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Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in shallow Mediterranean rocky reefs

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Abstract Underwater observations on fish and asteroid consumers (i.e. predators and scavengers) of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, were carried out at several locations in shallow Mediterranean rocky reefs. Observations conducted in the marine reserve of Torre Guaceto (Adriatic Sea) revealed that sparid fishes, *Diplodus sargus* and *D. vulgaris*, are the main fish predators of small (<1 cm in test diameter) and medium (1–4 cm) sea urchins, whereas the labrids *Coris julis* and *Thalassoma pavo* preyed only upon small sea urchins. Large *D. sargus* were able to prey upon small and medium, and occasionally large (>4 cm) sea urchins, whereas medium and small *Diplodus* preyed mainly upon small sea urchins. The number of sea urchins preyed upon by fishes was negatively related to sea urchin size for both species. *P. lividus* appeared to be subject to higher predation levels than *A. lixula*. The scavenger guild comprised 11 fish species, with *D. sargus*, *D. vulgaris*, *Coris julis* and *Chromis chromis* accounting for about 80% of scavenger fishes. Observations performed at several locations in the Mediterranean on the predatory asteroid *Marthasterias glacialis* revealed that only 3% of the detected individuals were preying upon sea urchins. Due to the importance of sea urchins for assemblage structure and functioning of Mediterranean rocky reef ecosystems, these results may have also important implications for management of fishing activities.

Keywords Sea urchins · Predators · Scavengers · Rocky reefs · Mediterranean Sea

Introduction

It is well known that predation is one of the most important biological processes affecting community structure and ecosystem functioning (Hairston et al. 1960; Duffy and Hay 2001, and references therein). Besides direct effects on their preys, predators may also influence community structure indirectly whenever their prey species strongly interact with other species of the community (Power 1992). The effects of predators, therefore, may extend well beyond the prey consumed throughout the so-called “trophic cascades” (Paine 1980; Witman and Dayton 2001).

In shallow sublittoral rocky reefs in the Mediterranean Sea, as seen in other temperate regions (Andrew and Underwood 1993; Tegner et al. 1995; Scheibling 1996, and references therein), sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) may strongly influence marine benthic communities, in some cases driving the transition from erect macroalgal assemblages to coralline barrens (Sala et al. 1998, and references therein; Guidetti et al. 2003). Abundance, size structure, and feeding behavior of sea urchins may be influenced by predation (Duggins 1980; Tegner and Dayton 1981; McClanahan and Shafir 1990; Sala and Zabala 1996; Scheibling 1996; Guidetti et al. 2003), which stresses the potentially great functional importance of consumers of echinoids in the control of sea urchin populations and, furthermore, the structure of entire communities associated with rocky substrates.

Potential predators of sea urchins in Mediterranean sublittoral rocky habitats encompass large crustaceans (*Eriphia spinifrons*, *Maja squinado*, *Palinurus elephas*), asteroids (*Marthasterias glacialis*) and fishes (e.g. *Diplodus* spp., *Coris julis*) (Sala et al. 1998, and references therein). There is no clear scientific evidence, however, that *E. spinifrons* and *M. squinado* are important predators of sea urchins in shallow rocky reefs (Sala et al. 1998). As regards the spiny lobster, *P. elephas*, it has to be considered that this crustacean usually lives in deeper habitats than the shallow rocky reefs where *P. lividus* and *A. lixula* thrive (Boudouresque and Verlaque 2001). Al-

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though Goñi et al. (2001) reported that ‘echinoidea’ can be found in the stomachs of spiny lobsters, the lack of spatial overlap leads to the conclusion that spiny lobsters are not involved in the control of sea urchin populations in shallow rocky reefs. The starfish *M. glacialis* was reported feeding upon *P. lividus* in *Posidonia oceanica* seagrass beds by Dance and Savy (1987 a), who estimated that about 10% of adult sea urchins might annually be removed by starfish predation. In their cage experiments, however, these authors removed any alternative prey, and thus probably overestimated predation rates of *M. glacialis* upon sea urchins. Although Fanelli et al. (1999) reported negative correlations between *M. glacialis* and sea urchin density in shallow rocky reefs in SE Italy, there is no clear evidence so far to show that this starfish is an efficient sea urchin predator in the field. Fishes have been reported by many authors as the most important and diverse guild of sea urchin consumers in the Mediterranean Sea (Sala 1997, and references therein). Although a great number of fish species have been indicated as potential sea urchin consumers (that includes predators and scavengers), recent studies have provided evidence that only a few fish, which may be grouped into two main guilds, are actually important as predators: (1) predators of adult and juvenile sea urchins (chiefly *D. sargus* and *D. vulgaris*); and (2) predators of juvenile sea urchins only (e.g. *Coris julis*). Both these guilds include several fish species of economic importance (mainly the two *Diplodus* spp.; Harmelin et al. 1995). A decrease in their abundance (e.g. due to fishing) may have consequences on their prey (i.e. sea urchins) and, in the end, on the entire benthic community in shallow rocky reefs. Many fish species among those that are known as consumers, conversely, are actually scavengers (Sala 1997), but these latter obviously cannot control sea urchin populations.

The present knowledge about sea urchin consumers in the Mediterranean, however, is still fairly scanty and spatially limited to a few areas in the basin (Sala 1997). This stresses the need to widen the spatial scale of observations in order to look for general patterns. Furthermore, in situ observations allowing quantification of the importance of a species as predator or scavenger (McClanahan 1995; Sala 1997) have referred exclusively to *P. lividus*. No data are available about consumers of *A. lixula*, which co-occurs with *P. lividus* in shallow rocky reefs, and in some case shows higher density and/or biomass, mainly in the southern sectors of the Mediterranean (Guidetti et al. 2003, 2004).

This paper aims to provide information about predators and scavengers of the sea urchins *P. lividus* and *A. lixula* in shallow Mediterranean rocky reefs.

Methods

Observations on fish consumers

Observations on fish predators and scavengers were made by means of SCUBA diving within the marine protected area (MPA) of

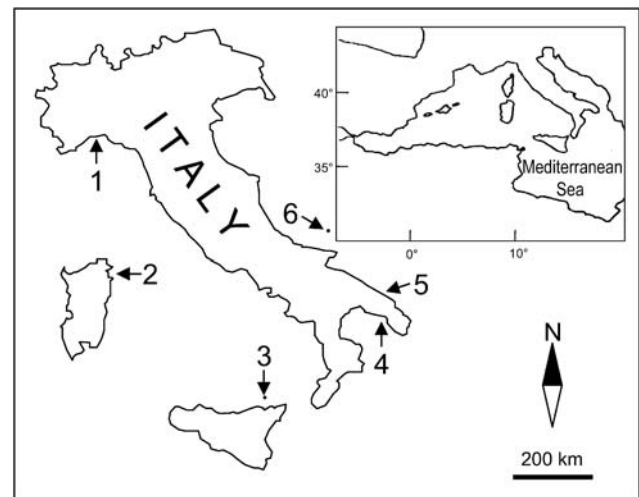


Fig. 1 Study locations along the coast of Italy. 1 Arenzano; 2 Olbia; 3 Lipari Island; 4 Porto Cesareo; 5 Torre Guaceto; 6 Tremiti Islands

Torre Guaceto (southern Adriatic Sea; Fig. 1) from May 2002 to July 2003. The whole reserve, established in 1992, covers about 2,220 ha, and the two no-take zones cover about 180 ha. This MPA is successfully enforced, and observations were made inside the two no-take zones since predation by fish was expected to be far greater here, and thus easier to observe, than in fished areas.

Sea urchins, i.e. *P. lividus* and *A. lixula*, were collected by SCUBA diving in areas outside the reserve (inside they show very small densities; unpublished data), taking care to avoid any damage to spines. A total of 300 sea urchins (150 *P. lividus* and 150 *A. lixula*) were collected, measured with a calliper and assigned to three size categories: small (test diameter without spines less than 1 cm; $n=50$ for each species), medium (from 1 to about 3.5 cm; $n=50$) and large (more than 3.5 cm; $n=50$). Sea urchins were positioned (with the oral side on the substratum) in five groups of five specimens each over rocky substrate at about 4–7 m depth within the two no-take zones of the Torre Guaceto MPA. The observer, hidden behind a boulder at a distance of about 5–10 m (depending on water clarity) from the baited sites, noted for approximately 15 min the number of sea urchins preyed upon, and the species and number of ‘consumer’ fishes, assigning them to one of two guilds: (1) predator guild (i.e. species able to open sea urchins by breaking the tests); (2) scavenger guild (i.e. species feeding upon already opened sea urchins). The size of predatory fishes was evaluated by using three size categories (i.e. small, medium and large) on the basis of the maximum total length reached by each species (Fischer et al. 1987).

As predatory fishes usually become aggressive after having broken a sea urchin, which may keep away other fish (i.e. scavengers) (Sala 1997), sea urchins of both species which had already been opened by the observer were also offered to get a more exhaustive list of scavenger fishes.

Observations on starfish predation

Underwater observations on predatory patterns of the starfish *M. glacialis* were made in shallow rocky reefs (2–10 m depth) by means of SCUBA diving from June 2001 to July 2003 in several areas of the Mediterranean basin (Fig. 1): Arenzano (Ligurian Sea); Olbia (Sardinia Island, central Tyrrhenian Sea); Lipari Island (southern Tyrrhenian Sea); Porto Cesareo (Ionian Sea); Torre Guaceto (southern Adriatic Sea); and Tremiti Archipelago (central Adriatic Sea). Each starfish detected was turned upside down to check whether it was (1) feeding on a sea urchin or other prey, (2)

moving, or (3) inactive (immobile but not feeding). Whenever a sea urchin was observed to be preyed upon by a starfish, its species, size (test diameter without spines), and position relative to that of the predator were recorded.

Results

Fish consumers

Eighteen fish species were observed to consume sea urchins at the MPA of Torre Guaceto. All 18 fish species consumed *P. lividus*, whereas only 14 of them consumed *A. lixula* (Table 1). Four species were observed to be successful as predators of sea urchins: *D. sargus*, *D. vulgaris*, *Coris julis* and *T. pavo*, and their relative importance varied depending on species and size of sea urchins (Fig. 2).

A total of 37 (24.7%) out of the 150 *P. lividus* offered to predatory fishes were actually eaten. The number of sea urchins preyed upon by fishes was highest (24 out of 50) for small-sized, intermediate (12 out of 50) for medium-sized, and smallest (1 out of 50) for large-sized *P. lividus* (Fig. 2). Small-sized *P. lividus* were preyed to nearly the same extent by the two *Diplodus* species and *Coris julis*, and to a lesser extent by *T. pavo*. *D. sargus* was the most important predator of medium-sized *P. lividus*, followed by *D. vulgaris*, whereas a single large-sized *P. lividus* was preyed upon by *D. sargus*.

The total number of individuals of *A. lixula* preyed upon by fishes (13, i.e. 8.7%, out of 150) was lower than

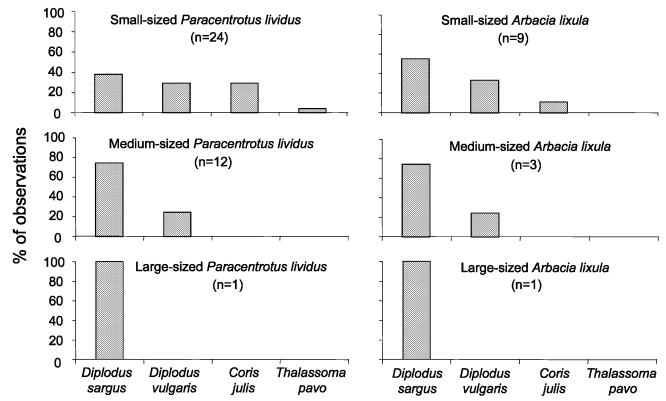


Fig. 2 Fish species (predator guild) observed to successfully attack sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) of different sizes

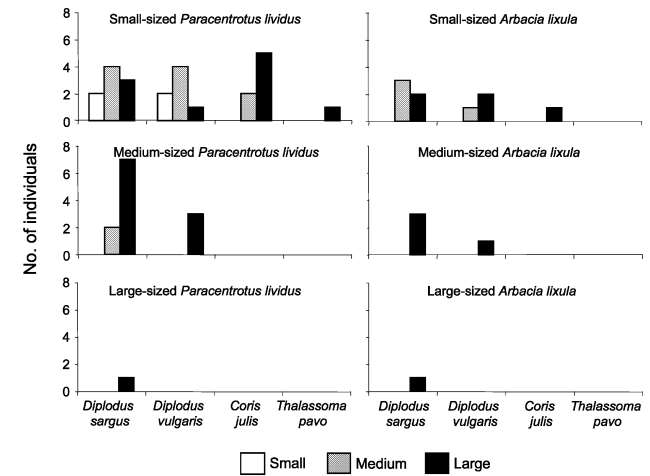


Fig. 3 Size category and number of individuals of predatory fish species observed preying upon sea urchins (*P. lividus* and *A. lixula*) of different sizes

Table 1 Fish species observed to consume sea urchins (*P. lividus* predators; *S* scavengers) (*Paracentrotus lividus* and *Arbacia lixula*) in the no-take zones of the MPA of Torre Guaceto

Family	<i>P. lividus</i>		<i>A. lixula</i>	
	P	S	P	S
Blenniidae				
<i>Parablennius gattorugine</i>		●		●
<i>P. rouxi</i>		●		●
Gobiidae				
<i>Gobius bucchichii</i>		●		
Labridae				
<i>Coris julis</i>	●	●	●	●
<i>Symphodus doderleini</i>		●		
<i>S. mediterraneus</i>		●		●
<i>S. ocellatus</i>		●		●
<i>S. roissali</i>		●		
<i>S. rostratus</i>		●		
<i>S. tinca</i>		●		●
<i>Thalassoma pavo</i>	●	●		●
Pomacentridae				
<i>Chromis chromis</i>		●		●
Serranidae				
<i>Serranus cabrilla</i>		●		●
<i>S. scriba</i>		●		●
Sparidae				
<i>Diplodus annularis</i>		●		●
<i>D. sargus</i>	●	●	●	●
<i>D. vulgaris</i>	●	●	●	●
<i>Oblada melanura</i>		●		●

that of *P. lividus* and, similarly to the other sea urchin, predation by fish decreased with increasing sea urchin size. Overall, nine small-sized, seven medium-sized, and one large-sized *A. lixula* (out of 50 of each size category) were successfully preyed upon (Fig. 2). *D. sargus* was observed to be the most relevant predator of this sea urchin. Small-sized *A. lixula* were mostly preyed upon by *D. sargus*, followed by *D. vulgaris* and *Coris julis*. Medium-sized *A. lixula* were successfully attacked by *D. sargus*, and to a lesser extent by *D. vulgaris*, whereas only *D. sargus* was observed to break a large specimen of *A. lixula* in one case (Fig. 2).

The success of the above predatory fishes in breaking sea urchin tests was related to predator size (Fig. 3). Small sea urchins were eaten by small *Diplodus*, but also by medium- and large-sized specimens of all four predatory fishes. Most medium- and large-sized sea urchins, however, were successfully preyed upon by large *D. sargus* individuals and, to a lesser extent, *D. vulgaris*. Only very large *D. sargus* (around 40 cm TL) were observed to bite

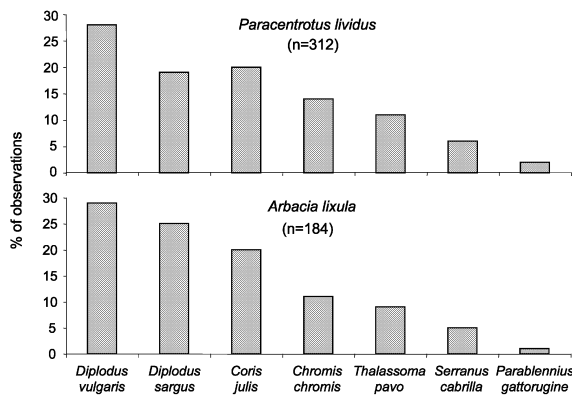


Fig. 4 Fish species (scavenger guild) observed to eat carcasses of the sea urchins *P. lividus* and *A. lixula*

and break sea urchins larger than 3.5 cm in diameter (Fig. 3).

Six species of scavenger fishes were observed feeding upon carcasses of *P. lividus* and *A. lixula* previously broken by predatory fishes. *D. vulgaris* was the most frequent scavenger, followed by *Coris julis* and *D. sargus*, and with decreasing importance by *Chromis chromis*, *T. pavo*, *Serranus cabrilla* and *Parablennius gattorugine*. In particular, *Chromis chromis* individuals were observed eating small sea urchin fragments floating in the water at a short distance (10–20 cm) from the carcasses where all species usually crowded. The species composition of the scavenger guild was similar for the two species of sea urchins (Fig. 4).

The list of fish species potentially acting as scavengers of sea urchins, however, includes species not directly observed to eat sea urchins broken by predatory fishes. On the whole, I observed 18 fish species eating already-opened *P. lividus*, and 14 species biting already-opened *A. lixula*. It is worth noting that all species observed to prey upon sea urchins were also active as scavengers (Table 1).

Starfish predation

A total of 132 *M. glacialis* individuals were detected at the six investigated locations over the two years of study. Due to the comparatively low number of observations at each location (the starfish showed very low density everywhere), data were pooled to provide an overall picture of the predatory activity of *M. glacialis* in shallow rocky reefs (Fig. 5). Less than 10% of the detected individuals were inactive, which suggests that this starfish is also an active predator during daytime. About 27% of starfishes were foraging for prey (e.g. when offered prey such as medium-sized gastropods, *Hexaplex trunculus*, they promptly assumed the typical predatory behaviour). Most of the starfishes (about 35%) were observed to prey upon the rock-boring mollusc *Lithophaga lithophaga* (date mussel), whose valves are kept open by the starfish podia, while the prey is digested inside its hole by the everted stomach of *M. glacialis*. Mollusc gastropods,

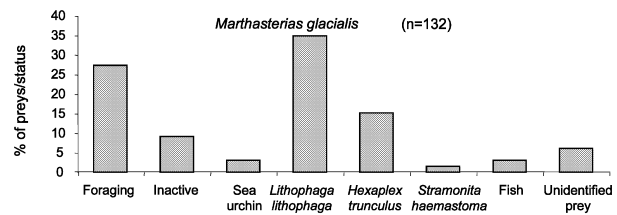


Fig. 5 Frequency of prey items of the starfish *Marthasterias glacialis* over rocky substrates

namely *H. trunculus* and *Stramonita haemastoma* (in a single case) constituted about 17% of the prey of *M. glacialis*, whereas about 6% of the starfishes were found eating ‘unidentified prey’ (i.e. the starfish’s stomach was everted inside a small crevice but the prey was not identifiable). Four specimens (3%) of *M. glacialis* were found to eat small fishes, probably acting as scavengers. Finally, another four *M. glacialis* specimens (3%) were found preying on *P. lividus* ranging in size (test diameter) from 2.8 to 3.5 cm. They were digested by the everted stomach of the starfish, after the sea urchins had been turned upside down.

Discussion

The results of the present study provide evidence that many fish species consume sea urchins, i.e. *P. lividus* and *A. lixula*, in shallow Mediterranean rocky habitats, while only a few species actually prey upon them by breaking their tests. Predation, in addition, appears to be dependent on both prey and predator size, and was found to be greater on *P. lividus* than on *A. lixula*.

The most relevant fish predators of sea urchins are *D. sargus* and *D. vulgaris*. *D. sargus*, in particular, has been observed to prey upon small, medium and large specimens of both sea urchin species. However, only very large *D. sargus* (around 40 cm TL) are able to open sea urchins larger than 4 cm in test diameter, while *D. sargus* of any size prey upon small sea urchins. In contrast, the labrids *Coris julis* and, to a lesser extent, *T. pavo*, prey only on small sea urchins. These results substantially agree with the observations from other marine reserves in the western Mediterranean: *D. sargus* has been reported as the main predator of sea urchins in Medes (Spain) and Scandola (Corsica, France) where the role of *T. pavo* was negligible, whereas in Cabrera (Spain) *D. sargus* was found to be functionally replaced by *D. vulgaris*, and *T. pavo* represented an important predator of juvenile *P. lividus* (Sala 1997). The relative importance of the two *Diplodus* species and the two labrids as predators thus seems to vary among the marine reserves considered, probably due to the actual density that these species achieve locally. Inside the MPA of Torre Guaceto, *D. sargus* is slightly more common than *D. vulgaris* (especially large individuals), and *Coris julis* is far more abundant than *T. pavo*, which could explain their different

relative importance as consumers of sea urchins over a local scale.

Predation rates on *P. lividus* and *A. lixula* appear to be negatively related to sea urchin size (Sala 1997; present study). Many authors have reported that the more sea urchins are susceptible to predation, the more they tend to shelter (Guidetti et al. 2003, and references therein). Large *P. lividus* individuals (>4–5 cm) are often found outside shelters, whereas most smaller individuals are found in shelters (Sala and Zabala 1996). This suggests that *P. lividus* may escape fish predation after having achieved approximately 4 cm in test diameter. Specimens of *A. lixula*, in contrast, can be observed in open areas of sublittoral rocky substrates even with 2.5–3 cm diameter (unpublished data). This suggests that *A. lixula* may escape predation at a smaller size and may be subject to lower predation rates than *P. lividus*. Reasons for this may be: differences between the two sea urchins in palatability, test robustness, and/or effectiveness of protective structures (e.g. length and/or robustness of spines) (see also Tegner and Dayton 1981). Fish predation could thus affect density and cryptic behaviour of the two co-occurring echinoids differently, depending on their specific strategies to encounter fish predation. Differences in cryptic behaviour and susceptibility to predation among co-occurring sea urchin species have also been observed elsewhere (e.g. for the two genera *Diadema* and *Echinometra*), and have been hypothesised to reduce niche overlap (McClanahan 1999). This involves potential (and in some case unexpected) repercussions on the structure of the benthic macroalgal assemblages grazed by sea urchins (McClanahan 1999; Guidetti et al. 2004).

The pool of fish species acting as scavengers was much richer than the predatory guild, with the scavenger guild including all four species that have been directly observed to prey upon sea urchins. Similar findings have been reported for both tropical and temperate seas by McClanahan (1995, 1999) and Sala (1997). From this perspective, in situ underwater observations can provide a proper understanding of these relationships, while analyses of gut contents do not allow scavengers to be distinguished from predators.

The method used in this study to observe fish predation potentially suffers from some sources of bias. Observations were only conducted during daytime, only on exposed sea urchins, and in the presence of a diver-observer. Although there is evidence that predatory fishes of sea urchins in the Mediterranean Sea are mainly active during daytime (Savy 1987a), it cannot be excluded that patterns and intensity of predation may be different during night-time when, for example, *P. lividus* tends to move out of shelters (Shepherd and Boudouresque 1979). Sea urchins, in addition, were offered outside their natural shelters, which could have led to an overestimation of predation since exposed sea urchins are more susceptible. The method used in the present study may thus allow the determination of potential predators, but might be less effective in determining the actual relative frequency of predators under the natural condition of shel-

tered sea urchins. Finally, it cannot be excluded that the presence of the observer using SCUBA may have biased the observations, considering that there are fishes, such as *Sparus aurata*, which have been reported to prey upon *P. lividus* (Savy 1987a; personal observation), but are much more shy in the presence of divers than the species I have directly observed preying on sea urchins.

Previous papers have reported that the starfish *M. glacialis* is a predominantly nocturnal predator (Dance and Savy 1987; Savy 1987a), although Savy (1987b) noted that this starfish may also be active during daytime. Most of the individuals I detected during daytime were found feeding, or foraging for prey. Only in a few cases were starfishes observed to prey upon sea urchins (as observed outside the Mediterranean; see Verling et al. 2003), specifically upon medium-sized *P. lividus*. The fact that many starfishes were found feeding suggests, on the one hand, that the observations may reliably represent prey preferences of the starfish, but on the other hand it cannot be excluded that predation patterns during night-time are different from those observed during daylight. However, the findings that *M. glacialis* is usually at very low densities everywhere, and that it preys only occasionally upon sea urchins in the field, suggest that this starfish is probably unable to control sea urchin populations (see also Boudouresque and Verlaque 2001). In some areas of the southeastern Italian rocky coast, where predatory fish densities are low due to overfishing, the density of *M. glacialis* persists at a very low level, while sea urchins may reach densities of about 30 individuals m^{-2} (Guidetti et al. 2003). This agrees with data from other regions of the Mediterranean, and elsewhere, where predation rates by invertebrate predators of sea urchins such as large gastropods and starfishes are generally very low, even where overfishing has caused a decline in predatory fish stocks (McClanahan and Muthiga 1989; Sala and Zabala 1996).

Many points raised by the present study may have implications for management policies of Mediterranean littoral ecosystems. For many areas of the basin, there is a diffused concern that the increasing sea urchin populations may cause an enlargement of barren grounds in rocky littoral ecosystems (see Guidetti et al. 2003, and references therein). There is increasing evidence that predation by fish exerts an important role in the dynamics of sea urchin populations (Scheibling 1996; Sala et al. 1998). *D. sargus* and *D. vulgaris* are among the most important coastal fish species from a commercial point of view, and are targeted by many kinds of fishery (e.g. spearfishing, trammel nets, angling), whereas *Coris julis*, chiefly large individuals, is mainly affected by angling (Harmelin et al. 1995). *T. pavo* is chiefly distributed in the southern parts of the Mediterranean, although it is currently spreading northwards (Guidetti et al. 2002). Its importance thus depends on the considered location, and although there are no data about the possible effects of fishing on this species, it may be affected by angling just as *Coris julis* is, considering that the two labrids have similar size and general habits. Several studies have

demonstrated that densities of predatory fishes tend to be negatively related to sea urchin densities (McClanahan 1999; Guidetti and Sala, in preparation), and that predatory fish size is positively related to the success of predatory attacks (Sala 1997; present study). Therefore, fisheries' regulations should focus on the population recovery of these functionally important predatory fishes, which may be assigned to the status of 'keystone species' (see Piraino et al. 2002 for a review), or members of a 'keystone guild' (McClanahan 1995), as their simultaneous removal has the potential to profoundly alter assemblage structure and functioning of benthic rocky ecosystems (McClanahan and Sala 1997; Sala et al. 1998; Pinnegar et al. 2000).

Sea urchin fishery is practiced in many areas of the Mediterranean (see Guidetti et al. 2004, and references therein). Only *P. lividus* is edible, and it is thought (often based on anecdotal knowledge) that where this echinoid is heavily fished, *A. lixula* might compensate for the reduction in *P. lividus*, with no relevant effects of this fishing on the benthic assemblages. Whether or not the two species are ecologically redundant is still a matter of debate (Bulleri et al. 1999; see Boudouresque and Verlaque 2001 for a review). The present paper suggests that the two species could be differently susceptible to predation. Guidetti et al. (2004) reported that, in areas with strong *P. lividus* harvesting, *A. lixula* does increase, thus compensating for the reduction in *P. lividus* biomass. This does not imply, however, that benthic communities remain unaffected. Substantial differences between the two echinoids in their pattern of grazing (Boudouresque and Verlaque 2001), and in the rate of predation they are subject to (this study), suggest that species may be not redundant. Sea urchin fishery management should take into account that *A. lixula* populations might be less efficiently controlled by predation than *P. lividus*.

To properly support management policies of fishing activities in littoral systems, more experimental evidence is obviously needed. Studies based on direct observations similar to those reported here may contribute to a better understanding of basic ecological aspects of rocky reef ecosystems: this is fundamental for the development of ecologically-founded hypotheses that can be tested experimentally (Dayton and Sala 2001).

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