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Rare predation by the intertidal crab *Pachygrapsus marmoratus* on the limpet *Patella depressa*

Ana Silva*, Diana Boaventura*‡, Augusto Flores*, Pedro Ré* and Stephen J. Hawkins†

*Laboratório Marítimo da Guia/IMAR—Faculdade de Ciências da Universidade de Lisboa, Estrada do Guincho, 2750-374 Cascais, Portugal. Escola Superior de Educação João de Deus, Avenida Álvares Cabral, 1269-094 Lisboa, Portugal. †Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, PL1 2PB, UK and Division of Biodiversity and Ecology, School of Biological Sciences, Biomedical Sciences Building, University of Southampton, Southampton, SO16 7PX, UK.
‡Corresponding author, e-mail: dianab@fc.ul.pt

The predatory effects of *Pachygrapsus marmoratus* on populations of the intertidal limpet *Patella depressa* were analysed on rocky shores located on the central coast of Portugal. Nocturnal observations on crab feeding behaviour were conducted and experimental exclusion cages were set in the substratum to assess density effects on limpets. The results indicated that although crabs feed on adult limpets the predatory level was minimal. Crabs used consistent tactics to detach limpets from the substratum but the majority of the attacks were unsuccessful, possibly due to morphological and behavioural adaptations of limpets. An alternative recruitment hypothesis is advanced to explain non-significant differences between experimental treatments and a possible predatory role on shaping levels of recruitment on lower levels of the shore is considered.

INTRODUCTION

Predation has been viewed as a primary biotic factor affecting the structure and dynamics of marine intertidal communities (Paine, 1974). The nature and intensity of predatory effects can vary greatly and a wide scope of outcomes is possible as predation may be responsible for distribution limits of prey, decrease in prey abundance, changes in age and size-structure of prey communities, morphological adaptations of prey to their predator, alteration of prey behaviour, and changes in competitive interactions among prey or in shaping intertidal assemblages (e.g. ap Rheinallt, 1986; Stachowicz & Hay, 1999; Hamilton, 2000). Direct evidences of crab predation on limpets have been found in previous studies (Lowell, 1986; Cannicci et al., 2002).

Patella depressa Pennant, 1777 is the most common limpet species in the Portuguese central coast (Boaventura et al., 2002), colonizing the entire eulittoral zone. *Pachygrapsus marmoratus* (Fabricius, 1887) is the dominant intertidal brachyuran in the Cabo Raso rocky shore (Flores & Paula, 2001) and its habitat includes the whole intertidal zone. In this study, the predatory role of *P. marmoratus* on *P. depressa* populations, and its variation between two different seasons and on two shores was investigated. Direct observations of crabs were made over a period of nine months, in order to evaluate limpet–crab interactions. Simultaneously, we tested the effects of crab predatory activity on the density of limpets.

MATERIALS AND METHODS

Study sites and planning

The study sites used were two rocky shores, Cabo Raso and Raio Verde, on the central coast of Portugal (38°42′N 09°29′W). Tides are semidiurnal in this region, and tidal amplitude varies around 3 m. Both shores are composed of limestone rocks with a moderate slope and the sites are exposed to wave action.

The study was divided into two phases. First, *in situ* nocturnal observations of crab predatory behaviour were made at two sites at Cabo Raso (A,B) and two sites at Raio Verde (C,D). Secondly, an experiment with predator exclusion cages was made at two sites in Cabo Raso. Care was taken to select lower eulittoral areas very similar to each other in terms of biotic characteristics, mainly dominated by *Chthamalus* spp. (*C. montagui* and *C. stellatus*) and *Patella depressa*. Observations on crab behaviour were carried out in both autumn–early winter (September 2001–January 2002) and spring–early summer (April 2002–July 2002), and the experiments of exclusion cages were only made in spring–early summer (April 2002–July 2002).

Sampling protocol

Direct observation of crab behaviour

Observation sessions lasted approximately three hours and were exclusively made at nocturnal low tides, when *Pachygrapsus marmoratus* reaches the greatest activity period. The observation sites consisted of vertical walls of 18 m^2 each, on which the crabs fed actively. In general, the four observation sites (A,B,C,D) were sampled twice per month. The sum of the nocturnal observation period comprised a total of 70 hours in autumn–early winter and 44 hours in spring. Mean densities of *Patella depressa* were analysed monthly using ten replicate quadrats of 50×50 cm in each of these areas. Although crabs did not respond to artificial lights, a red filter was used in the lamps to minimize any disturbances to their normal activity.

Table 1. *Analysis of variance on* Patella depressa *monthly mean densities at* Pachygrapsus marmoratus *observation sites (Cabo Raso sites—A and B, Raio Verde sites—C and D).*

		October		December		April		July	
Source of variation	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Shores=Sh	1	8294.4	12.55 n.s.	0.63	0.26 n.s.	24.49	0.49 n.s.	20.20	0.21 n.s.
Areas=Ar (Sh)	2	660.9	0.99 n.s.	2.42	35.35***	50.00	21.41***	97.00	66.94***
Residual	36	664.27		0.07		2.34		1.5	
Cochran's test		C=0.50 n.s.		C=0.36 n.s.		C=0.41 n.s.		C=0.41 n.s.	
Transformation:		(none)		Ln (X)		Sqrt (X+1)		Sqrt (X+1)	
Student–Newman–Keuls tests				Ar (Sh) SE=0.08		Ar (Sh) SE=0.48		Ar (Sh) SE=0.38	
				Cabo Raso A<B** Raio Verde C=D n.s.		Cabo Raso A<B** Raio Verde C=D n.s.		Cabo Raso A<B** Raio Verde C=D n.s.	

n.s., not significant; **, $P<0.01$; ***, $P<0.001$.

Experimental design

In order to test the null hypothesis that there is no predatory effect of *Pachygrapsus marmoratus* on *Patella depressa* populations, three distinct experimental treatments were set: uncaged controls (C)—no cage, allowing total movements of predators, half-cage (HC)—half of the cage area allowing crab access (cage control), and exclusion (E)—cage totally closed preventing predator entrance. Three replicates per treatment were placed on two vertical and two horizontal areas—total of 36 plots—to test for the influence of treatments and substrate inclination. Cages made of a square mesh (13×13 mm) welded plastic coated steel wire were placed randomly and attached to the rock by screws fixed into rawplugs in holes drilled by a petrol driven drill (Ryobi ER 160). Rubber tap washers were used to hold the mesh to the substratum. Cage dimensions were 25×25×7 cm. Control plots with the same dimensions as the cage were marked using rawplugs in holes drilled in the substratum. The total number of limpets inside the cage area was counted on the first day of the experiment and every month subsequently.

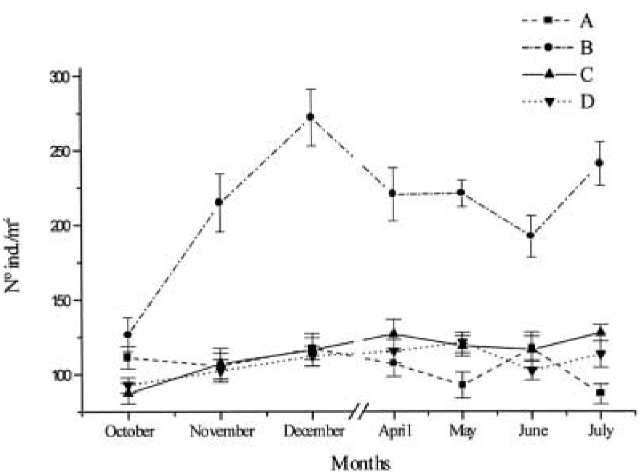

Figure 1. Mean (±SE) of monthly densities of *Patella depressa* in the four observation sites. A,B—Cabo Raso C,D—Raio Verde.

Data analysis

Mean densities of limpets at the crab observation sites were analysed using a two-way analysis of variance (ANOVA). The factors tested were 'shores' (fixed, orthogonal, two levels) and 'areas' (random, nested within shores, two levels). The predation experiment results were analysed using a three-way ANOVA. The factors tested were 'treatments' (fixed, orthogonal, three levels), 'surfaces' (fixed, orthogonal, two levels) and 'areas' (random, nested within surfaces, two levels) with three replicates for each treatment. Cochran's C-test was used to check homogeneity of variance. Whenever there were significant differences among means, Student–Newman–Keuls (SNK) *a posteriori* comparison tests were made. Tests of homogeneity, ANOVA and SNK tests were done using GMAV5 for Windows Statistical Software (Institute of Marine Ecology, Sydney, Australia).

RESULTS

Site B at Cabo Raso had the highest number of *Patella depressa* while the other areas were very similar to each other, except for October, when all densities were very close (Figure 1). An increased density until December can also be observed followed by a decrease in the spring months. The density peak in December can be related to a

Table 2. *Predator and prey characteristics in the predation events registered during observation periods.*

	Crab		Limpet
Areas	Carapace width (mm)	Sex	Shell length (mm)
A	24.6	Male	6.6
A	31.8	Female	14.3
B	20.4	Female	14.7
C	24.2	Male	12.5
D	17.4	Male	6.2
D	28.2	Female	21.2
D	33.9	Female	28.0

Table 3. *Analysis of variance of mean densities of* Patella depressa *in the predator exclusion study.*

		0 months		3 months	
Source of variation	df	MS	*F*	MS	*F*
Predation=Pr	2	6.58	0.09 n.s.	1.36	1.53 n.s.
Surface=Su	1	2738.78	3.82 n.s.	17.2	3.28 n.s.
Area (Surface)=Ar (Su)	2	716.94	17.31 ***	5.24	12.82 ***
PrxSu	2	20.03	0.28 n.s.	0.47	0.53 n.s.
PrXAr (Su)	4	71.03	1.71	0.89	2.18 n.s.
Residual	24	41.42		0.41	
Cochran's test		C=0.31 n.s.		C=0.32 n.s.	
Transformation:		(none)		Sqrt (X+1)	
Student–Newman–Keuls tests		Ar (Su), SE=2.15		Ar (Su), SE=0.21	
		Horizontal		Horizontal	
		Ar 1=Ar 2 n.s.		Ar 1=Ar 2 n.s.	
		Vertical		Vertical	
		Ar 1< Ar 2 **		Ar 1< Ar 2 **	

n.s., not significant; **, $P<0.01$; ***, $P<0.001$.

recruitment period for *P. depressa*. The areas had significant differences in the number of limpets at the beginning and end of each observation period (except in October), due to a higher density at Site B than at the other sites (Table 1).

During direct field observations on feeding behaviour, very few limpets were seen to be eaten by *Pachygrapsus marmoratus* (Table 2), although some attempts to detach limpets were registered. All directly observed successful prising attacks resulted in the shell being detached. The limpet body was seen to be totally eaten, with the exception of the foot. The whole process of limpet detachment and feeding lasted always more than 10 min, reaching a maximum of 30 min. This may indicate high rates of energy and time expenditure.

The statistical analysis showed no significant differences in limpet density among treatments, both at the beginning and end of the experiment (Table 3). Therefore, crab predation on limpets did not appear to interfere with limpet abundance during the experimental period. In relation to surfaces, Table 3 shows that there was only a significant difference between vertical walls in the beginning and at the end of the experiment possibly related to higher recruitment levels on the vertical area 2 (V_2).

DISCUSSION

From this study, there is no evidence that the crab *Pachygrapsus marmoratus* has any effect on the structure and abundance of limpet communities in Cabo Raso and Raio Verde since there were no significant differences among experimental treatments, and the number of predation events during the observation period was low. The only observed predatory behaviour was the 'prising' proceeding: *Pachygrapsus marmoratus* continuously criss-crossed the feeding area in search of food items until they located a feeding limpet with an elevated shell. Once the prey was located, an attempt was made to prise the margin of the limpet shell away from the substratum, using walking legs placed between the limpet shell and the substratum. This behaviour was very similar to the prising technique described by Lowell (1986) which was common in temperate and tropical eastern Pacific crabs; unsuccessful events resulted from failure in the introduction of the appendages underneath the shell margin. Even so, Lowell (1986) found a small percentage of success of this prising technique compared with the numerous attempts. Also the surface orientation does not seem to represent a limiting factor in crab limpet feeding, because significant differences between surfaces were not detected except for the special case of vertical area 2 (V_2). In fact, the main restriction to crab activity appears to be the presence of size-related refuges, namely crevices and holes.

In this study the behaviour of *Patella depressa* by quickly clamping down, when in contact with moving crabs, may represent a response to prevent the introduction of appendages underneath the shell margin and thus avoid the most common predatory crab strategy (prising proceeding). This event was frequently recorded in nocturnal observations. The adhesion force of limpets supplants the prising force of crabs, although there are various ways of removing limpets from the substratum (see Gregon & Walker, 1981).

This resistance is much less in juvenile prey but the present work failed to identify any crab preference for smaller limpets. A recent study by Cannicci et al. (2002) on feeding habits of *Pachygrapsus marmoratus*, which included the Portuguese shores, revealed that in its selective omnivorous diet, the most common animal prey were limpets and mussels (barnacles were also present), whereas preferred plant items were filamentous algae. Altogether, these results indicate that *P. marmoratus* does not exert any effective control on adult *Patella depressa* abundance. Several hypotheses can be advanced to explain this. Firstly, high recruitment rates may be important in maintaining population numbers on a local habitat scale, preventing detection of any controlling predatory factor. Secondly, the non-significant effect suggested by the data does not exclude the hypothesis of a more active role of *Pachygrapsus marmoratus* exerted on new recruits

(S. Cannicci, personal communication). However, settlement processes are not well studied in *Patella* species and while it is known that they recruit to tide pools on Irish shores (see Delany et al., 1998), no study has been made in Portugal on this subject.

REFERENCES

ap Rheinallt, T., 1986. Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*; the importance of mechanical factors. *Marine Ecology Progress Series*, **29**, 45–53.

Boaventura, D., Ré, P., Cancela da Fonseca, L. & Hawkins, S.J., 2002. Intertidal rocky shore communities of the Portuguese coast: analysis of distribution patterns. *Marine Ecology*, **23**, 69–90.

Cannicci, S., Gomei, M., Boddi, B. & 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.

Delany, J., Myers, A.A. & McGrath, D., 1998. Recruitment, immigration and population structure of two coexisting limpet species in mid-shore tidepools, on the West Coast of Ireland. *Journal of Experimental Marine Biology and Ecology*, **221**, 221–230.

Flores, A.A.V. & Paula, J., 2001. Intertidal distribution and species composition of brachyuran crabs at two rocky shores in Central Portugal. *Hydrobiologia*, **449**, 171–177.

Gregon, J.F. & Walker, G., 1981. The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology*, **54**, 277–308.

Hamilton, D., 2000. Direct and indirect effects of predation by common eiders and abiotic disturbance in an intertidal community. *Ecological Monographs*, **70**, 21–43.

Lowel, R.B., 1986. Crab predation on limpets: predator behaviour and defensive features of the shell morphology of the prey. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **171**, 577–596.

Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93–120.

Stachowicz, J.J. & Hay, M., 1999. Reduced mobility is associated with compensatory feeding and increased diet breadth of marine crabs. *Marine Ecology Progress Series*, **188**, 169–178.

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