

Population structure, recruitment and distribution patterns of *Patella depressa* Pennant, 1777 on the central Portuguese coast

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Received January 2003. Accepted December 2003.

ABSTRACT

Using in situ individual measurements at two levels of the shore during a one-year period, recruitment peaks of *Patella depressa* Pennant, 1777, possibly related to breeding periods, were identified during autumn-winter. Recruits were associated with lower levels on the shore, and juveniles mainly inhabited *Mytilus galloprovincialis* Lamarck, 1819 patches. Niche partitioning, intraspecific competition, and desiccation stress are discussed as decisive factors in the different size-class distributions found. A mark-recapture growth study was made at two substrata within study sites, one substratum with irregular depressions mainly composed of *Chthamalus* spp., and a second regular substratum comprising mostly bare rock. Our results indicated lower growth increments in the irregular substratum zone, probably due to space availability and limited foraging activity.

Keywords: Limpet, population distribution, recruitment pattern, growth, environmental conditions.

RESUMEN

Estructura de la población, reclutamiento y modelos de distribución de *Patella depressa* Pennant, 1777 en la costa central de Portugal

Utilizando mediciones individuales in situ a dos niveles de la orilla durante un año, se han identificado en otoño-invierno los picos de reclutamiento de *Patella depressa* Pennant, 1777 relacionados, posiblemente, con los periodos de reproducción. Los reclutamientos se asocian con bajos niveles en la orilla y juveniles ocupando principalmente pequeñas extensiones junto a *Mytilus galloprovincialis* Lamarck, 1819. Se discute la influencia del reparto de nichos, la competencia intraespecífica y el estrés por desecación como factores decisivos en la distribución de las distintas clases de tallas encontradas. Se ha hecho un estudio de marcado y recaptura en dos sustratos comparando uno con otro: un primer sustrato con depresiones irregulares compuesto principalmente por *Chthamalus* spp. y un segundo, regular, compuesto fundamentalmente por rocas desnudas. Nuestros resultados indicaron incrementos bajos de crecimiento en la zona de sustrato irregular, probablemente debido a la limitada disponibilidad de espacio y a la actividad de forraje.

Palabras clave: Lapa, distribución de población, modelo de reclutamiento, crecimiento, condiciones ambientales.

INTRODUCTION

There is a vast amount of literature dealing with limpet dynamics and ecological interactions. In an initial phase, the work of Orton (1928a,b, 1929) on the British Islands resulted in an integrative view of the overall dynamics of the common limpet *Patella vulgata* L. Since then, marine ecologists have analysed a wide range of subjects, encompassing specific biological aspects and general ecological processes.

The important role of limpets in structuring communities is also well documented and, in addition, several marine ecologists have assessed the grazing activity of limpets as a structuring force in intertidal algal communities (e.g., Underwood, 1980; review in Branch, 1981; Jernakoff, 1983; Della Santina *et al.*, 1993). In fact, limpets were found to be responsible for setting some algae species' upper limits of distribution (e.g., Underwood and Jernakoff, 1981, 1984; Boaventura *et al.*, 2002) by grazing early sporeling propagules (Lewis, 1954). Similar adverse effects have been reported between barnacles and limpets, because the latter may be responsible for reduced survival of the post-settlement barnacles, which are bulldozed off the rocks where limpets are grazing (Dayton, 1971; Denley and Underwood, 1979). Conversely, barnacles may positively contribute to limpet juvenile survival by conferring protection against desiccation and shelter (Lewis and Bowman, 1975; Choat, 1977).

Limpets are widespread all over the intertidal shores and, although geographical similarities may arise, there are also regional differences, mainly in the life cycles. Such is the case of *Patella depressa* Pennant, 1777. Bowman and Lewis (1986) indicated that similar general patterns could be found in British and continental European populations, but noted the existence of local variations in life-cycle events. Guerra and Gaudêncio (1986) reported, simultaneously with the work of Bowman and Lewis (1986), the general ecological parameters of *Patella* spp. (*P. vulgata* and *Patella ulyssiponensis* Gmelin) for the Portuguese coast. However, local specific analyses on recruitment levels and on particular patterns of distribution are still limited for the central coast of Portugal, where *P. depressa* dominates the eulittoral zone.

The present study investigates the population structure of *P. depressa* at different levels on the shore at two stations located on the central

Portuguese coast. Monthly sampling was used to identify recruitment peaks. The hypothesis that recruits and juveniles are associated with lower levels on the shore was tested. Complementary data was gathered on *P. depressa* individual growth rates at two different substrata (regular *versus* irregular) at the two studied sites. Thus, our results contribute to expanding current ecological knowledge on the structure of *P. depressa* populations, particularly regarding recruitment and distribution and also, to providing information on growth features.

MATERIALS AND METHODS

Study sites

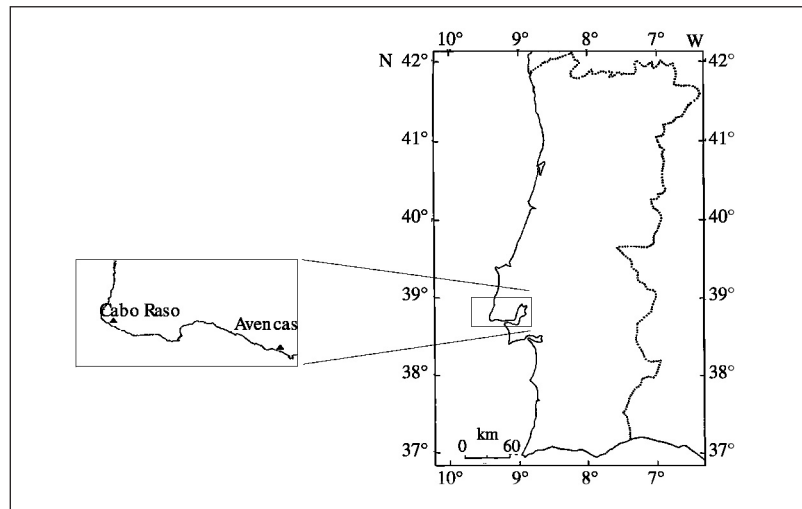
We focused on the size structure of *P. depressa* populations' growth and distribution patterns on two rocky shores located on the central Portuguese coast, Cabo Raso (38° 42' N, 09° 29' W) and Avenças (38° 41' N, 09° 21' W) (figure 1).

Sampling methods

Population structure and recruitment

To examine the limpet population size structure over time, the maximum shell length of approximately 400 individuals was measured at both sites, 200 in the upper eulittoral area dominated by *Chthamalus* spp., and 200 in the lower eulittoral area characterised by the presence of *Mytilus galloprovincialis* Lamarck. The study was conducted during one year, and sampling was conducted on a monthly basis at both study sites. Quadrat plots of 50 cm × 50 cm were randomly placed, until a minimum of 200 individuals had been measured in each area. A fixed minimum number of individuals was selected instead of a fixed plot number to enable a comparison of structure and recruitment among areas and over time with a similar sample size. Therefore, the number of plots was not always the same, depending on the density of the area. For instance, in the upper eulittoral area the number of plots required to reach 200 limpets was generally higher than in the lower eulittoral area. The maximum shell length, to the nearest 0.1 mm, was obtained in situ without removing the animals, with the aid of vernier callipers with extensions to

Figure 1. Study sites



reach limpets in crevices or in clumps. This non-destructive procedure prevented the mortality associated with the process of substratum detachment (Hawkins and Jones, 1992).

Growth

In order to determine growth rates, 200 individuals of *P. depressa* were tagged for a period of 7 months on different rock substrata at both study sites. Thus, 100 limpets were tagged on an irregular surface with depressions and dominated by *Chthamalus* spp., and 100 organisms were tagged on a regular smooth area almost solely composed of limpets and bare rock. The limpets were selected randomly, including all the size classes within an area of 2 m². A small plastic numbered tag was glued (with Superglue) to each limpet shell, and then covered with the same glue for further tag protection. Limpets of *Patella* spp. have a well-fixed homing behaviour, returning to a home scar after every foraging excursion (Branch, 1975; Hartnoll and Wright, 1977); therefore, the tagged individuals were easily re-measured in each sampling month. Growth rates were calculated using only those limpets that survived the entire sampling period.

Data analysis

Population structure and recruitment data were analysed by monthly size-frequency distributions obtained by splitting size records into 1-mm classes.

The recruitment peaks were identified using size-frequency histograms. Growth rate regressions were analysed using initial lengths data plotted with growth increments data for the two substrata at both study sites. Comparison of regression lines, in terms of residual variance, slope and elevation (regression coefficients), was made for each site, using the methodology described by Snedecor and Cochran (1989).

RESULTS

Population structure and recruitment

Size-frequency histograms are shown in figures 2 and 3. They are presented in chronological order for both shore levels. The number of sampled individuals is given in the size-class histograms. Juveniles are present almost year-round, but peaks are mostly found in winter months for both shores. December-February are the winter months when spat presence is stronger, mainly in the lower eulittoral. The major recruit mode was 5 mm on both shores, but the frequency was much higher at Cabo Raso than Avencas, indicating that the recruitment level was also higher on Cabo Raso.

Moreover, histograms show that, independently of the eulittoral level and the sampled month, the distribution frequency on Cabo Raso is mainly directed towards lower shell sizes, a situation opposite to that of Avencas (figures 2 and 3). In the upper eulittoral zone, the higher mean size-class was 17 mm in July 2002 on Cabo Raso and 18 mm at

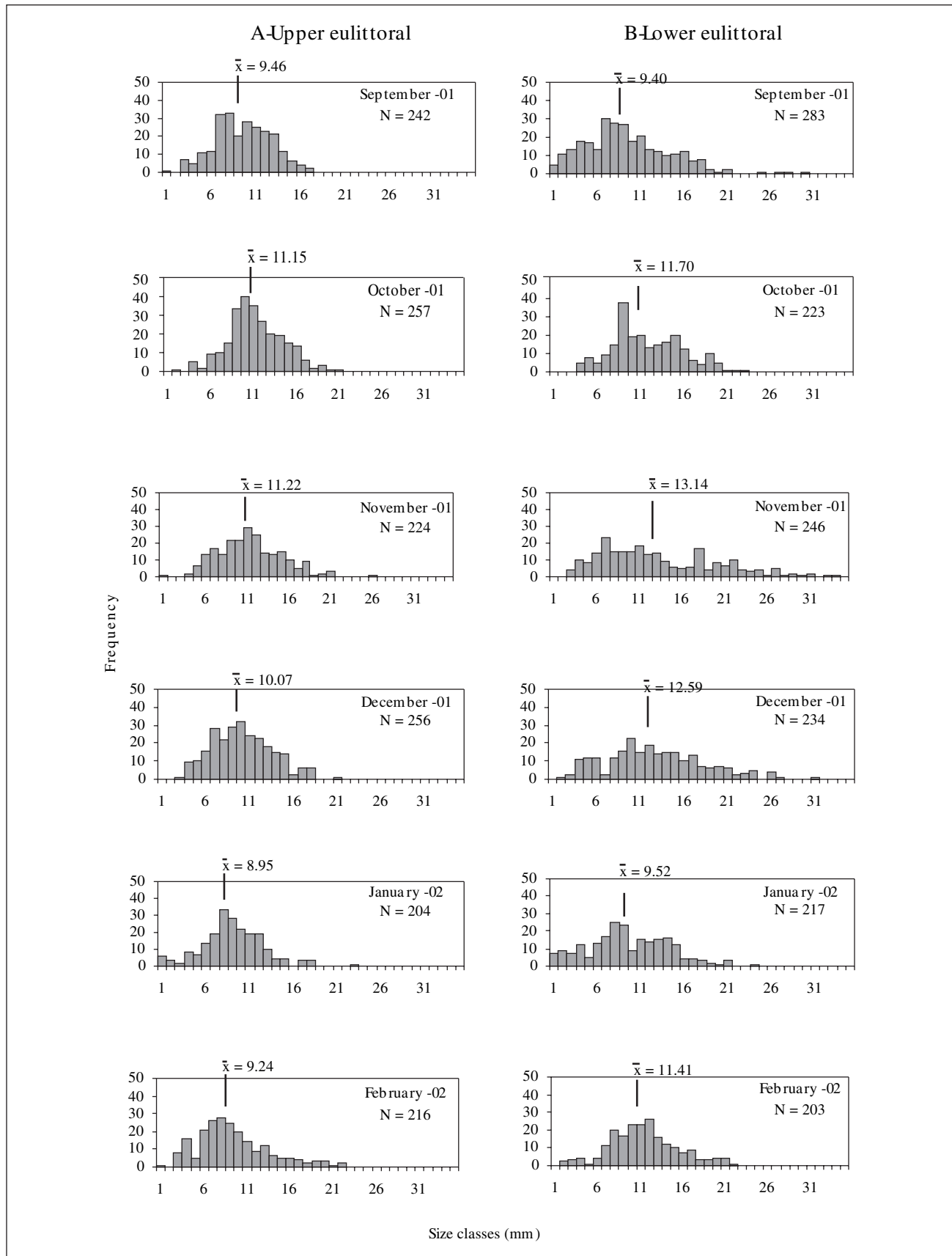


Figure 2. Monthly distribution of *P. depressa* size-frequencies on both shore levels at Cabo Raso. (01): 2001; (02): 2002

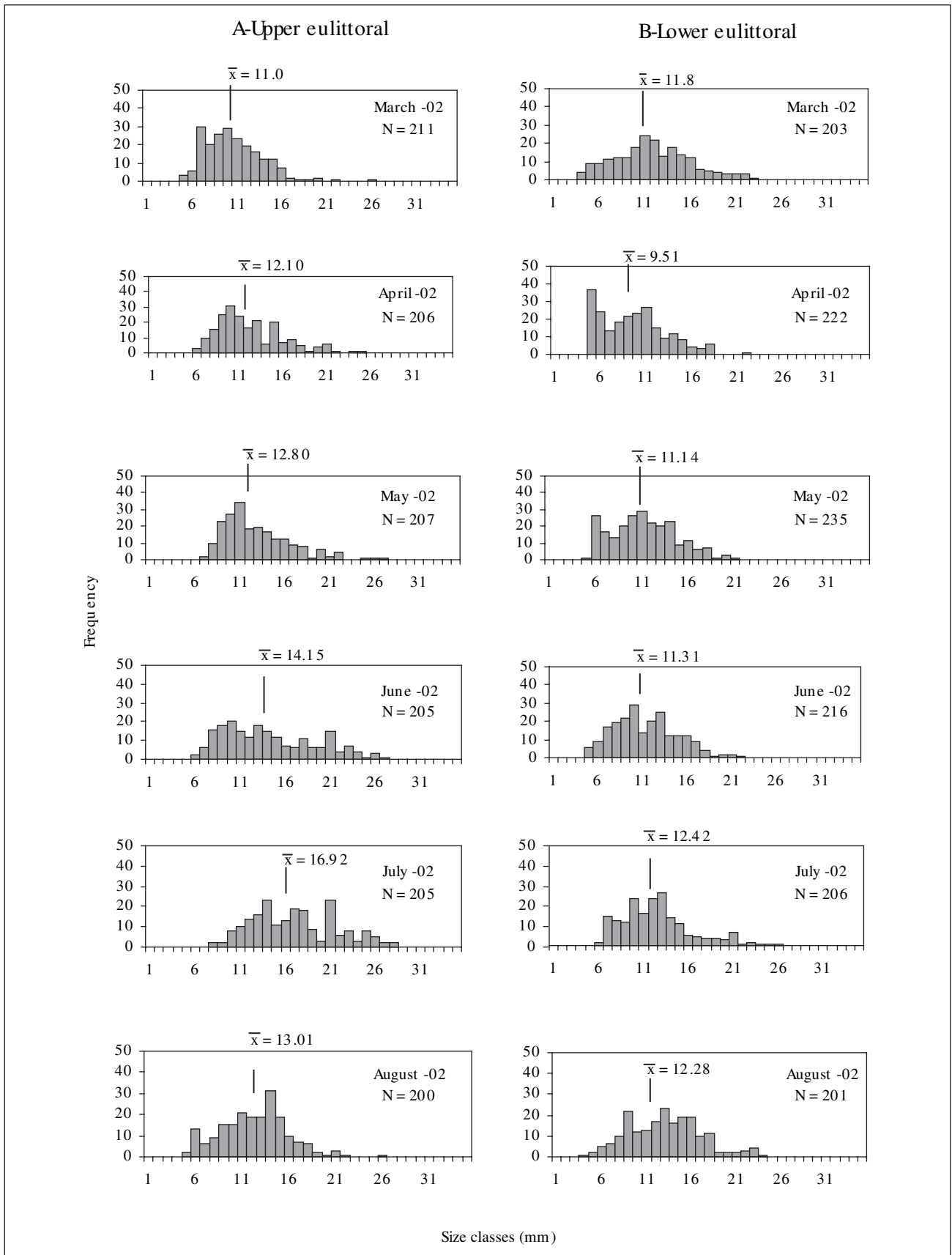


Figure 2 (continuation)

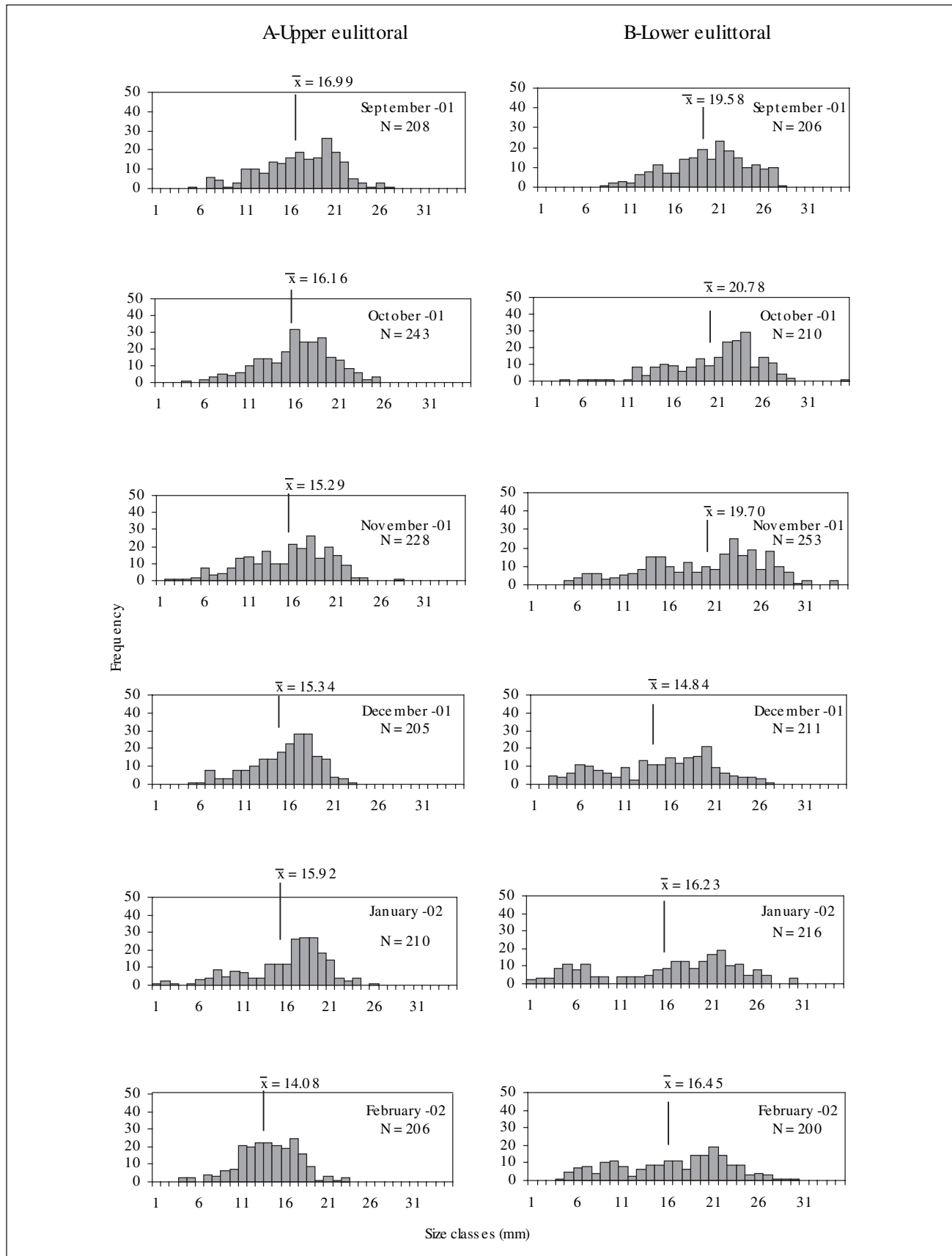


Figure 3. Monthly distribution of *P. depressa* size-frequencies on both shore levels at Avencas. (01): 2001; (02): 2002

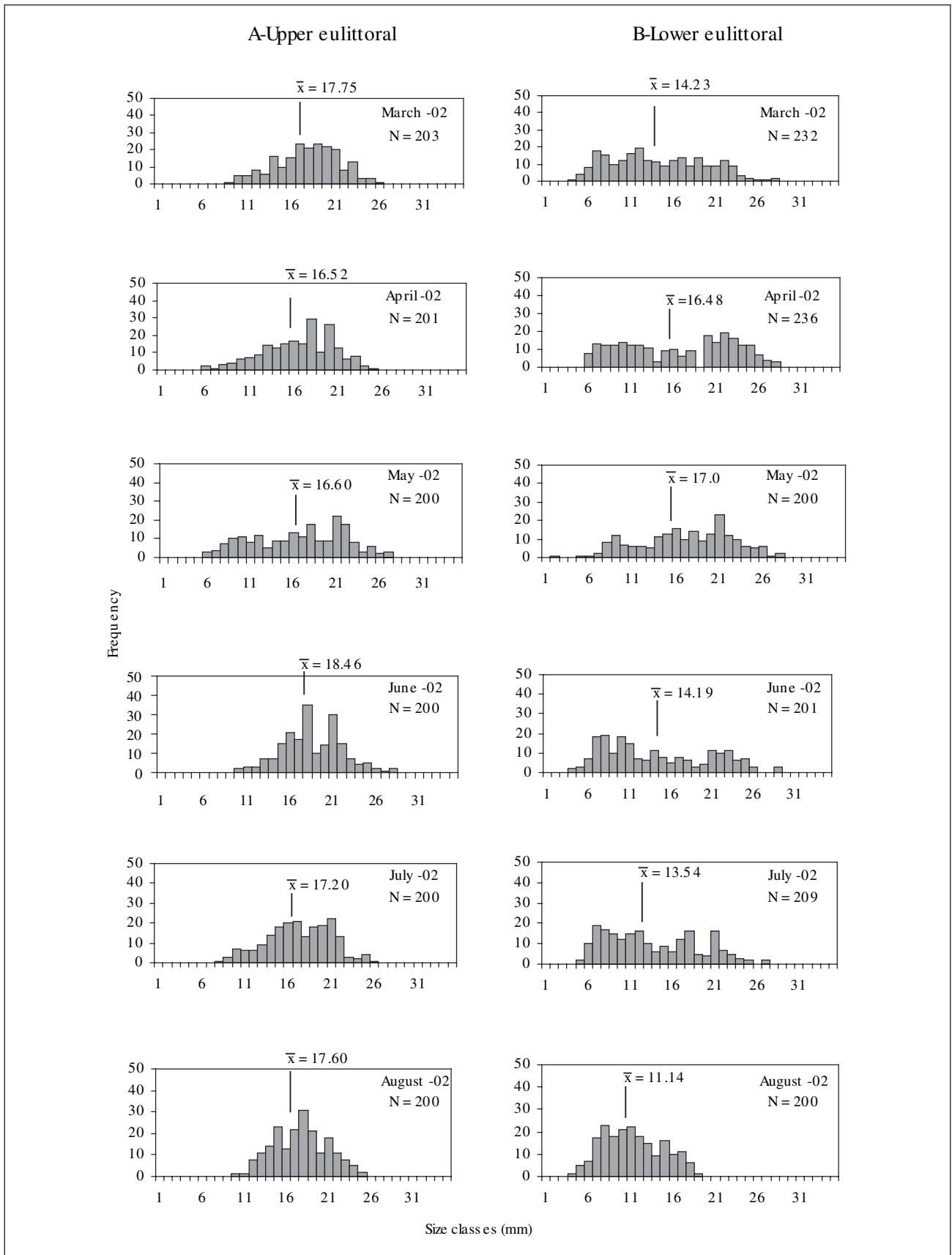


Figure 3 (continuation)

Avencas (table I). As for the lower eulittoral zone, the maximum mean size was 13 mm for Cabo Raso and 21 mm for Avencas (table I). These data suggest the presence of larger limpets in Avencas, and seem to confirm the previously stated hypothesis of a lower recruitment frequency at this site. These results could also indicate increased growth rates for both levels at Avencas. In general, we found that larger limpets were more frequent in the upper eulittoral than in the lower eulittoral zone (figures 2 and 3). In fact, individuals smaller than 5 mm were only sporadically found in the upper eulittoral zone, and only in small depressions with some degree of humidity.

Growth

The results of *P. depressa* growth during a period of 7 months are given in figure 4. Regression analysis showed that, for any given size and at both study sites, *P. depressa* had lower growth increments in the irregular substratum area than in the regular substratum. This is indicated by the less accentuated slope for the irregular substratum, and the more ac-

centuated slope regular substratum (figure 4). The slopes of the linear regression lines also indicate that growth increments are lower for Cabo Raso (regular substratum: 0.42; irregular substratum: 0.24) than for Avencas (regular substratum: 0.55; irregular substratum: 0.37). Growth increments were slightly variable in the regular substratum for both shores, particularly between 11 and 20 mm; some limpets increased only 4 mm during the study period, whereas others increased as much as 19 mm. For irregular substrata, the main variation occurred for limpets between 11 and 20 mm of initial shell length, with a minimum increment of 2 mm and a maximum increment of 10 mm (figure 4).

The two-tailed F test, which compared residual mean squares of regression for each substrata, indicated that residual variances were homogeneous for the two sites. The slopes of the incremental growth regressions were not parallel on Cabo Raso ($F_{1,117} = 9.20$, $p = 0.003$), nor at Avencas ($F_{1,126} = 6.64$, $p = 0.010$), indicating that the rate of change in length was not similar for the two surface types at each site. According to Snedecor and Cochran (1989), further comparison of elevations of the surfaces regression lines is only meaningful if the lines are parallel. However, our data shows that, for any given size, limpets on regular substrata had a higher growth increment than those on irregular substrata for both study sites. For example, in Avencas, a limpet of 15 mm initial size grew an average of 6 mm of linear shell growth on the irregular substratum, while a similarly sized limpet on the regular substratum grew around 13 mm.

Table I. Mean size (\pm SE) of *P. depressa* at the two studied sites (central Portuguese coast) for different shore levels and sampling dates

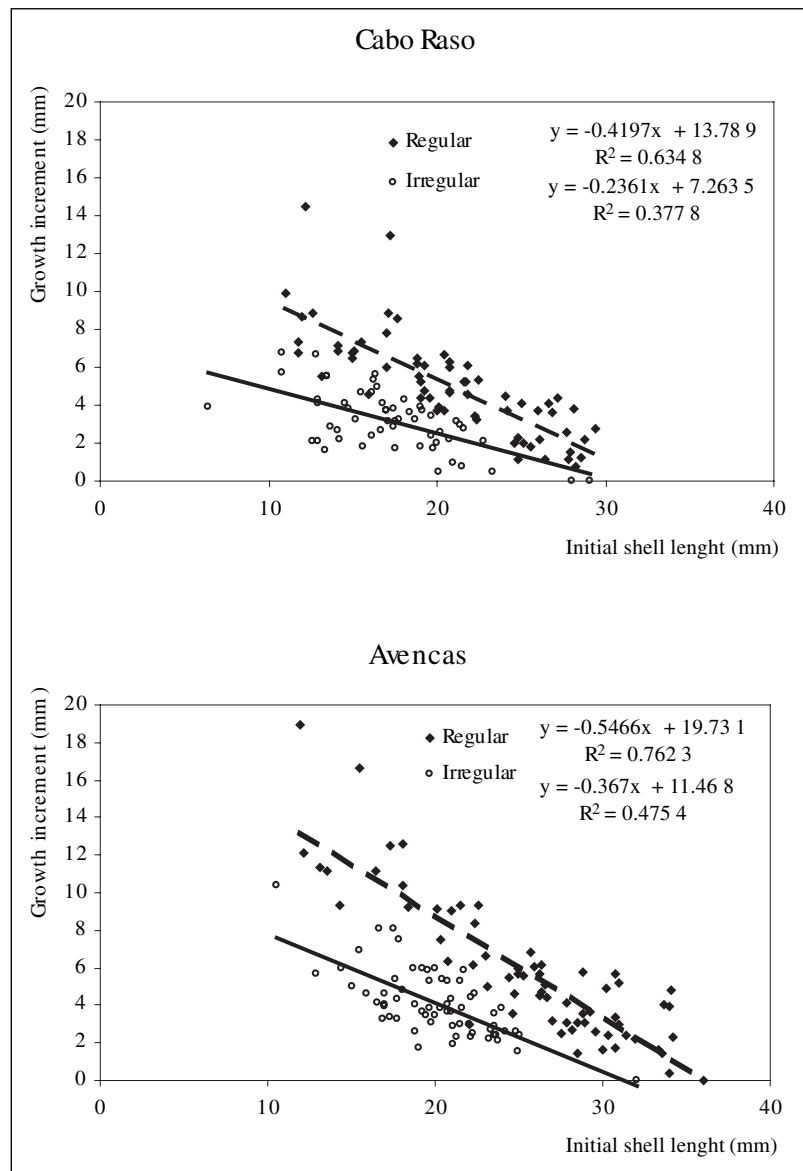
	Month	Avencas	Cabo Raso	
Upper eulittoral	September 2001	16.99 \pm 0.30	9.46 \pm 0.20	
	October 2001	16.16 \pm 0.19	11.15 \pm 0.16	
	November 2001	15.29 \pm 0.22	11.22 \pm 0.22	
	December 2001	15.34 \pm 0.26	10.07 \pm 0.18	
	January 2002	15.92 \pm 0.32	8.95 \pm 0.24	
	February 2002	14.08 \pm 0.24	9.24 \pm 0.28	
	March 2002	17.75 \pm 0.25	11 \pm 0.23	
	April 2002	16.52 \pm 0.28	12.10 \pm 0.26	
	May 2002	16.60 \pm 0.37	12.80 \pm 0.26	
	June 2002	18.46 \pm 0.24	14.15 \pm 0.36	
	July 2002	17.20 \pm 0.26	16.92 \pm 0.32	
	August 2002	17.60 \pm 0.22	13.01 \pm 0.26	
	Lower eulittoral	September 2001	19.58 \pm 0.30	9.40 \pm 0.30
		October 2001	20.78 \pm 0.23	11.70 \pm 0.23
November 2001		19.70 \pm 0.30	13.14 \pm 0.40	
December 2001		14.84 \pm 0.41	12.59 \pm 0.30	
January 2002		16.23 \pm 0.49	9.52 \pm 0.31	
February 2002		16.45 \pm 0.43	11.41 \pm 0.27	
March 2002		14.23 \pm 0.37	11.80 \pm 0.29	
April 2002		16.48 \pm 0.42	9.51 \pm 0.24	
May 2002		17 \pm 0.38	11.14 \pm 0.23	
June 2002		14.19 \pm 0.45	11.31 \pm 0.25	
July 2002		13.54 \pm 0.38	12.42 \pm 0.28	
August 2002		11.14 \pm 0.24	12.28 \pm 0.28	

DISCUSSION

The two study sites were broadly similar in terms of *P. depressa* population structure and growth. However, some important differences were detected, such as a higher recruitment on Cabo Raso, and larger size classes at Avencas.

Successful recruitment is strongly dependent on the local habitat conditions; specifically, physical factors like temperature, topography, wetness of the surface, tidal and level, and biological factors, such as the presence of mussels and barnacles (Lewis and Bowman, 1975). In fact, physical and biological factors can act together, although one may prevail over the other, depending on local habitat characteristics. Previous work on limpet recruit-

Figure 4. Growth increment (mm) observed in the study period plotted with regard to initial sizes at Cabo Raso (irregular substratum: N = 57; regular substratum: N = 64) and Avencas (irregular substratum: N = 64; regular substratum: N = 66), on both substrata. Regression equations and regression coefficient are shown in the graphic



ment and spat settlement indicates that temperature is the major factor influencing the reproductive process (Lewis, 1986). Brazão *et al.* (2003), also working on the central Portuguese coast detected two main spawning peaks for *P. depressa* (January and May/August). Moreover neuter, developing, and spawning gonads were found almost in every monthly sample, meaning that spawning is asynchronous and takes place several times during the year. The recruitment observed in the present study was higher towards the autumn-winter period. Newly recruited limpets can only be detected on the shore when they reach a minimum size of 1 to 2 mm. Blackmore (1969) found that spat settlement occurred predominantly during the more

frequent rougher sea conditions, typical of colder months, whilst other studies have cited low temperature as a stimulus for spawning (Bowman and Lewis, 1977, 1986; Thompson, 1979). The enhanced recruitment observed on Cabo Raso may therefore be related to more exposed climacteric and local sea conditions. The resultant temporal pattern in spawning events could explain the observed annual presence of juveniles and the identified recruitment peaks. Another difference in population size structure between sites was the general presence of larger limpets at Avencas. Several factors may account for this: 1) the lower recruitment may contribute to reduced intraspecific competition; 2) increased growth rates due to a higher

availability of food supply or lesser intraspecific interactions can also play an important role; and 3) the fact that Avencas shore is less exposed than Cabo Raso as far as wave action is concerned. These issues require further investigations.

The juvenile preferential distribution in the lower eulittoral zone (in *M. galloprovincialis* patches) may possibly be an outcome of desiccation refuge, since crevices and spaces between mussels enable maintenance of humidity levels. Studies by Orton (1929) and by Delany, Myers and McGrath (1998) reported that the juvenile association of other *Patella* species (*P. vulgata* and *P. ulysiponensis*) is strongly associated with mid-shore tidepools and damp conditions. Although desiccation may in fact control juvenile distribution, strong intraspecific competitive interactions were experimentally demonstrated in previous studies for *P. depressa* (Boaventura, 2000; Boaventura, Cancela da Fonseca and Hawkins, 2002), which could account for smaller scale niche partitioning within size classes. Thus, the lower shore distribution pattern of juveniles can be simultaneously issued to reduced mortality by desiccation (Lewis and Bowman, 1975), as in other gastropods (Underwood, 1979; Branch, 1981) and, to some extent, to size-class competitive interactions.

P. depressa adults could be found at all sampled shore levels, but the majority inhabited the upper eulittoral area, where it is closely linked with *Chthamalus* spp. Although barnacles can positively affect limpets by conferring enhanced desiccation and wave action protection (Choat, 1977), our analysis on the growth increments for irregular substrata showed that they eventually reduce growth rates. Such constraint may not have solely negative effects, since field observations seem to indicate that larger limpets may be prevented from feeding on these areas due to space availability constraints and, therefore, smaller individuals may be submitted to reduced competitive stress (Lewis and Bowman, 1975), with increased survival rates (Branch, 1975).

Our finding of lower shell increment in substratum areas occupied by barnacles is similar to that of Lewis and Bowman (1975) and Thompson (1980) for *P. vulgata*, which had reduced growth and smaller maximum sizes in habitats with dense barnacle cover. Differences in the increments for different substrata may be due to the fact that limpets on regular substrata have access to an increased availability of grazing space, and here algae spores are likely to grow without space limitation, thus

making possible more effective foraging activities. The opposite appears true for limpets on irregular substrata, since movements are quite limited because of the high barnacle cover and the presence of crevices. In conclusion, our analysis indicates that limpet population dynamics seem to be clearly related to specific local habitat conditions and to environmental variations. However, more specific studies (e.g., chlorophyll analysis) are required to clarify all of the causes related to behavioural and morphological adaptations.

ACKNOWLEDGEMENTS

We would like to thank Dr Terence Ocaña, who assisted in the final review of the manuscript, and also Dr Darren Fa, who substantially improved the manuscript with comments and suggestions.

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