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Population structure of the intertidal crab *Cyrtograpsus altimanus* (Brachyura: Varunidae) in a northern Patagonia mussel bed

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The population structure, size at maturity, reproductive period, recruitment and habitat use were studied in a population of the grapsoid crab Cyrtograpsus altimanus *in an intertidal mussel bed at San Antonio Bay, Argentina. Samples were taken from October 2000 to January 2002. Crabs were sized and sexed to estimate size–frequency distributions (SFD). Modal groups of males and females were the same. Growth, evidenced by the shift to right of SFD modal classes, was observed in spring, summer and autumn. Size at maturity of females varied seasonally. Ovigerous females were found in winter, spring and summer, but two discrete recruitment events (in spring and autumn) are proposed. Based on the maximum male and female sizes found in the mussel bed, a size constraint is proposed that forces large crabs to migrate to cobblestone adjacent habitats.*

Keywords: size distribution, population structure, refuge, marine crustaceans

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INTRODUCTION

Crabs are conspicuous inhabitants of intertidal areas and, sometimes, form dense populations which play important ecological roles. Many species, belonging to different families have a set of physiological and behavioural traits that allow them to cope with the changing environmental conditions of such habitats. Particularly important among these traits is the usage of refuges. The quality and quantity of refuges (burrows in muddy or sandy shores, cobbles or crevices in rocky shores) are important factors regulating populations and may restrict the abundance of a specific size-class or ontogenetic stage, thus creating a shelter limitation bottleneck (Caddy, 1986).

The varunids (Varunidae) are an example of crabs that live both in soft and hard intertidals. The south-western Atlantic temperate shores are dominated by three species of varunids: *Neohelice granulata* (formerly known as *Chasmagnathus granulatus*) is an estuarine crab that burrows in soft sediments; *Cyrtograpsus angulatus* is a highly euryhaline species that inhabits both estuarine sandy or muddy beaches and marine rocky shores and it is relatively independent of the refuge availability; and *Cyrtograpsus altimanus* is restricted to areas rich in refuges in marine coasts and, occasionally, in the lowest part of estuaries (Scelzo & Litchestein de Bastida, 1978; Spivak, 1997). The present knowledge about the natural history, population and reproductive biology and ecological role of these three species is disparate: *N. granulata* and *C. angulatus* have been intensely studied, and the former became a standard model for studies of physiological and biochemical adaptations to transitional environments between the sea and land (Anger *et al.*, 2008; Spivak, 2010); *C. altimanus*, instead, has been scarcely studied in spite of being frequently found in many areas along their distribution range (Boschi, 1964).

Cyrtograpsus altimanus Rathbun is a small crab (maximal size 20 mm carapace width (CW)) endemic to the south-western Atlantic. This species was described by Rathbun (1918) from individuals of a population inhabiting a mussel bed in northern Patagonia. It may reach high densities in marine shores covered with stones or shells, used as refuge (Spivak, 1997). In spite of being a common constituent of the intertidal communities along its distribution range between Río Grande (Brazil) and Chubut (Argentina), the only studies related to its ecology and life history correspond to Buenos Aires coastal areas. Scelzo & Lichtschtein de Bastida (1978) described the larval development in the laboratory with some comments about its ecology, Gavio (2003) studied the population structure, growth, maturity size, reproductive period and mating system in a population from Santa Clara (36°56′S 58°11′W) and López-Greco & Rodríguez (2004) estimated the fecundity, reproductive effort and maturity size of females from a population at Jabalí Island (40°32′S 62°15′W)

The purpose of the present study was to describe the structure and dynamics of a population of *C. altimanus* inhabiting the extensive intertidal beds of the small mussel *Brachidontes rodriguezi*[1] in San Matías Gulf (northern Patagonia, Argentina), under the hypothesis that this complex structure

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[1] *Brachidontes rodriguezi* is synonymous with *Brachydontes rodriguezi, Brachydontes rodriguezii* and *Brachidontes rodriguezii*, all variants commonly used in the literature for the same species.

provides crabs suitable refuge for settlement and development. Additionally, new information on reproductive traits is reported.

MATERIALS AND METHODS

Study area

The sampling site is located in San Antonio Bay (40°46′S 64°50′W), an inlet of the north-western coast of San Matías Gulf, Río Negro province, Argentina. Semidiurnal high amplitude tides (9 m) characteristic of the Patagonian coast cover and uncover twice a day an extensive cobblestone intertidal area. Parallel to the main channels that drain the intertidal along 8 km, huge populations of the small mussel *Brachidontes rodriguezi*, form a dense belt of several metres width and about 10 cm thickness. This three-dimensional structure hosts high number of invertebrate species (crustaceans, annelids, molluscs and sponges among others) in the spaces among shells (Vázquez, personal observation) as was observed in populations at other localities (Scelzo *et al.*, 1996; Adami *et al.*, 2004). Average winter and summer temperatures are 7.8°C and 22.6°C (July and January respectively) (Servicio Meteorológico Nacional, Argentina).

Sample processing and data analysis

The mussel bed was sampled 11 times from October 2000 to January 2002, monthly during spring and the beginning of autumn (October to April 2001), bimonthly in winter (June to August) and monthly during the following summer (December 2001, January 2002). Each time, ten 1200 cm^3 samples were collected (except January, June and August 2001, when $N = 5$) randomly with a cylindrical sampler of 100 mm diameter. Each sample consisted of several thousands of *B. rodriguezi* individuals adhered among them and to cobbles by their byssal threads, thus forming a complex structure with free spaces which hosted *C. altimanus* and other invertebrate species.

Since all crabs collected on the mussel bed were smaller than the maximum sizes reported for the species, an ancillary sampling was performed in February 2007 at the cobblestone area adjacent to mussel beds. There, all crabs present in 10 square areas 0.5×0.5 m, placed at random along the narrow area about 2 m width between the low tide edge and the mussel bed, were collected by hand at low tide. To minimize the possibility of escape, a square frame was kept surrounding each sample, while cobbles were removed cautiously.

Samples were immediately transported to the laboratory and frozen at −20°C before processing. Crabs were separated by hand and fixed in 4% formalin after de-freezing, sized (maximal CW) and separated into four classes: males; non-ovigerous females; ovigerous females; and juveniles (= morphologically undifferentiated crabs).

Crab density was expressed as the number of crabs/1200 cm^3. Monthly crab densities were compared with one-way analysis of variance (ANOVA) and the *a posteriori* Tukey test was applied when significant differences existed (Zar, 2010). Sex-ratios departures from expected 1:1 ratio for each month and for all months together were analysed with Chi^2 test. Crabs were grouped in size-classes of 0.25 mm for juveniles (<3mm CW, genital pores not evident) and of 0.5 mm for larger individuals. Size–frequency distributions (SFD) were constructed separately for males, females and juveniles. Modal components of each distribution were estimated with a modification of the method developed by McDonald & Pitcher (1979) where observed SFD were fitted to the expected values of a mixture of normal distributions by the least squares method (see Bas *et al.*, 2005 for details of procedure, parameters and restrictions of the method). Growth data obtained by Spivak (1999) and Gavio (2003) for this species were used as guide to evaluate the reliability of the differences between successive modes. Given that the number of replicates of each group was variable (larger modes appeared only in some samples, see below) it was not possible to use a two-way ANOVA and differences among consecutive modes and between sexes were evaluated separately with one-way ANOVAs. Since no differences appeared between sexes (see below), comparisons among consecutive modes were made pooling modal values of males and females. Modes 1 to 8 were compared in one analysis and modes 9 to 11 in another, since the last group presented greater variances than the former, as expected.

Between 10 and 42 females per sample, from all the size-range, were used to estimate the size of morphological maturity, measuring the maximal width of the third abdominal segment (AW) and the CW. Females were considered mature when the third abdominal segment reached the coxae of the adjacent pereiopods (Spivak, 1999). However, a broad range of forms of the abdominal segments were present in a wide range of CW and so, the maturity condition was not easily assigned to one of each category. Because of that, the size at 50% maturity was estimated following Somerton (1980). According to this method, the data from the smallest and biggest individuals, that could be surely defined as immature and mature respectively, are used to fit straight lines by regression and then, data of uncertain immature and mature individuals are assigned iteratively to the closest line until the best assignment is obtained. After evaluating the statistical significance of the fitting, compared to the fitting to a single line, the size of 50% maturity is estimated by fitting a logistic function to the proportion of mature and immature individuals assigned to each size-class. After all samples were sized, it was evident that in some months, the maximal sizes of females with immature characteristics were larger than in others. In consequence, monthly samples were grouped based in the similitude of those ranges and separately analysed.

To analyse the availability of refuge in the mussel bed, the structural components of 250 ml sub-samples of each sample were subsequently separated and their elements classified as *B. rodriguezi* shells, other biological components (mainly barnacle and mollusc shells), cobblestones and fine material (sand and shells debris). The volume of each fraction was estimated by volume displacement in a graduated 200 ml test tube. *Brachidontes rodriguezi* shells were sized (shell length, SL) and monthly SFD histograms were plotted.

RESULTS

A total of 1470 individuals were measured in samples from mussel beds, 595 males, 680 females and 195 juveniles. The density of crabs was variable among samples (average 14.7 ± 9.2 crabs/1200 cm^3) in all sampled months.

Differences among sampling dates were significant (ANOVA, F = 4.84; $P < 0.001$). The *a posteriori* Tukey test showed no clearly separated groups. The highest average densities occurred in March and April (autumn) and the lowest in most of summer months (Figure 1). The sex-ratio was biased to females (Chi^2 = 5.66; $P = 0.017$) when all samples were pooled. In the monthly analysis, November and December 2000 were dominated by females while males were the majority in February 2001; in the remaining months, the sex-ratio was 1:1 (Table 1)

The SFD of crabs were polymodal (Figure 2). The smallest and largest size-groups of crabs were not always present. The intermediate modal groups, however, appeared in all samples, even when their proportion varied. Seven modes were detected in male SFD, ten in female SFD and two in juvenile SFD. Modal values were denominated M1 to M12; M1 and M2 corresponded to juveniles, M3 to M9 to both males and females, and M10 to M12, the largest crabs detected, were females present only in winter and at the beginning of spring.

In the ancillary sample from cobblestone area adjacent to the mussel's bed, 283 individuals were sized: 174 females and 109 males. The sex-ratio was biased to females (Chi^2 = 14.92, $P < 0.001$). The average density was 137 ind./ m^2. Crabs below 3 mm CW (juveniles) were not present. Modal values of 'cobble' females corresponded to modes M4 to M12, of 'mussel bed' females. Larger crabs were more represented (maximum CW = 13.3 mm). The first five modes of 'cobble' males corresponded to mussels bed modes M4 to M8 and four larger groups (M9 to M12) appeared, reaching 16.6 mm CW (Figure 3).

The comparison between modes of males and females showed no significant differences at least until M9 (Table 2). M10 to M12 were not statistically compared because of the low number of replicates. All modes differed from each other (ANOVA M1 to M8: df = 7; F = 1278.25; $P < 0.01$ and ANOVA M9 to M12: df = 3; F = 57.37; $P < 0.01$; Tukey tests, all pair wise comparison $P < 0.01$). Growth was evidenced by the shift of SFD modal classes to the right in successive months; however, in June and August, the SFD were almost identical, suggesting that growth was interrupted during the cold season. The differences between successive modes decreased with size: the difference was highest (more than 50%) between M1 and M2, it diminished to ~20% in the intermediate size-groups and to ~10% in the largest ones (Table 3). The smallest modal group (M1) appeared only in January and March, but M2, the following group of juveniles was usually present, except in winter and at the beginning of spring.

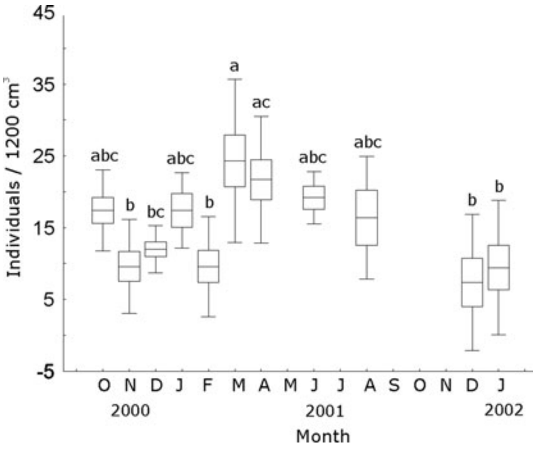

Fig. 1. *Cyrtograpsus altimanus.* Average density of crabs per sample at each sampled month. Horizontal lines inside boxes: mean. Box: standard error. Vertical lines: standard deviation. Different letters indicate significant differences among densities.

Table 1. *Cyrtograpsus altimanus.* Results of the Chi^2 tests of the monthly and total deviations of the estimated 1:1 sex-ratio in samples from the mussel bed area. Significant *P* values in bold.

Year	Month	N	Chi^2	df	*P*
2000	October	169	1.33	1	0.24
	November	73	4.94	1	**0.02**
	December	116	4.96	1	**0.02**
2001	January	71	1.14	1	0.28
	February	87	17.29	1	**0.00003**
	March	177	1.27	1	0.25
	April	185	1.21	1	0.27
	June	91	1.32	1	0.24
	August	75	2.25	1	0.13
	December	55	2.2	1	0.13
2002	January	176	2.75	1	0.09
All months		1275	5.66	1	**0.01**

N, number of adult individuals.

Ovigerous females were present in 7 of the sampled months at the mussel bed and were considered as an indication of reproductive activity. Reproduction peaked in spring, diminished until a minimum at mid-summer, and reached later a second peak at the end of that season. Autumn appeared as a resting period with no ovigerous females, and a new reproductive peak was present in winter, with more than 80% of females carrying eggs at that season (Figure 4).

The linear growth functions (after transforming data as ln x) for AW versus CW were significantly different for immature and mature females. Size at maturity differed between winter–spring and summer–autumn females too. In samples from June, August, October, November and December 2001 and 2002 (winter and spring), immature and mature lines almost did not overlap and all females above 6 mm CW were mature; the SM$_{50}$ for this group was 7.72 mm CW (95% confidence interval, 7.43–8.01 mm) (Figure 5a). In samples from January, February, March and April 2001, January 2002 and in the ancillary sample from February 2007 (summer–autumn), in contrast, lines overlapped extensively and many females above 6 mm CW (and even larger than 8 mm CW) were immature; the SM$_{50}$ for this group was 8.57 mm CW (95% confidence interval, 8.32–8.92) (Figure 5b).

The 80% of the mussel bed was composed of *Brachidontes rodriguezi* shells, other biogenic structures (mollusc and barnacle shells) and cobblestones; the proportion of each component was relatively constant through the year (Figure 6). The remaining 20% of volume was fine material (sand and shells debris). A total of 4427 *B. rodriguezi* shells were measured. Their population structure was very stable along the sampling period, with an average of 82% (±9%) of the individuals included in one modal group (SL = 25 mm) and the remaining 18% (±5.9%) grouped into two small modes (SL between 7 and 17 mm; Figure 7).

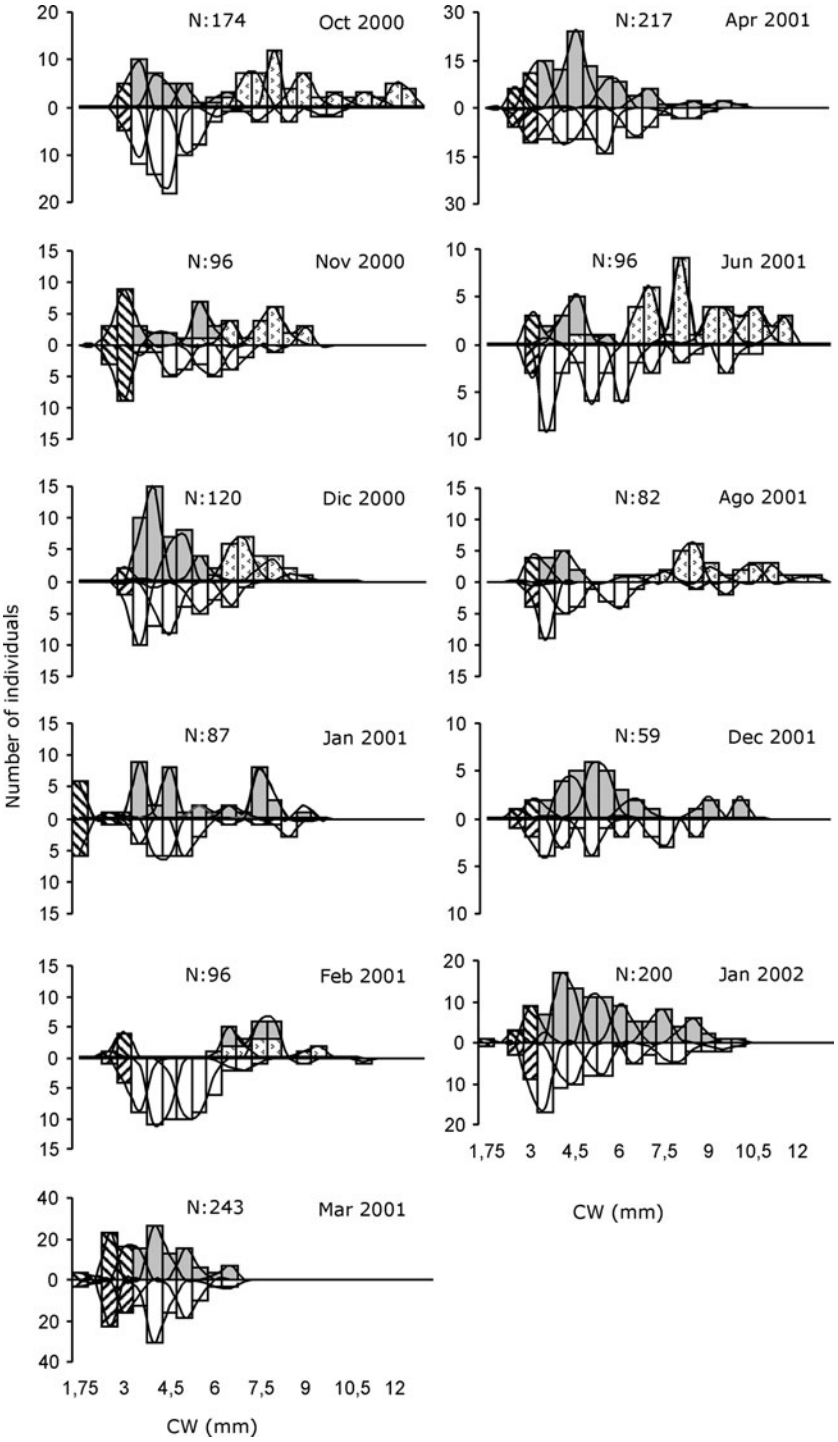

Fig. 2. *Cyrtograpsus altimanus*. Size–frequency distributions (carapace width (CW), mm) at each sampled month. Stripped bars: juveniles (half of the total number was assigned to each sex); white bars: males; grey bars: non-ovigerous females; spotted bars: ovigerous females.

DISCUSSION

Population structure and growth

Size–frequency analysis depends on the clear identification of modes in the distributions. When this is possible, the analysis is simple and computer-based approaches are powerful tools. Nevertheless, since these approaches are flexible and need assumptions and starting points established by the user, they have to be used and interpreted with caution (Hartnoll, 2001). The results of this study were consistent: the modes in SFD of *Cyrtograpsus altimanus* from San Antonio were markedly separated in spite of the small number of individuals in some size-classes, and little variation was detected among modal values among samples. In addition, the differences between successive modes matched very well with the moult increments measured in juvenile and adult males and females of *C. altimanus* captured in the field and kept in

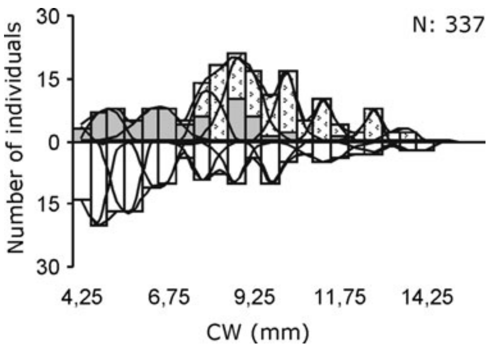

Fig. 3. *Cyrtograpsus altimanus*. Size–frequency distributions (carapace width (CW), mm) of the ancillary sampling in February 2007. References as in Figure 2.

captivity no longer than seven days (Gavio, 2003), and with growth data of crabs reared in the laboratory, from C1 to C6 (Spivak, 1999). The average M1 size (1.73 mm CW) corresponded to the size of the smallest modal class reported by Gavio (2003: 1.72 mm CW) and with the average size of the first stage crab cultured and described by Scelzo & Lichstein de Bastida (1978: 1.6 mm CW) both from populations from Buenos Aires Province, northward of San Antonio. However, the first stage of crabs obtained from megalopae of Mar Chiquita (Buenos Aires Province) were larger (Spivak, 1999: average 2.33 mm CW). In spite of the latter discrepancy, it seems reasonable to consider that M1 corresponded to the smallest (recently metamorphosed) settled crabs. The presence of M2 in all spring and summer samples suggests that, even when M1 settlers were not always detected, recruitment was more or less continuous between November and March. If this is so, eggs carried by females in winter would produce the new settlers of mid-spring (November), in accordance with a slower embryonic and larval development at low temperature

Reproduction

Two different strategies are commonly found in Brachyura living in warm-temperate coastal waters of the south-western Atlantic. The reproduction of some species takes place only in spring and summer: *Neohelice granulata* (Ituarte *et al.*, 2006) or *Uca uruguayensis* (Spivak *et al.*, 1991). Other species carry eggs almost all the year: *Cyrtograpsus angulatus* (Boschi, 1964) and the platyxanthid *Platyxanthus patagonicus* (Leal *et al.*, 2008). Gavio (2003) found ovigerous females of *C. altimanus* only in spring and summer in the intertidal population of Santa Clara, Buenos Aires (37°50′S 57°30′W), but Silva (2009) found them all year round except in April and May (autumn) in Mar del Plata harbour, 15 km southward. In San Antonio (this study) proportions of ovigerous females higher than 60% were present in spring, summer and winter months. The maximal proportion of ovigerous females in winter could be the result of a massive and synchronized event of mating after the resting period or just an effect of accumulation because of the slowing down of embryonic development at low temperature. Unfortunately, no information is available about any of these possible facts.

Table 2. *Cyrtograpsus altimanus*. Analysis of variance table for the comparison between females and males modal sizes for each detected mode.

Comparison	SS	MS	df	*F*	*P*
M3	0.0225	0.0225	1	0.615	0.443
M4	0.0049	0.0049	1	0.0922	0.765
M5	0.0754	0.0754	1	0.765	0.392
M6	0.0178	0.0178	1	0.335	0.57
M7	0.0788	0.0788	1	1.346	0.269
M8	0.076	0.076	1	1.352	0.267
M9	0.217	0.217	1	2.921	0.122

M3 to M9: modes 3 to 9 of the size–frequency distributions.

Table 3. *Cyrtograpsus altimanus*. Average modal value of carapace width (CW: in mm) and growth increment (as a percentage ± standard deviation (SD)) between consecutive modes.

Mode	Average CW ± SD	Average % growth ± SD
M1	1.75 ± 0.04	
		49.55 ± 11.45
M2	2.62 ± 0.19	
		26.50 ± 5.28
M3	3.31 ± 0.19	
		31.57 ± 5.62
M4	4.35 ± 0.23	
		23.80 ± 4.60
M5	5.39 ± 0.31	
		20.72 ± 4.32
M6	6.51 ± 0.23	
		16.60 ± 2.65
M7	7.59 ± 0.25	
		11.73 ± 2.07
M8	8.48 ± 0.24	
		11.80 ± 2.69
M9	9.48 ± 0.30	
		11.95 ± 1.57
M10	10.61 ± 0.45	
		9.99 ± 1.51
M11	11.67 ± 0.64	
		10.05 ± 1.11
M12	12.84 ± 0.71	

M1 to M12: modes 1 to 12 of the size–frequency distributions.

Sexual maturity of females

The variation in the size at maturity among individual females from the same population is commonly reported even when

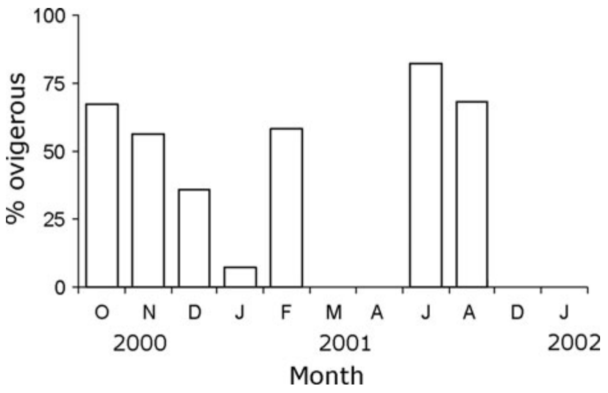

Fig. 4. *Cyrtograpsus altimanus*. Percentage of ovigerous females at each sampled month.

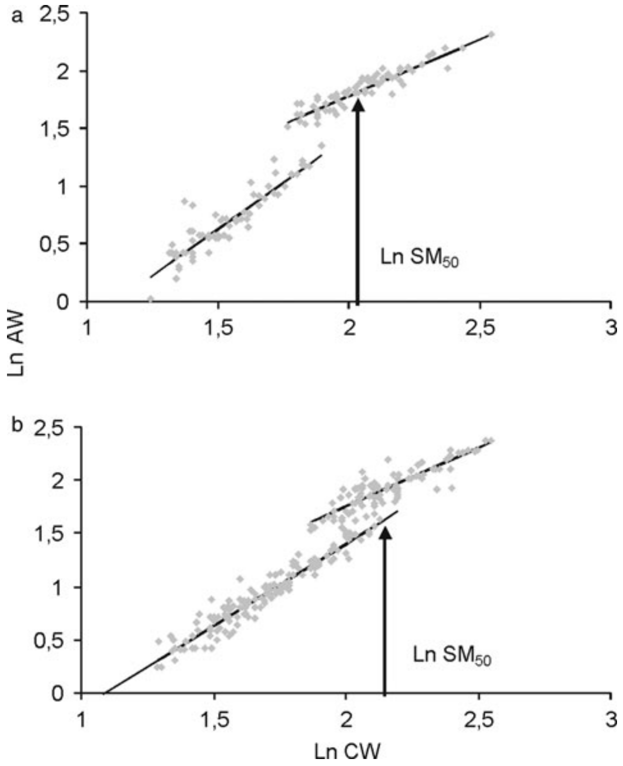

Fig. 5. *Cyrtograpsus altimanus.* Estimated Ln of the size (carapace width (CW)) at which 50% of the females are morphologically mature (size of maturity$_{50}$, SM$_{50}$) in females from: (a) winter–spring; (b) summer–autumn.

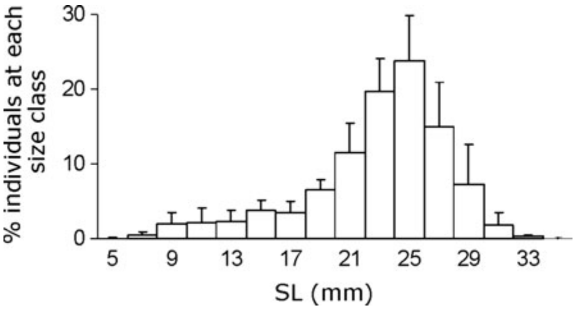

Fig. 7. Size–frequency distributions (shell length (SL)) of the mussel *Brachidontes rodriguezi* shells from all samples pooled.

not explicitly referred and so, the size of mature and immature females are ranges that overlap and the intrapopulational differences in size at puberty moult between the largest and the smallest females in some species reach values of 300% (Hartnoll, 1982). The overlapping in size between mature and immature *C. altimanus* females was wider and the size at maturity larger, in summer–autumn than in winter–spring females. Size at maturity data have not been usually analysed on a seasonal basis, with the exception of a detailed study of growth in natural populations of *Rhithropanopeus harrisii tridentatus* at the Loire estuary (Marchand, 1979). *Rhithropanopeus harrisii tridentatus* females from the beginning and the end of the reproductive season reached maturity at a smaller size than those from mid-summer; this change in size at maturity was attributed to the higher temperatures and food availability at that moment (Marchand, 1979). Both factors have proved to exert a positive effect on growth rate (Hartnoll, 2001) and may explain the seasonal variation observed in *C. altimanus*: there are marked temperature differences between winter–spring and summer–autumn and presumably food availability is higher in warm months, allowing immature individuals to reach a larger size before the puberty moult. The same factors (temperature and food availability) and others, such as density or genetics, have been used to explain interpopulational differences in size at maturity of females of different decapod species (Gardner *et al.*, 2006; Mellville-Smith & De Lestang, 2006).

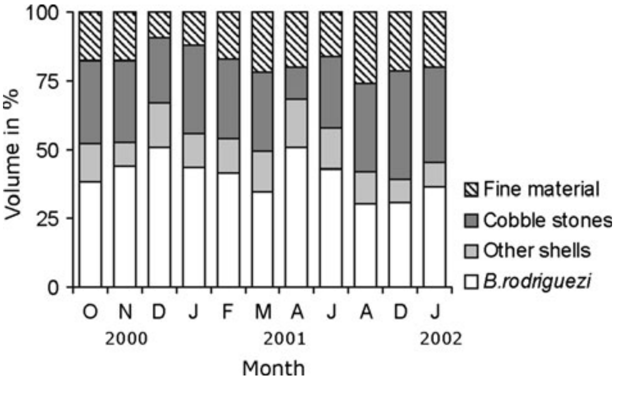

Fig. 6. Proportion of each structural element, forming the bed of the mussel *Brachidontes rodriguezi*, at each sampled month.

Refuge use

Mussel beds are excellent refuges for invertebrates (Adami *et al.*, 2004) and megalopae of *C. altimanus* settling on *B. rodriguezi* beds could have high possibilities of survival to adult age. Nevertheless, habitat structure determines the maximal body size of associated fauna by constraint of their access and movement inside the spaces used as refuge (Hacker & Steneck, 1990). The refuge availability is related to the size of shells and the degree of packing and was proposed to be a function of the fractal dimension of the refuge (Gutiérrez *et al.*, 2003). Maximum size of *B. rodriguezi* is only 33 mm length, and they are densely packed, leaving small free spaces. Even when no attempts were made to estimate the real availability of free space, it appears to be stable along the year with no change in the proportion or size of mussel bed components, as was observed in other populations of *B. rodriguezi* (Adami *et al.*, 2004). Then, crabs should leave this habitat when their body size and/or density reached dimensions incompatible with those available as refuge to establish in the adjacent stone bed where they reach bigger sizes. Flores & Negreiros-Franzoso (1999) observed a similar process in a *Pachygrapsus transversus* population inhabiting biogenic substrates of the mussel *Brachidontes solisanus* and the polychaete *Phragmatopoma lapidosa*. From the analysis of SFD and field observations, they concluded that crabs in that population settled in those substrates, but moved later, after reaching juvenile size, to rocky intertidal. Some experimental work should be necessary to accurately determine this migratory process in the *C. altimanus* population, and the possibility of a differential growth between habitats (and refuge size) cannot be discarded. Nevertheless, the fact that SFD of crabs from cobbles agree with, but also complement, those from mussel beds support the migration idea. In the same sense, it is worth noting that the largest size of females at mussel beds was 12.5 mm CW, and the largest male measured 10.5 mm CW (most large males have 9 mm CW). This difference could be explained by refuge size too, taking into account the high sexual dimorphism of this species. *Cyrtograpsus altimanus* males show positive allometry in chelar growth after reaching sexual maturity (6.7 mm CW: Gavio, 2003), and as a consequence their total volume is higher than those of females of the same CW.

This study is far from a comprehensive analysis of the life history and ecology of *C. altimanus*. Nevertheless, some relevant aspects were established and would serve as a basis to compare with other populations living in different environments in order to evaluate the effect of the environment on life history traits and the plasticity of the species. The presence of the mussel bed appears to be an important feature in the recruitment of *C. altimanus* in San Matías Gulf, where this species reaches the highest density reported. It would be of interest to study the settlement of this species in close areas where *B. rodriguezi* is absent to evaluate their effect on the mortality of the smallest size-classes.

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