

Predation: a regulating force of intertidal assemblages on the central Portuguese coast?

SÓNIA A.E. BRAZÃO¹, ANA C.F. SILVA² AND DIANA M. BOAVENTURA^{1,3}

¹Laboratório Marítimo da Guia, Centro de Oceanografia, Faculdade de Ciências da Universidade de Lisboa, Avenida Nossa Senhora do Cabo, 939, 2750-374 Cascais, Portugal, ²University of Plymouth, Marine Biology & Ecology Research Centre, Drake Circus, Plymouth, PL4 8AA, UK, ³Escola Superior de Educação João de Deus, Avenida Álvares Cabral, 69, Lisboa 1269-094, Portugal

*Predation has long been recognized as an important biological force driving community patterns in intertidal rocky shores throughout the world. Little is known, however, about the role of predation by mobile marine predators in shaping intertidal prey populations in Portuguese rocky shores. The abundance and population structure of crabs were assessed during nocturnal low-tides on two rocky shores to characterize potential predator species. To assess the effect of predation on intertidal species including limpets, barnacles and mussels, predator exclusion experiments using full cage, partial cage and no cage treatments, were set up for two months on two shores on the central Portuguese coast. *Pachygrapsus marmoratus* (Fabricius) and *Eriphia verrucosa* (Forsskål) were the most abundant crabs. Results from predator exclusion experiments suggested that predators do not exert a significant control on abundance of limpets, mussels or barnacles on the midshore during the experimental period. Despite the fact that these crabs are known to feed on the analysed prey, several factors may account for the observed absence of impact on prey abundance and these are discussed.*

Keywords: top-down control, crabs, exclusion, barnacles, limpets, mussels

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INTRODUCTION

Intertidal communities vary in space and time (Underwood & Chapman, 1998a; Underwood *et al.*, 2000). The interplay between biological (e.g. competition, predation, settlement and recruitment) and physical forces (e.g. wave exposure and topographical heterogeneity of the shore) has been reported to drive patterns of distribution of species on the shore (Paine, 1966, 1974; Dayton, 1971; Menge & Sutherland, 1976; Sousa, 1984; Sih *et al.*, 1985; Menge, 1991; Benedetti-Cecchi *et al.*, 2000; Boaventura *et al.*, 2002b). Among these forces, predation has been widely recognized as a key force influencing the structure and dynamics of intertidal communities (Paine, 1974; Menge & Sutherland, 1976; Sih *et al.*, 1985; Menge, 2000).

The most evident effect of predation encompasses changes on prey density and distribution limits, while indirectly it can change diversity within the community (Paine, 1974; Chilton & Bull, 1984; Sih *et al.*, 1985; Hall *et al.*, 1990; Yamada & Boulding, 1996). Controlled manipulative field experiments using predator exclusion cages have been widely used in rocky intertidal systems to assess the impact of predators on prey populations (e.g. Menge & Sutherland, 1976; Hall *et al.*, 1990; Connell, 1997; Navarrete & Castilla, 2003; Silva *et al.*, 2004; Felsing *et al.*, 2005; Sams & Keough, 2007), and used in this study to assess predation effects on intertidal prey populations.

Crabs, fish, sea stars, birds, humans and even small rodents are considered to be important predators of intertidal prey on Atlantic and Pacific shores such as limpets, mussels and barnacles by controlling their abundance and distribution (Navarrete & Castilla, 1993; Norberg & Tedengren, 1995; Castilla, 1999; Coleman *et al.*, 1999; Carlton & Hodder, 2003; Rius & Cabral, 2004; Monteiro *et al.*, 2005; Cannicci *et al.*, 2007; Markowska & Kidawa, 2007). In turn, these prey are known to be key space occupiers; their absence or reduced abundance will strongly influence intertidal community composition (Hawkins, 1999; Hawkins *et al.*, 2000; Boaventura *et al.*, 2002a; Cannicci *et al.*, 2002). Patellid limpets are the most common limpets on Portuguese shores (Boaventura *et al.*, 2002a) and are considered to be dominant grazers, playing a key role on European rocky shores by controlling algae abundance and distribution (Hawkins, 1999). It is therefore important that we understand the role of predation in controlling their populations and consider possible cascade effects for the algae assemblages.

On Portuguese rocky shores, the limpet *Patella depressa* Pennant, the mussel *Mytilus galloprovincialis* Lamarck and the barnacle *Chthamalus* spp. are dominant mid-shore space occupiers (Boaventura *et al.*, 2002a). Thus, this study tested for predation effects on the populations of these species on the mid-shore, where prey reach higher densities. Although this somewhat limits the comparison of our findings with that of similar studies made on other areas of the shore (e.g. Chilton & Bull, 1984), they remain valid and pertinent for the hypothesis tested and add to our knowledge on the subject. Crab species such as *Pachygrapsus marmoratus* (Fabricius) and *Eriphia verrucosa* (Forsskål) have been reported to be predators of limpets, mussels and barnacles on Portuguese rocky shores (Flores *et al.*, 2001; Cannicci

Corresponding author:
S.A.E. Brazão
Email: soniabrazao@gmail.com

et al., 2002; Silva *et al.*, 2004). Also, small benthic fish such as blennies have been reported to include limpets in their diet on Portuguese shores (Monteiro *et al.*, 2005) and thus, the predation effect of crabs and fish was considered in the present study, as exclusion cages would also prevent the feeding of both on the experimental plots.

Despite the extensive body of literature on predator–prey interactions and caging experiments on rocky shores throughout the world, little is still known about the role of predation by mobile aquatic predators in shaping intertidal prey populations on Portuguese rocky shores (but see Silva *et al.*, 2004), while predation is long recognized as a key structuring force on North-American shores (Paine, 1974; Rilov & Schiel, 2006). Previous observations on the central coast of Portugal, detected weak predatory effects of the crab *Pachygrapsus marmoratus* on populations of the intertidal limpet *Patella depressa* (Silva *et al.*, 2004). The present study adds to the existing information by analysing the predatory effect of crabs on important intertidal prey including mussels and barnacles and it examined the following hypotheses: (i) crabs are abundant predators on rocky shores and their abundance varies spatially between shores; and (ii) there is a significantly higher survival of limpets, mussels and barnacles in complete cages than on open cages or control plots.

MATERIALS AND METHODS

Study sites

Two rocky shores were surveyed on the central Portuguese coast: Paimogo (39°17'N 9°20'W) and Peralta (39°14'N 9°20'W), separated by approximately 5 km. In this region, tides are semidiurnal and tidal amplitude varies around 3–4 m. Two sampling sites (about 100 m apart and in minimum 20 m long) were selected at each shore representing continuous rock platforms (1 km long). Each shore was typical of the region.

Predator characterization

Due to logistic limitations and because previous studies in the region had reported that crabs are relevant predators of the prey analysed in the present study (Flores *et al.*, 2001; Cannicci *et al.*, 2002; Silva *et al.*, 2004), crabs were the only predators sampled although other predators such as small blennies may have been excluded by the cages in this study. Similar experiments using exclusion cages have, however, demonstrated the value of this experimental approach (Rilov & Schiel, 2006; Silva, 2008; Silva *et al.*, 2008). To establish the identity, abundance and population structure of crabs, four nocturnal one hour searches were made by two observers between July and August 2007 on each shore at spring low-tides. This was because crabs reach their greatest activity period during nocturnal periods (Flores *et al.*, 2001; Cannicci *et al.*, 2002; Silva *et al.*, 2004). Searches were made by counting crabs that were actively feeding on the rock surface and thus easily detectable with a torch.

Predator exclusion experiments

In order to test the null hypothesis that there were no significant predation effects on the abundance of limpets, barnacles

and mussels, three experimental treatments were set up during spring 2007 (April–June): (i) uncaged treatment (UC), no cage but plot marked on the rock surface; (ii) partial cage (PC), half of the cage area with open sides which allowed predator entrance and a roof (cage control); and (iii) complete cage (CC), totally closed cage which prevented predator entrance. Cages (30 × 30 × 15 cm) were made of square mesh (6 × 6 mm welded plastic coated steel wire) covered with a 25 × 25 mm mesh galvanized metal for support and resistance. The partial cage treatment was considered to allow access to locally abundant crabs such as *P. marmoratus*, *E. verrucosa* and *Necora puber* and small fish such as Blenniidae and Gobiidae, but no other predators such as large fish (e.g. wrasse) and birds, while the total cage treatment was considered to exclude all predators. Six replicates of each treatment were randomly set at mid-shore level on the two sites per shore. Care was taken in cage design (e.g. mesh size) and maintenance (manual algae removal) to control cage artefacts such as shading, reduction of water flow, abnormally high algal growth and increased sedimentation within cages and prey movements (see Hall *et al.*, 1990; Connell, 1997; Englund, 1997; Navarrete & Castilla, 2003; Miller & Gaylord, 2007). Care was also taken to select mid-intertidal areas very similar to each other in terms of biotic and abiotic characteristics, and also dominated by all the three prey species analysed in this study. The abundance and shell length of limpets and percentage covers of mussels and barnacles within the experimental plots were assessed in the beginning of the experiment (T₀) and after two months (T₂) (Figures 1 & 2). Because limpets were the only mobile prey considered these were marked at T₀ with nail polish in order to identify predation effects on prey specific to each plot and to examine any migration or emigration. Potential cage artefacts were examined by comparing uncaged treatments to partial cages.

Data analysis

In order to test the hypothesis that there was no predation effect on the abundance of limpets and percentage cover of barnacles and mussels, the change in their abundance and/or percentage cover data between T₀ and T₂ were analysed using a 3-way mixed model ANOVA. We also examined the change in the average shell length growth data for limpets between T₀ and T₂ for all plots to test if that recruitment or growth was not likely to influence our results. The factors tested were 'treatment' (fixed, orthogonal and 3 levels), 'shore' (random, orthogonal and 2 levels) and 'site' (random, nested in shore and 2 levels) with six replicates per treatment. Time was not considered as a factor in the design to avoid non-independence of data, since the same plots were measured at both times of the experiments. For all statistical analyses, Cochran's test was done prior to ANOVA to test for homogeneity of variances. Where variances were heterogeneous data were transformed and, after this the limitation persisted and thus analysis was made using non-transformed data, but a more conservative *P* value was used ($P < 0.01$) (Underwood, 1997). Where results were significant, the pairwise comparisons between groups were determined using SNK (Student–Newman–Keuls) *a posteriori* comparison tests. Tests of homogeneity, ANOVA and SNK tests were done using GMAV5 for

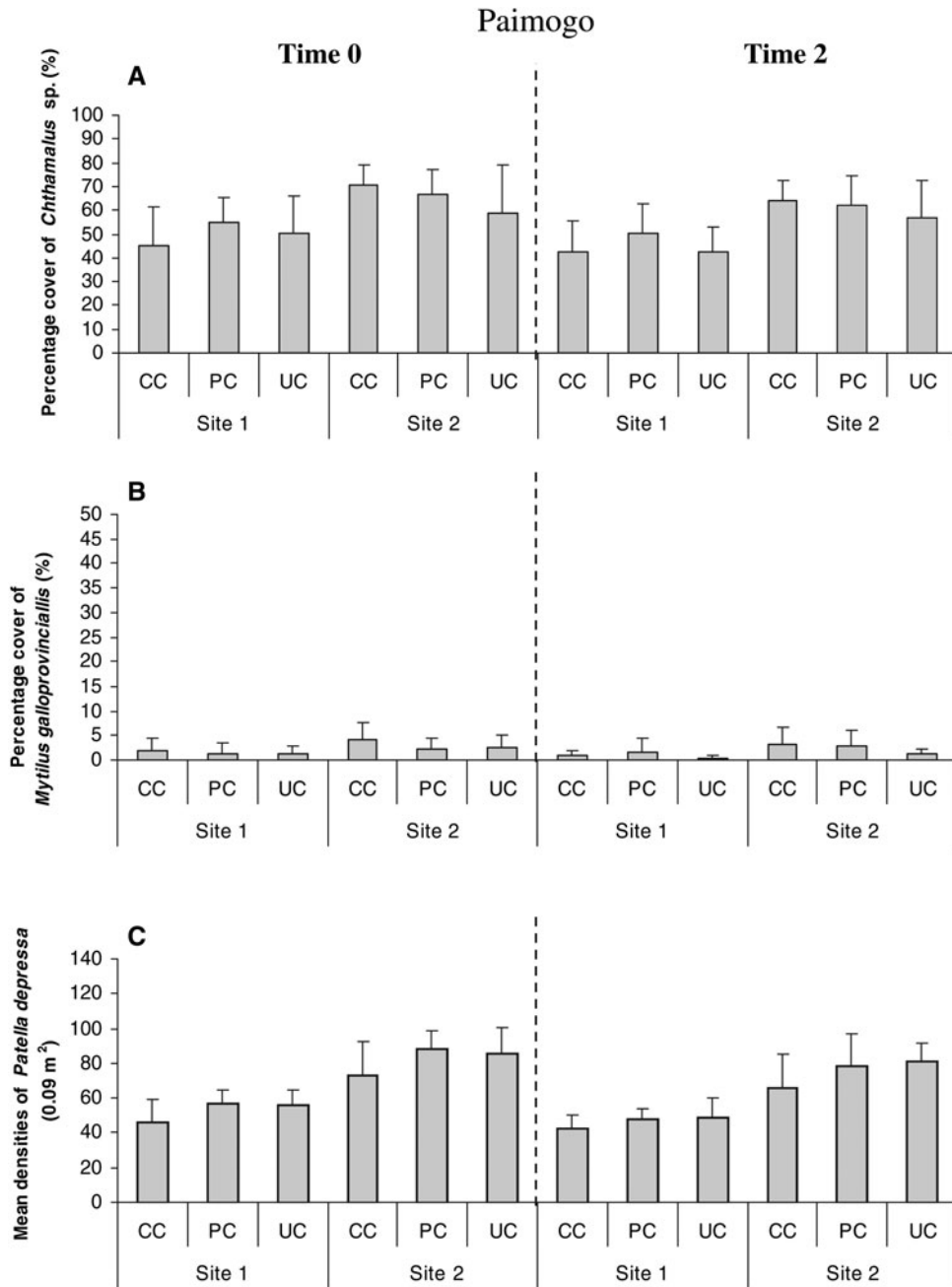


Fig. 1. Percentage cover of *Chthamalus* sp. (A) and *Mytilus galloprovincialis* (B) and mean densities of *Patella depressa* (C) (\pm SE) in the predator exclusion study in the beginning (T0) and after two months of exclusion (T2) in Paimogo. CC, complete cage; PC, partial cage; UC, uncaged treatment.

Windows Statistical Software (Underwood & Chapman, 1998b).

RESULTS

Predator characterization

The total number of crab species recorded on all four nights and both shores was: *P. marmoratus* (N = 536) and *Eriphia verrucosa* (N = 133), while *Carcinus maenas* (Linnaeus) (N = 6) and *Necora puber* (Linnaeus) (N = 4) were seldom detected. In Paimogo, *P. marmoratus* (N = 64) and *E. verrucosa* (N = 65) were both the dominant species while in

Peralta, the most abundant species was by far *P. marmoratus* (N = 472), followed by *E. verrucosa* (N = 68). Crab abundance was very high with an average of 67 individuals of *P. marmoratus* species and an average of 17 individuals of *E. verrucosa* species being collected per night per shore.

Predator exclusion experiments

There was no evidence for the occurrence of cage artefacts: any algae growth was successfully removed when detected, no sedimentation was detected and limpet marking allowed tracking all individuals. All limpets were found to be very faithful to their home scars, only 295 individuals (out of 5383 at the start of the experiment—5.5%) were detected

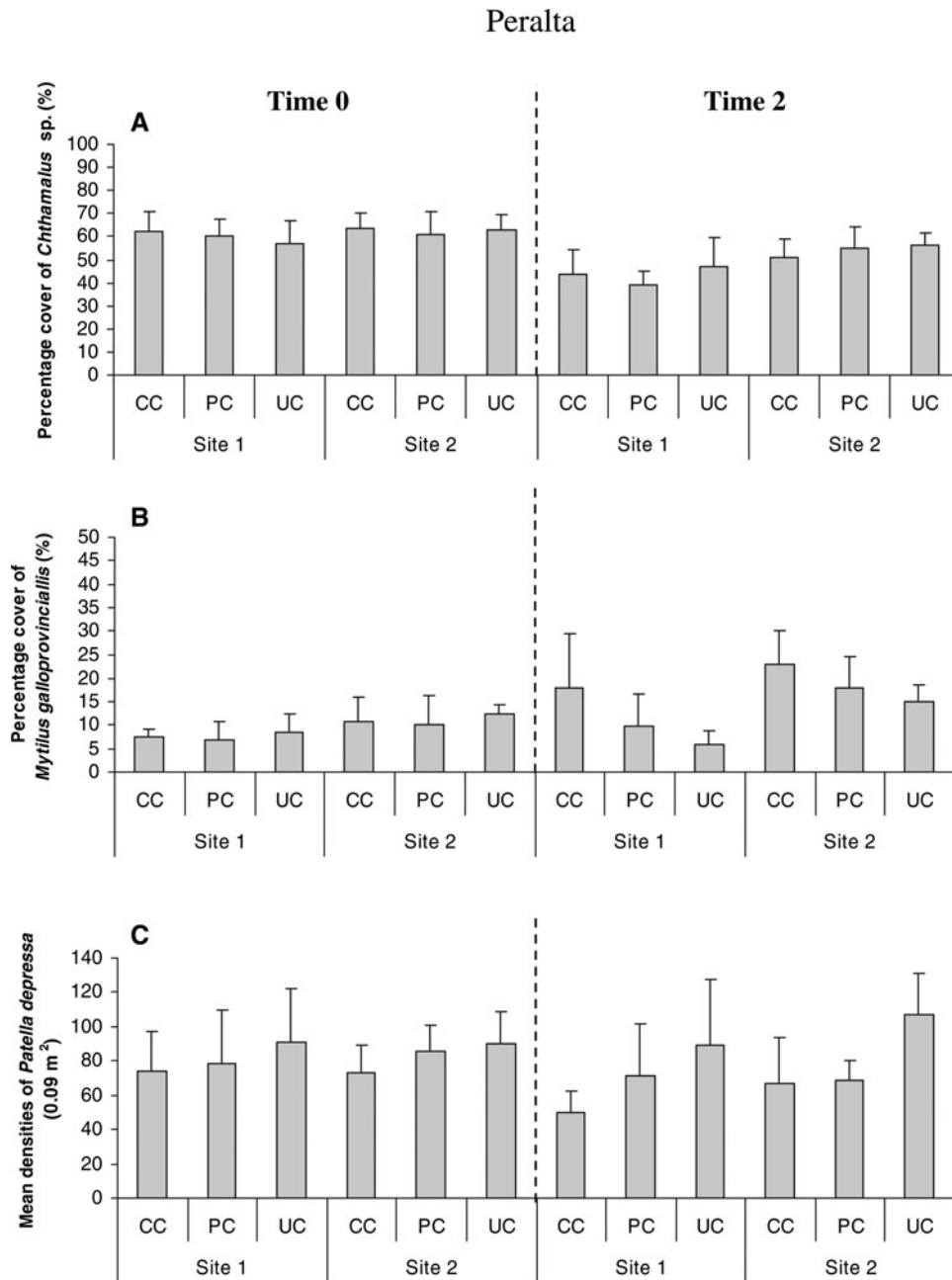


Fig. 2. Percentage cover of *Chthamalus* sp. (A) and *Mytilus galloprovincialis* (B) and mean densities of *Patella depressa* (C) (\pm SE) in the predator exclusion study in the beginning (T₀) and after two months of exclusion (T₂) in Peralta. CC, complete cage; PC, partial cage; UC, uncaged treatment.

outside the plots but still within 30 cm of the open cage or plot edge. Reduced limpet emigration and immigration rates in similar exclusion experiments have been shown for patellid limpets in south-west Britain (Silva *et al.*, 2008). ANOVA analyses on the abundance and/or percentage cover data of each of the target species revealed no significant differences between T₀ and T₂ in any of the tested factors (treatments, shores or sites) ($P > 0.05$; Table 1).

Since there were no significant differences between treatments at T₂, predation was found not to be a significant force controlling the abundance and/or percentage cover of limpets, barnacles and mussels for the duration of the experimental period. However, a significant interaction was detected on the percentage cover of mussels between the

factors 'treatment' and 'shore' (treatment \times shore $F_{2,4} = 34.75$, $P < 0.01$; Table 1). SNK comparison tests revealed that significant differences between treatments were only detected in Peralta, where the complete cage treatment (CC) had significantly higher percentage cover of mussels than the uncaged (UC) and partial cage treatments (PC) (SNK tests, Table 1; Figure 2). We also examined the change in the average shell length growth data for limpets between T₀ and T₂ for all plots and there were no significant differences between treatments (ANOVA, $F_{2,2} = 0.04$, $P = 0.963$).

Due to the weak predator-prey interaction detected in the above ANOVA, power analyses were made for all three prey species on the non-significant factor 'treatment', to show that there was sufficient replication and power on the design

Table 1. Analysis of variance testing for differences in the percentage cover of *Chthamalus* spp. and *Mytilus galloprovincialis* and in the abundance of *Patella depressa*, after two months of the predator exclusion study (T2) (N = 6). Significant effects are in bold.

Source of variation	df	<i>Chthamalus</i> spp.			<i>Mytilus galloprovincialis</i>			<i>Patella depressa</i>		
		MS	F	P	MS	F	P	MS	F	P
Treatment = Tr	2	74.06	0.68	0.59	200.72	1.09	0.48	1074.43	1.23	0.45
Shore = Sh	1	1042.72	3.59	0.20	672.22	8.83	0.10	4.50	0.01	0.92
Site = Si (Sh)	2	290.72	3.15	0.05	76.11	2.82	0.07	348.11	2.25	0.11
Tr × Sh	2	108.72	1.21	0.39	183.39	34.75	0.003	877.04	2.36	0.21
Tr × Si (Sh)	4	90.06	0.98	0.43	5.28	0.20	0.94	372.07	2.40	0.06
Res	60	92.30			27.00			154.82		
Cochran's test		C = 0.2534 ns			C = 0.4514 (P < 0.01)			C = 0.1967 ns		
Transformation		None			None ^a			None		
SNK tests					Treatment × shore SE = 0.6632 Paimogo, CC = PC = UC ns Peralta, CC > PC > UC**					

ns, not significant; **P < 0.01; Pa, Paimogo; Pe, Peralta; S1, Site 1; S2, Site 2; CC, complete cage; PC, partial cage; UC, uncaged treatment; SNK, Student–Newman–Keuls. ^a, Data were not transformed, but a conservative P < 0.01 was used.

and thus certify that any effects of predation would have been detected by the experiments if they occurred. Because the present study has similar methods and experimental design to Silva *et al.* (2008), also made in European rocky shores but where strong predatory effects were detected, power was calculated using the effect size (a reduction of around 0.50 in limpets abundance) measured by those authors, in order to compare both experiments. Power calculations indicated that the experiment conducted in the present study was sufficiently replicated and was powerful enough to detect any effects of predation if they occurred (Power = 0.85 in barnacles, Power = 0.99 in mussels and Power = 0.99 in limpets). Power calculated using the effect size measured by Silva *et al.* (2008) in south-west Britain revealed that the experimental design used in the present study would be sufficiently replicated and powerful to detect predatory effects if it was run in south-west Britain instead of the central Portuguese coast (Power = 0.97), strengthening our results that predators had weak effects in our study.

DISCUSSION

This study was successful in examining the effects of predation on important intertidal species, thus adding new and valuable information on predator–prey interactions which had remained relatively unknown for Portuguese shores. Potential cage artefacts such as shading by algae growth were controlled and limpet emigration and/or immigration were considered minimal.

Our results support the hypothesis that for a two month period during the spring (April–June), predatory effects of crab and small fish on abundance of barnacles, mussels and limpet communities can be very weak on the Portuguese coast. These findings were considered to be consistent and valid as the study included large replication for each treatment (6) at large (km) and small (m) spatial scales. Power calculated using the effect size measured by Silva *et al.* (2008) in south-west Britain, where strong predatory effects were detected, revealed that the experimental design used in the present study would be sufficiently replicated and powerful to detect predatory effects if it was run in south-west Britain instead

of the central Portuguese coast (Power = 0.97). This strengthens our conclusion that predators had weak effects on Portuguese rocky shores during the period of this experiment.

Our main result of no predation effects contrasts with most similar studies which report severe predation effects (Paine, 1974; Rilov & Schiel, 2006; Silva *et al.*, 2008). However, these so-called negative results are important to report due to the emphasis placed on strong predator–prey interactions as major community drivers on rocky shores and the often overlooked meaning of reduced predation effects. According to Hall *et al.* (1990), predators do not always play major roles in shaping community structure and these so-called negative results are under-reported. Other studies have also reported weak predator–prey interactions (Hall *et al.*, 1990; Connell, 2001; Sams & Keough, 2007) and a similar minimal predatory effect on abundance of limpets has also been already reported in other Portuguese rocky shores (see Silva *et al.*, 2004).

Despite the lack of a clear predation effect on prey abundance, a significant interaction between the factors treatment and shore was detected on the percentage cover of mussels. Significant differences between treatments were only detected in Peralta (see SNK tests), where the complete cage treatment (CC) showed a significantly higher percentage cover of mussels than uncaged treatment (UC) and partial cage (PC), indicating that mussel abundance reductions in PC and UC could be attributed to the effect of predators and/or could be possibly related to potential cage artefacts since significant differences were detected between UC and PC treatments, in Peralta.

Several hypotheses can be advanced to explain the relatively weak predatory effects shown by our data. It is possible that predators may remove prey but this effect may be weak relative to other processes that shape the abundance of prey such as recruitment. A recruitment ‘confounding’ effect on detection of predation effects has been reported for barnacles on the coast of south central Alaska by Carroll (1996). On central Portuguese rocky shores, Silva *et al.* (2003) found that, despite juveniles limpets were present almost year-round, recruitment peaks were mostly found in winter months (December–February), mainly on the lower shore. Range & Paula (2001) recorded densities of 17 recruits cm⁻² *Chthamalus* spat on the central west coast of Portugal and

found that *Chthamalus* spp. recruited almost continuously throughout the year, with a peak between July and September and also found that recruitment was usually stronger on the lower shore levels but extended for a longer period higher on the shore. Unfortunately, no known data are available for peaks of mussel recruitment on the central Portuguese coast. Hence, high settlement and recruitment levels may have influenced prey abundance and thus preventing the detection of the predation effect in the examined time scale. Nevertheless, we examined the change in the average shell length growth data for limpets between T₀ and T₂ for all plots and these were very similar, indicating that recruitment or growth was not likely to influence our results.

Another explanation may be that predation has an effect in abundance of these prey species but the experiment may have run for a too short time to detect it. It seems likely that this is not a satisfactory explanation since, for example, strong effects of crab predation on the abundance of limpets were detected for the same exclusion time (two months) for south-west Britain in similar exclusion experiments (Silva *et al.*, 2008) and, according to Connell & Anderson (1999) approximately 3.5 months is sufficient time to assess the effects of predators (fish) on the structure of established assemblages. Furthermore, several other studies with longer experimental exclusion times (between 3 and 3.5 months) have also revealed weak predatory effects (Connell, 2001; Silva *et al.*, 2004). Hall *et al.* (1990) suggested that predators do not always play major roles in shaping community structure and the effects of predation may be location and/or time specific. In times of plenty, when many alternative resources may be available for predators, or when predators are present in lower numbers, the consequences of predation may be more subtle and difficult to detect.

Although our results pertain only to the mid-shore for the reasons outlined before, our results also do not exclude the hypothesis of a more effective pressure by predators exerted on prey present lower on the shore, where recruits are common and where prey will be accessible for longer periods of submersion to subtidal predators such as crabs and fish. For example, predation pressure on limpets by crabs has been reported to be higher on smaller limpets which are more commonly found on the lower shore (Silva, 2008; Silva *et al.*, 2008). These grazers are known to display avoidance behaviours such as clamping down when in contact with moving predators (Branch & Marsh, 1978; Branch, 1981; Espoz & Castilla, 2000; Silva *et al.*, 2004) and this resistance is known to be less effective in juvenile prey (Navarrete & Castilla, 1993; Coleman *et al.*, 1999).

Finally it is also possible that the existing accentuated human exploitation of intertidal resources on the Portuguese coastline may be involved to a certain extent on the weak predation effects. Crustaceans are very important for the public in general in Portugal to supplement diet, commerce or for bait (Oliveira *et al.*, 2000; Rius & Cabral, 2004; Silva, 2006; Barrento *et al.*, 2008). A significant human-driven reduction of predator abundance could be related to the weak predatory effects detected in the present study. Anthropogenic effects on intertidal dynamics have been reported throughout the world (e.g. Castilla, 1999, 2000; Thompson *et al.*, 2002; Davenport & Davenport, 2006). Further experiments are required to examine this hypothesis, possibly using predator inclusions or comparing effects between protected and non-protected marine areas. Our study contrasts with numerous

similar studies by showing weak predator–prey interactions on rocky shores, suggesting that predation may not always play major roles in shaping intertidal community structure.

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REFERENCES

- Barrento S., Marques A., Pedro S., Vaz-Pires P. and Nunes M.L. (2008) The trade of live crustaceans in Portugal: space for technological improvements. *ICES Journal of Marine Science* 65, 551–559.
- Benedetti-Cecchi L., Bulleri F. and Cinelli F. (2000) The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. *Oecologia (Berlin)* 123, 406–417.
- Boaventura D., Ré P., Cancela da Fonseca L. and Hawkins S.J. (2002a). Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. *Marine Ecology* 23, 69–90.
- Boaventura D., Alexander M., Santina P.D., Smith N.D., Ré P., Cancela da Fonseca L. and Hawkins S.J. (2002b). The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain. *Journal of Experimental Marine Biology and Ecology* 267, 185–206.
- Branch G.M. (1981) The biology of limpets, physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology: an Annual Review* 19, 235–380.
- Branch G.M. and Marsh A.C. (1978) Tenacity and shell shape in six *Patella* species, adaptive features. *Journal of Experimental Marine Biology and Ecology* 34, 111–130.
- Cannicci S., Gomei M., Boddi B. and Vannini M. (2002) Feeding habits and natural diet of the intertidal crab *Pachygrapsus marmoratus*, opportunistic browser or selective feeder? *Estuarine, Coastal and Shelf Science* 54, 983–1001.
- Cannicci S., Gomei M., Dahdouh-Guebas F., Rorandelli R. and Terlizzi A. (2007) Influence of seasonal food abundance and quality on the feeding habits of an opportunistic feeder, the intertidal crab *Pachygrapsus marmoratus*. *Marine Biology* 151, 1331–1342.
- Carlton J.T. and Hodder J. (2003) Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology Progress Series* 256, 271–286.
- Carroll M.L. (1996) Barnacle population dynamics and recruitment regulation in southcentral Alaska. *Journal of Experimental Marine Biology and Ecology* 199, 285–302.
- Castilla J.C. (1999) Coastal marine communities, trends and perspectives from human-exclusion experiments. *Tree* 14, 280–283.
- Castilla J.C. (2000) Roles of experimental marine ecology in coastal management and conservation. *Journal of Experimental Marine Biology and Ecology* 250, 3–21.

- Chilton N.B. and Bull C.M.** (1984) Influence of predation by a crab on the distribution of the size-groups of three intertidal gastropods in South Australia. *Marine Biology* 83, 163–169.
- Coleman R.A., Goss-Custard J.D., Le V dit Durell S.E.A. and Hawkins S.J.** (1999) Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*, a preference for solitary prey items. *Marine Ecology Progress Series* 183, 253–261.
- Connell S.D.** (1997) Exclusion of predatory fish on a coral reef: the anticipation, pre-emption and evaluation of some caging artefacts. *Journal of Experimental Marine Biology and Ecology* 213, 181–198.
- Connell S.D. and Anderson M.J.** (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.
- Connell S.D.** (2001) Predatory fish do not always affect the early development of epibiotic assemblages. *Journal of Experimental Marine Biology and Ecology* 260, 1–12.
- Dayton P.K.** (1971) Competition, disturbance, and community organization, the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41, 351–389.
- Davenport J. and Davenport J.L.** (2006) The impact of tourism and personal leisure transport on coastal environments, a review. *Estuarine, Coastal and Shelf Science* 67, 280–292.
- Englund G.** (1997) Importance of spatial scale and prey movements in predator caging experiments. *Ecology* 78, 2316–2325.
- Espoz C. and Castilla J.C.** (2000) Escape responses of four Chilean intertidal limpets to seastars. *Marine Biology* 137, 887–892.
- Felsing M., Glencrossa B. and Telfer T.** (2005) Preliminary study on the effects of exclusion of wild fauna from aquaculture cages in a shallow marine environment. *Aquaculture* 243, 159–174.
- Flores A.A.V., Cruz J. and Paula J.** (2001) Intertidal distribution and species composition of brachyuran crabs at two rocky shores in Central Portugal. *Hydrobiologia* 449, 171–177.
- Hall S.J., Raffaelli D. and Turrell W.R.** (1990) Predator-caging experiments in marine systems, a reexamination of their value. *The American Naturalist* 136, 657–672.
- Hawkins S.J.** (1999) Experimental ecology and coastal conservation, conflicts on rocky shores. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9, 565–572.
- Hawkins S.J., Corte-Real H.B.S.M., Pannacciulli F.G., Weber L.C. and Bishop J.D.D.** (2000) Thoughts on the ecology and evolution of the intertidal biota of the Azores and other Atlantic islands. *Hydrobiologia* 440, 3–17.
- Markowska M. and Kidawa A.** (2007) Encounters between Antarctic limpets, *Nacella concinna*, and predatory sea stars, *Lysasterias* sp., in laboratory and field experiments. *Marine Biology* 151, 1959–1966.
- Menge B.A.** (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146, 69–100.
- Menge B.A.** (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250, 257–289.
- Menge B.A. and Sutherland J.P.** (1976) Species diversity gradients, synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist* 110, 351–369.
- Miller L.P. and Gaylord B.** (2007) Barriers to flow, the effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. *Journal of Experimental Marine Biology and Ecology* 344, 215–228.
- Monteiro N.M., Quinteira S.M., Silva K., Vieira M.N. and Almada V.C.** (2005) Diet preference reflects the ontogenetic shift in microhabitat use in *Lipophrys pholis*. *Journal of Fish Biology* 67, 102–113.
- Navarrete S.A. and Castilla J.C.** (1993) Predation by Norway rats in the intertidal zone of central Chile. *Marine Ecology Progress Series* 92, 187–199.
- Navarrete S.A. and Castilla J.C.** (2003) Experimental determination of predation intensity in an intertidal predator guild, dominant versus subordinate prey. *Oikos* 100, 251–262.
- Norberg J. and Tedengren M.** (1995) Attack behaviour and predatory success of *Asterias rubens* L. related to differences in size and morphology of the prey mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology* 186, 207–220.
- Oliveira R.F., Machado J.L., Jordão J.M., Burford F.L., Latruffe C. and Mcgregor P.K.** (2000) Human exploitation of male fiddler crab claws: behavioural consequences and implications for conservation. *Animal Conservation* 3, 1–5.
- Paine R.T.** (1966) Food web complexity and species diversity. *The American Naturalist* 100, 65–75.
- Paine R.T.** (1974) Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15, 93–120.
- Range P. and Paula J.** (2001) Distribution and recruitment of *Chthamalus* (Crustacea: Cirripedia) populations along the central coast of Portugal. *Journal of the Marine Biological Association of the United Kingdom* 81, 461–468.
- Rilov G. and Schiel D.R.** (2006) Trophic linkages across seascapes: subtidal predators limit effective mussel recruitment in rocky intertidal communities. *Marine Ecology Progress Series* 327, 83–93.
- Rius M. and Cabral H.N.** (2004) Human harvesting of *Mytilus galloprovincialis* Lamarck, 1819, on the central coast of Portugal. *Scientia Marina* 68, 545–551.
- Sams M.A. and Keough M.J.** (2007) Predation during early post-settlement varies in importance for shaping marine sessile communities. *Marine Ecology Progress Series* 348, 85–101.
- Sih A., Crowley P., McPeck M., Petranka J. and Strohmeier K.** (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16, 269–311.
- Silva A.C.F.** (2006) *A apanha artesanal de recursos vivos marinhos no concelho da Lourinhã*. Lourinhã, Portugal: Câmara Municipal da Lourinhã.
- Silva A.C.F.** (2008) *Predation by crabs on rocky shores in North-East Atlantic*. PhD thesis. University of Plymouth, UK.
- Silva A., Boaventura D. and Ré P.** (2003) Population structure, recruitment and distribution patterns of *Patella depressa* Pennant, 1777 on the central Portuguese coast. *Boletín Instituto Español de Oceanografía* 19, 461–471.
- Silva A.C.F., Boaventura D., Flores A., Ré P. and Hawkins S.J.** (2004) Rare predation by the intertidal crab *Pachygrapsus marmoratus* on the limpet *Patella depressa*. *Journal of the Marine Biological Association of the United Kingdom* 84, 367–370.
- Silva A.C.F., Hawkins S.J., Boaventura D.M. and Thompson R.C.** (2008) Predation by small mobile aquatic predators regulates populations of the intertidal limpet *Patella vulgata* (L.). *Journal of Experimental Marine Biology and Ecology* 367, 259–265.
- Sousa W.P.** (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15, 353–391.
- Thompson R.C., Crowe T.P. and Hawkins S.J.** (2002) Rocky intertidal communities, past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* 29, 168–191.

Underwood A.J. (1997) *Experiments in ecology, their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press.

Underwood A.J. and Chapman M.G. (1998a) Spatial analyses of intertidal assemblages on sheltered rocky shores. *Australian Journal of Ecology* 23, 138–157.

Underwood A.J. and Chapman M.G. (1998b) *GMAV5 for Windows*. Institute of Marine Ecology, University of Sydney.

Underwood A.J., Chapman M.G. and Connell S.D. (2000) Observations in ecology, you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250, 97–115.

and

Yamada S.B. and Boulding E.G. (1996) The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *Journal of Experimental Marine Biology and Ecology* 204, 59–83.

Correspondence should be addressed to:

S.A.E. Brazão

Laboratório Marítimo da Guia, Centro de Oceanografia

Faculdade de Ciências da Universidade de Lisboa

Avenida Nossa Senhora do Cabo, 939, 2750-374 Cascais, Portugal

email: soniabrazao@gmail.com