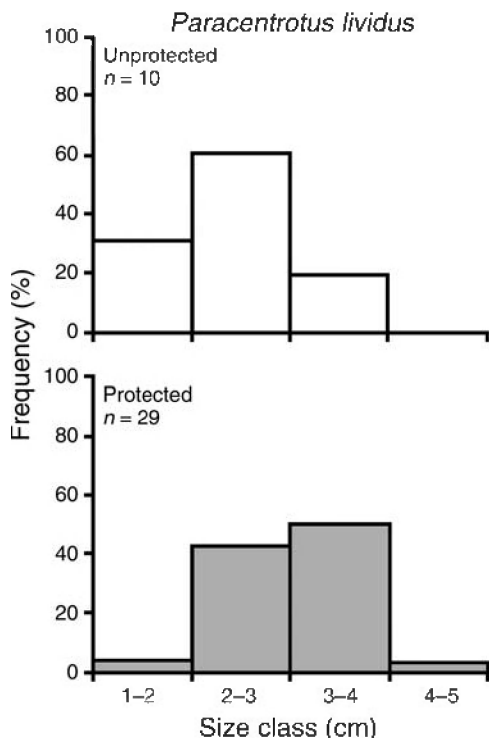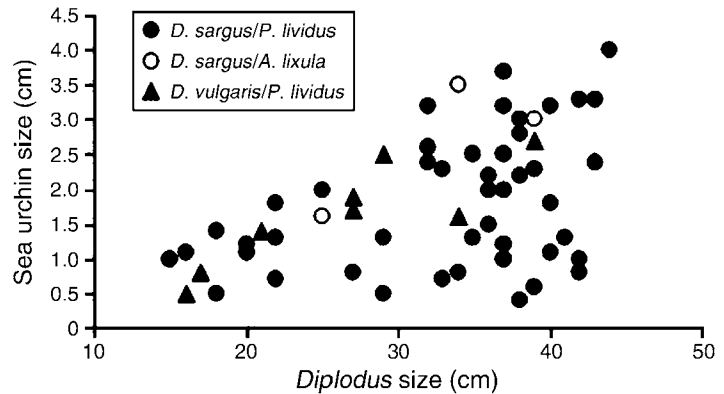
FIG. 9. Relationship between prey size (sea urchins) and predator size (*Diplodus* fish). Sea urchin size was estimated from stomach content remains.

not differ between protected and unprotected locations, probably due to their lower palatability to urchins (Boudouresque and Verlaque 2001). This lower palatability makes their abundance unrelated to local levels of urchin grazing. These results are consistent with the patterns observed in rocky reefs in New Zealand, where some macroalgae showed higher cover within reserve sites than in nonreserve sites and responded significantly to an experimental reduction of sea urchin grazing (Shears and Babcock 2002).

Cover of sessile zoobenthic organisms did not show any difference between protected and unprotected locations. Sea urchins have little chance to directly affect adult sessile animals. Nevertheless, especially when at dramatically high density (Guidetti et al. 2003 and references therein), they may affect zoobenthic assemblages by bulldozing propagules of sessile animals at the time of settlement (Maldonado and Uriz 1998). However, only long-term investigations could highlight whether or not protection may cause significant changes in the animal component of sessile benthos.

These results suggest that intense and unselective sea urchin grazing on sessile animal propagules and macroalgae at the time of recruitment, along with the inhibitory effect of some encrusting algae associated with barrens (Bulleri et al. 2002), can prevent recolonization of barrens once they are formed and make them persistent in time as a stable-state alternative to macroalgal beds (Knowlton 2004). Adopting this perspective, the temporal variability I observed in the cover of some macroalgal categories could simply be the result of two opposing mechanisms: the macroalgae recolonization of the available spaces provided by barrens contrasted with intense urchin grazing pressure.

The available studies dealing with community-wide changes in marine reserves suggest that trajectories of change are not obvious (Sala et al. 1998, Edgar and Barret 1999, Pinnegar et al. 2000, Shears and Babcock 2002, 2003, Micheli et al. 2004, Guidetti et al. 2005). In Mediterranean rocky reefs, P. Guidetti and E. Sala (*unpublished data*) and Verlaque (1987) identified thresholds in the density of consumers (i.e., *Diplodus* fish and

urchins) for the realization of trophic cascades. This would suggest, for example, that only marine reserves that are actually protected and have the proper characteristics for supporting dense populations of predators should be expected to undergo the back-transition from barrens to macroalgal beds. From a management perspective, these results suggest that any measure aimed at reducing the impact on populations of key predators (e.g., by using selective fishing gear) and preventing related ecosystem-wide changes could be complementary to the establishment of marine reserves.

Predation levels upon sea urchins assessed by tethering experiments inside and outside the TGMR were positively related with density and size of *Diplodus* fish. This demonstrates that the lower density of sea urchins inside the reserve is related to higher levels of fish predation (McClanahan 1999, Shears and Babcock 2002). Tethering experiments, in addition, showed that predation was higher on *P. lividus* than on *A. lixula*, and higher on medium- than large-sized urchins. Such results are consistent with those reported by Guidetti (2004a), who observed (by offering fish-consumers already opened urchin tests) a similar palatability of *P. lividus* and *A. lixula*; Guidetti and Mori (2005), reported that *A. lixula* displays greater attachment tenacity, test robustness, and spine length (providing protection against fish attacks) than *P. lividus*. Such morpho-functional features, in addition, are positively associated with urchin size for both species (Guidetti and Mori 2005).

At protected locations, size distribution of *P. lividus* was bimodal, while at the unprotected location it was unimodal. Bimodality in *P. lividus* populations has often been attributed to selective predation on urchins of intermediate size (e.g., Tegner and Dayton 1981, Sala and Zabala 1996, Shears and Babcock 2002). Medium-sized *P. lividus* seemed to be subject to the highest predation impact by fish, probably because large urchins can escape predation due to their size, whereas very small urchins usually shelter under stones and in crevices (Sala et al. 1998, Guidetti and Mori 2005, Hereu et al. 2005). *A. lixula* displayed lower density at the protected locations (similarly to *P. lividus*), but population size

PLATE 1.   (Left) Macroalgal bed and (right) a group of sea urchins feeding on macroalgae. Photo credit: P. Guidetti.

structure did not differ between protected and unprotected reefs. Predation on this urchin was slightly greater inside the TGMR than outside. This suggests that slightly greater predation could, in the long term, control *A. lixula* populations and/or that predation on juveniles (not evaluated here) is strong enough to control adult population density. Overall, even though there are many factors potentially capable of affecting population density of sea urchins (see Hereu et al. 2004), in the study area (at least during the study years), fish predation seems to exert an important role, although the observed patterns of urchin size distribution, especially the bimodal distribution, could change with time leading to few large adults.

The pattern for greater predation upon intermediate sea urchins may have implications for the trajectories of community change after having established a no-take reserve. Rocky reef communities, in fact, could display delays in the back-transition from extensive barrens to flourishing macroalgal beds because of the time taken by predator fish populations to fully recover, but also the for the oldest, biggest, and less preyed-upon urchins to die off naturally. Only at this stage will predators be capable of preventing smaller urchins replacing older ones, thus maintaining urchin density below the threshold required to form and maintain barrens. From this perspective, considering the abovementioned thresholds in the density of predatory fish to control sea urchins (P. Guidetti and E. Sala, *unpublished data*) and of sea urchins to cause the formation of barrens (Verlaque 1987), these results suggest that the patterns observed at the TGMR and adjacent fished areas could be described in terms of ecosystem shifts attributed to alternative, stable states (Scheffer and Carpenter 2003).

The greater size of sea urchins preyed upon in natural conditions at protected than at unprotected rocky reefs, and the expanded range of urchin size with increasing fish predator size (a general pattern of invertebrate prey use by predatory fish [Scharf et al. 2000]) provide further evidence that predation on sea urchins is more effective

in the marine reserve than outside due to the higher density and size (and therefore predatory efficiency; Guidetti 2004*a*) of *Diplodus* fish within the TGMR.

In conclusion, these results demonstrate that fishing bans (e.g., within no-take reserves) may allow density and size of the most effective fish predators of sea urchins to increase in Mediterranean, sublittoral rocky reefs. From this perspective, the use of fishing gear that does not impact key predators could be useful to the same purpose. Recovery of predatory fish seems to reestablish natural patterns of predation upon sea urchins. Due to higher predation in marine reserves, the urchins decrease in density (and so does their grazing impact on macroalgae), which results in less extended barrens and greater erect macroalgal cover at protected than at unprotected rocky reefs. It is interesting to note that before the establishment of the TGMR, wide barrens along with high sea urchin density characterized the rocky reefs that have been included in the reserve (M. Spoto and F. De Cristofaro, *personal communication*). Such reefs, at present, are almost completely colonized by benthic assemblages dominated by erect macroalgae. This study thus shows that fishing may cause ecosystem-wide changes in temperate rocky reefs and supports the use of no-take marine reserves as management tools capable not only of recovering fish populations of target species, but also of inverting the transition from macroalgal beds to barrens by reestablishing lost predatory interactions.

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APPENDIX

Results of three-factor ANOVA examining density of *Diplodus sargus*, *D. vulgaris*, *Coris julis*, *Paracentrotus lividus*, and *Arbacia lixula*; and cover of barrens, coarse sediment, algal turf, branched-erect macroalgae, unbranched-erect macroalgae, calcified-erect macroalgae, sponges, anthozoans, and other sessile invertebrates at each of the four sampling times between two levels of protection, between two protected and two unprotected locations, and two sites within location (*Ecological Archives* A016-037-A1).