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Activity pattern and spatial strategy in *Pachygrapsus marmoratus* (Decapoda: Grapsidae) from Mediterranean and Atlantic shores

Abstract The spatial strategies and activity patterns of two populations of *Pachygrapsus marmoratus* (Fabricius), from Italy and Portugal, were studied in the field. The Mediterranean site was a non-tidal splash zone about 30 cm wide, while the Atlantic site was a 30 m wide intertidal belt. Almost all *P. marmoratus* of both populations were active on the emerged rocks, rarely entering the sea. The Mediterranean crabs actively fed on the algal turf throughout the 24 h, while in Portugal active crabs were more numerous at night. In the Italian population, all crabs were packed together, although large males had larger activity areas than females and smaller males. In Portugal, the large males were more concentrated in the sublittoral fringe, while both small males and females were confined to the eulittoral and littoral fringe. The Italian *P. marmoratus* performed feeding loops within areas smaller than 9 m^2. Although most Portuguese crabs showed the same spatial strategy, some of them performed feeding migrations to the sublittoral fringe, covering distances of up to 20 m. Environmental factors (e.g. temperature), physical factors (e.g. refuge availability) and biotic factors (e.g. competitors and predators) of the different shores probably determine the behavioural plasticity of *P. marmoratus*.

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Introduction

Among the Decapoda, the family Grapsidae is one of the richest in terms of intertidal species. In fact, most of the Sesarminae and Grapsinae are well distributed and abundant in intertidal environments (Hartnoll 1988).

In spite of the broad distribution of both Grapsinae and Sesarminae on hard- and soft-bottomed shores, knowledge of morphological and behavioural adaptations to the intertidal environment is mostly confined to the latter. Sesarminae are adapted to semi-terrestrial or truly terrestrial life styles (Warner 1977; Hartnoll 1988). The intertidal species are active during aerial phases, while they shelter themselves in refuges during high tide or avoid submersion by migrating away from the water's edge. Most of these species rely on internal clocks as well as on external stimuli to synchronise their periods of activity and their migrations with the tidal phases (Seiple 1981; Palmer 1995; Vannini et al. 1995). Moreover, they can rapidly return to specific shelters at the end of the activity phase (Vannini and Cannicci 1995).

There is little information about behavioural adaptations in the Grapsinae, even though they play a predominant ecological role on rocky shores. Activity patterns are partially known only for two American *Pachygrapsus*, *P. crassipes* (see Hiatt 1948) and *P. transversus* (see Abele et al. 1986), and for *Grapsus grapsus* (see Kramer 1967), all of which are active during low tide. Spatial patterns of behaviour are known only for *P. transversus*; it is faithful to specific territories, returning to them after migrations to feed on algae of the lower intertidal belt (Abele et al. 1986).

The aim of the present study was to investigate the spatial and temporal patterns of activity of an East Atlantic and a Mediterranean population of *Pachygrapsus marmoratus* and their possible plasticity with respect to different environmental and physical factors of the two habitats.

Materials and methods

Italian site: study area and methods

Observations and experiments took place at Villa Domizia Bay, near Porto S. Stefano, on the southern coast of Tuscany, Italy, during July and August 1995. The site is a gently sloping sandstone shore sheltered by a group of small immersed rocks but never completely covered with water (Fig. 1). During the observation period the average tidal excursion was about 20 cm and the splash zone was very narrow; the covering of *Chthamalus stellatus* ended at a maximum of 25 cm above the mean water level (MWL), while *Melarhaphe neritoides* was recorded within a 40 cm belt above the MWL.

In this area a 15 × 15 m quadrate was delimited, including the rocky shore and some of the small immersed rocks (Fig. 1). During 3 d, 66 adult *Pachygrapsus marmoratus* (Fabricius) were captured by hand or with fishing line baited with limpets. All captured crabs were individually marked with numbered Dymo tags glued to the carapace and released at the capture site no more than 5 min later, after their sex and carapace length (CL) had been determined.
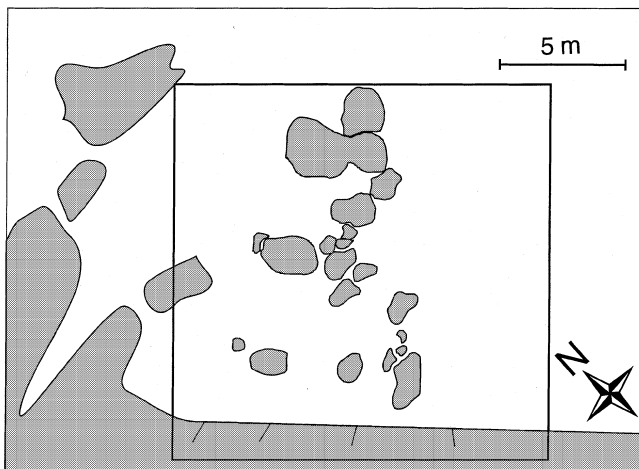
Within the quadrate, all crevices and holes suitable as refuges were marked with white paint to facilitate observations and records. Only four large crevices were present on the rocky coastline, while there were many holes and crevices among the immersed rocks. All holes within three 1-m^2 sub-quadrates, chosen at random, were counted.

At various points in the quadrate, reference dots were painted at 5-cm intervals perpendicular to the sea to estimate the distance of active crabs from the water level.

Standardised surveys were taken almost daily (4 d were missed) for 1 month, starting from the day following the marking, and included the full range of light and tide conditions. All surveys were carried out by two observers, who stood in the quadrate for 30 min and recorded the relative position of each active crab in the quadrate and its distance from the water level. Electric torches were used during nocturnal sessions, and diving masks were used to record crabs under water. Focal crabs were followed during their feeding activity and their excursions were accurately drawn on a map.

Portuguese site: study area and methods

The second experimental site was Praha do Luz, near Lagos, on the Algarve coast, Portugal, where studies were carried out during June and July 1996. This moderately exposed sandstone shore is crossed by large crevices and marked by many rock pools *Pachygrapsus marmoratus* hid in great numbers both in the large crevices, and in smaller holes and crevices at the border of the pools.

The moderate slope of the shore, combined with the tidal amplitude, ranging from about 3.5 m (from MLW to MHW at spring tide) to 2.0 m (at neap tide), account for an intertidal belt about 35 m wide. Preliminary linear transects indicated that the portion of the sublittoral fringe emerging during spring low tides was about 10 m wide and was dominated by large populations of *Paracentrotus lividus*, *Mytilus galloprovincialis* and of the red algae *Corallina elongata* and *Lythophillum incrustans*.

Above this belt, the 12 m wide eulittoral was dominated by *Chthamalus montagui*, *Siphonaria pectinata* and *Patella depressa*. Finally, large populations of *Melarhaphe neritoides* and *Ligia oceanica* characterised a 12 m littoral fringe, in which great numbers of *P. depressa* and *Monodonta lineata* were still present.

A 35 × 35 m area was delimited within the intertidal belt and 148 adult *Pachygrapsus marmoratus* were captured, measured, individually marked – as described for the Italian site – and released at the capture sites. All the rock pools and crevices in the experimental area were marked with painted numbers.

For 25 d, standardised 1-h surveys by two observers were carried out daily in conditions of night, day, dawn, dusk and of low, high, ebb and flood tide. A few snorkeling inspections were performed to record the presence of active crabs under water.

Only marked crabs still active in the survey quadrate from the fourth day after the marking date were considered in the analysis of spatial strategies. This procedure excluded about 20% of the marked crabs at each site and might have biased the analysis toward the more sedentary part of the population. Nevertheless, it was followed to exclude from consideration (1) crabs that suffered from the marking procedure (about half of the excluded crabs were found dead within the first 4 d), and (2) crabs that inhabited neighbouring areas and were caught by accident within the experimental quadrate, but could not be followed throughout the study period.
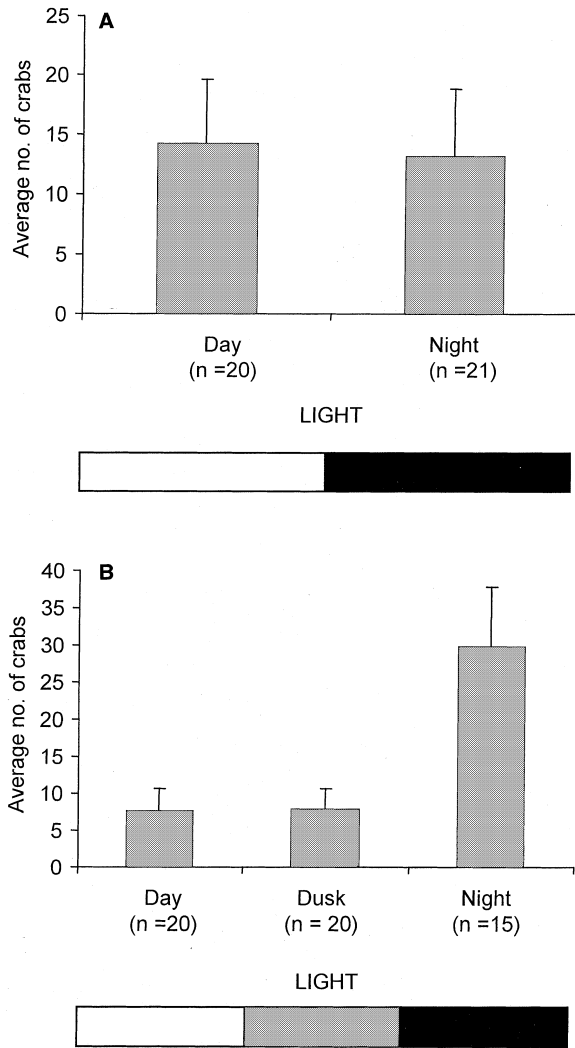
Results

The CL distribution of the two marked populations did not differ significantly ($n = 65$ and 148; $z = 0.701$; $P = NS$, Mann-test); both the distributions were bimodal, with modal values of 15 and 20 mm. Accordingly, the crabs were divided into two size classes: small (CL ≤ 17 mm) and large (CL > 17 mm), whose numbers were similar in the two samples (32 small vs 33 large for Villa Domizia; 119 small vs 129 large for Praha do Luz).

The sex ratio was different in the marked samples. In Italy it was clearly shifted towards females, m:f = 0.69 (27 and 39), while in Portugal marked males (90) were more numerous than females (58), m:f = 1.56.

Activity patterns

Villa Domizia population

A four-factor ANOVA of Box–Cox transformed data (Sokal and Rohlf 1995) showed that the number of active *Pachygrapsus marmoratus* in the Villa Domizia population was not affected by sex and size nor by environmental factors (Figs. 2, 3). Crabs were active

Fig. 1 Schematic map of the Italian study site, Villa Domizia Bay, showing the four large crevices along the sandstone shore, the disposition of the immersed rocks and the boundaries of the experimental quadrate
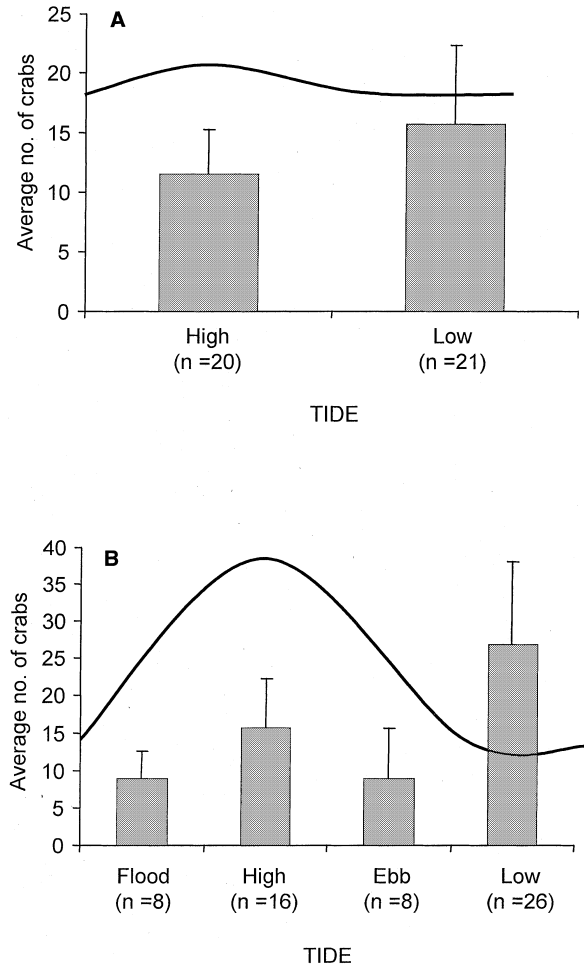
5 m

Fig. 2 *Pachygrapsus marmoratus*. Average numbers, with standard errors, of crabs active during different light conditions at **A** Villa Domizia and **B** Praha do Luz. The number of surveys performed under each condition is shown in parentheses

throughout the 24 h, always within a narrow belt between 20 cm above and 10 cm below the relative water level, with an average distance of 6.5 ± 0.67 cm above (*n* = 87).

Praha do Luz population

The overall activity in the Praha do Luz *Pachygrapsus marmoratus* population was influenced by environmental factors (Table 1). On average, 29.75 crabs were active at night, while only 7.69 were recorded during the day 7.81 in the crepuscular hours (dawn and dusk hours combined) (Fig. 2).

The tide also affected *Pachygrapsus marmoratus* activity; the crabs were active in greater numbers at low tide than in any other tidal phase (Fig. 3; Table 2). Moreover, a greater number of crabs were observed at

Fig. 3 *Pachygrapsus marmoratus*. Average numbers, with standard errors, of crabs active during different tidal phases at **A** Villa Domizia and **B** Praha do Luz. The number of surveys performed in each phase is shown in parentheses

high tide than at ebb and flood tide, although there was a very small area not covered by water.

ANOVA revealed significant interactions among light conditions, sex and size. The number of males active on the shore was significantly greater at night and at dusk, in agreement with the unbalanced sex ratio of the marked sample, while no differences between sexes were recorded during daytime activity (Table 3). Moreover, small crabs were significantly less active at night, showing a clear temporal separation in their activity.

Spatial strategies

In both populations, the maximum distance travelled by each crab was independent of the period in which it was followed (*R* = 0.131, *n* = 49, *P* = 0.369, for Villa Domizia and *R* = 0.151, *n* = 101, *P* = 0.131, for Praha do Luz). Thus the activity of the marked crabs was confined to defined areas, at least over a 25 to 33 d period.

Table 1 *Pachygrapsus marmoratus*, Praha do Luz population. Influence of light conditions and tide on the activity of adult crabs of different sex and size (small CL ≤ 17 mm; large > 18 mm). Average numbers of active crabs (Av.) together with their standard errors (SE), the *F*-ratio value and probability level (*P*) are shown for every condition. Four-factor ANOVA of Box–Cox transformed data. Higher order interactions were not significant

Source	Av.	SE	Av.	SE	F-ratio	P
Size (large vs small)	16.04 ± 3.62		14.12 ± 2.34		0.48	0.51
Sex (males vs females)	18.00 ± 3.55		12.17 ± 2.30		38.40	< 0.001
Tide (flood vs high vs	9.00 ± 1.85		15.58 ± 3.34			
ebb vs low)	9.00 ± 3.40		26.75 ± 5.72		97.62	< 0.001
Light (day vs dusk vs	7.69 ± 1.49		7.81 ± 1.41			
night)	29.75 ± 4.14				282.38	< 0.001
Sex × Size					10.71	0.02
Sex × Light					8.90	0.02
Size × Light					9.08	0.01
Sex × Tide					0.71	0.58
Size × Tide					3.00	0.12
Light × Tide					7.24	0.01

Table 2 *Pachygrapsus marmoratus*, Praha do Luz population. Comparisons among the number of crabs active in different tidal phases; data from the ANOVA in Table 1 (++ indicates statistical significance of the contrast test above the 0.01 level; – stands for no significant difference)

Contrast	Low	Flood	High	Ebb
Low		++	++	++
Flood			++	–
High				++

Table 3 *Pachygrapsus marmoratus*, Praha do Luz population. Comparisons between means of crabs of different sex and size active in different light conditions. Data from the ANOVA in Table 1. Means, *F*-ratio and probability level (*P*) also shown

	Means	F-ratio	P
Sex vs light			
Female, day vs males, day	8.18 & 9.64	1.52	0.26
Female, dusk vs males, dusk	7.38 & 10.41	6.57	0.04
Female, night vs males, night	22.01 & 30.22	48.12	< 0.001
Size vs light			
Large, day vs small, day	8.15 & 9.68	1.67	0.244
Large, dusk vs small, dusk	8.07 & 9.71	1.91	0.216
Large, night vs small, night	28.41 & 23.82	15.06	0.008

Villa Domizia population

Crabs from Villa Domizia never crossed water surfaces of more 1.5 m nor water deeper than about 50 cm. Relationships among excursion distances of the marked crabs and their sex, their size and the area that they occupy (the shore or the isolated rocks) were investigated with three-factor ANOVA (Table 4). On the isolated rocks, where the refuges numbered $18 \pm 1.52 \ m^{-2}$ and the crabs were densely packed (2.43 ind. m^{-2}), the distances travelled were significantly shorter than those covered by the crabs living along the shore, where crevices were 0.5 m^{-2} and the population was less dense (0.32 ind. m^{-2}).

Observations of focal crabs showed that the activity ranges of the larger males never overlapped. However, the activity areas of the large males were divided into a number of small territories also occupied by smaller males or females (Fig. 4).

Praha do Luz population

During the observation period, marked crabs remained faithful to areas with an average diameter of 3.64 ± 0.45 m, $n = 84$, within which they visited an average of 2.09 ± 0.11 pools. Although active crabs were recorded throughout the intertidal belt and crevices were common within the whole belt, crabs were significantly more abundant in the crevices of the eulittoral and the littoral fringe ($G = 17.346$, $df = 2$, $P < 0.001$, Table 5).

The five crabs permanently inhabiting the sublittoral fringe were significantly larger (average CL = 29 ± 2.49 mm) than those of the eulittoral (CL = 20.22 ± 0.93 mm) and the littoral fringe (CL = 16.23 ± 0.85 mm) ($\chi^2 = 16.042$, $df = 2$, $P = 0.0003$, Wilcoxon/Kruskal–Wallis test).

Table 4 *Pachygrapsus marmoratus*, Villa Domizia population. Influence of sex, size and area inhabited (shore or isolated rocks) on the distance travelled by adult crabs. Means, standard errors (SE), *F*-ratio value and probability level (*P*) are shown. Three-factor ANOVA of Box–Cox transformed data. Higher order interactions were not significant

Source	Av.	SE	Av.	SE	F-ratio	P
Size (large vs small)	2.32 ± 0.37		2.19 ± 0.38		2.06	0.16
Sex (males vs females)	2.56 ± 0.43		2.04 ± 0.34		3.47	0.07
Area (shore vs rocks)	4.51 ± 1.07		1.82 ± 0.20		11.61	0.001
Sex × Size					3.16	0.08
Sex × Area					1.10	0.30
Size × Area					0.37	0.54
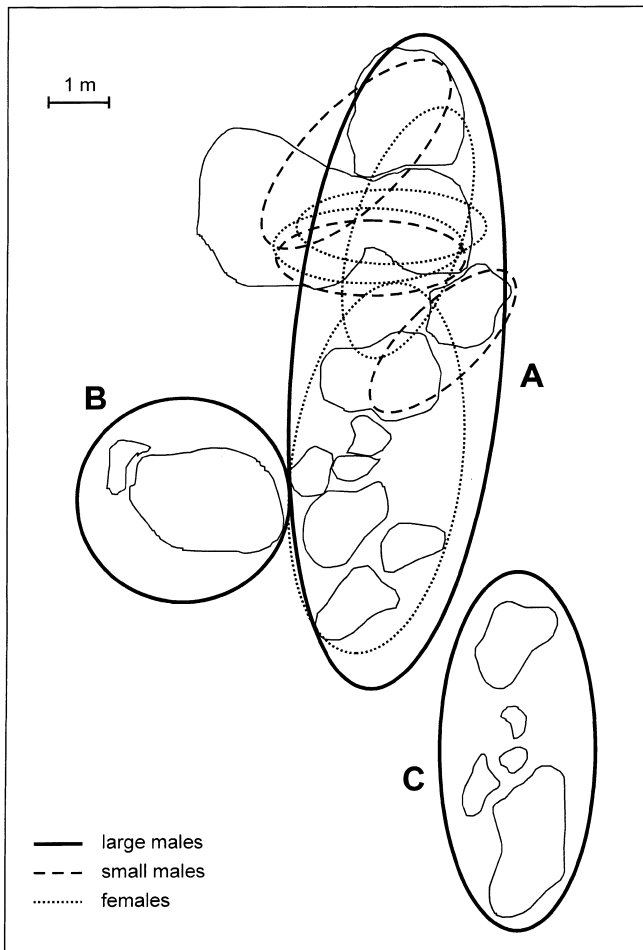
Fig. 4 *Pachygrapsus marmoratus*. Schematic close-up view of the isolated rocks (*fine continuous lines*) in the experimental quadrate at Villa Domizia. The activity areas of three large male crabs (*A*, *B* and *C*) are represented by *ellipses* that enclose the points at which the crabs were observed. For the area belonging to Male A, sub-areas shared with marked small males and females are also shown

Table 5 *Pachygrapsus marmoratus*, Praha do Luz population. Comparison between the number of suitable pools, i.e. with crevices in them, and the number of crabs resident at the three intertidal levels. Approximate width of levels and density of resident crabs are shown

Level	Suitable pools	Resident crabs	Width (m)	Crabs (m^{-2})
Sublittoral fringe	14	5	10	0.014
Eulittoral	22	36	12	0.094
Littoral fringe	17	43	12	0.112

As at the Italian site, the relationships among the excursion distances of marked crabs permanently living at the eulittoral and littoral fringe and their sex and size were investigated with three-factor ANOVA (Table 6). Larger crabs travelled significantly greater distances (average 4.18 ± 0.65 m) than the smaller ones (2.82 ± 0.69 m).

At low tide, 23.3% (*n* = 10) of the crabs inhabiting the littoral fringe migrated at least twice to feed on the sublittoral fringe and then returned to their crevices (Fig. 5), while the proportion of eulittoral crabs migrating seawards was higher, 41.6% (*n* = 15). In contrast, crabs of the sublittoral fringe and eulittoral were never observed within the more landward belts, probably remaining covered during high tide.

Discussion and conclusions

Like most Grapsinae (Hiatt 1948; Kramer 1967; Abele et al. 1986), *Pachygrapsus marmoratus* shows a strong tendency to a semi-terrestrial lifestyle. At both sites, the crabs were active outside the water, seldom entering the sea, and colonised the whole intertidal belt regardless of its width. Indeed, during 1 month, crabs at the Italian site never crossed shallow water surfaces wider than 1.5 m, confirming a strong avoidance of swimming.

The activity patterns and the spatial distribution and behaviour of the Mediterranean and Atlantic populations differed strongly.

The Mediterranean site was a non-tidal sheltered shore with a strong asymmetry in hole density and a very narrow feeding belt exploited by the crabs. *Pachygrapsus marmoratus* always maintained itself a few centimetres above the water, on the wet algal turf, and was active throughout the 24-h period (Fig. 2).

The Atlantic site was a wide intertidal belt with high availability of refuges (Table 5). Most crabs were active far from the water level, up to 30 m away, but mainly walked and fed at night (Table 1; Fig. 2). Although this shore was under strong tidal influence, the number of active crabs observed during high tide (with an emerged feeding area about one-third the total intertidal fringe) was still relevant (Table 2).

Which environmental and/or physical factors can account for the behavioural differences recorded at the two locations?

This semi-terrestrial crab probably must cope with increased water loss during its activity, especially during daytime (average temperature 30 °C in Tuscany and 29 °C in Algarve). At the non-tidal Italian shore, where all marked crabs were active within a few centimetres above the water level, the availability of cold sea water could help the crabs to cope with thermal stress and prevent excessive water loss.

The Atlantic *Pachygrapsus marmoratus*, instead, can feed on a far wider belt, rich in algae and sessile fauna. However, like most truly terrestrial and semi-terrestrial crabs (Wolcott 1988), they are probably forced to be active during the nocturnal hours (average *T* = 18 °C) to avoid major thermal stress. Although tidal pools were present along the whole eulittoral and littoral fringe (Table 5), the water in them reached very high temperatures during the day and was probably of little help in thermoregulation.

Table 6 *Pachygrapsus marmoratus*, Praha do Luz population. Influence of sex, size and inhabited shore level on the distance travelled by adult crabs. Means, standard errors (SE), *F*-ratio value and probability level (*P*) are also shown. Three-factor ANOVA of Box–Cox transformed data. Higher order interactions were not significant

Source	Av.	SE	Av.	SE	*F*-ratio	*P*
Size (large vs small)	4.18	± 0.65	2.82	± 0.69	3.86	0.05
Sex (males vs females)	3.79	± 0.68	3.27	± 0.67	0.18	0.67
Shore level (littoral fringe vs eulittoral)	3.31	± 0.67	3.86	± 0.67	0.66	0.42
Size × Shore level					2.17	0.14
Size × Sex					0.73	0.39
Shore level × Sex					1.67	0.20
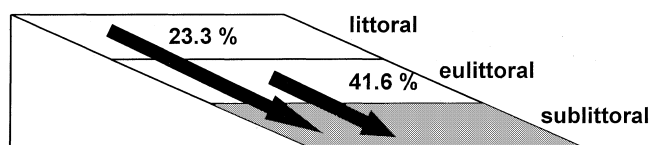
Fig. 5 *Pachygrapsus marmoratus*. Schematic diagram showing the percentage of crabs colonising the eulittoral and littoral fringe of Praha do Luz that migrated towards the sublittoral fringe (*in grey*) to feed on algal turf

Another possible reason for the nocturnal peaks in activity is predator avoidance. However, during the entire observation period, no diurnal predators, such as seagulls, were observed to prey on the marked crabs at either site. The most dangerous predator of this species proved to be the crab *Eriphia spinifrons*, whose predatory acts were recorded more often at night.

The overall activity pattern of *Pachygrapsus marmoratus* seemed to be only weakly related to the tidal cycle. This was true not only for the Italian site, where the tidal influences on activity were obviously nil (Fig. 3), but also for the densely populated Portuguese littoral fringe (Table 5), where crabs actively fed at night regardless of the tidal phase (Table 1). Although this lack of tidal periodicity in the activity of *P. marmoratus* contrasts with the activity rhythms of many intertidal crabs (see Palmer 1995), it has also been observed in other intertidal Grapsidae, e.g. *Sesarma reticulatum* (Seiple 1981) and *S. leptosoma* (Vannini et al. 1995).

Pachygrapsus marmoratus did not walk at random but confined its activity to stable areas, the size of which varied according to the sex and size, as well as different abiotic factors (Tables 4, 6).

At the Mediterranean site, the spatial distribution was probably affected only by the symmetry in refuge availability, the marked crabs were packed together where the refuge density was higher. In this area, the territories of larger males never overlapped, but were divided into many small areas also occupied by smaller males and females (Fig. 4). The symmetry in availability of a resource, i.e. refuges, probably led to strong competition among the larger males for the territories rich in refuges and thus attractive to many females. The larger males probably tolerate smaller ones because they do not compete for females but only for food, which is likely not a limiting factor.

This spatial distribution is similar to the one recorded by Abele et al. (1986) for *Pachygrapsus transversus* living on an intertidal flat strongly affected by the tidal regime. They found that, in this smaller species (max. carapace width = 17 mm), the larger males acted like those of the Italian *P. marmoratus*.

On the Portuguese shore, refuges were present throughout the wide intertidal belt, where a spatial segregation of different size crabs occurred. Only the larger males colonised the crevices of the sublittoral fringe, while small and medium-size crabs were confined to the crevices of the eulittoral and littoral fringe. Moreover, about 50% of the smaller crabs and 25% of the medium-size ones relied on the sublittoral fringe to feed (Fig. 5). One possible explanation for this zonation pattern is the presence in the sublittoral fringe of two other decapod species, *Pachygrapsus transversus* and *Eriphia spinifrons*. The congeneric species is surely a competitor of the smaller *P. marmoratus* crabs for refuges, while both *E. spinifrons* and the larger conspecific males can exert strong predatory pressure on them. The results of the activity pattern analysis also support this hypothesis, revealing a slight temporal segregation of activity between small and large crabs (Table 3). This behavioural mechanism is known to be associated with the avoidance of cannibalism in other crab species (Vannini 1987; Wolcott 1988).

The overall results suggest that *Pachygrapsus marmoratus* is a very adaptable rocky shore dweller, capable of modifying its use of time and space according to the different characteristics of the shores it inhabits. Environmental factors (e.g. temperature variation), physical factors (e.g. refuge availability) and biotic factors (e.g. presence/absence of competitors and predators) all seem to be involved (and inter-related) in shaping the plastic and variable behaviour of *P. marmoratus*.

Further studies are needed to assess the relative contributions of genetic differences and phenotypic plasticity in controlling the behavioural traits of these populations.

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