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Relationships among predatory fish, sea urchins and barrens in Mediterranean rocky reefs across a latitudinal gradient

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Abstract

Previous studies conducted on a local scale emphasised the potential of trophic cascades in Mediterranean rocky reefs (involving predatory fish, sea urchins and macroalgae) in affecting the transition between benthic communities dominated by erected macroalgae and barrens (i.e., bare rock with partial cover of encrusting algae). Distribution patterns of fish predators of sea urchins (*Diplodus sargus sargus*, *Diplodus vulgaris*, *Coris julis* and *Thalassoma pavo*), sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) and barrens, and fish predation rates upon sea urchins, were assessed in shallow (3–6 m depth) sublittoral rocky reefs in the northern, central and southern sectors of the eastern Adriatic Sea, i.e., on a large spatial scale of hundreds of kilometres. No dramatic differences were observed in predatory fish density across latitude, except for a lower density of small *D. sargus sargus* in the northern Adriatic and an increasing density of *T. pavo* from north to south. *P. lividus* did not show any significant difference across latitude, whereas *A. lixula* was more abundant in the southern than in the central Adriatic. Barrens were more extended in the southern than in the central and northern sectors, and were related with sea urchin density. Fish predation upon adult sea urchins did not change on a large scale, whereas it was slightly higher in the southern sector for juveniles when predation rates of both urchins were pooled. Results show that: (1) assemblages of predatory fish and sea urchins, and barren extent change across latitude in the eastern Adriatic Sea, (2) the weak relations between predatory fish density and predation rates on urchins reveal that factors other than top-down control can be important over large scale (with the caveat that the study

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was conducted in fished areas) and (3) patterns of interaction among strongly interacting taxa could change on large spatial scales and the number of species involved.

1. Introduction

Sea urchins are important grazers in marine subtidal communities in temperate regions (Sala et al., 1998 and references therein). When at high density, they can cause the transition from macroalgal forests to coralline barrens, i.e., bare rocks with encrusting algae (Tegner and Dayton, 1981; McClanahan and Shafir, 1990; Sala et al., 1998), with repercussions for rocky-reef ecosystem structure and functioning (Sala et al., 1998). Predators can affect density, behavior and population structure of sea urchins (Tegner and Dayton, 1981; McClanahan and Shafir, 1990; Scheibling, 1996; Sala et al., 1998; Shears and Babcock, 2002; Tuya et al., 2004; Guidetti, 2006), which means they may indirectly influence the structure of benthic communities by mediating urchin grazing pressure (Shears and Babcock, 2002).

Benthic communities in the shallow Mediterranean rocky sublittoral range from coralline barrens (dominated by sea urchins and encrusting algae) to diverse macroalgal beds (which harbour hundreds of species of algae and invertebrates). The sea urchins *Paracentrotus lividus* and *Arbacia lixula* (that may coexist in rocky reefs; Bulleri et al., 1999) can cause the transition between these two community states (Sala et al., 1998; Boudouresque and Verlaque, 2001; see also Bulleri et al., 2002). The sea breams *Diplodus sargus sargus* and *D. vulgaris* (actively preying upon juvenile and adult sea urchins) and large-sized individuals of the wrasses *Coris julis* and *Thalassoma pavo* (preying upon urchins <1 cm in test diameter) are the only predators that may effectively prey upon sea urchins (Sala, 1997; Sala et al., 1998; Guidetti, 2004; Hereu et al., 2005).

The available studies about the relationships between predatory fish, sea urchins and macroalgae in the Mediterranean Sea chiefly took into account *P. lividus* (e.g., Verlaque, 1987; Sala and Zabala, 1996; Sala et al., 1998), but there is increasing evidence that *A. lixula* may exert an important role (Guidetti et al., 2003; Micheli et al., 2005). This sea urchin, in fact, is more effective in scraping rocky surfaces (Boudouresque and Verlaque, 2001) and less impacted by predation (Guidetti and Mori, 2005; Guidetti, 2006). Predation upon sea urchins is generally higher where predatory fish are abundant and large (e.g., within MPAs; Sala and Zabala, 1996; Guidetti, 2006), but, on the other hand, the patterns observed are not obvious (Guidetti and Sala, unpublished data), nor consistent in time or at large spatial scale (Sala et al., 1998; Guidetti, 2006; Guidetti et al., 2005; Micheli et al., 2005). Latitudinal differences in the diversity of assemblages of predator and prey species may affect the way strongly interacting taxa (e.g., fish and urchins) interact (Tegner and Dayton, 2000; Steneck et al., 2002). No previous studies were done, however, that investigated the relationships among predator fish, sea urchins and barrens in the Mediterranean Sea across latitude. Such knowledge, however, is necessary for predicting the consequences of the ongoing large-scale changes in the distribution patterns of thermophilous species through the Mediterranean Sea (including e.g., *T. pavo* and *A. lixula*; Francour et al., 1994; Guidetti et al., 2002; Dulčić, 2003) as a response to seawater warming

(Astraldi et al., 1994; Dulčić and Grbec, 2000; Dulčić et al., 2004), which could have potential wide-community effects.

This study, therefore, aims at assessing the relationships between predatory fish, sea urchins and barrens in sublittoral rocky reefs across a latitudinal gradient in the eastern Adriatic Sea.

2. Materials and methods

2.1. Study area

This study was done along the eastern Adriatic coast, from Trieste (northern Adriatic Sea; NE Italy) to Dubrovnik (southern Adriatic Sea; southern Croatia) (Fig. 1). Climatic conditions markedly change along this latitudinal gradient (e.g., lowest sea water temperature and salinity decrease from south to north; Gačić et al., 1999; Dulčić and Grbec, 2000). Three sectors, i.e., northern, central and southern Adriatic Sea, were arbitrarily chosen across latitude and sampled in late summer-early autumn 2004: two locations (situated 80–130 km apart from each other; Trieste and Rovinj in the northern Adriatic; Zadar and Split in the central Adriatic; around Makarska and Dubrovnik in the southern Adriatic; Fig. 1) were randomly selected within each of the three sectors, with three random sites (located 5–20 km apart from each other) sampled within each location. The assessment of distribution patterns of predatory fish, sea urchins and barrens, and the experimental evaluation of fish predation intensity on sea urchins were done in shallow (3–6 m depth) rocky reefs. This depth was chosen because it was common to all sites and locations studied.

2.2. Distribution patterns of predatory fish, sea urchins and barrens

Predatory fish density was assessed by visual census along 25×5 m transects (Harmelin-Vivien et al., 1985). Ten transects (i.e., replicates) were done at each site within location
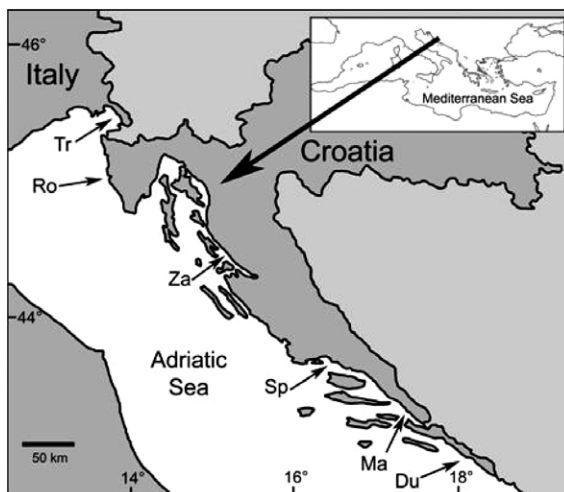

Fig. 1. Sampling locations: Tr = Trieste, Ro = Rovinj (northern Adriatic); Za = Zadar, Sp = Split (central Adriatic); Ma = Makarska, Du = Dubrovnik (southern Adriatic) (see Section 2).

and sector (for a total of 180 censuses). Settlers and recruits (<2 cm total length, TL) were excluded from the study as their numerical contribution may greatly influence mean density values, while having no predatory effect on sea urchins. Only large-sized *C. julis* and *T. pavo* (>2/3 of maximum size that equals 25 cm TL; Fischer et al., 1987) were included in the analysis as they are the only wrasses able to effectively prey upon sea urchins. Small-sized *D. sargus sargus* and *D. vulgaris* (<33% of the maximum size of 45 cm TL; Fischer et al., 1987) were treated separately from adults (i.e., fish >33% of maximum size). Small *Diplodus*, in fact, prey only upon juvenile sea urchins, while adult *Diplodus* eat juveniles, medium- and, to a lesser extent, large-sized sea urchins (Sala, 1997; Guidetti, 2004; Guidetti, 2006).

Counts of sea urchins were done within quadrats of 1 m² (20 replicates) at each sector, location and site (for a total of 360 counts). This method is suitable for assessing the adult (>1 cm in diameter) fraction of sea urchin populations (Sala and Zabala, 1996). Care was taken to look for urchins into crevices and under boulders. Sampling of *P. lividus* and *A. lixula* was made by separate series of quadrats to insure independence of data.

Percent cover of barrens was evaluated using quadrats of 1 m² ($n = 20$) at each sector, location and site (for a total of 360 samples). Each sample consisted of superimposing a quadrat with a grid of 25 small squares (each representing 4% of the quadrat). The extent of barrens was quantified according to Dethier et al. (1993) and Guidetti (2006) and references therein.

2.3. Fish predation impact on adult and juvenile sea urchins

Predation intensity upon adult urchins was estimated using tethering (Sala and Zabala, 1996; Shears and Babcock, 2002) carried out directly in the field. Tethering involved inserting a thin nylon filament (0.25 mm diameter) ~50 cm long, by means of a thin needle, through the dorsal and ventral surface of each urchin test, as far away from the oral-aboral axis as possible. Each experimental unit (EU) was formed by ten sea urchins tied by means of thin monofilaments to a main thick nylon monofilament (1.0 mm diameter) 8–10 m long. Separate EUs were made for each species of urchin (*P. lividus* and *A. lixula*), and for each of two size classes considered (medium: 2–3.5 cm in test diameter without spines; large: >3.5 cm; Guidetti, 2006). Laboratory trials and previous studies (e.g., Shears and Babcock, 2002 and references therein) revealed low mortality due to tethering, except for sea urchins <2 cm, not included in the experiment. Replicate EUs ($n = 3$), therefore, consisted of 10 tethered urchins for each single species and each size class placed at each site, location and sector (for a total of 216 EUs). The percentage of urchin tests missing (but remains were often close to the EUs) or opened in the latero-ventral part (typically attacked by *Diplodus* fish) was assessed 5 days later (Sala and Zabala, 1996; Guidetti, 2006). None of the dead individuals still tied to the EUs had its test intact.

Predation intensity on juvenile urchins was assessed using urchins 0.5–1.0 cm in diameter, carefully collected with tweezers, and put into experimental arenas (EAs) formed by artificial grass bands delimiting a 1 m² quadrat of rock without crevices where small urchins could conceal. Laboratory trials in aquaria showed that juvenile urchins do not cross such bands. Replicate EAs ($n = 5$) with 10 juveniles of each species of sea urchin were made at each sector, location and site (for a total of 180 EAs). Each EA was watched for some minutes after preparation to check for possible attraction of fish caused by the diver; then the diver moved away, but EAs remained in sight or visible to the diver. About

20 min later the number of juvenile urchins still present within each EA was counted (see also Hereu et al., 2005).

Estimates of predation obtained by tethering and EAs are to be considered as measures of the predation potential (Sala and Zabala, 1996; Shears and Babcock, 2002; see also Barbeau and Scheibling, 1994; Aronson et al., 2001 for further discussion about tethering). On the whole, the experiments were completed within 2 weeks.

2.4. Statistical treatment of data

Analysis of variance (ANOVA; GMAV5 package, University of Sydney) was used to test for differences in predatory fish density (small *D. sargus sargus* and *D. vulgaris*; adult *D. sargus sargus* and *D. vulgaris*; large *C. julis* and *T. pavo*), sea urchin density (*P. lividus* and *A. lixula*) and percent extent of barrens 'among sectors', 'between locations' and 'among sites'. The factor 'Sector' (*Se*; 3 levels: northern, central, and southern Adriatic Sea) was fixed, 'Location' (*Lo*; 2 levels) was random and nested within 'Sector', and 'Site' (*Si*; 3 levels) was random and nested within 'Location'.

ANOVA was also used to analyze predation intensity upon adult and juvenile sea urchins. With regard to predation intensity upon adult *P. lividus*, we first tested for possible differences among sectors, locations, and sites, and between size classes. The factors *Se*, *Lo* and *Si* were treated as reported above; 'Size class' (*Sc*; 2 levels: medium vs large) was considered as fixed and orthogonal. As *A. lixula* was not found in the three northernmost locations (see Results), we tested for possible differences in the predation intensity between species (*Sp*; 2 levels: *P. lividus* vs *A. lixula*), size classes, among locations (considering only the three southernmost locations where the two species coexist) and sites. The factors *Lo* was random, *Si* was random and nested in *Lo*, while *Sp* and *Sc* were fixed and orthogonal.

Predation intensity on juvenile sea urchins was evaluated following the same criteria used for adult sea urchins, without considering, obviously, the factor 'size class'.

Prior to analysis, homogeneity of variance was tested by Cochran's test and, whenever necessary, data were appropriately transformed (Underwood, 1997). If transformations did not produce homogeneous variances, ANOVA was used on non-transformed data after setting $\alpha = 0.01$ to compensate for the increased likelihood of Type I error. SNK test was used for *post-hoc* comparisons, when appropriate (Underwood, 1997).

Relationships between relevant variables (e.g., barren extent and sea urchin density, predation intensity and predatory fish density) averaged within each study site were examined by correlation analysis.

3. Results

3.1. Distribution patterns of predatory fish, sea urchins and barrens

Assessment of the variability in the distribution patterns of predatory fishes, sea urchins and barrens at the different scales investigated is reported in Tables 1 and 2.

Density of small *D. sargus sargus* was significantly higher in the central and southern sectors than in the northern Adriatic (Fig. 2a), while density of adults did not change among sectors (Fig. 2b). Density of small and adult *D. vulgaris*, and of large *C. julis* did not change along the latitudinal gradient (i.e., among sectors; Figs. 3a and b; 4a).

Table 1
ANOVA on density of fish predator of sea urchins among the 3 sectors, between 2 locations per sector, and among 3 sites per location

Source of variation	df	Diplodus sargus sargus						Diplodus vulgaris						Coris julis			Thalassoma pavo		
		Small-sized			Adults			Small-sized			Adults								
		MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Sector	2	4.38	10.82	0.04*	4.32	1.32	0.39	142.49	1.67	0.33	254.45	0.80	0.53	10.07	2.28	0.25	102.11	735.16	0.0001***
Location (sector)	3	0.40	0.57	0.64	3.27	5.06	0.02*	85.35	5.17	0.02*	319.88	3.43	0.06	4.42	11.86	0.0007***	0.14	0.02	0.99
Site(location (sector))	12	0.71	3.23	0.0003***	0.65	2.74	0.002**	16.50	4.63	0.0001***	93.32	7.54	0.0001***	0.37	3.92	0.0001***	6.74	13.33	0.0001***
Residual	162	0.22			0.23			3.56			12.38			0.09			0.51		

Significance level: * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$.

Table 2
ANOVA on density of sea urchins and percent extent of barrens among the 3 sectors, between 2 locations per sector, and among 3 sites per location

Source of variation	df	*Paracentrotus lividus*			*Arbacia lixula*			Barren		
		MS	F	P	MS	F	P	MS	F	P
Sector	2	11.14	5.59	0.10	202.81	36.34	0.008**	6137.39	30.87	0.01**
Location(sector)	3	1.99	1.67	0.23	5.58	5.46	0.012*	198.80	2.30	0.12
Site(location(sector))	12	1.19	4.05	0.0001***	1.02	0.68	0.77	86.37	1.51	0.12
Residual	342	0.29			1.50			57.29		

Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.
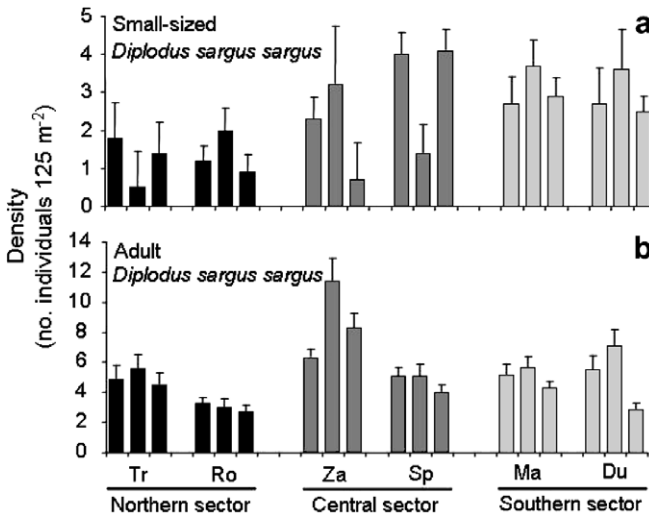
Fig. 2. Mean (±SE) density of small-sized (a) and adult (b) *Diplodus sargus sargus* at each location (with three sites sampled at each location; codes as in Fig. 1) and sector studied.

Although the inspection of the graph would suggest a lower density of *C. julis* in the northern sector (it was absent at Trieste), the significant variability among locations and sites is likely to have masked the differences among sectors. Density of large *T. pavo* was higher in the southern Adriatic than in the central sector, while the species was not recorded in the northern Adriatic (Fig. 4b).

Density of *P. lividus* did not change among sectors (Fig. 5a). Density of *A. lixula* was higher in the southern Adriatic than in the central sector, while the species was not recorded in the northern Adriatic (Fig. 5b).

Percent extent of barrens was significantly higher in the southern than in the northern and central Adriatic Sea, with no significant differences between these two latter sectors (Fig. 6).

Relationships between mean density of each sea urchin species (*P. lividus* and *A. lixula*) and the percent extent of barrens at each sampling site were both positive, but the correlation was less strict for *P. lividus* than for *A. lixula* (Fig. 7a and b).
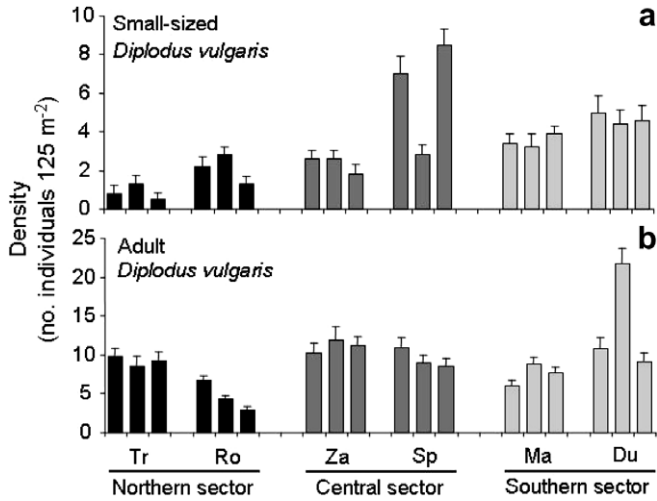
Fig. 3. Mean (±SE) density of small-sized (a) and adult (b) *Diplodus vulgaris* at each location (with three sites sampled at each location; codes as in Fig. 1) and sector studied.
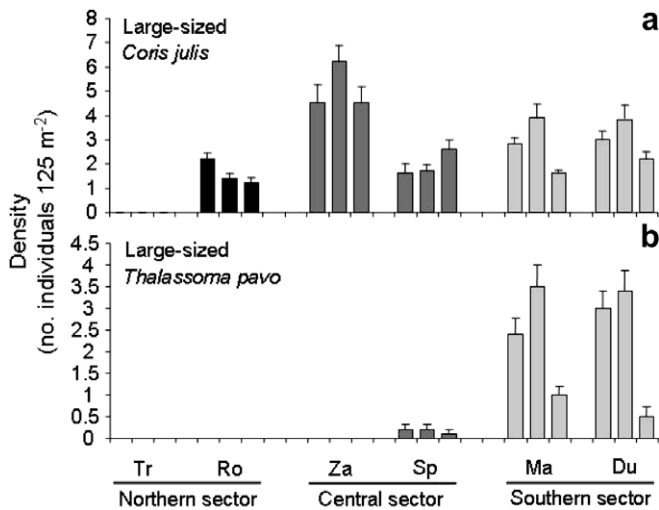

Fig. 4. Mean (±SE) density of large-sized *Coris julis* (a) and *Thalassoma pavo* (b) at each location (with three sites sampled at each location; codes as in Fig. 1) and sector studied.

3.2. Fish predation intensity on adult and juvenile sea urchins

Predation upon adult *P. lividus* did not change across latitude, and it was higher upon medium-sized than large-sized individuals at all locations, although the magnitude of the difference was not the same between locations within sector. ANOVA, moreover, revealed a significant interaction between 'size class' and 'location' ($Sc \times Lo(Se)$; Table 3, Fig. 8).
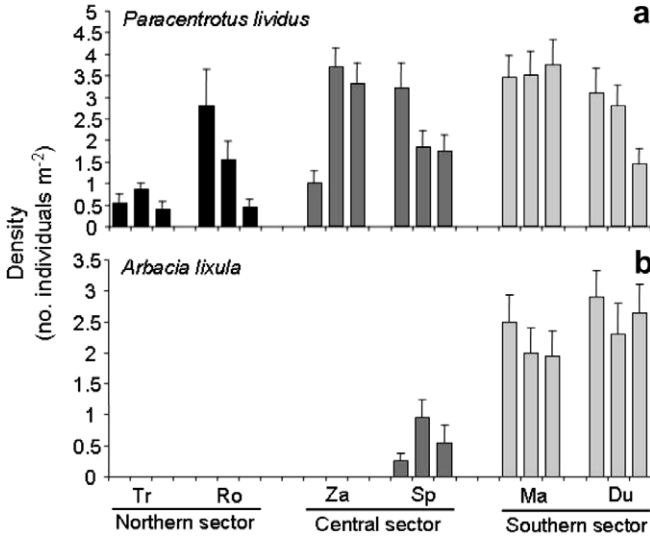
Fig. 5. Mean (±SE) density of *Paracentrotus lividus* (a) and *Arbacia lixula* (b) at each location (with three sites sampled at each location; codes as in Fig. 1) and sector studied.
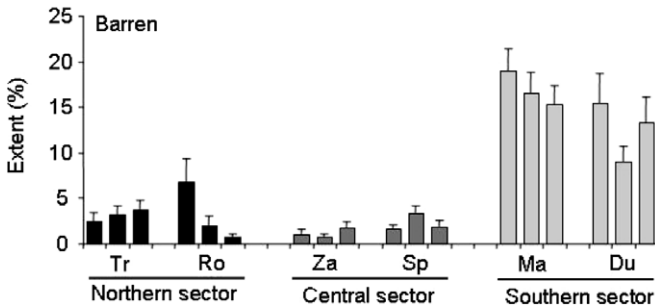

Fig. 6. Mean (±SE) percent extent of barrens at each location (with three sites sampled at each location; codes as in Fig. 1) and sector studied.

Predation intensity upon adult *P. lividus* and *A. lixula* at the three locations where the two sea urchins coexist (i.e., Split, Makarska, Dubrovnik) differed 'between species', and such a difference was not the same for the two size classes considered (Table 4, Fig. 8). ANOVA detected, in fact, a significant interaction between the factors 'species' and 'size class' ($Sp \times Sc$), and SNK tests revealed that, for both *P. lividus* and *A. lixula*, medium-sized individuals were subject to a significantly higher predation than large-sized individuals, but such a difference was greater for *P. lividus* than for *A. lixula*. Overall, medium-sized *P. lividus* showed the greatest predation intensity (Fig. 8).

Density of fish preying upon adult sea urchins (i.e., adult *D. sargus sargus* and *D. vulgaris*) and predation intensity upon both medium- and large-sized *P. lividus* and *A. lixula* were not significantly correlated (Fig. 9a–d).

Predation impact upon juvenile *P. lividus* did not show any significant difference across latitude in the eastern Adriatic, or at the scale of locations and sites (Table 5, Fig. 10).
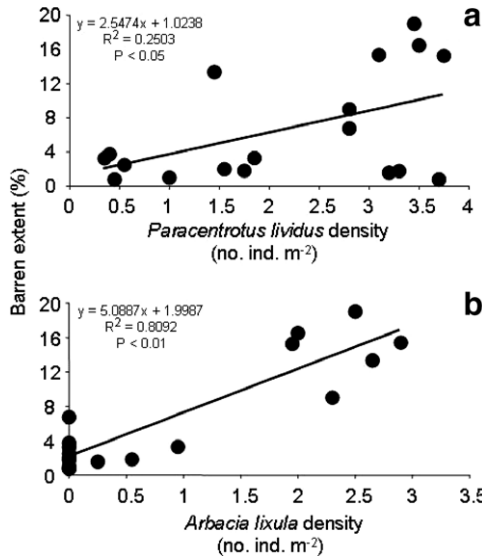
Fig. 7. Relationships between sea urchin density (a: *Paracentrotus lividus*; b: *Arbacia lixula*) and the percent extent of barrens at the studied sites.

Table 3
ANOVA on fish predation intensity upon adult *Paracentrotus lividus* between 2 size classes (medium- and large-sized urchins), among the 3 sectors, between 2 locations per sector, and among 3 sites per location

Source of variation	df	MS	F	P
Size class	1	13868.89	40.53	0.008**
Sector	2	335.56	0.29	0.77
Location(sector)	3	1151.11	24.67	0.0001***
Site(location(sector))	12	46.67	0.32	0.98
Size class × sector	2	148.89	0.44	0.68
Size class × location(sector)	3	342.22	11.85	0.0007***
Size class × site(location(sector))	12	28.89	0.20	0.99
Residual	144	146.11		

Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Predation intensity upon juvenile sea urchins at the three locations where *P. lividus* and *A. lixula* coexist differed 'between species' (Table 6), and SNK test revealed that predation was significantly greater upon *P. lividus* than *A. lixula* (Fig. 10).

Predation intensity on juvenile *P. lividus* and density of predatory fish was not significantly correlated (Fig. 11a). Conversely the relationship between predation intensity upon juvenile *A. lixula* and density of predatory fish was positive and significant (Fig. 11b).

4. Discussion

D. sargus sargus, *D. vulgaris* and *C. julis* did not show any dramatic difference in density across latitude (except for a significantly lower density of small-sized *D. sargus sargus* in the northern Adriatic and the absence of adult *C. julis* only in the northernmost location,
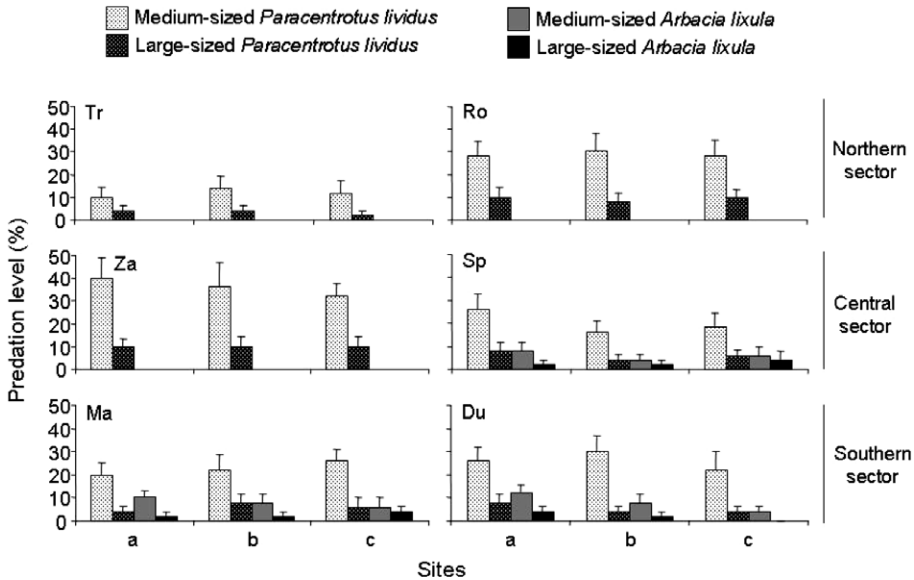
Fig. 8. Mean (±SE) predation intensity on adult sea urchins in relation to size (medium and large) at each location studied (a, b and c indicate the three random sites sampled at each of the six locations within each of the three sectors investigated; codes as in Fig. 1). The experiment was not done on *A. lixula* in the locations where it was absent.

Table 4
ANOVA on fish predation intensity upon adult sea urchins between the 2 species (*Paracentrotus lividus* and *Arbacia lixula*), between 2 size classes (medium and large), among 3 locations (Split, Makarska, Dubrovnik; see Methods), and among 3 sites per location

Source of variation	df	MS	F	P
Species	1	4013.89	233.06	0.004**
Size class	1	5445.00	66.67	0.015*
Location	2	43.89	0.54	0.61
Site(location)	6	81.67	0.96	0.45
Species × size class	1	1680.56	97.58	0.011*
Species × location	2	17.22	0.58	0.59
Species × site(location)	6	29.44	0.35	0.91
Size class × location	2	81.67	3.13	0.12
Size class × site(location)	6	26.11	0.31	0.93
Species × size class × location	2	17.22	0.69	0.54
Species × size class × site(location)	6	25.00	0.29	0.94
Residual	144	85.00		

Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

i.e., at Trieste). *T. pavo*, instead, showed a higher abundance in the southern Adriatic than in the central sector, and it was absent in the northern sector. The peculiar hydroclimatic conditions in the northern Adriatic, in particular the lowest seawater temperature during winter (Mosetti, 1988; Zore-Armanda, 1991), could be invoked to explain the absence of *T. pavo* (and in part of *C. julis*) in this area. This hypothesis is consistent with the ecological traits of *T. pavo*. This wrasse, in fact, is a typically thermophilic fish thriving in the
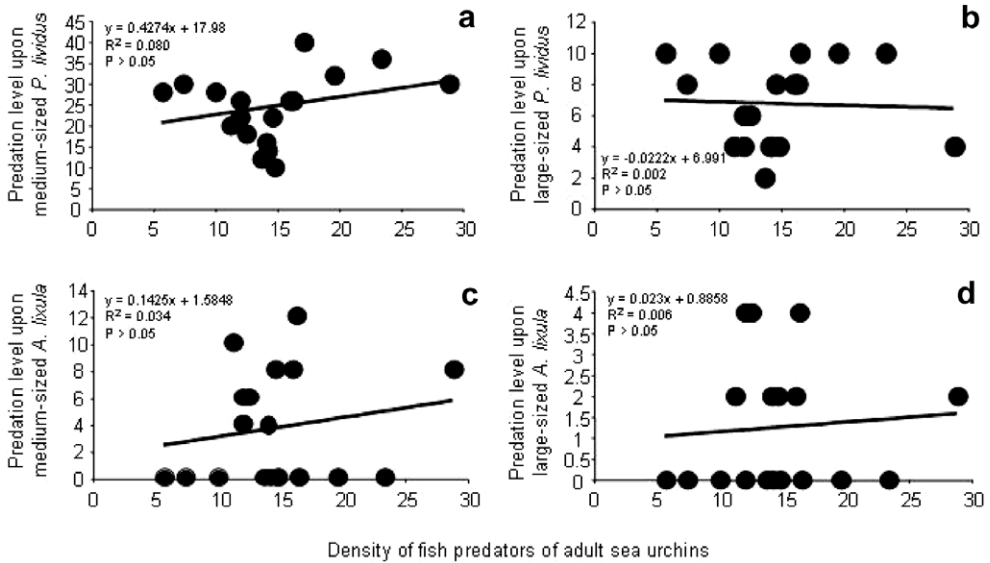
Fig. 9. Relationships between density (no. ind. 125 m^{-2}) of fish preying upon adult sea urchins and the levels of predation (%) measured in the field (a: medium-sized *Paracentrotus lividus*; b: large-sized *P. lividus*; c: medium-sized *Arbacia lixula*; d: large-sized *A. lixula*).

Table 5
ANOVA on fish predation intensity upon juvenile *Paracentrotus lividus* among the 3 sectors, between 2 locations per sector, and among 3 sites per location

Source of variation	df	MS	F	P
Sector	2	130.00	1.21	0.41
Location(sector)	3	107.78	3.34	0.06
Site(location(sector))	12	32.22	0.10	0.99
Residual	72	314.44		

Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

southern and eastern Mediterranean Sea (Francour et al., 1994; Guidetti et al., 2002). Its distribution limits, however, are currently expanding northwards in the western Mediterranean and the Adriatic Seas (Guidetti et al., 2002; Dulčić, 2003 and references) as a response to the ongoing water warming (Astraldi et al., 1994; Dulčić and Grbec, 2000). Parallel to this, the frequency of occurrence of *C. julis* has been recently found to increase in northern Croatia and Slovenia (Hanel, 2005; Lipej, personal communication), i.e., close to Trieste, where it could appear in a short time. No explanation can be provided, instead, to interpret the distribution of small-sized *Diplodus* as there are no data about temperature preferences of juvenile sea breams.

P. lividus did not show any significant difference across latitude, whereas *A. lixula* was significantly more abundant in the southern than in the central Adriatic and it was not recorded in the northern sector (although some specimens were observed at very shallow depth; Guidetti, personal observation). Total sea urchin density thus tended to increase from north to south, parallel to the barrens extent. *A. lixula* is a thermophilic species (Kempf, 1962) which significantly increased in density in the NW Mediterranean in recent
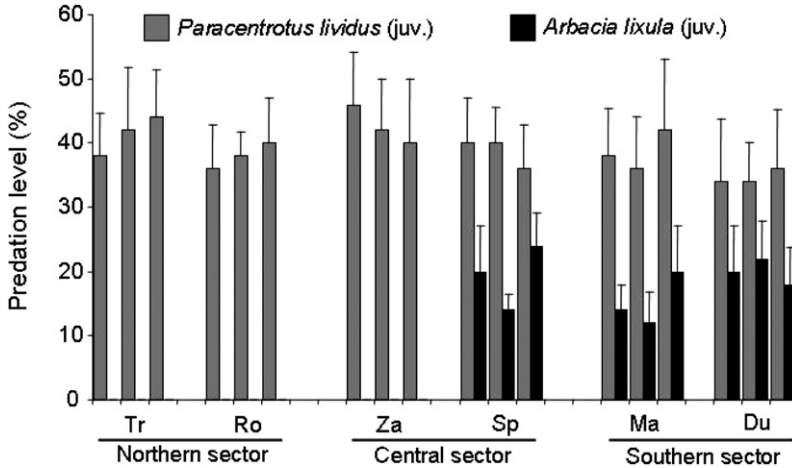
Fig. 10. Predation impact on juvenile sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) at each location (three sites sampled at each location; codes as in Fig. 1) and sector studied. The experiment was not done on *A. lixula* in the locations where it was absent.

Table 6
ANOVA on fish predation intensity upon juvenile sea urchins between the two species (*Paracentrotus lividus* and *Arbacia lixula*), among 3 locations (Split, Makarska, Dubrovnik; see Methods), and among 3 sites per location

Source of variation	df	MS	F	P
Species	1	8217.78	58.24	0.017*
Location	2	34.44	0.63	0.56
Site(location)	6	54.44	0.22	0.97
Species × location	2	141.11	2.82	0.14
Species × site(location)	6	50.00	0.21	0.97
Residual	72	243.89		

Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

decades (Francour et al., 1994). The warm-water affinity of *A. lixula*, as for *T. pavo*, could explain the distribution patterns observed in the eastern Adriatic. Although these data suggest that the overall density of sea urchins is greater in the southern sector, there are records of population explosions and collapses in the northern Adriatic that may alternatively cause formation of large barrens or almost complete recolonization by erect macroalgae (Boudouresque and Verlaque, 2001; Hanel, 2005). This suggests that rocky reef communities in this region may display a very large variability in time. In this study, however, the extent of barrens was found to be greater in the southern Adriatic, where total sea urchin density was highest. Although the relationship between barren extent and urchin density was generally positive, this pattern was more evident for *A. lixula*. This supports the hypothesis that *A. lixula* may play an important role in the process of formation and maintenance of barrens in the Mediterranean (Bulleri et al., 1999; Micheli et al., 2005). From this point of view, the current expansion of this sea urchin northwards in the Mediterranean could have the potential of inducing changes to coastal phytobenthos (see Francour et al., 1994) by enhancing, for instance, the chance of transition from macroalgal beds to barrens.
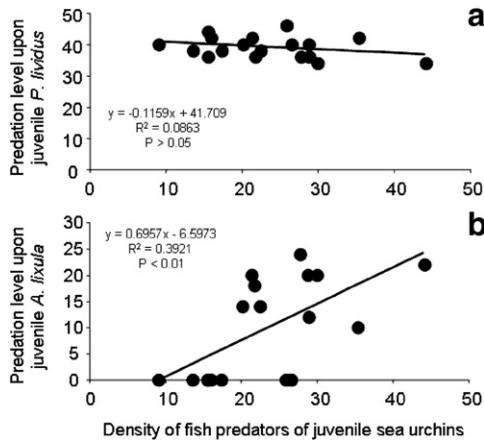
Fig. 11. Relationships between density (no. ind. 125 m^{-2}) of fish predators and the intensity of predation (%) on juvenile urchins (a: *Paracentrotus lividus*; b: *Arbacia lixula*).

Predation intensity was significantly higher upon *P. lividus* than *A. lixula*, and greater upon medium-sized than large-sized urchins for both species, as also observed in the SW Adriatic Sea (Guidetti, 2006). Attachment tenacity, test robustness and spine length are greater in *A. lixula* than *P. lividus*, and positively related with urchin size for both species. *A. lixula* (and in general large-sized urchins) could therefore be more resistant to fish predation (Guidetti and Mori, 2005), which could suggests that the more abundant *A. lixula* (or the higher the *A. lixula*:*P. lividus* ratio within the urchin assemblage), the less predatory fish could be effective in controlling sea urchin density, with increasing effects of grazing on benthic communities.

Predation intensity upon juvenile and adult *P. lividus* did not vary significantly across latitude. Similarly, predation intensity upon both juvenile and adult of *A. lixula* did not differ among the locations where this species occurred. If total predation intensity on adult sea urchins (even pooling predation rates on *P. lividus* and *A. lixula*) did not change with latitude, for juveniles overall predation on urchins (*P. lividus* plus *A. lixula*) tended to be slightly higher in the southern Adriatic Sea. Distribution patterns of fish, urchins and barrens, and related predation rates, did not match with a classic trophic cascade model (Sala et al., 1998). This suggests that trophic interactions within shallow rocky-reefs may change over large scale due to factors (e.g., urchin recruitment or mortality during early life-stages; Hereu et al., 2004, 2005) other than top-down control, which may result in different effects of predators on sea urchins and benthic communities (at least in the study area).

The relationship between predatory fish density and levels of predation was significant only for juvenile *A. lixula*. The weak relationship between overall densities of predatory fish and adult sea urchin preys could be explained considering that predators such as *Diplodus* seem to be effective in controlling urchin populations when at densities exceeding 15–20 fish 100 m^{-2} (Guidetti and Sala, unpublished data). Along the investigated coast, where sampling was done in fished areas, this threshold has seldom been exceeded. Although habitat complexity and pressure of micropredators (e.g., polychaetes, crustaceans, starfishes) could also be important to control sea urchin density (Sala and Zabala, 1996; Sala et al., 1998; Hereu et al., 2005), these outcomes may involve that only if marine protected

areas (MPAs) were put in place there is the potential for predatory fish populations to increase in abundance and size, and for top-down control to become effective in affecting rocky-reef community structure. From this perspective, there is an increasing evidence suggesting that within MPAs there are clear symptoms of top-down control of predatory fishes on urchins and, indirectly, on benthic communities in sublittoral rocky reefs (Sala et al., 1998; Micheli et al., 2005; Guidetti, 2006 and references therein).

This study also suggests that there could be significant differences in the way predatory fishes and sea urchins interact in rocky reefs across latitude due to diversity of assemblages of predators and preys (i.e., in terms of species number and relative abundances of predatory fishes and sea urchins that change among sectors in the eastern Adriatic Sea). This possibly involves different consequences on benthic communities over large spatial scale, as observed in marine rocky intertidal and subtidal communities elsewhere (Paine, 1980; Fowler-Walker and Connell, 2002; Steneck et al., 2002). We observed, in fact, that diversity of predatory fish and urchin assemblages (2 predatory fish and 1 urchin in the northernmost location; 4 fish predators and 2 urchins in the south) increased from north to south in the eastern Adriatic Sea, parallel to total sea urchin density and barren extent. Differences in consumer diversity may affect the strength of the relationships among the species involved in the cascade (Williams et al., 2004) varying across a latitudinal gradient. The extent of barrens was higher where both urchins coexist (e.g., in the southern sector) than where only *P. lividus* was found (i.e., in the northern sector), which again suggests that *A. lixula* could be more important than, or could interact with *P. lividus*, in forming and maintaining barrens (see also Micheli et al., 2005). It is difficult, however, to draw conclusions about the effects of changing consumer diversity on the trophic cascade, as diversity is here confounded (*sensu* Underwood, 1997) with changing overall consumer density (see Benedetti-Cecchi, 2004 and references about components of diversity). We analyzed in this study only distribution patterns, while proper experiments are needed to test whether or not the observed patterns are consistent with the hypothesis that the greater diversity of predators and herbivores, the lower is the chance of realization of trophic cascades (see Steneck et al., 2002).

In conclusion, predatory fishes did not appear to have a general top-down controlling impact on sea urchin abundance on the west coast of the Adriatic (there was no relationship between fish abundance and predation levels), and both fish and urchins (and barrens) were more abundant in the southern Adriatic. This suggests that other factors can be important in controlling the distribution of sea urchins across large spatial scale. However, the densities of predatory fish were generally below the critical density required to impact on urchin populations, and this has been shown to be the case in many areas which are fished compared to MPAs (Guidetti and Sala, unpublished data). It is possible that if fish densities were higher (e.g., creating MPAs) there would have been a positive relationship with predation levels and clearer trophic effects. This study, finally, shows that the number and evenness of strongly interacting species involved in the trophic cascade may change across latitude and this may reflect into different patterns of species interaction and related effects on benthic communities. This poses new questions about the potential effects of human impacts like fishing (impacting on *Diplodus* fish or *P. lividus*; Sala et al., 1998; Guidetti et al., 2004; Guidetti, 2006) and climate changes (e.g., influencing *A. lixula* and *T. pavo*; Francour et al., 1994; Guidetti et al., 2002) in affecting diversity (structural and functional) of assemblages of fish predators and sea urchins, with potential effects on community structure of Mediterranean rocky reef ecosystems.

Acknowledgements

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