

Negative interactions between two SW Atlantic intertidal crabs in soft-bottom habitats

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Abstract The intertidal crabs *Chasmagnathus granulatus* and *Cyrtograpsus angulatus* coexist across the SW Atlantic intertidal. Previous studies in this region suggest that *C. granulatus* displace *C. angulatus* in soft sediment, where *C. granulatus* build burrows (“burrowing beds”). We examined variation in abundance, size-frequency distribution, sex ratio, incidence of autotomies, and diet of both species in *C. granulatus* crab beds and adjacent areas without burrows. We also experimentally tested the hypothesis that in the absence of *C. granulatus*, *C. angulatus* will build burrows. Only large sized individuals of *C. angulatus* venture into *C. granulatus* crab beds. The sex ratio of *C. angulatus* was always biased towards females, with higher bias outside crab beds (1:8 outside, 1:2 inside). Although the items consumed in the crab beds did not differ from those consumed outside, the males of *C. angulatus* had a higher frequency of empty stomachs in crab beds. The incidence of limb autotomies of *C. angulatus* was higher

outside *C. granulatus* crab bed areas. After a long rainy period in which *C. granulatus* was absent from these areas, the pattern of habitat use of *C. angulatus* changed. During this period *C. angulatus* showed higher abundance in the areas, where *C. granulatus* previously constructed burrows, and there were no differences between areas in any of the measured parameters. In the absence of *C. granulatus*, *C. angulatus* built their own burrows and never used *C. granulatus* burrows. The interaction between *C. granulatus* and *C. angulatus* may be a good example of competitive exclusion, when the shared resource is the access to surface soft-sediment.

Introduction

Competition for space and direct interference within and among species is usually not a dominant process in three-dimensional soft-substratum habitats (e.g., Peterson 1991; Wilson 1991), although exploitative competition for limiting food resources may be important (Lenihan and Micheli 2001). The common explanation for this pattern is that in soft-sediments, food rather than space is the limiting resource (Peterson 1992). The three-dimensional structure of soft-sediment allows vertical and horizontal partitioning of space, minimizing opportunities for direct competition for space by living at different depths within sediments (Wilson 1991). Another possible mechanism that prevents saturation, and hence exclusion, may be a lack of sufficient larvae to settle and saturate available space (Lewin 1986). Whatever the factors involved, the coexistence of competing species is a major unresolved issue in the understanding of soft-bottom communities.

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Although there is evidence that competition is important when the resource is space (e.g., Wilson 1991), habitat displacement has been reported in few cases (e.g., Peterson 1977; Peterson and Andre 1980; Wilson 1980; Brenchley and Carlton 1983; Kurihara et al. 1989). The examples of competitive interaction generally involve soft-substratum dwellers, such as gastropods and polychaetes, which share access to the sediment surface (Woodin 1974, 1976; Levin 1981). Habitat displacement in soft-sediment habitats due to competition for space has been proposed to explain differences in habitat use by the SW Atlantic intertidal crabs *Chasmagnathus granulatus* and *Cyrtograpsus angulatus* (Iribarne et al. 2003; Martinetto 2006). Both crabs are common in SW Atlantic coastal and estuarine areas (i.e., Spivak 1997a, b; Iribarne et al. 1997), but only rarely are they found sharing the same microhabitat (Spivak et al. 1994; Iribarne et al. 2003). The burrowing crab *C. granulatus* is the dominant species in soft-sediments and vegetated intertidal areas from southern Brazil to the northern Argentinean Patagonia, where it produces dense and extensive burrowing beds (Boschi 2000; Spivak et al. 1994; Iribarne et al. 1997). The geographical distribution of the mud crab *C. angulatus* overlaps with *C. granulatus*, but it also inhabits areas to the south (northern and central Argentinean Patagonia; see Spivak 1997a, b; Boschi 2000; Iribarne et al. 2003). There are populations of *C. angulatus* that construct and live in burrows, generating dense burrowing beds, but this is rare when coexisting with *C. granulatus* (Iribarne et al. 2003; Palomo et al. 2007). Where both species coexist, burrowing beds of *C. angulatus* are restricted to small sandy-muddy areas. However, when *C. granulatus* were experimentally excluded within their burrowing beds, new settlers of *C. angulatus* made burrows and maintained them until they reached large size (Botto and Iribarne 1999). Other field experiments showed that adults of *C. granulatus* always displace *C. angulatus* from burrows. Furthermore, in several sites located south of the limit of distribution of *C. granulatus* at the Patagonian coast, soft intertidal areas are dominated by burrowing beds of *C. angulatus* mixed with the congener *C. altimanus* (Iribarne et al. 2003). As a result of competition, some population traits such as density (Morin 1999), size (Hesthagen and Heggenes 2003; Morin 1999), and sex ratio (Svensson et al. 2000; Boaventura et al. 2002) may be affected. For instance, abundances of *C. angulatus* could be lower in areas inhabited by *C. granulatus*; individuals of larger sizes and males may perform better than females facing an aggressive encounter (see Morin 1999) and individuals with no limb autotomies better than those with multiples

autotomies (see Juanes and Smith 1995). Despite this background information, little is known about the mechanisms of competition and how the population characteristics of *C. angulatus* are affected by competition with *C. granulatus*.

In this study, we investigated how the presence of *C. granulatus* and its burrows affect *C. angulatus*' abundance, size frequency distribution, incidence of limb autotomies, sex ratio, diet, and burrowing behavior. For this purpose, we measured these variables on crabs captured from inside and outside *C. granulatus*' burrowing bed areas and tested the hypothesis that in absence of *C. granulatus*, *C. angulatus* will use *C. granulatus*' burrows or will form their own burrows if *C. granulatus*' burrows are not available.

Materials and methods

Study site

The study was conducted in the Mar Chiquita coastal lagoon (Argentina, 37° 32'S and 57° 19'W), a body of brackish water ($\approx 46 \text{ km}^2$) affected by a microtidal regime ($\leq 1 \text{ m}$) and characterized by mudflats surrounded by a large *Spartina densiflora* marsh area (Fasano et al. 1982; Bortolus and Iribarne 1999). The burrowing crab *C. granulatus* inhabits both *S. densiflora* areas and mudflats, but our study was done in open intertidal mudflats, given that it is the area daily flooded by tides where inhabit *C. angulatus*. Surveys and experiments were carried out at the low intertidal near the mouth of the lagoon. Given that the main objective was to compare crab densities, sex ratio, size frequency distribution (sfd), incidence of limb autotomies and diet between areas, sampling was done in paired areas with active *C. granulatus* bioturbation (thereafter "crab beds") and without burrows (thereafter "outside crab beds"; see Iribarne et al. 1997, 2000; Martinetto et al. 2005). Knowing the limitations on the inference, we selected two paired (crab bed/outside crab bed) areas mainly due to logistic constraints and because they present similar tidal heights and general environmental characteristics that have been extensively described in previous works contrasting other effects of crabs (e.g., Botto and Iribarne 1999; Botto et al. 2000; Escapa et al. 2004; Martinetto et al. 2005). Crabs in these areas were sampled during January, February, March and December 2000; January, February, June, July and December 2001; and monthly from January to March 2002. During this period of time, we covered differences in salinity and water level of the lagoon due to dry and rainy weather conditions that

affect crab activity (see Iribarne et al. 2003; Martinetto 2006). Each month, samples were obtained over three to five consecutive days. The number of days varied due to weather constraints, especially in winter months.

Abundance and size of *C. granulatus* burrows

To evaluate *C. granulatus*' activity, burrow abundances and diameters were measured in each area and sampling month. Based on the tidal level, each area was divided into four intertidal zones parallel to the shore, each one limited by a drop of 0.2 m in tidal height. Burrow abundance was determined during low tide by counting the number of burrows inside ten squares (0.5 m-side) randomly distributed in each intertidal zone at both areas. Burrow sfd was calculated by measuring (accuracy 0.5 mm) 20 burrows in each intertidal zone. Differences in burrow abundance and sfd between intertidal zones and month were evaluated using a repeated measure two-way ANOVA (Zar 1999), with month as the repeated measure. Planned comparisons were used when significant interactions were found (Underwood 1997).

Abundance, size, and sexual proportion of *C. angulatus* inside and outside *C. granulatus* burrowing beds

To evaluate if the presence of *C. granulatus* affects population characteristics of *C. angulatus*, the abundances, sfd, and sex ratio of crabs were measured in both areas (inside and outside crab bed) through time. Crabs were collected using a beach seine (1 cm mesh size) towed for 50 m, parallel to the shore during flooding tide (1 h before high tide). The seine was towed during high tide by two people handling a 7 m rope, to keep a constant net opening, thus covering 350 m² each time. The captured crabs were sorted by species and sex, counted, and measured (carapace width, accuracy 0.5 mm). Because more than three consecutive days were sampled in some months, the data were unbalanced. A repeated measures two way-ANOVA Type III for unbalanced data (Shaw and Mitchell-Olds 1993) was used to evaluate the null hypothesis of no difference in catch per tow of each species between areas (inside and outside crab beds) and sampling months, using month as the repeated measure. A Kolmogorov–Smirnov test (Hollander and Wolfe 1999) was used to evaluate if sfd of each species, according to sex, differed between areas by month. To determine if the sex ratio of *C. granulatus* and *C. angulatus* differed from 1:1, the proportion of males and females was calculated in each area and month. A *Z* test (Devore

2000) was applied to evaluate the null hypothesis of no difference between proportions of males and females of each species in each area by sampling month. Differences in the sex ratio between areas were evaluated using Chi-square test (Zar 1999). When the null hypothesis of no differences between proportions was rejected, a Tukey-type test of multiple comparisons for proportions was done to identify those months when the sex ratio differed between areas (Zar 1999).

Diet of *C. angulatus* inside and outside *C. granulatus* burrowing beds

To assess whether the presence of *C. granulatus* affects the diet of *C. angulatus* and if there is overlap in the diet of both species, 10–25 crabs of each species were collected inside and outside crab beds in June and December 2001, January to March and June to July 2002. Crabs were collected during daylight hours using a beach seine and preserved in 5% formalin. The foregut of each crab was removed and stored in 70% ethanol. Carapace width and sex was recorded for each individual. Foregut contents were examined under a binocular dissecting microscope. Prey items were sorted into broad taxonomic groupings. Differences in the percentage of empty stomachs were evaluated using *Z* tests (Devore 2000). Frequency of occurrence (FO) was calculated for each prey item by dividing the number of crabs in the sample whose foregut contained a given prey by the total number of crabs in the sample with food in their stomachs. Food item proportions were compared between habitats according to sex using Chi-square test for more than two proportions (Zar 1999).

Incidence of limb autotomy in *C. angulatus* inside and outside *C. granulatus* burrowing beds

Given that *C. angulatus* have a high incidence of limb autotomy in our study site (Mar Chiquita coastal lagoon; Spivak and Politis 1989), the percentage of autotomized crabs was recorded according to sex and area. The type of limb lost (walking legs or chelae) was also recorded. *Z* tests (Devore 2000) were used to evaluate if the proportion of autotomized crabs differed between area, sex and type of limb lost for the overall data sets.

Use and construction of burrows by *C. angulatus* inside *C. granulatus* burrowing beds

To evaluate if *C. angulatus* can build burrows in areas where *C. granulatus* form burrowing beds, an inclusion/

exclusion experiment of *C. angulatus* and *C. granulatus* was performed during February 2006. Since individuals of *C. angulatus* living in burrows in central Patagonia are smaller than free living individuals in Mar Chiquita (Iribarne et al. 2003), the experiment was designed to evaluate if there are limitations to building and maintaining burrows associated with crab size. Forty inclusion fences (1 cm mesh, 40 cm side, with top and no bottom) were installed in two sites (20 inclusion fences each) with *C. granulatus* burrowing beds. The treatments were randomly assigned to: (a) inclusion of small *C. angulatus* (<2.7 cm) with a *C. granulatus* burrow, (b) inclusion of small *C. angulatus* with no burrow, (c) inclusion of large *C. angulatus* (>3.3 cm) with a *C. granulatus* burrow, and (d) inclusion of large *C. angulatus* with no burrow. The inclusion fences were revised after 5 and 15 days, to record the number of cages in each treatment with *C. angulatus* burrows or with *C. angulatus* using *C. granulatus* burrows. Data from the two sites were pooled by treatment and differences among treatments were evaluated using a Chi-square test (Zar 1999).

Results

Abundance and size of *C. granulatus* burrows

Chasmagnathus granulatus burrow densities showed significant interaction between intertidal zones and months ($df = 30$, $F = 54.287$, $P < 0.001$). The a posteriori analysis showed that from January 2000 to July 2001 burrow density was higher in the high intertidal and decreased toward lower intertidal (Fig. 1). From December 2001 to March 2002, densities were lower than other months and there were no differences between intertidal levels (Fig. 1).

Size frequency distribution of burrow diameters also showed interaction between intertidal zones and months ($df = 27$, $F = 2.897$, $P < 0.001$). The a-posteriori analysis showed that from January 2000 to June 2001, average burrow diameter increased from high to low intertidal zones (Fig. 2). From July 2001, average burrow diameters increased in the highest levels no different among the intertidal levels since January 2002 (Fig. 2).

Abundance, size, and sexual proportion of *C. angulatus* inside and outside *C. granulatus* burrowing beds

A significant interaction between area and month was observed in *C. granulatus* males ($df = 9$, $F = 12.328$, $P < 0.001$; Fig. 3a) and females ($df = 8$, $F = 23.296$, $P < 0.001$; Fig. 3b). The a posteriori analysis showed

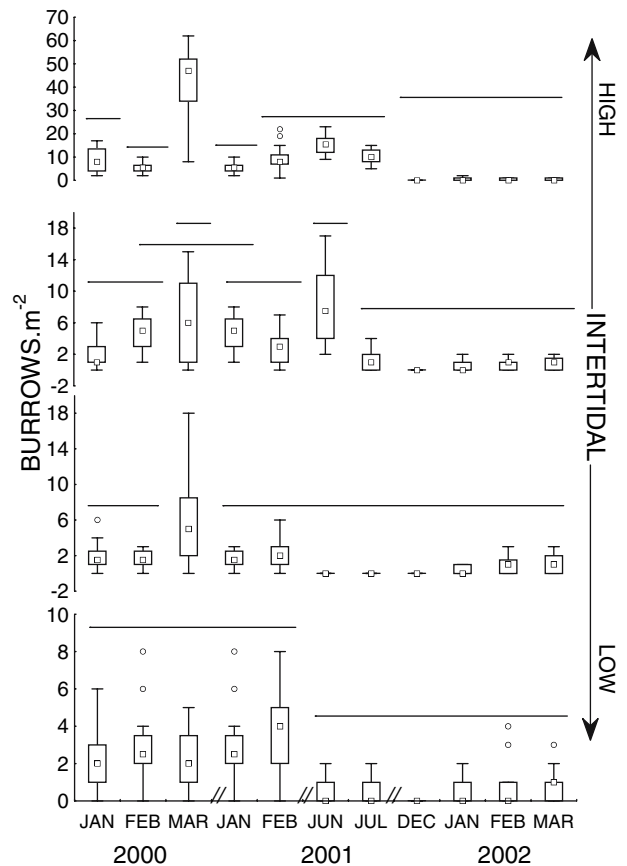


Fig. 1 *Chasmagnathus granulatus* burrow densities at four intertidal levels. Here and thereafter, box plots are constructed with limits of boxes being the 75th and 25th percentile, lines represent 10th and 90th percentiles, points inside boxes are medians, and circles are outliers. Horizontal lines indicate no significant differences

that in both cases, from January 2000 to February 2001, and in March 2002, abundances were higher in crab beds. Between June 2001 and February 2002, abundances were lower than the preceding months and there were no differences between areas. In addition, in July 2001, no individuals of *C. granulatus* were captured outside or inside the crab beds.

Cyrtograpsus angulatus males and females also showed a significant interaction between area and month (male: $df = 10$, $F = 2.598$, $P = 0.016$; Fig. 3c, female: $df = 10$, $F = 7.304$, $P < 0.001$; Fig. 3d). The a posteriori analysis showed that abundances of males and females were higher outside crab beds from January 2000 to February 2001, and in March 2002. In June and December 2001 they were more abundant in crab beds and there were no differences between areas in July 2001, and in January and February 2002.

Size frequency distribution of males of *C. granulatus* differed between areas in January 2000 and 2001, February 2001, and March 2002 with large individuals

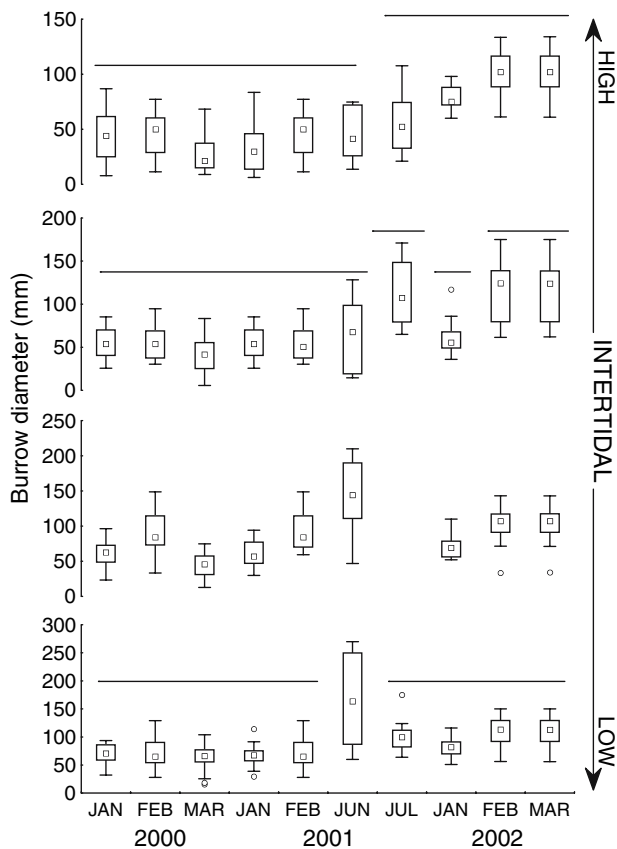


Fig. 2 Size frequency distributions of *Chasmagnathus granulatus* burrow diameters at four intertidal levels. Horizontal lines indicate no significant differences

more common outside crab beds (Fig. 4). Females of *C. granulatus* also showed a greater proportion of large sizes outside crab beds during January 2000, February 2001, and March 2002 (Fig. 4). Statistical analysis for the overall data set shows that males were larger outside crab beds ($D = 0.165$, $P = 0.004$, n inside crab bed = 362, n outside = 162) and females showed no differences ($D = 0.109$, $P = 0.149$, n inside crab bed = 523, n outside = 138).

Size frequency distribution of males of *C. angulatus* showed differences in January, February, July, and December 2001, and February 2002, with a bias towards larger sizes inside crab beds (Fig. 5). Females of *C. angulatus* also showed a greater proportion of large sizes in crab beds during January and February 2000, and January and June 2001 (Fig. 5). Statistical analysis for the overall data set shows that males ($D = 0.106$, $P = 0.009$, n inside crab bed = 471, n outside = 501) and females ($D = 0.152$, $P < 0.001$, n inside crab bed = 831, n outside = 859) were larger inside crab beds.

The sex ratio of *C. granulatus* in crab beds was biased towards males in January and March 2002 and

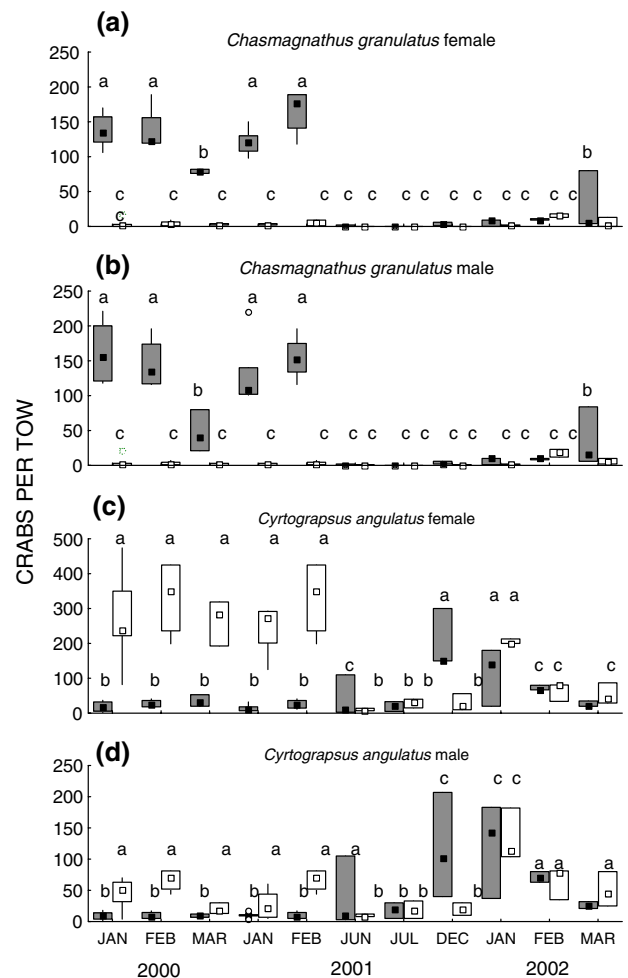
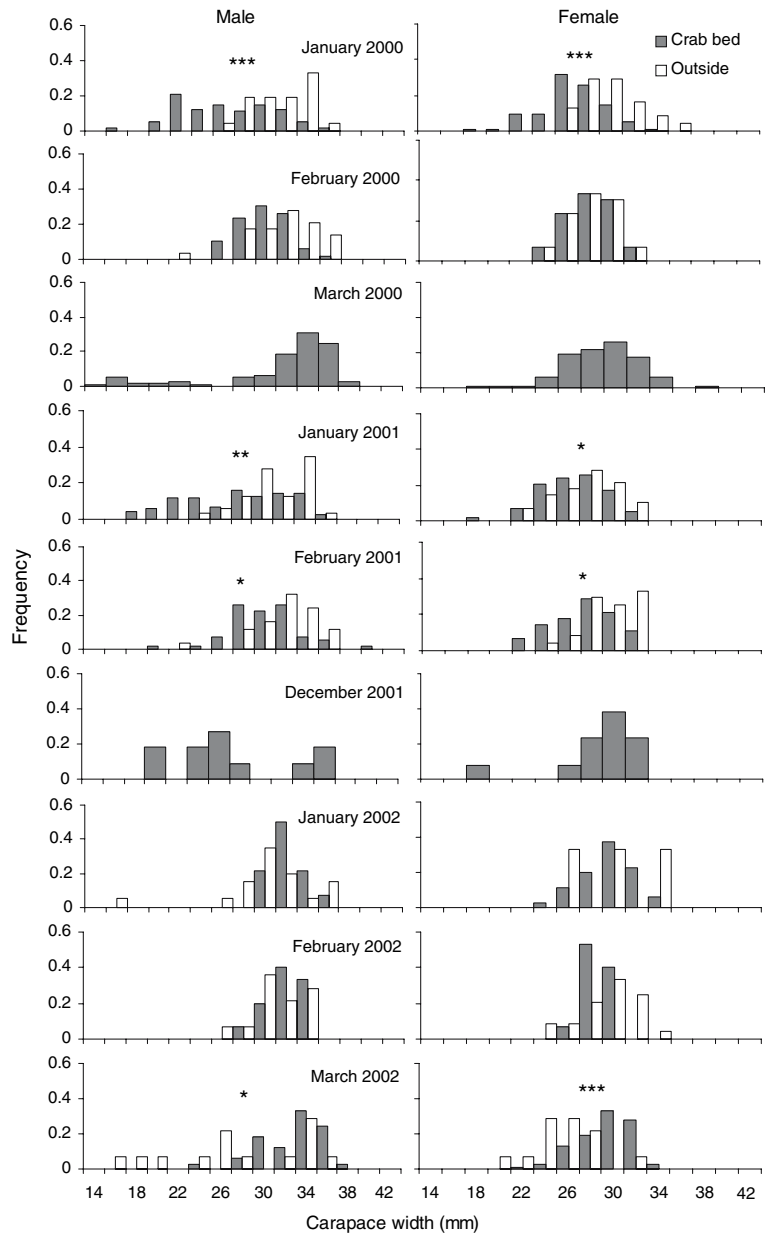


Fig. 3 *Chasmagnathus granulatus* and *Cyrtograpsus angulatus* abundances inside (filled boxes) and outside (open boxes) *C. granulatus* burrowing beds. Different letters indicate differences in abundance between areas and sampling months

towards females in March 2000 (Table 1; Fig. 6a). The sex ratio outside crab beds was biased towards males in January 2000 and March 2002 and towards females in March 2000 and, in January and February 2001 (Table 1; Fig. 6a). Overall, sex ratio of *C. granulatus* calculated for the entire study period shows no difference from 1:1 (Table 1). There was no difference between areas in the sex ratio during the study period (Fig. 6a).

The sex ratio of *C. angulatus* was biased towards males in crab beds only in January 2002. During all other months, the sex ratio was biased towards females, except that in June 2001, February and March 2002 in both areas and July 2001 in crab beds only, there was no bias (Table 1; Fig. 6b). Overall, sex ratio of *C. angulatus* calculated for the entire study period shows a higher proportion of females (Table 1). The bias towards females was higher outside than inside

Fig. 4 *Chasmagnathus granulatus* size frequency distributions (*sfd*) inside (filled bars) and outside (open bars) *C. granulatus* burrowing beds. Asterisks indicate differences in the *sfd* between areas (Kolmogorov–Smirnov test; *** $P < 0.001$, ** $P < 0.010$, * $P < 0.050$)



crab beds from January 2000 to February 2001, and in January 2002 (Fig. 6b).

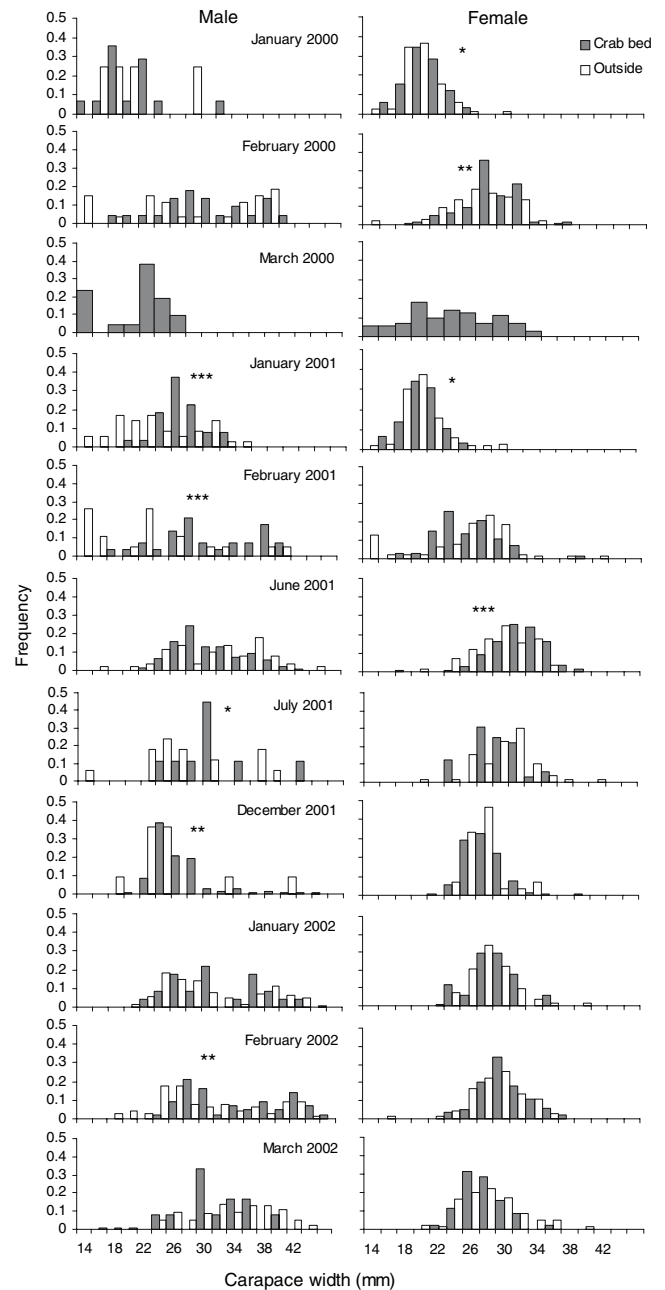
Diet of *C. angulatus* inside and outside *C. granulatus* burrowing beds

Since during winter months, abundances of *C. granulatus* were too low or even null, diet was analyzed from December 2001 to March 2002. In December, *C. granulatus* was absent outside crab bed areas. Inside crab beds, the percentage of empty stomachs was higher for females than males (Table 2). In summer 2002, the percentage of empty stomachs was higher outside than inside crab beds mainly in the case of males (Table 2).

In all cases, stomachs contained benthic microalgae and sediment; there were only three crabs (two males and one female) from inside crab beds that had polychaete pieces in their stomachs.

The percentage of empty stomachs of *C. angulatus* was higher inside crab beds for males in spring 2001 and summer 2002; and for females in summer and winter 2002 (Table 2). The percentage of empty stomachs was higher outside than inside crab beds in winter 2002 for males and in winter and spring 2001 for females (Table 2). As in *C. granulatus*, sediment and microalgae were often found in *C. angulatus* stomachs; other items such as polychaetes, crab pieces, ostracods and foraminifers were also common in their stomachs

Fig. 5 *Cyrtograpsus angulatus* size frequency distributions (*sfd*) inside (filled bars) and outside (open bars) *C. granulatus* burrowing beds. Asterisks indicate differences in the *sfd* between areas (Kolmogorov–Smirnov test; *** $P < 0.001$, ** $P < 0.010$, * $P < 0.050$)



(Table 3). The proportion of different food items was not different between areas for either sex (Table 4).

Incidence of limb autotomy in *C. angulatus* inside and outside *C. granulatus* burrowing beds

The incidence of limb autotomies in *C. angulatus* showed differences between sexes, areas, and type of lost limb (Fig. 7). The percentage of autotomized individuals was higher outside crab beds than inside for both males ($Z = -2.987$, $P = 0.001$) and females ($Z = -2.353$, $P = 0.009$). The percentage of autotomized females was higher than males both inside

($Z = 3.579$, $P = 0.001$) and outside crab beds ($Z = 2.223$, $P = 0.023$). The percentage of females with lost walking legs was higher than those for males ($Z = 5.555$, $P < 0.001$), while males showed a higher incidence of lost chelae than females ($Z = -5.105$, $P < 0.001$).

Use and construction of burrows by *C. angulatus* inside *C. granulatus* burrowing beds

The mud crab *C. angulatus* was never found using *C. granulatus*' burrows. After 5 days, 50% of the cages with small crabs and no *C. granulatus* burrows and

Table 1 *Chasmagnathus granulatus* and *Cyrtograpsus angulatus* male proportion of individuals captured from inside and outside *C. granulatus* crab bed

	<i>Chasmagnathus granulatus</i>				<i>Cyrtograpsus angulatus</i>			
	Crab bed		Outside		Crab bed		Outside	
	N	Male proportion	N	Male Proportion	N	Male proportion	N	Male proportion
January 2000	1,794	0.54	52	0.61*	168	0.28***	1,876	0.13***
February 2000	1,133	0.51	26	0.48	148	0.25***	1,588	0.17***
March 2000	379	0.35**	13	0.31**	133	0.23***	857	0.07***
January 2001	1,280	0.52	22	0.40**	123	0.44*	1,321	0.10***
February 2001	1,278	0.48	31	0.42**	141	0.28***	1,588	0.17***
June 2001	4	0.50	1	0	242	0.49	56	0.49
July 2001	0		0		113	0.49	140	0.36**
December 2001	20	0.52	1	0	948	0.34***	147	0.45*
January 2002	38	0.76**	8	0.5	702	0.58*	1,012	0.41*
February 2002	57	0.49	101	0.54	427	0.50	390	0.50
March 2002	195	0.61*	32	0.72**	153	0.51	308	0.49
Total	6,178	0.51	287	0.50	3,298	0.42*	9,283	0.20***

Asterisks indicate bias toward a 1:1 sex-ratio (Z test; * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$)

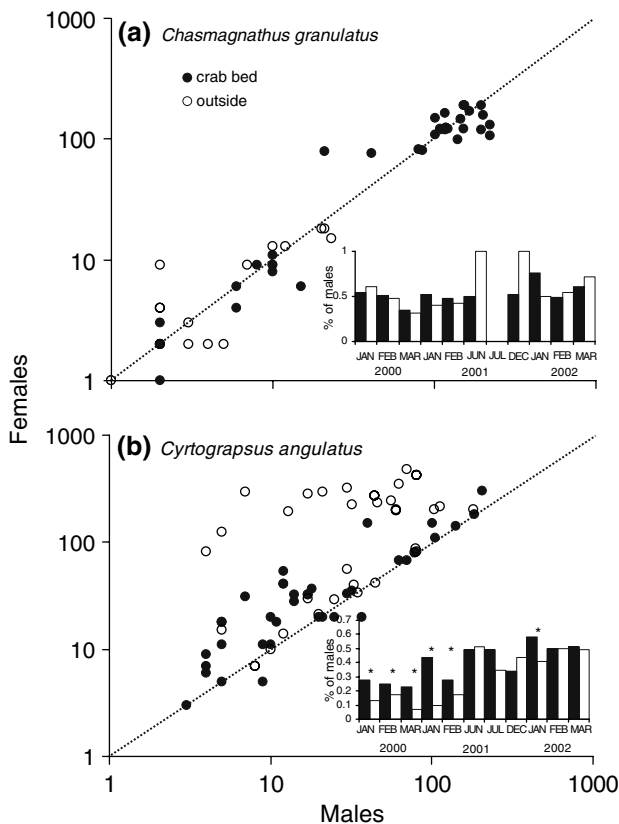


Fig. 6 *Chasmagnathus granulatus* (a) and *Cyrtograpsus angulatus* (b) sex ratio inside (black circles and bars) and outside (empty circles and bars) *C. granulatus*' burrowing beds. Asterisks indicate differences in the sex ratio between areas. The axes are in logarithmic scale

20% of the cages with large crabs and no *C. granulatus* burrows showed *C. angulatus* burrows (Fig. 8). The mud crab *C. angulatus* did not form burrows in treatments that included *C. granulatus* burrows. After

15 days, at least 1 cage in each treatment showed *C. angulatus* burrows and the percentage of cages with burrows was higher in the treatment with small crabs and no *C. granulatus* burrows (Fig. 8). Small crabs were more likely to maintain burrows than large crabs. In addition, 43% of those crabs that built burrows after 5 days and 66% of those that did not were found dead after 15 days.

Discussion

Our results show that the presence of *C. granulatus* constraints the distribution and modified the population characteristics and burrowing behavior of *C. angulatus*. Differences in abundance, sfd, sex ratio, diet, and incidence of autotomies of *C. angulatus* between inside and outside *C. granulatus* burrowing bed areas provide evidence for this.

Inside *C. granulatus*' burrowing beds, *C. angulatus* showed lower abundances, larger sizes, and a higher percentage of males than outside crab bed areas, suggesting a partitioning of habitat dominated by *C. granulatus*. This pattern shifted through the study period when densities of *C. granulatus* and its burrows were very low or even null. Densities of both *C. granulatus* and its burrows declined after December 2001. This decrease in *C. granulatus*' burrow density in mudflat areas has been related to a long rainy period with precipitation exceeding the average for this region (data from the Argentinean National Weather Forecast Service—ANWFS), during which, *C. granulatus* moved from mudflats to the salt marsh (Iribarne et al. 2003). During this period, mudflats remained mostly covered

Table 2 Percentages of *Chasmagnathus granulatus* and *Cyrtograpsus angulatus* with empty stomachs in areas with *C. granulatus* burrows (CB) and in nearby areas without burrows (OS)

	Male				Female			
	N analyzed		Percentage of empty		N analyzed		Percentage of empty	
	CB	OS	CB	OS	CB	OS	CB	OS
<i>Chasmagnathus granulatus</i>								
Spring 2001	11	0	18.18	0	13	0	23.08	0
Summer 2002	15	8	20	37.5	19	12	5.26	8.33
<i>Cyrtograpsus angulatus</i>								
Winter 2001	9	17	0	0	31	57	0	3.51
Spring 2001	14	4	14.29	0	30	16	3.33	25
Summer 2002	30	37	33.33	29.73	30	41	20	14.63
Winter 2002	33	11	6.06	9.09	20	12	10	0

Table 3 Prey item occurrence frequency in *Cyrtograpsus angulatus* stomach contents

Items	Male								Female							
	Winter 2001		Spring 2001		Summer 2002		Winter 2002		Winter 2001		Spring 2001		Summer 2002		Winter 2002	
	CB	OS	CB	OS	CB	OS	CB	OS	CB	OS	CB	OS	CB	OS	CB	OS
Sediment	0.89	0.88	0.86	0.25	0.43	0.65	0.82	0.73	1.00	0.92	0.93	0.62	0.63	0.76	0.90	0.92
Microalgae	0.44	0.41	0.29	0.50	0.10	0.19	0.54	0.64	0.55	0.32	0.27	0.19	0.37	0.39	0.60	0.50
<i>Laonereis Acuta</i>	0.11	0	0.36	0.50	0.07	0.11	0.06	0.09	0.32	0.03	0.27	0.31	0.10	0.07	0.10	0.42
<i>Neanthes succinea</i>	0	0	0	0	0	0.05	0.06	0	0	0.02	0	0.06	0.10	0	0.10	0
Crabs	0.22	0	0	0	0.33	0.30	0.24	0.18	0.16	0.09	0	0.06	0.10	0.10	0	0
Foraminifer	0.67	1.00	0.36	0.25	0.03	0.11	0	0	0.77	0.96	0.67	0.19	0.07	0.17	0	0
Ostracods	0.11	0.47	0.36	0	0.07	0.13	0	0	0.39	0.40	0.60	0.12	0.13	0.19	0.05	0
<i>C. angulatus</i> eggs	0.67	0.94	0	0	0	0	0	0	0.64	0.60	0	0	0	0.02	0	0

CB *Chasmagnathus granulatus* crab bed, OS outside *C. granulatus* crab bed areas

Table 4 Results of analysis comparing proportions of food items found in *Cyrtograpsus angulatus* stomachs from inside and outside *Chasmagnathus granulatus*' burrowing beds

	Male			Female		
	df	χ^2	P	df	χ^2	P
Winter 2001	5	4.180	0.524	7	6.785	0.452
Spring 2001	3	2.341	0.505	5	5.509	0.357
Summer 2002	7	2.778	0.905	8	0.059	1.000
Winter 2002	5	1.431	0.921	4	5.285	0.259

by freshwater, affecting crab burrowing activity (see Iribarne et al. 2003). Although we did not experimentally manipulate the abundance of *C. granulatus*, these weather-induced variations in its abundance, allowed to evaluate changes in *C. angulatus*' abundances under different *C. granulatus* densities in different areas. The decrease of *C. granulatus*' densities corresponded to an increase in *C. angulatus* density inside *C. granulatus*' burrowing areas, and no differences in sfd or sex ratio were found between different areas. Thus, the presence of *C. granulatus* seems to control the access of *C. angulatus* to these areas.

The diet analysis also suggested that *C. granulatus* controls the use of intertidal areas by *C. angulatus*. The

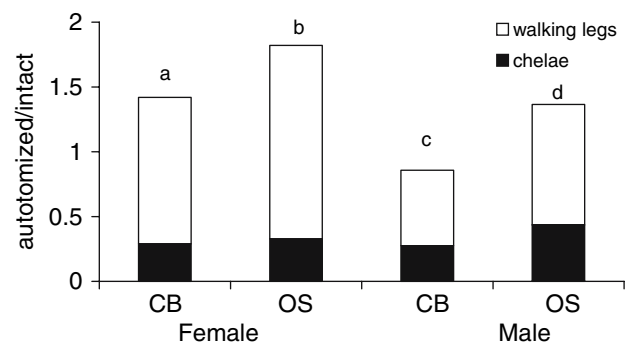


Fig. 7 Ratio between the number of intact and autotomized *Cyrtograpsus angulatus* males and females captured inside (CB) and outside (OS) *Chasmagnathus granulatus*' burrowing beds. Different letters indicate significant differences in the ratio between areas and sex

mud crab *C. angulatus* is very flexible in its diet. For instance, in a population in Dos Patos lagoon (Southern Brazil) *C. angulatus* is an omnivore, preferably consuming the eelgrass *Zostera marina* and to a lesser extent, small mollusks (*Heleobia australis* and *Erodona mactroides*) and peracarid crustaceans (Capitoli and Ortega 1993). In Caleta Valdez (northern Patagonia, Argentina), this species is mostly a deposit feeder, and

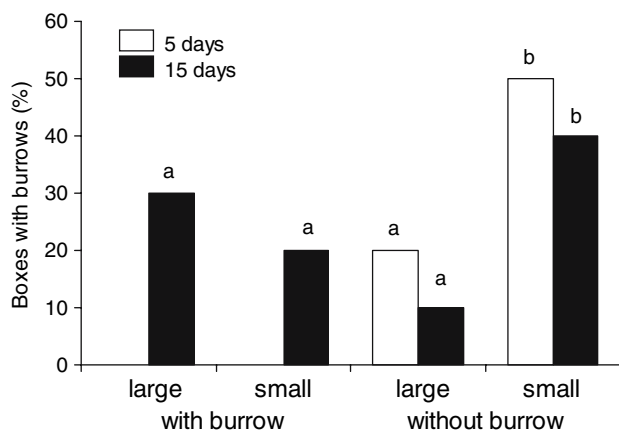


Fig. 8 Percentage of boxes with *Cyrtograpsus angulatus* burrows after 5 (open bars) and 15 (black bars) days, including large (>3.3 cm) or small (<2.7 cm) crabs, and with or without *Chasmagnathus granulatus* burrows. Different letters indicate differences among treatment (χ^2 test, $P < 0.001$)

constructs and lives in burrows forming similar burrow assemblages to those of *C. granulatus* (Palomo et al. 2003). A study performed in the inner part of Mar Chiquita lagoon on *C. angulatus* associated to reef of the polychaete *Ficopomatus enigmaticus* also showed a large variety of items consumed by this crab (Schwindt et al. 2001). Of 60 *C. angulatus* stomachs sampled, 45% contained algae, in addition to other prey items, including foraminifers, *C. angulatus* eggs, nematods, polychaetes (*Laeonereis acuta*, *Neanthes succinea*, and *Nephtys fluviatilis*), gastropods (*Heleobia conexa*), ostracods, dipters larvae, and detritus. A food web study using stable isotopes showed that the C and N signatures in *C. angulatus* do not differ between crab beds and outside areas indicating no differences in the nutrient sources used by this species (Botto et al. 2005). In contrast, the C signatures between crab species differed, indicating that different crab species assimilated different nutrient sources (Botto et al. 2005). The individuals from Mar Chiquita analyzed in our study ingested a wide range of food items including sediment and microalgae as well as polychaetes and crabs. Although the items consumed in the crab beds did not differ from those consumed outside, the percentage of empty stomachs did differ. The males of *C. angulatus* had higher frequency of empty stomachs in crab beds, but this pattern shifted to a higher frequency outside crab beds during summer and winter 2002 when *C. granulatus* was almost absent. Therefore, the presence of *C. granulatus* seems to interfere with the feeding activity of *C. angulatus*, at least in males.

The Mar Chiquita population of *C. angulatus* has been characterized as having high incidence of multiple limb autotomies (Spivak and Politis 1989). In this

study, we found that the incidence of autotomies in *C. angulatus* was higher outside than inside *C. granulatus* crab bed areas. One possible explanation for this pattern is that, only those individuals with less autotomies or without autotomies are able to deal with *C. granulatus*. But this could be also an indirect result of the dominance of *C. granulatus* relative to *C. angulatus*. Field experiments showed a positive relationship between the number of autotomies and the mortality rates in *C. angulatus* with sizes between 2.5 and 3 cm, and mortality was primarily due to cannibalism (Gavio and Iribarne 1994). Intraspecific predation has been also observed in the laboratory, mostly with juvenile crabs eating recruits (Luppi 1999) and has been proposed as a possible mechanism to explain the high incidence of autotomies in *C. angulatus* in Mar Chiquita lagoon (Spivak and Politis 1989). Indeed, we observed a higher incidence of autotomies outside crab beds, where *C. angulatus* density and small size frequencies are higher. The high incidence of autotomies observed outside crab beds could be a result of the increased abundance of *C. angulatus* in these areas, with a concomitant increase in encounters between individuals. Thus, we hypothesize that the constraints imposed by *C. granulatus* on the distribution of *C. angulatus* indirectly increase the incidence of limb autotomies.

Although sympatric occurrence of brachyuran crabs, mostly members of the families Varunidae (e.g., species of the genera *Pachygrapsus*, *Helice*, and *Hemigrapsus*, formerly in the family Grapsidae) and Ocypodidae (e.g., species of the genera *Macrophthalmus* and *Uca*), are common in estuaries, there are only few reports of interactions between these crabs (Ringold 1978, 1979; Willason 1981; Jones and Simons 1982; Kurihara et al. 1989; Daleo et al. 2003; Iribarne et al. 2003). Habitat segregation between crab species has been explained mostly by differential tolerance to desiccation, feeding habit, and burrowing adaptation related to the different substratum, but interactions such as competition and direct predation have been shown in few studies (Kurihara et al. 1989; Daleo et al. 2003). In the case of *C. granulatus* and *C. angulatus*, a combination of factors could drive habitat segregation. Although both species construct burrows, they play a key role in the life of *C. granulatus*, whereas for *C. angulatus*, burrows seem to be less important. Evidence of this is that some populations of *C. angulatus* form burrow assemblages similar to those of *C. granulatus* (e.g., in Caleta Sara and Caleta Valdez, Patagonia Argentina: Iribarne et al. 2003) but others do not, as is the case for the population from our study site and from Dos Patos lagoon (Brazil; Capitoli and Ortega 1993). The requirement of a permanent burrow for *C. granulatus* converts the stable and

compacted substratum, where it constructs burrows into a limiting resource. Indeed, our experiments showed that *C. angulatus* built burrows when *C. granulatus* was excluded and does not use *C. granulatus*' burrows when those were available. Moreover, in an experiment performed in Mar Chiquita where both species were included in cages, *C. granulatus* was observed displacing *C. angulatus* from its burrows, while the opposite was never found (Palomo et al. 2007). Therefore, the habitat for burrow construction could be the limiting resource that promotes territorial behavior in *C. granulatus*. Our results clearly show that *C. granulatus* displaces *C. angulatus* from those areas, where *C. granulatus* construct their burrows. Territorial behavior in this species has been inferred in a previous study (Iribarne et al. 2003), and aggressive encounters between male individuals of both species have been also observed in the boundary of crab bed areas with *C. granulatus* always as the dominant species (P. Martinetto, personal observation). Indeed, our results showed that only few individuals of *C. angulatus* enter *C. granulatus* crab beds, and those that were found inside crab beds seem to be the strongest (larger, with a higher proportion of males, and with a lower incidence of autotomies than those from outside crab bed). However, this pattern shifted when abundance of *C. granulatus* was very low or even null. During this period, abundances of *C. angulatus* were higher inside *C. granulatus* crab bed areas and there were no differences between areas in sfd, sex ration, incidences of autotomies, or in the percentage of empty stomachs. Thus, the area usually dominated by *C. granulatus* became an area in which *C. angulatus* was no longer constrained.

In soft-sediment habitats it is known that other factors, such as disturbance and predation, rather than competition, limit the distribution of organisms (Peterson 1979, 1991) although there is some evidence of competitive interactions among soft-bottom organisms that affect spatial distribution (see Wilson 1991). The most common explanation is that, in contrast to sessile epifauna of rocky shores, benthic species in soft bottoms are mobile enough to reduce the intensity of local competition (Peterson and Andre 1980). Beside the limitations on the inference imposed by the sampling design in this study (only two paired areas of crab bed/ outside crab bed), the results obtained were steady. Our results consistently demonstrate that competition for substrate can occur in the soft sediment intertidal areas, showing that functional traits of the non-dominant species could change.

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