Are marine protected areas useful for the recovery of the Mediterranean mussel populations?

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ABSTRACT

1. Mussel beds are important intertidal communities in the Mediterranean Sea and have traditionally been exploited by humans.

2. Marine protected areas are management tools for recovering over-fished populations, normally top predator populations, which may in turn undermine prey abundance. Therefore, mussel populations might not recover inside protected areas, as they are affected by increasing fish populations.

3. To study the effects of both human and fish predation on mussels, three locations were selected: the Reserve (R), where all types of exploitation were banned and fish were abundant; the Partial Reserve (PR), where only angling was permitted, and fish abundance was low; and the Non-Reserve (NR), where no protection existed and fish were rare.

4. Data from mussel bed surveys indicate that recruitment is critical to sustain mussel populations, and similar size structures were found at all three locations. However, the overall biomass in the PR was nearly double that in both R and NR, suggesting disturbance of some sort at these latter two sites.

5. A tethering experiment showed that fish predation greatly affected mussels in R, while the analysis of harvester collections from the NR showed that the most harvested size classes were those least abundant in the mussel bed.

6. Both protected and non-protected areas are unable to increase mussel populations due to trophic cascade effects, while partial reserves, where fish populations are exploited and mussels protected, are areas where the Mediterranean mussel populations can recover.
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INTRODUCTION

Human exploitation of marine resources can be responsible for dramatic changes in the trophic structure of ecosystems (Pauly *et al.*, 1998; Coleman and Williams, 2002). On rocky shores, human harvesting significantly alters intertidal communities (Moreno *et al.*, 1984; Hockey and Bosman, 1986; Underwood, 1993). Mussel communities are a very important ecological component of aquatic environments worldwide (Suchanek, 1985; Dye *et al.*, 1994), especially regarding their role as ecosystem engineers (Jones *et al.*, 1994; Crooks, 2002). In the Mediterranean Sea, the indigenous mussel *Mytilus galloprovincialis* is one of the dominant intertidal species (Ceccherelli and Rossi, 1984; Bulleri and Airoldi, 2005). This species has traditionally been removed from the Mediterranean shores by humans to supplement diet, for commerce or for bait. On the Mediterranean coast of France, shell middens have been dated at 400 000 years before present (BP) (de Lumley, 1975). However, no studies have focused on the present condition of the *M. galloprovincialis* natural populations in the Mediterranean Sea and relatively little is known regarding the effects of their exploitation (Airoldi *et al.*, 2005).

Along non-protected coastlines, only remote sites provide refuge from intense harvesting; accessibility to rocky shores has proven to be the factor regulating human pressure on intertidal ecosystems (Addessi, 1994; Rius and Cabral, 2004). Along the Spanish coast, although exploitation of natural mussel beds is an illegal activity (Anonymous, 1995), no control has been established and mussel collection is nowadays common, especially during holiday periods (M. Rius and M. Zabala, personal observation). A preliminary study in Punta de la Mora (Tarragona, north-east coast of Spain) during summer 2001 showed that, in some areas, intense human harvesting on *M. galloprovincialis* beds caused 100% mussel mortality by the end of the summer months (M. Orta and M. Rius, unpublished data).

Marine protected areas (MPAs) are commonly used as management tools in order to allow previously over-fished populations to recover (Hyrenbach *et al.*, 2000). Most studies of MPAs have focused on the recovery of top predators such as fish (Harmelin, 1987; Buxton, 1993; Wantiez *et al.*, 1997; Lipej *et al.*, 2003) or gastropods (Castilla and Durán, 1985; Moreno *et al.*, 1986); fewer studies have focused on lower trophic level organisms (Castilla and Bustamante, 1989; Branch and Odendaal, 2003; Rius *et al.*, 2006). Trophic cascades have important effects on ecosystem structures, especially in MPAs (Sala *et al.*, 1998a; Pinnegar *et al.*, 2000) where prey abundance can be largely undermined by the high abundance of predators (Castilla, 1999). The pressure of top predators on sessile communities can be extremely important in regulating rocky intertidal communities (Connell and Anderson, 1999; Halpern *et al.*, 2006). Regarding predation on mussels, one example is the muricid gastropod *Concholepas concholepas*, which was recovered in a Chilean MPA and has eliminated *Perumytilus purpuratus* (Castilla, 1999). Concerning fish, Osman and Whitlatch (1998) suggested that the cunner *Tautogolabrus adspersus* was the most probable cause of mortality of the blue mussel *Mytilus edulis*, and Lloret *et al.* (2005) described *Diplodus sargus* preying on *M. galloprovincialis* populations close to the Cap de Creus MPA (north-east coast of Spain). At a nearby rocky shore, inside the Medes Islands MPA, two sparidae fish (*Sparus aurata* and *D. sargus*) were observed actively preying on mussels (M. Rius and M. Zabala, personal observation). At this location, removal of man as predator has allowed recovery of the previously over-fished fish populations (García-Rubies and Zabala, 1990). As a result, the high abundance of large fish may have a severe impact on mussel beds inside the MPA.

Little is known about size-dependent fish predation on benthic communities (Hereu *et al.*, 2005). Regarding mussels, our hypothesis is that fish would preferably feed on large mussels as their meat content is comparatively higher. However, the largest mussels may achieve a 'size-refuge' from fish predation as a result of the size and strength of their shell, as has been proven with other organisms (Elner and Hughes, 1978; Griffiths and Seiderer, 1980; Peharda and Morton, 2006). Outside MPAs, fish predators are uncommon due to commercial and recreational fishing (Harmelin *et al.*, 1995; Claudet *et al.*, 2006), while

M. galloprovincialis populations are exploited by harvesters preferably preying on the largest specimens (Tsuchiya and Bellan-Santini, 1989; Rius and Cabral, 2004).

Therefore, at least two key factors affect mussel populations inside MPAs: the prevention of human harvesting leads to an increase in mussel populations, while the recovery of fish predator populations negatively impacts mussel beds. In terms of the mussel size preferred by predators, it is hypothesized that mussel beds would be affected by fish (inside MPAs) and humans (outside MPAs) with greatest effects on medium and large size mussels, respectively.

The aim of this study was to determine if MPAs could be proposed as a useful tool for the recovery of the historically harvested populations of *M. galloprovincialis*.

METHODS

Study site

The study was conducted at the Medes Islands MPA (42°03′N, 03°13′E) and at the adjacent unprotected area. Three locations (Reserve, Partial Reserve and Non-Reserve) were selected based on their level of protection from human pressure. The Reserve (R) is a group of islands located 1 km offshore from the town of l'Estartit (Figure 1), where all types of extractive uses have been banned since 1983. The second location, the Partial Reserve (PR), is the stretch of coastline north of l'Estartit, where angling is allowed but the collection of intertidal animals has been prohibited since 1990. The last location, the Non-Reserve (NR), is the continuous stretch of coastline north of PR where no protection exists. The three locations are in close proximity (maximum distance 2 km between R and NR) and are calcareous rocky shores containing the same type of intertidal communities, with *M. galloprovincialis* beds present at all locations. Between 1992 and 2005, yearly visual census transects were made at the three locations in order to assess the size and abundance of *D. sargus* and *S. aurata*, following García-Rubies and Zabala (1990). A high abundance of large individuals from both species was encountered only in R (see Results). Anglers were often observed at NR and PR, while harvesters were reported only in NR (Rius and Zabala, unpublished data).

Experimental design

The experimental design was based on a comparative study of the three locations, in order to assess the relative influence that both human exploitation and fish predation have on mussel populations. Three
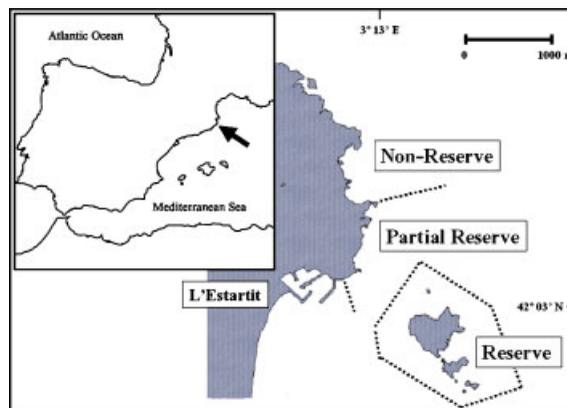

Figure 1. Map of the study area showing the positions of the survey locations. This figure is available in colour online at www.interscience.wiley.com/journal/aqc

methodologies were used: one to assess the abundance of *M. galloprovincialis* populations in the different locations based on samplings of mussel beds; another to test the influence of fish on mussels by means of a tethering experiment; and thirdly, to analyse harvester collections with the purpose of determining the quantity and size range of exploited mussels.

Mussel surveys

Four surveys of all the mussel beds were performed, with two undertaken in summer (July 2003 and August 2004) and two in winter (January 2003 and December 2004).

For every location, three north-east facing sites in close proximity to one another were selected, and at each site three rocky reefs between 0 and 1 m in depth containing mussel beds were randomly selected. On each reef, scrapings were performed in three random 0.1×0.1 m quadrats on mussel beds with 100% cover using a chisel.

All individuals from the samples were separated, counted and the maximum shell length was measured to the nearest millimetre using digital callipers (with 0.01 mm precision). Only specimens with shell length of 10 mm or larger were considered, as these mussels have survived post-settlement mortality (Suchanek, 1985; Griffiths and Hockey, 1987; McQuaid and Lawrie, 2005). The exclusion of specimens with shell length less than 10 mm avoided high background variability in the data and, in addition, this study found that small mussels were not targeted by human or fish predators (see below).

Biomass measurements were made using the July 2003 samples, with the purpose of comparing mussel condition between locations. Five size classes (from 10 to 60 mm) were established and three mussels were randomly selected per size class for each of the 27 scrapings. Mussels were dried at 100°C until a constant dry weight was obtained. Subsequently, the soft tissue was ashed at 450°C for 4 h to determine the organic weight (OW) of the tissue with an accuracy of 0.01 g in all cases (Palmerini and Bianchi, 1994; Babarro *et al.*, 2000).

Tethering experiment

A tethering experiment was undertaken in August 2005 at the same reefs where the scrapings were taken. The experiment involved the translocation of 30 mussels (between 30 and 39 mm) to a stone plate 0.2×0.2 m. This size class was selected as previous results showed that R contained a lower abundance of this size class than both NR and PR (see below). Mussels were collected from the sea-facing side of the l'Estartit harbour breakwater, placed on the plates and covered tightly with shade cloth mesh (4 mm) to allow them to reattach to the plate. This procedure was based on the evidence that *M. galloprovincialis*, when removed from its original mussel bed, can reattach by creating new byssus threads (Rius and McQuaid, 2006). Three nylon screws were glued onto each of the nine reefs using bicolour putty in order to support the meshed plates. The plates were attached to the screws and, after two weeks, when the mussels were firmly attached, the mesh was removed. At that point (8:00 am) the experiment began. Every 2 h, the mussels were visually counted. The experiment ended with the fourth survey (i.e. 4:00 pm), when the results showed an established pattern.

Harvester collections

Local harvesters kindly provided the shells from five mussel collections gathered at NR between December 2005 and May 2006, after they had removed the flesh. Maximum shell lengths were measured to the nearest millimetre using callipers.

Data analysis

All data were tested for normality using Shapiro–Wilk's W test and for homoscedascity using Levene's test. When data failed to meet the assumptions of the parametric test, and heterogeneous variances could not be rectified by transformation, the data were analysed using non-parametric tests.

Fish survey data were analysed using a repeated measures analysis of variance (RM-ANOVA) test in order to compare the abundance of each fish species at the different locations. Significant results were analysed using the Tukey test for *post hoc* multiple comparisons of means.

Shell length data obtained from the scrapings were contrasted with three factors: location (R, PR, NR), season (summer and winter) and year (2003 and 2004). Comparisons between locations were made using the Kruskal–Wallis ANOVA test followed by the multiple comparisons Kruskal–Wallis tests (Zar, 1984), while to test the influence of year and season, data were analysed using the Mann–Whitney U test. In order to compare size frequency distributions the two-sample Kolmogorov–Smirnov test was used for each factor.

OW data were square root transformed and compared using the one-way ANOVA test. For the predation experiment, a RM-ANOVA test was used in order to assess differences in percentage survival between locations. In both cases, analyses were followed by the Tukey test for *post hoc* multiple comparisons of means.

Manly's selectivity measure ($\alpha_i = (r_i/n_i)(1/\Sigma(r_j/n_j))$) (Krebs, 1989) was used to assess whether harvesters size-select their prey or not, as it is one of the best selective predation indexes for most situations (Chesson, 1978; Heisey, 1985). The frequency of a particular prey type being preyed upon in relation to all available prey types is 'r', while 'n' is the frequency of occurrence of this prey type in the ecosystem. In the present study, the prey types were the different size classes that harvesters collected, and the frequency of occurrence of a particular prey type was calculated from all the mussel surveys done at NR. If there is a selective feeding on prey type i, α_i is greater than $1/m$ (m = total number of prey types), if $\alpha_i = 1/m$ prey selection does not occur, and if $\alpha_i < 1/m$ then prey type i is avoided.

Statistical analyses were done using the software SPSS (SPSS Inc., 2003, version 12.0) and STATISTICA (Statsoft Inc, 2001, version 6.1), and a critical probability of 5%.

RESULTS

Fish surveys

The highest numbers of *D. sargus* and *S. aurata* in terms of abundance and size were encountered in R (Figure 2). When data were analysed throughout the 14 year study period significant differences between
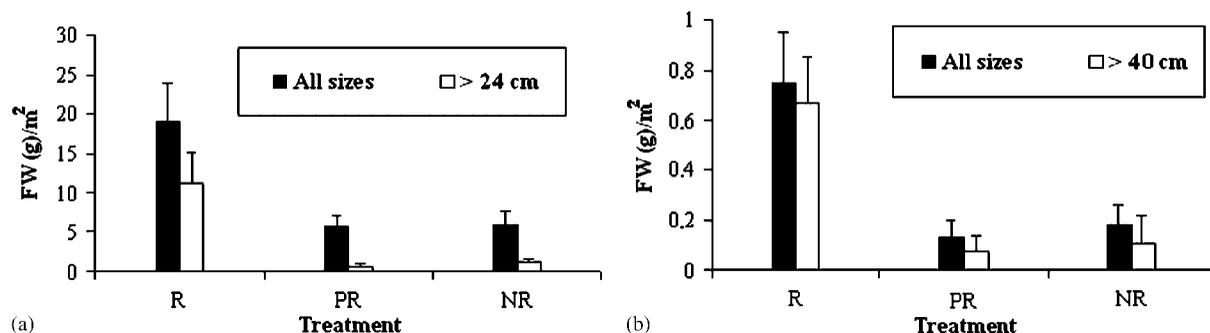

Figure 2. Fish census. Mean biomass (fresh weight (g)) m^{-2} of (a) *Diplodus sargus* and (b) *Sparus aurata* for each location (R, PR and NR) of all visual census. Biomass of individuals > 24 cm for *D. sargus* and > 40 cm for *S. aurata*, represented separately to illustrate the relative importance of large fish in the total biomass. Vertical bars denote standard errors.
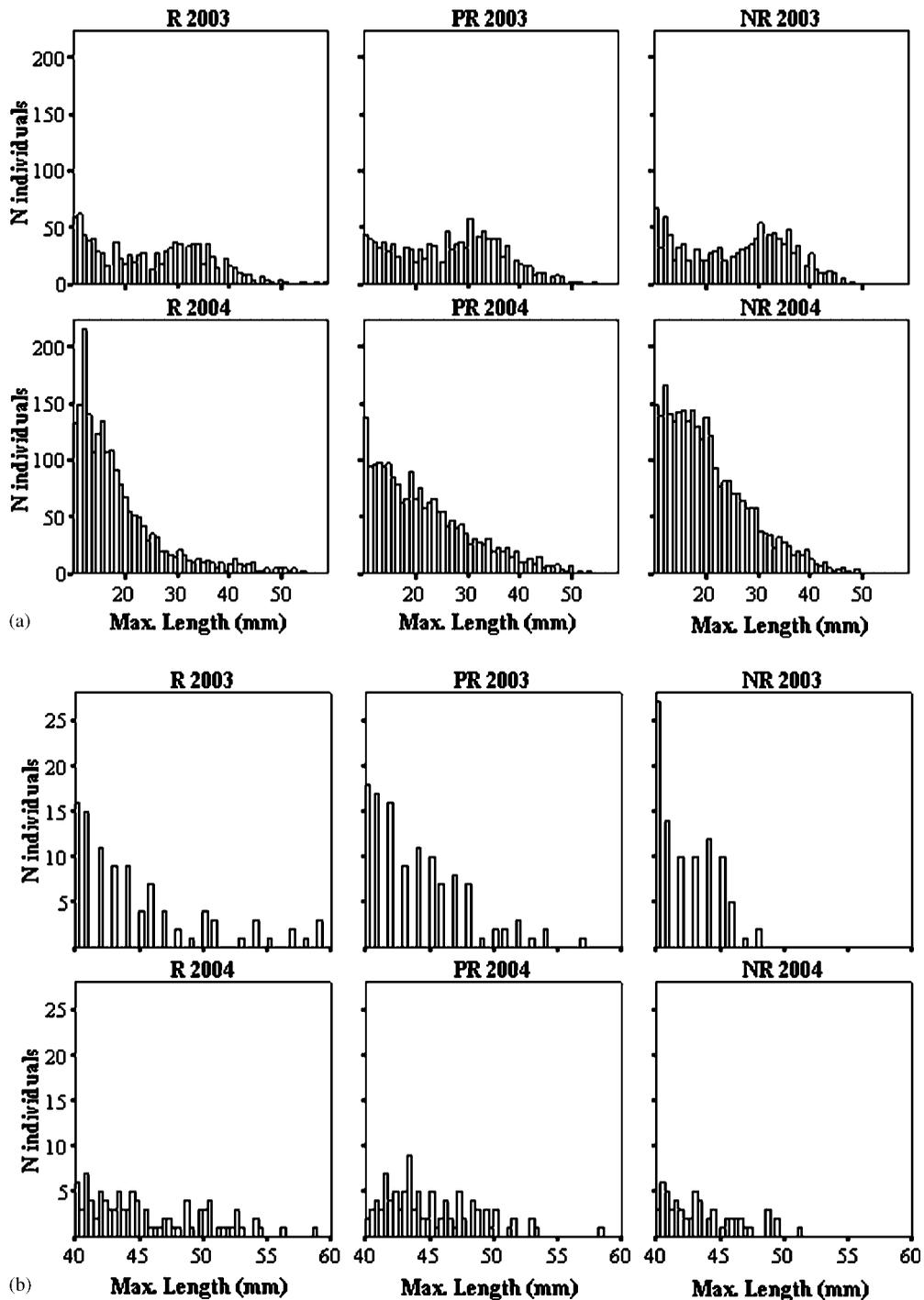
Figure 3. (a) Size structure of each year (2003 and 2004) and location (R, PR, NR) of all mussel surveys. *N* refers to the total number of *Mytilus galloprovincialis* measured. The same graph is shown in (b) but only for individuals ⩾40 mm.

locations were found for both species (RM-ANOVA, *D. sargus*, $F_{2,3} = 12.671$, $P = 0.034$; *S. aurata*, $F_{2,3} = 90.838$, $P = 0.002$), and these differences between R and the other two locations were significant (Tukey tests, $P < 0.05$, all cases).

Mussel surveys

The size structure data obtained from the scrapings showed similar distributions among locations but very different distributions between years (Figure 3(a)). A massive entry of new recruits in 2004 (the total number of individuals doubled in each location) changed the 2003 bimodal distribution to unimodal in 2004. In both years R showed a lower abundance of mussels of size between 30 and 40 mm than PR or NR while, for the largest mussels (from 40 to 60 mm) (Figure 3(b)), R and PR showed a higher abundance than NR, especially regarding mussels from the largest size classes ($\geqslant 45$ mm).

The Kruskal–Wallis ANOVA test on shell length found significant effects of location ($H_{2,10211} = 138.184$, $P < 0.001$). The multiple comparisons Kruskal–Wallis tests found differences in mean shell length between all three locations ($P < 0.001$). These differences showed the same pattern ($\mu_{PR} > \mu_{NR} > \mu_R$), which was maintained across both years (Figure 4). Differences between years were significant (Mann–Whitney U test, $Z = 24.695$, $P < 0.001$), and mainly due to the variability in recruitment that resulted in a decrease in the overall mean shell length from 2003 to 2004 at all locations (Figure 4). The size structures for each year and season (pooling locations) showed that in 2003 only a single recruitment event occurred in summer, while in 2004, high recruitment was observed in both seasons (Figure 5). No differences in mean length were found between seasons (Mann–Whitney U test, $Z = 1.098$, $P = 0.272$). When the size–frequency distributions across the different factors were analysed, significant effects of all factors (two-sample Kolmogorov–Smirnov tests, $P < 0.001$, all situations) were found.

In summer 2003 the condition of mussels, calculated as mean OW for each size class, was greatest in R for all size classes, followed by PR and then NR (Figure 6). However, no differences were found in the mean OW between locations (one-way ANOVA, $F_{2,78} = 0.491$, $P = 0.615$). These OW data were used to create biomass histograms for each location to obtain the total biomass distributions. These were calculated by multiplying each size class mean OW by the total number of individuals from all surveys of the corresponding size class per location, pooling years and seasons (Figure 7). These size–biomass histograms
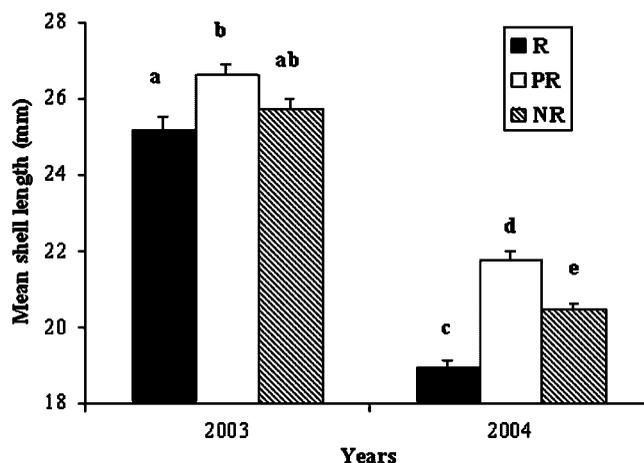

Figure 4. Mean shell length of *Mytilus galloprovincialis* from the mussel surveys for each year and location (R, PR, NR), pooling seasons. Vertical bars denote standard error. Letters indicate homogenous groups as determined by multiple comparison Kruskal–Wallis tests.
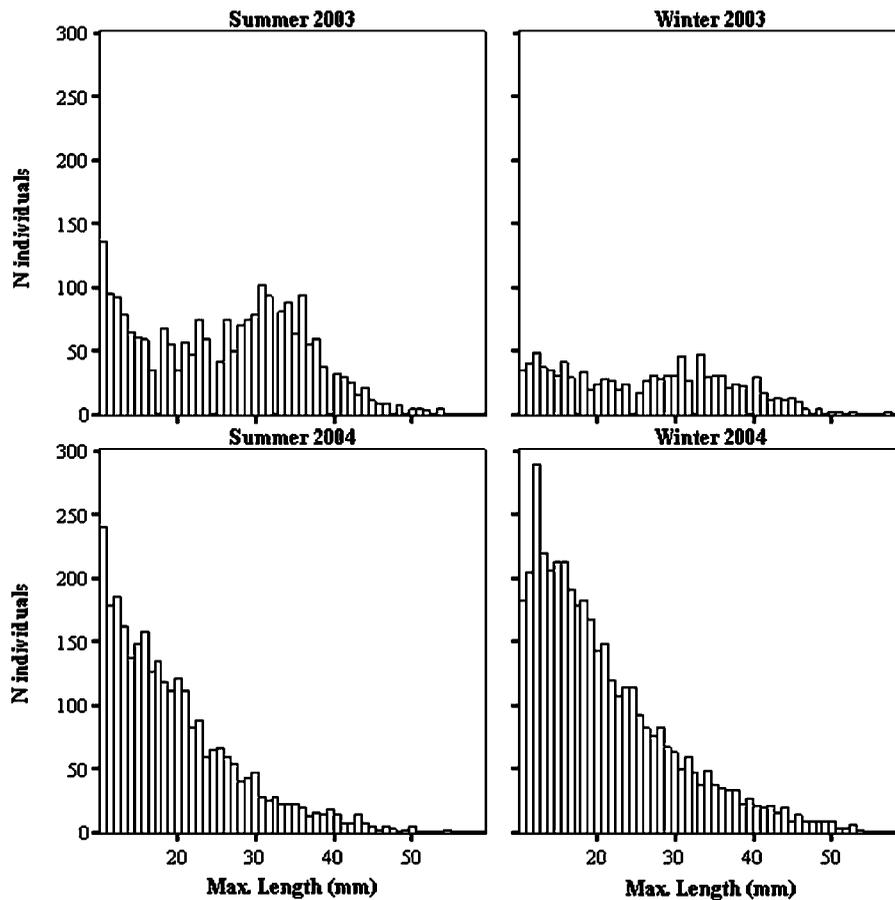
Figure 5. Size structure of *Mytilus galloprovincialis* for each year (2003 and 2004) and season (summer and winter) for all mussel surveys.

showed that mussels of the size class 30–39 mm were the main contributors to the mussel bed population in all locations, while the most abundant small mussels scarcely contributed to the overall biomass of mussel beds. The overall biomass for each location showed that PR supports nearly double the biomass of the other two locations, and that the pattern found with the mean shell data between locations was observed again regarding the location's biomass. Comparing locations for each size class, it was noticeable that both R and PR had almost the same biomass numbers of the largest size class (50–59 mm) and that these were higher than NR (Figure 7). In the middle size classes (30–39 and 40–49 mm), both R and NR showed a similar lower biomass than PR.

Tethering experiment

The initial mortality (10–20%) was most likely due to the fact that a few individuals did not successfully attach to the plate. After the first 2 h, a dramatic decrease in the number of individuals was found in R (Figure 8). In PR, an initial increase in mortality of around 50% was observed, although in the following observations the trend stabilized at around 38% survival. Similar results were observed in NR, even though in this location the loss of individuals was more gradual than PR, and it stabilized at
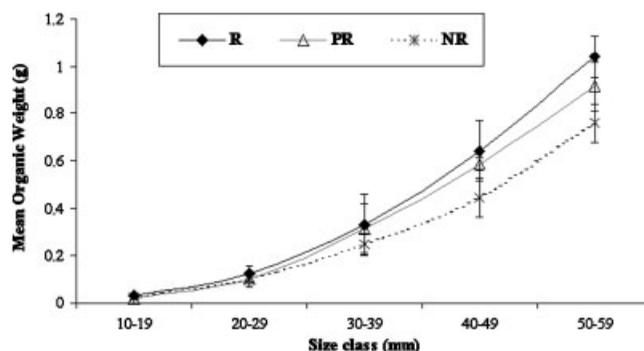
Figure 6. Mean biomass (organic weight (g)) of *Mytilus galloprovincialis* for each size class, obtained from the summer 2003 mussel survey. Vertical bars denote standard error.
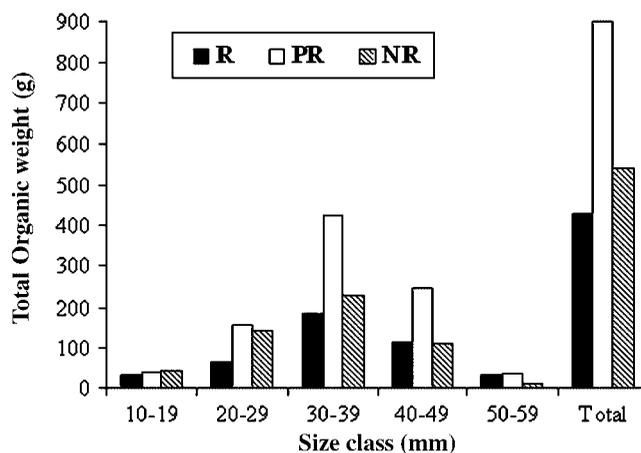

Figure 7. Biomass–size distributions of *Mytilus galloprovincialis* for each location (R, PR, NR), pooling years and seasons of all mussel surveys. The total biomass at each location is shown on the right-hand side.

around 57% survival. The RM-ANOVA test found significant differences between locations ($F_{2,24} = 6.8179$, $P = 0.004$), with the differences being between R and the other two locations (Tukey tests, $P < 0.05$).

Harvester collections

The mean number of mussels found per harvester collection was 125.4 ± 15.96 (mean $\pm$ standard error). The size structure histogram of all collections was a unimodal distribution that ranged from 30 to 66 mm with the most frequently exploited size class being between 50 and 59 mm.

Comparisons between the histograms obtained from the scrapings at NR and the harvester collections showed that the sizes exploited by harvesters were the least abundant sizes found in the mussel bed (Figure 9). Subsequently, Manly's index was calculated for each size class. As no mussels larger than 59 mm could be found at NR from the mussel surveys, it was not possible to calculate Manly's alpha for the largest
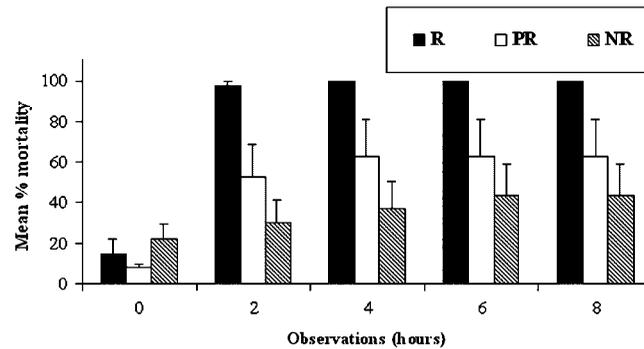
Figure 8. Tethering experiment. Mean percentage mortality of *Mytilus galloprovincialis* on the experimental plates for each observation (h) and location (R, PR, NR). Vertical bars denote standard error.
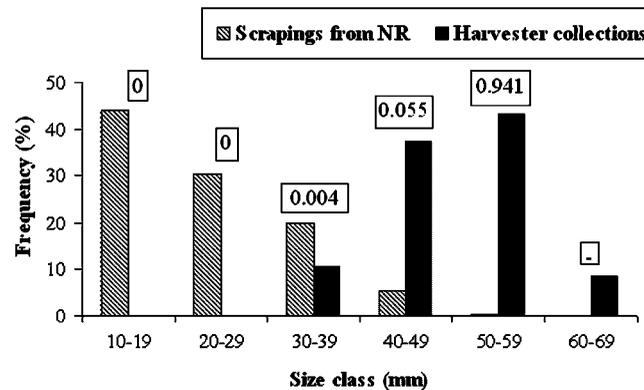

Figure 9. Harvester collections. Frequency (%) of each size class of *Mytilus galloprovincialis* from the harvester collections and NR scrapings. The frequency was calculated from the total number of the samples obtained in each situation. Numbers inside boxes are Manly's alpha values obtained for each size class; if $\alpha > 0.2$, prey is preferred.

size class (60–69 mm). As a result, only five prey types could be considered, and the resulting α_i values for each prey type were compared with 0.2 ($1/m$). The only size class that showed prey preference (i.e. α_i greater than $1/m$) was that between 50 and 59 mm (Figure 9). Although the other four prey types showed lower values than $1/m$, size classes between 30 and 49 mm showed α_i values greater than 0.

DISCUSSION

This study has shown that both the medium and large size classes of *M. galloprovincialis* populations, which were generally the least abundant in the mussel beds but the most important in terms of biomass, were subject to top down processes (i.e. fish and human predation). On the other hand, the abundance of small mussels was highly variable and recruitment was an important factor for *M. galloprovincialis* populations.

M. galloprovincialis reproductive cycles in the Mediterranean Sea are well documented, with the major spatfall taking place in spring (Sarà *et al.*, 1998) and summer (Abada-Boudjema and Dauvin, 1995), with less individuals spawning in autumn (Mazzola *et al.*, 1999). The largest settlement has been reported in summer or late summer (Marguš and Teskeredžić, 1986; Ardizzone *et al.*, 1996). In the present study, the high abundance of small mussels in summer suggests that the spring spatfall resulted in a successful

recruitment in summer, while in the winter of 2004 the recruits detected were most likely from the major settlement, which had arrived in late summer. On the other hand, the fact that the abundance of large mussels (> 30 mm) was higher in 2003 than 2004 (and the small mussels showed the inverse pattern) suggests that large mussels detected in 2003 (the ones reproductively more active) produced an important arrival of recruits the following year.

Ceccherelli and Rossi (1984) studied *M. galloprovincialis* growth rate in a highly productive Mediterranean lagoon (eutrophic waters) and found that 14.5 months after settlement, mussels reached 50 mm in shell length. Sarà *et al.* (1998) studied the growth rate of mussels on the northern coast of Sicily at a site with oligotrophic waters and found that in 1 year mussels reached a maximum shell length of between 30 and 40 mm, and after the second year they reached 60 mm in length. The Medes Islands MPA waters are mesotrophic (Ribes, 1998), which suggests that mussels here might have an intermediate growth rate somewhere between the values mentioned in the studies of Ceccherelli and Rossi (1984) and Sarà *et al.* (1998). Consequently, mussel populations in and around the Medes Island MPA are composed of relatively young individuals (less than 2 years old). As mussel populations are subject to environmental pressures (Erlandsson *et al.*, 2006; Zardi *et al.*, 2006) and biotic stresses (Griffiths and Seiderer, 1980; Carroll and Highsmith, 1996; this study), they have the evolutionary need for a highly dynamic population strategy in order to ensure self-sustainable populations.

Many authors worldwide have reported a high abundance of predatory fish that achieve large sizes inside MPAs (Harmelin, 1987; Polunin and Roberts, 1993; Willis *et al.*, 2003; Rius, 2007). In contrast, studies of sea urchins have not detected differences in density or mean size between protected and fished areas (Sala *et al.*, 1998b). Similarly, in the present study, remarkably different mussel size structures between locations were not found, although statistical analysis showed significant differences in terms of both mean shell length and size structure among locations. Biomass proved to be a good indicator of each size class contribution to the mussel bed population structure. The fact that PR persistently showed a higher mean shell length and biomass than the other locations in both years, suggested that the presence of predators was affecting both R and NR mussel populations.

The tethering experiment indicated that fish predators caused significantly higher mussel mortality in R than at the other two locations where predators were not abundant. The losses reported in PR and NR were most likely due to wave action, which affected mussels with looser byssus threads (Zardi *et al.*, 2006). This idea was reinforced by the fact that the mussels that were not removed within the first 4 h remained until the end of the experiment. Tethering experiments provide information about predation, although they do not always accurately reflect natural patterns (Aronson *et al.*, 2001). The mussels used in this experiment were easier to prey upon than natural populations as neither their attachment nor the substratum on which they were attached were as suitable as those of natural populations. However, mortality was so extreme and quick in R that, besides these methodological limitations, only fish predators could cause such rapid mortality of mussels in R. The present study pointed out that MPAs where top predators are recovered are not going to contribute to the enhancement of *M. galloprovincialis* populations, as mussel beds are subjected to trophic cascade effects through fish predation. The same has been found for urchins (Hereu *et al.*, 2005) and lobsters (Díaz *et al.*, 2005) in the same MPA. As a result, the creation of the Medes Island MPA has only benefited particular species, namely top fish predators.

Human exploitation of intertidal organisms has been reported to be a very selective activity, targeting the largest individuals in many regions around the world (Moreno *et al.*, 1984; Lasiak and Dye, 1989; this study). R and PR have been completely protected from human harvesting for 17 years, and consequently showed a higher abundance of larger mussels (⩾ 40 mm) than NR. As a result, no increase in the abundance of large mussels (i.e. harvestable size) can be expected in mussel beds in non-protected areas. However, the high turnover rate of the mussel populations studied suggests that mussel populations in harvested areas in the north-western Mediterranean are not at risk, and seem able to withstand the current human harvesting pressure.

The fact that R and NR showed similar total biomass suggests that the effects of harvesters and fish at NR and R, respectively, had similar effects on the mussel populations. Therefore, *M. galloprovincialis* populations can only be completely recovered in partial reserves, where recreational fishing maintains top predator abundance at low levels (Denny and Babcock, 2004). If the aim of the Medes Island MPA is to recover the entire benthic community, a broader conservation approach should be considered in future management plans.

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REFERENCES

Abada-Boudjema YM, Dauvin JC. 1995. Recruitment and life span of two natural mussel populations *Perna perna* (Linnaeus) and *Mytilus galloprovincialis* (Lamark) from the Algerian coast. *Journal of Molluscan Studies* **61**: 467–481.

Addessi L. 1994. Human disturbance and long-term changes on a rocky intertidal community. *Ecological Applications* **4**: 786–797.

Airoldi L, Bacchiocchi F, Cagliola C, Bulleri F, Abbiati M. 2005. Impact of recreational harvesting on assemblages in artificial rocky habitats. *Marine Ecology Progress Series* **299**: 55–66.

Anonymous. 1995. Regulació de la pesca marítima recreativa. Diari Oficial Generalitat de Catalunya. Decret 109/1995. Article 24.1.

Ardizzone GD, Belluscio A, Gravina MF, Somaschini A. 1996. Colonization and disappearance of *Mytilus galloprovincialis* Lam. on an artificial habitat in the Mediterranean Sea. *Estuarine, Coastal and Shelf Science* **43**: 665–676.

Aronson RB, Heck KL, Valentine JF. 2001. Measuring predation with tethering experiments. *Marine Ecology Progress Series* **214**: 311–312.

Babarro JMF, Fernández-Reiriz MJ, Labarta U. 2000. Growth of seed mussel (*Mytilus galloprovincialis* Lmk): effects of environmental parameters and seed origin. *Journal of Shellfish Research* **19**: 187–193.

Branch GM, Odendaal F. 2003. The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. *Biological Conservation* **114**: 255–269.

Bulleri F, Airoldi L. 2005. Artificial marine structures facilitate the spread of a nonindigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology* **42**: 1063–1072.

Buxton CD. 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes* **36**: 47–63.

Carroll ML, Highsmith RC. 1996. Role of catastrophic disturbance in mediating *Nucella-Mytilus* interactions in the Alaskan rocky intertidal. *Marine Ecology Progress Series* **138**: 125–133.

Castilla JC. 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution* **14**: 280–283.

Castilla JC, Bustamante RH. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Durvilleales). *Marine Ecology Progress Series* **50**: 203–214.

Castilla JC, Durán LR. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* **45**: 391–399.

Ceccherelli VU, Rossi R. 1984. Settlement, growth and production of the mussel *Mytilus galloprovincialis*. *Marine Ecology Progress Series* **16**: 173–184.

Chesson J. 1978. Measuring preference in selective predation. *Ecology* **59**: 211–215.

Claudet J, Pelletier D, Jouvenel J-Y, Bachet F, Galzin R. 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation* **130**: 349–369.

Coleman FC, Williams SL. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution* **17**: 40–44.

Connell SD, Anderson MJ. 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology* **241**: 15–29.

Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* **97**: 153–166.

de Lumley H. 1975. Cultural evolution in France in its paleoecological setting during the Middle Pleistocene. In *After the Australopithecines*: *Stratigraphy*, *Ecology and Culture in the Middle Pleistocene*, Isaac GL, Butzer KW (eds). Mounton: The Hague; 745–808.

Denny CM, Babcock RC. 2004. Do partial marine reserves protect reef fish assemblages? *Biological Conservation* **116**: 119–129.

Díaz D, Zabala M, Linares C, Hereu B, Abelló P. 2005. Increased predation of juvenile European spiny lobster (*Palinurus elephas*) in a marine protected area. *New Zealand Journal of Marine and Freshwater Research* **39**: 447–453.

Dye AH, Schleyer MH, Lambert G, Lasiak TA. 1994. Intertidal and subtidal filter-feeders in Southern Africa. In *Rocky Shores*: *Exploitation in Chile and South Africa*, Siegfried RW (ed.). Springer-Verlag: Berlin; 57–74.

Elner RW, Hughes RN. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenus*. *Journal of Animal Ecology* **47**: 103–116.

Erlandsson J, Pal P, McQuaid CD. 2006. Re-colonisation rate differs between co-existing indigenous and invasive intertidal mussels following major disturbance. *Marine Ecology Progress Series* **320**: 169–176.

García-Rubies A, Zabala M. 1990. Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands Marine Reserve (NW Mediterranean). *Scientia Marina* **54**: 317–328.

Griffiths CL, Hockey PAR. 1987. A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. *South African Journal of Marine Science* **5**: 547–556.

Griffiths CL, Seiderer JL. 1980. Rock-lobsters and mussels — limitations and preferences in a predator–prey interaction. *Journal of Experimental Marine Biology and Ecology* **44**: 95–109.

Halpern BS, Cottenie K, Broitman BR. 2006. Strong top-down control in Southern California kelp forest ecosystems. *Science* **312**: 1230–1232.

Harmelin J-G. 1987. Structure et variabilité de l'ichtyofaune d'une zone rocheuse protegeé en Mediterranée (Parc National de Port-Cros, France). *Marine Ecology* **8**: 263–284.

Harmelin J-G, Bachet F, García F. 1995. Mediterranean marine reserves: fish indices as tests of protection efficiency. *Marine Ecology* **16**: 233–250.

Heisey DM. 1985. Analysing selection experiments with log-linear models. *Ecology* **66**: 1744–1748.

Hereu B, Zabala M, Linares C, Sala E. 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Marine Biology* **146**: 293–299.

Hockey PAR, Bosman AL. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* **46**: 3–14.

Hyrenbach KD, Forney KA, Dayton PK. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* **10**: 437–458.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.

Krebs CJ. 1989. *Ecological Methodology*. Harper and Row: New York.

Lasiak TA, Dye AH. 1989. The ecology of the brown mussel *Perna perna* in Transkei, southern Africa: implications for the management of a traditional food resource. *Biological Conservation* **47**: 245–257.

Lipej L, Bonaca MO, Šiško M. 2003. Coastal fish diversity in three marine protected areas and one unprotected area in the Gulf of Trieste (Northern Adriatic). *Marine Ecology* **24**: 259–273.

Lloret J, Galzin R, Gil de sola L, Souplet A, Demestre M. 2005. Habitat related differences in lipid reserves of some exploited fish species in the north-western Mediterranean continental shelf. *Journal of Fish Biology* **67**: 51–65.

Marguš D, Teskeredžić E. 1986. Settlement of mussels (*Mytilus galloprovincialis* Lamarck) on rope collectors in the estuary of the River Krka, Yugoslavia. *Aquaculture* **55**: 285–296.

Mazzola A, Favaloro E, Sarà G. 1999. Experiences of integrated mariculture in a southern Tyrrhenian area (Mediterranean Sea). *Aquaculture Research* **30**: 773–780.

McQuaid CD, Lawrie SM. 2005. Supply side ecology of the brown mussel, *Perna perna*: an investigation of spatial and temporal variation in, and coupling between, gamete release and larval supply. *Marine Biology* **147**: 955–963.

Moreno CA, Sutherland JP, Jara HF. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* **42**: 155–160.

Moreno CA, Lunecke KM, Lépez MI. 1986. The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from Man in southern Chile and the effects on benthic sessile assemblages. *Oikos* **46**: 359–364.

Osman RW, Whitlatch RB. 1998. Local control of recruitment in an epifaunal community and the consequences to colonization processes. *Hydrobiologia* **375/376**: 113–123.

Palmerini P, Bianchi CN. 1994. Biomass measurements and weight-to-weight conversion factors: a comparison of methods applied to the mussel *Mytilus galloprovincialis*. *Marine Biology* **120**: 273–277.

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998. Fishing down marine food webs. *Science* **279**: 860–863.

Peharda M, Morton B. 2006. Experimental prey species preferences of *Hexaplex trunculus* (Gastropoda: Muricidae) and predator–prey interactions with the Black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae). *Marine Biology* **148**: 1011–1019.

Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien M-L, Hereu B, Milazzo M, Zabala M, D'Anna G, Pipitone C. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation* **27**: 179–200.

Polunin NVC, Roberts CM. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**: 167–176.

Ribes M. 1998. Feeding activity and diet of benthic suspension feeders related to metabolic requirements and seston composition. PhD thesis, University of Barcelona.

Rius M. 2007. The effects of protection on fish populations in the Ses Negres Marine Reserve (NW Mediterranean, Spain). *Scientia Marina* **71**: 499–504.

Rius M, Cabral HN. 2004. Human harvesting of *Mytilus galloprovincialis* Lamarck, 1819, on the central coast of Portugal. *Scientia Marina* **68**: 545–551.

Rius M, McQuaid CD. 2006. Wave action and competitive interaction between the invasive mussel *Mytilus galloprovincialis* and the indigenous *Perna perna* in South Africa. *Marine Biology* **150**: 69–78.

Rius M, Kaehler S, McQuaid CD. 2006. The relationship between human exploitation pressure and condition of mussel populations along the south coast of South Africa. *South African Journal of Science* **102**: 130–136.

Sala E, Boudouresque CF, Harmelin-Vivien M. 1998a. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* **82**: 425–439.

Sala E, Ribes M, Hereu B, Zabala M, Alvà V, Coma R, Garrabou J. 1998b. Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area. *Marine Ecology Progress Series* **168**: 135–145.

Sarà G, Manganaro A, Cortese G, Pusceddu A, Mazzola A. 1998. The relationship between food availability and growth in *Mytilus galloprovincialis* in the open sea (southern Mediterranean). *Aquaculture* **167**: 1–15.

Suchanek TH. 1985. Mussels and their role in structuring rocky shore communities. In *The Ecology of Rocky Shores*, Moore PG, Seed R (eds). Hodder and Stoughton: London; 70–96.

Tsuchiya M, Bellan-Santini D. 1989. Vertical distribution of shallow rocky shore organisms and community structure of mussel beds (*Mytilus galloprovincialis*) along the coast of Marseille, France. *Mésogée* **49**: 91–110.

Underwood AJ. 1993. Exploitation of species on the rocky coast of New South Wales (Australia) and options for its management. *Ocean Coastal Management* **20**: 41–62.

Wantiez L, Thollot P, Kulbicki M. 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs* **16**: 215–224.

Willis TJ, Millar RB, Babcock RC. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**: 214–227.

Zar JH. 1984. *Biostatistical Analysis*. Prentice-Hall: New Jersey.

Zardi GI, Nicastro KR, McQuaid CD, Rius M, Porri F. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. *Marine Biology* **150**: 79–88.