Evidences of habitat displacement between two common soft-bottom SW Atlantic intertidal crabs

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Abstract

The intertidal burrowing crab *Chasmagnathus granulatus* Dana is the dominant species in soft sediments and vegetated intertidal areas along the SW Atlantic estuaries (southern Brazil 28°S to the northern Argentinean Patagonia 41°S) where it produces dense and extensive burrowing beds. The mud crab *Cyrtograpsus angulatus* Dana coexists with *Ch. granulatus* in this area, but it also inhabits areas to the south (northern and central Argentinean Patagonia). A survey covering both areas showed that *C. angulatus* rarely live in burrows when coexisting with *Ch. granulatus*, but form large burrowing beds when not coexisting with *Ch. granulatus*. When both species coexisted, burrowing beds of *C. angulatus* are restricted to sandy–muddy areas. Only rarely are burrows of *C. angulatus* found within *Ch. granulatus* beds. However, when *Ch. granulatus* were experimentally excluded within their burrowing beds, new settlers of *C. angulatus* made burrows and maintained them until they reached large size. Paired (inside and outside *Ch. granulatus* burrowing bed) sampling during high tide using beach nets showed that *C. angulatus* rarely venture inside the *Ch. granulatus* crab beds. Other field experiments showed that adults *Ch. granulatus* always displace *C. angulatus* from burrows. Furthermore, in several sites located south of the limit of distribution of *Ch. granulatus* at the Patagonian coast, soft bare intertidals are dominated by burrowing beds of *C. angulatus* mixed with the congener *C. altimanus* Dana. Together, these evidences suggest that the mud crab *C.*

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angulatus is displaced from soft bottom areas by the burrowing crab *Ch. granulatus*. It is an example of competitive exclusion through aggressive interference in soft-bottom habitats when the shared resource is the access to sediment surface, a two-dimensional well-defined resource.

1. Introduction

Vertical zonation of marine organisms in the rocky shore intertidal has yielded important insights into the role of interspecific interactions in community organization (see Menge and Branch, 2001). The general models to describe marine coastal assemblages of species have been based on the role of competition (Connell, 1961a,b, 1983), predation (Paine, 1966, 1974), disturbance (Sousa, 1979, 1980) and recently, the role of the supply of larvae (see Grosberg and Levitan, 1992 for review). There is no doubt that the supply of larvae is a key factor, but once larvae arrive, the other factors are all important (e.g. Dayton, 1971; Menge, 1976; Underwood et al., 1983). However, competition for space and direct interference within and among species is usually weaker in three-dimensional soft-substratum habitats (e.g. Peterson, 1979; Wilson, 1991), although exploitative competition for limiting food resources may be important (Lenihan and Micheli, 2001). Nevertheless, there are cases when the resource is space that competition becomes important (Wilson, 1991). Indeed, the few examples of competitive interaction among soft-substratum dwellers involve organisms that share access to the sediment such as gastropods (Levin, 1981) and suspension feeding polychaetes (Woodin, 1974, 1976), yet habitat displacement has been reported in a few cases (e.g. Peterson, 1977; Peterson and Andre, 1980; Wilson, 1980; Brenchley and Carlton, 1983). Differences in habitat use by the SW Atlantic intertidal crabs *Chasmagnathus granulatus* Dana and *Cyrtograpsus angulatus* Dana may be another example of habitat displacement in soft-substratum habitats due to competition for space. Both crabs are common in SW Atlantic coastal and estuarine areas (i.e. Spivak, 1997a,b; Iribarne et al., 1997), but they are rarely found in the same microhabitats (Iribarne et al., 1991; Spivak et al., 1994).

Soft bottom intertidals (and also salt marshes) of the SW Atlantic (southern Brazil 28°S to the San Matias Gulf 41°S, Argentina; Fig. 1) are dominated by the burrowing crab *Ch. granulatus* (Grapsoid; Boschi, 2000; D'Incao et al., 1990; Spivak et al., 1994; Iribarne et al., 1997; Bortolus and Iribarne, 1999; Botto and Iribarne, 1999, 2000; Bortolus et al., 2002). This species reaches as much as 60 mm in carapace width and excavates large (up to 20 cm diameter) semipermanent open burrows generating burrowing assemblages of many hectares (Spivak et al., 1994; Iribarne et al., 1997). Burrow density can exceed 60 crab m^{-2} extending up to 1 m into the sediment (Iribarne et al., 1997) modifying sediment characteristics and infaunal abundance (Botto and Iribarne, 1999, 2000; Bortolus and Iribarne, 1999). They are mainly deposit feeders in intertidal mud flats (creeks and channels) but herbivorous in salt marshes (Iribarne et al., 1997; Bortolus and Iribarne, 1999).
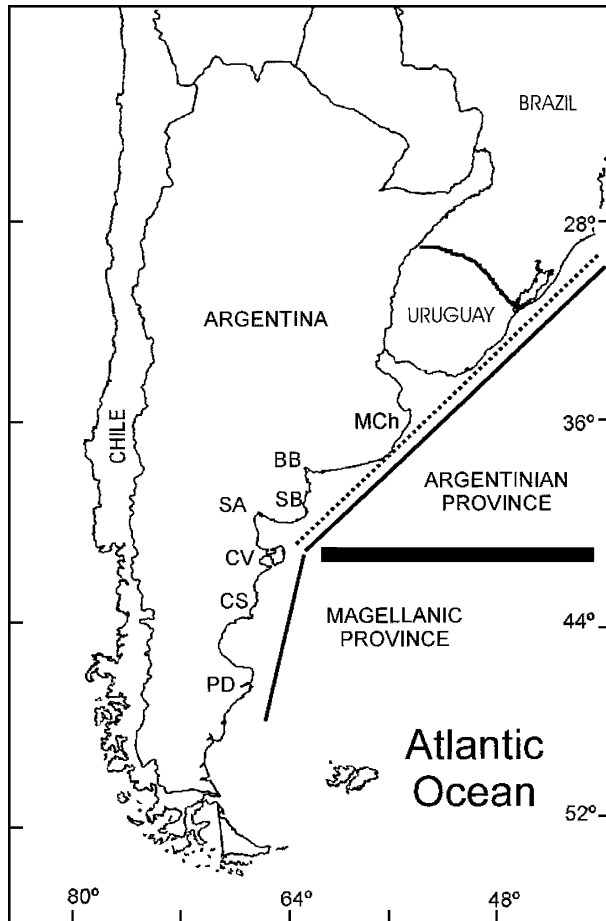
Fig. 1. Geographic distribution of *Ch. granulatus* (dotted line) and *C. angulatus* (solid line). The Argentine Province encompasses the coastal area of the northern part of Argentina, Uruguay and south of Brazil, while the Magellanic Province encompasses the Argentinean Patagonian coast. Samples were obtained from the Mar Chiquita coastal lagoon (MCh), Bahia Blanca (BB), Bahia San Blas (SB), Caleta Valdez (CV), and Caleta Sara (CS). Observations were also performed at Puerto Deseado (PD).

The grapsoid crab *C. angulatus* is similar in size, shape, and life history to *Ch. granulatus* (Boschi, 2000). In the Atlantic coast, this species lives in intertidal areas from Puerto Deseado (48°S; Argentina) to Rio de Janeiro (27°S; Brazil; Boschi, 2000; Fig. 1). This distribution encompasses two biogeographic provinces, the Argentinian Province (southern Brazil to Northern Argentinean Patagonia) and the Magellanic Province (Argentinean Patagonian coast and the south of Chile; see Spivak, 1997a,b; Boschi, 2000). Their main habitat is open-coast rocky shores, but this species also penetrates into brackish waters (Spivak, 1988). They are mainly mobile and active in the intertidal when the area is underwater, but most often they shelter under rocks or move to the shallow subtidal during low tide (Spivak et al., 1994). However, they have never

been reported as burrowers in soft-sediment habitats (see Spivak, 1988, 1990, 1997a,b; Spivak et al., 1994; Iribarne et al., 1991, 1997). Polychaetes and other crabs have been found in their stomach suggesting an omnivorous diet (Olivier et al., 1972; D'Incao et al., 1990).

Both species reproduce during spring–summer (Spivak et al., 1996) with similar reproductive output (Luppi et al., 1997). Larvae are released as zoea I that reinvade the estuarine environments approximately 1 month later as megalopae (Anger et al., 1994). Megalopae of both species are similar in size (1–2 mm carapace length) and can maneuver at the current speed usually present in their habitats (Valero et al., 1999). Based on a descriptive study comparing both species at the Mar Chiquita coastal lagoon (37°46′S, 57°27′W, Argentina; Fig. 1; Spivak et al., 1994), it has been inferred that that while *Ch. granulatus* prefer muddy soft sediments *C. angulatus* prefer rocky and structured habitats. This is indeed the pattern, but field experiments showed that when *Ch. granulatus* are excluded from their burrowing beds, new *C. angulatus* settlers constructed and lived in burrows (Botto and Iribarne, 1999). Furthermore, we have found adults living in burrows in marginal (to *Ch. granulatus*) habitats, which suggested that differences in habitat may be at least partially the result of interactions between both species.

In this study, we investigate the role of interactions between these two crabs, by combining large- and small-scale sampling, and field experiments. On a geographic scale, we explore the presence of shifts in habitat utilization in response to the lack of the other species. At a smaller spatial scale, we experimentally evaluate the role of interspecific interactions.

2. Material and methods

2.1. Study sites and sampling design

Most observations and experiments where the species are sympatric were performed at the Mar Chiquita coastal lagoon (MCh, Fig. 1). The lagoon, located along the northern Argentinean Atlantic coast (within the Argentinean Biogeographic Province, sensu Boschi, 2000), is a 46-km^2 body of brackish water affected by a semidiurnal tidal regime and characterized by mud flats and a large surrounding cord grass area (*Spartina densiflora* Brongn., Iribarne et al., 1997; Bortolus and Iribarne, 1999; Botto and Iribarne, 1999, 2000). Parts of the inner lagoon are covered by patches of the sea grass *Ruppia maritima* Linne (Bortolus et al., 1998). Intertidals of Bahia Blanca (BB, 38°53′S), Bahia San Blas (SB, 40°33′S) and Bahia San Antonio (SA, 40°48′S, Fig. 1) were also sampled.

Observations where only *C. angulatus* is present were performed at three sites of the Argentinean Patagonian coast, Caleta Valdez (CV, 42°S), Caleta Sara (CS, 44°S) and Puerto Deseado (PD, 47°45′S; Fig. 1), all south of the southern limit of distribution of *Ch. granulatus* and within the Magellanic Biogeographic Province (sensu Boschi, 2000; Fig. 1). These are sheltered areas with low wave energy and soft-bottom intertidal habitats.

2.2. C. angulatus burrowing beds within the Argentine Biogeographic Province

Sampling was done to identify areas inside the Mar Chiquita coastal lagoon where *C. angulatus* live in burrows. For this purpose, the lagoon was divided in three different sampling strata: (a) burrowing beds of *Ch. granulatus*, (b) patches of the sea grass *R. maritima* (see Bortolus et al., 1998), and (c) open areas without any of the other conditions. In each area, we randomly allocated at least 100 sampling units (1×1 m), and in each of these units, we counted the number of burrows of *C. angulatus*. The area was also excavated up to 0.5 m depth to avoid bias due to unnoticed buried crabs. Crab burrow entrances (maximum and minimum diameter), distance between them if there were more than one, burrow depth and carapace width of crabs found inside were also measured to the nearest millimeter. To evaluate spatial distribution of burrows in each stratum, we used a simple measure of S.D./x, but in order to see if the pattern was consistent across scales we also sampled changing the sampling frame up to 5×5 m.

Given that burrows of *C. angulatus* were found in only two of the strata previously described, their densities were compared using *t*-test with separate variances (thereafter t_c; Zar, 1999). The relationship between carapace width and crab burrow entrances or burrow depth was evaluated with correlation analysis (Zar, 1999). The size frequency distributions of crabs found in these areas were compared with a Kolmogoroff–Smirnoff test (Zar, 1999).

To evaluate if burrows were associated with particular sediment type, samples of the sediment (10 replicates per area; 10 cm diameter and 10 cm depth) were obtained from each stratum to evaluate grain size distribution by sieve and sedimentation analysis (Carver, 1971). With this methodology, the grains were separated in 2–1 mm (very coarse sand), 1–0.5 mm (coarse sand), 05–0.25 mm (medium sand), 0.25–0.125 mm (fine sand) and <0.0625 mm (very fine sand). We used the pipette technique to separate the smaller fraction in: 0.0625–0.0313, 0.0313–0.0156, 0.0156–0.00078, 0.0078–0.0039 and <0.00039 mm (silt–clay grain size distribution). Samples were then compared by pairs using a Kolmogoroff–Smirnoff test (Zar, 1999). Characteristics of burrows of *Ch. granulatus* have been exhaustively described before (Iribarne et al., 1997; Botto and Iribarne, 2000) and will not be described here.

Intertidals of Bahia Blanca (BB), Bahia San Blas (SB) and Bahia San Antonio (SA, Fig. 1) were also sampled to evaluate density of *Ch. granulatus* in soft-bottom areas, and to investigate if *C. angulatus* live in burrows. In all cases, at least five beds of *Ch. granulatus* burrows and nearby areas without crabs were sampled as described before in order to evaluate burrow density and to identify their inhabitants.

2.3. Habitat use of C. angulatus in areas with burrowing beds of Ch. granulatus

We evaluated the extent to which *C. angulatus* uses the burrowing beds of *Ch. granulatus* during high tide, and the relationship between densities of both crab species. A 15-m beach seine was used to sample these and nearby (separated by less than 50 m) areas without burrows at the same intertidal level (0.5 m above low tide level) of the Mar Chiquita coastal lagoon. Three similar paired areas were monthly sampled (one seining per habitat) from January 2000 to March 2002 to compare the relative abundances of both crab

species in both areas. Although this sampling may underestimate *Ch. granulatus* density in their burrowing bed, it serves to evaluate habitat use of *C. angulatus*. Samples were obtained monthly during summer, which is the higher crab activity period, and roughly bimonthly during winter due to low crab activity (see Spivak et al., 1994, 1996) and our own logistic constraints. These samples were obtained during ebbing tide. Each time, the net was towed 50 m by two people, and an 8-m rope tied to both handling bars was used to keep a constant net opening (covering 400 m^2). Seining was performed following previously demarcated paths at a constant tidal height. In each habitat (inside or outside the crab beds) sampled with the beach seine, 10 replicates of 1 m^2 area were randomly located during low tide to count the numbers of crab burrows and the crab species occupying them. Crab and burrow densities were compared between months and areas with a two-way ANOVA test. A log transformation was performed to adjust ANOVA assumptions. A posteriori LSD tests were used when necessary (Zar, 1999). All crabs were sexed and measured and the mean sizes of crabs inside and outside were compared with t_c-test (Zar, 1999).

2.4. Field experiments

To evaluate direct interaction between crab species, several experiments were performed in the intertidal habitats of the Mar Chiquita coastal lagoon. An experiment was performed to evaluate the success of new recruits of *C. angulatus* when their adults and adults of *Ch. granulatus* were present, and also to evaluate to what extent they constructed burrows. The experiment lasted 40 days (from March 2, 1999 until the recruitment period ended) and consisted of three treatments (10 replicates for each one): (1) inclusion of *Ch. granulatus*, (2) inclusion of *C. angulatus*, and (3) exclusion of adults of both crab species. Wire cages (50 × 50-cm area, 20 cm high, with a mesh size of 5 mm) were inserted 10 cm into the sediment so that crabs could not escape. After recruitment occurred, we counted the numbers of first-instars crabs that had recruited and the numbers of burrows constructed. No statistical test was necessary to test the hypothesis of no difference between treatments (see Results).

To evaluate if adults of *C. angulatus* are able to construct burrows, an experiment was performed which consisted of inclusion of adult crabs inside completely closed wire cages (10 replicates) as described above. In each cage, six individuals (three males and three females) within a size range of 30 to 35 mm were included. After a week, cages were inspected and the numbers of burrows constructed was counted.

An experiment was also performed to evaluate the effect of the inclusion of *Ch. granulatus* in *C. angulatus* burrowing beds. The experiment was performed in an intertidal habitat densely populated by the sea grass *R. maritima* (see Bortolus et al., 1998) with high density (up to 8 crab m^{-2}) of *C. angulatus* burrows. In these areas, exclusion cages were deployed with two treatments (10 replicate each one): (1) cages including undisturbed *C. angulatus* burrows and crabs, and (2) cages with *C. angulatus* burrows and crabs, where we added one *Ch. granulatus*. The experiment was run during 1 week, and at the end, we counted the number of *C. angulatus* that had lost their burrows in both treatments. The null hypothesis of no difference in the use of burrows by *C. angulatus* when *Ch. granulatus* was present was evaluated with a t_c-test (Zar, 1999).

An experiment was performed to evaluate colonization and maintenance of artificial burrows by adult *C. angulatus* inside and outside (but nearby) *Ch. granulatus* burrowing bed. Artificial burrows (10 cm diameter by 20 cm depth) similar to those used by crabs were built at two sites less than 50 m apart and in areas where burrowing beds of *Ch. granulatus* are common. One hundred artificial burrows were constructed inside three beds of *Ch. granulatus* and the same amount was constructed outside these areas. During 1 week, burrows were daily inspected to identify their crab inhabitants. A binomial test was used to evaluate the null hypothesis of no difference in the daily frequency of use of burrows by *C. angulatus* and *Ch. granulatus*.

2.5. Location and characterization of beds of C. angulatus south of the distributional limit of Ch. granulatus

To examine the hypothesis that *C. angulatus* use different habitats when *Ch. granulatus* is not present, surveys were performed in areas where both species are allopatric. *Ch. granulatus* has its southern distributional limit at the San Matias gulf (41°S), but *C. angulatus* has a much southern distribution encompassing the Magellanic Biogeographic province (Spivak, 1997a,b; Boschi, 2000; Fig. 1). Taking advantage on this difference, we investigated the habitat characteristics of *C. angulatus* at Caleta Valdez (CV) a site located at the tip of the Valdez Peninsula (Fig. 1), at Caleta Sara (CS) and at Puerto Deseado (PD), areas where *Ch. granulatus* is not present. In these areas, soft-bottom intertidal inlets were explored and crab habitats were recorded, paying attention to the presence of burrows and burrowing beds. When found, burrows and crabs were measured as previously described. Samples of sediments were also obtained from these sites and grain size analysis was then performed as described before.

3. Results

3.1. C. angulatus burrowing beds within the Argentine Biogeographic Province

Within the Mar Chiquita coastal lagoon, the study area where both crabs geographic distribution overlaps, a burrowing bed of *C. angulatus* was found in an area dominated by the seagrass *R. maritima* (see Fig. 1 in Bortolus et al., 1998). This area is located in the inner lagoon covering more than 13% of the lagoon area (Bortolus et al., 1998) with high-density patches. Mean density of *C. angulatus* burrows was 2.7 burrows m^{-2} (S.D. = 2.6, $n = 40$) and distribution of burrows was homogeneous (S.D./$x = 0.96$). Within the area dominated by *R. maritima*, this pattern held when the sampling frame was changed up to 5×5 m (2×2 m = 0.89, 5×5 m = 1.02). Most of these burrows (95%, $n = 150$) showed two entrances separated by a variable distance (up to 50 cm) with a perpendicular chamber (94% of them) in the middle of the tunnel, where the crab was usually sheltering. The distance between both entrances was positively correlated with entrance diameter ($r^2 = 0.68$, $n = 150$, $P < 0.05$). The ceiling of the straight tunnel that connected both entrances was usually the seagrass rhizome system, although the chamber was dug deeper (up to 30 cm) into the sediment. Some of the burrows (5%, $n = 100$) showed only one

entrance that spiraled into the sediment up to 35 cm depth. This tunnel was similar to the chamber found in the other burrows.

Density of burrows of *C. angulatus* in the area not covered by *R. maritima* was significantly lower ($x = 0.07$ burrows m^{-2}, S.D. $= 0.26$, $n = 10$; $t_c = 6.31$, $df = 44$, $P < 0.05$). These burrows had two entrances, and the distance between them was on average only 2.5 times the width of the burrow entrances (S.D. $= 0.6$, $n = 60$). Burrows were sparsely distributed and in patches (S.D./$x = 3.71$). Crab carapace width was positively correlated with burrow diameter ($r^2 = 0.23$, $n = 59$, $P < 0.0001$, Fig. 2A) and with burrow depth ($r^2 = 0.48$, $n = 60$, $P < 0.0001$, Fig. 2B).

Size-frequency distribution of crabs showed a mean size of 22.2 mm (S.D. $= 4.5$, $n = 100$) and not different between sites (K–S, $D = 0.24$, $n_1 = 62$, $n_2 = 25$; $P > 0.05$; Fig. 3 compare Mar Chiquita with Mar Chiquita-Ruppia). Few *Ch. granulatus* were found inside these burrows (0.3%; $n = 340$ burrows), although density of *Ch. granulatus* in the upper intertidal partially covered by *S. densiflora* (located less than 100 m away) was high ($x = 43$ crab m^{-2}, S.D. $= 12$, $n = 80$).

Sediment grain size in the *R. maritima* beds was finer than outside (K–S, $D = 17, 4$, $n_1 = n_2 = 100$, $P < 0.05$). Both areas were characterized by high proportion of sand (81% in *R. maritima* bed and 72% outside), but the proportion of silt and clay were higher in
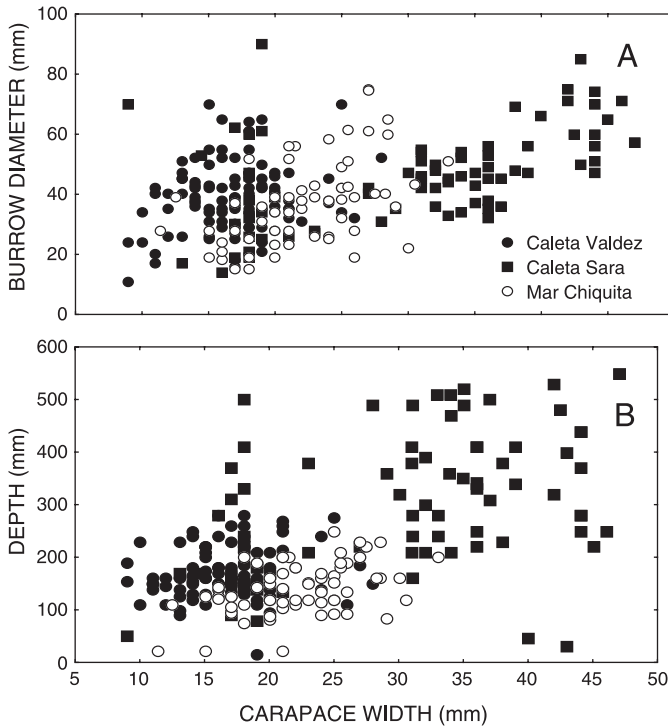

Fig. 2. Relationship between carapace width (mm) of *C. angulatus* and burrow diameter (A), and burrow depth (B) at Caleta Valdez (black circles), Caleta Sara (black squares) and Mar Chiquita coastal lagoon (empty circles).
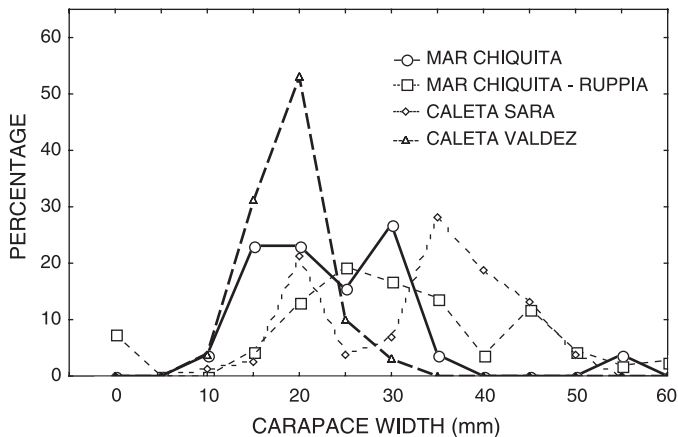
Fig. 3. Size frequency distribution of *C. angulatus* found in the burrowing beds of *Ch. granulatus* at Mar Chiquita coastal lagoon (circle), in the open area of the same lagoon (square), at Caleta Valdez (triangle), and at Caleta Sara (diamond).

vegetated areas (16% in *R. maritima* bed and 10% outside), while the proportion of gravel was higher outside (18%) the *R. maritima* bed (3%). However, these sediments were coarser than those obtained from nearby mud flat areas inhabited by *Ch. granulatus* (K−S, $D = 24$, 4, $n_1 = n_2 = 100$, $P < 0.05$).

All crab burrowing beds found at Bahia Blanca, Bahia San Blas and Bahia San Antonio were exclusively inhabited by *Ch. granulatus*. All sites are sheltered tidal bays with very low or no freshwater input. The seagrass *R. maritima* was not found in any of those sites. Density of *Ch. granulatus* inside burrowing beds at Bahia Blanca was 98 crabs m^{-2} (S.D. = 23, $n = 100$), 79 crabs m^{-2} (S.D. = 14, $n = 100$) in Bahia San Blas and 70 crabs m^{-2} (S.D. = 12, $n = 100$) in Bahia San Antonio. *C. angulatus* was generally restricted to areas underneath rocks, or they were wandering in shallow water tidal channels. However, flat areas located at the lower intertidals of Bahia San Blas showed extensive areas with 1.4 burrows m^{-2} (S.D. = 0.2, $n = 200$) of *C. angulatus*. The area is characterized by a high proportion of sand (82%), and low proportion of silt (16%) and gravel (2%). Burrowing beds of *Ch. granulatus* in this area were in the upper portion of the intertidal, areas with sediment grain size similar to those reported for Mar Chiquita, Bahia Samborombom and Bahia Blanca (see Iribarne et al., 1997; Botto and Iribarne, 2000).

3.2. Habitat use of C. angulatus in areas with burrowing beds of Ch. granulatus

Ch. granulatus burrow density during the sampling period was in general high inside burrowing beds, but reached low values during winter (JUN 01 and JUL 01) and during the summer 2001–2002 (Fig. 4A). This is interesting because these samples were obtained after a long rainy winter–spring season, when the crab beds have been reduced to very low density of *Ch. granulatus* with crabs moving into the marsh (Martinetto, personal observation). Thus, the area usually dominated by a bed of *Ch. granulatus* became a
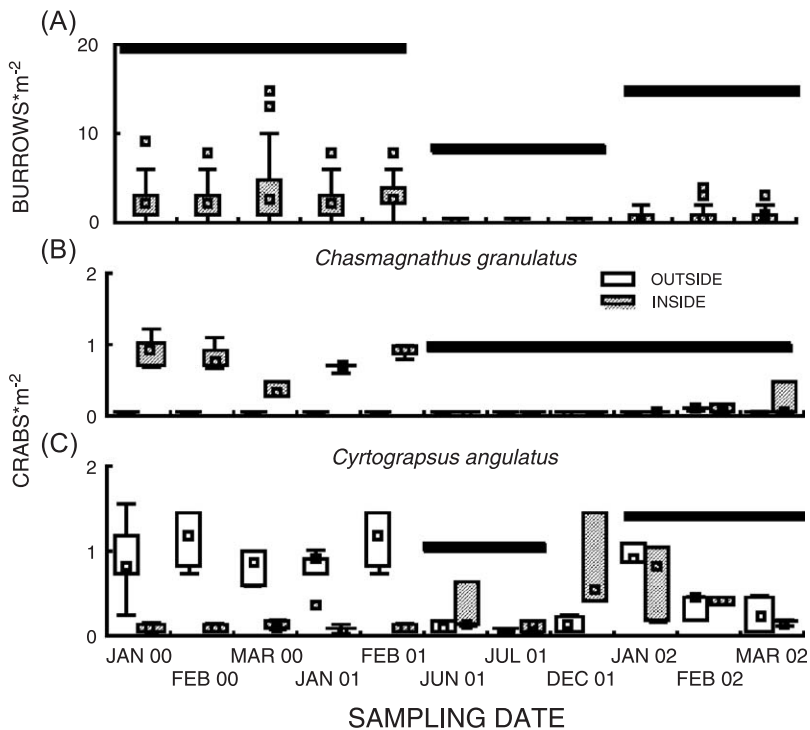
Fig. 4. Density of burrows of *Ch. granulatus* (A) and, density of *Ch. granulatus* (B) and *C. angulatus* (C) obtained with the seine netting inside (CRAB BED) and outside (OUTSIDE) the crab beds of *Ch. granulatus*. A two-way ANOVA test was used to compare densities between areas and months. A posteriori LSD test was performed to detect differences. Horizontal black lines encompass pairs of no significant differences between *Ch. granulatus* burrow densities (upper figure) or in densities between habitats for each species ($P > 0.05$). Box plots are constructed with limits of boxes being the 75th and 25th percentiles, lines represents 10th and 90th percentiles. Marks inside boxes are medians.

bare intertidal flat. *Ch. granulatus* was always restricted to the burrowing bed, their densities outside being very low.

Paired beach-seining samples performed during high tide showed that density of *C. angulatus* was always near zero inside the *Ch. granulatus* beds although their densities outside were similar to densities of *Ch. granulatus* (Fig. 4B,C). There is a small increase in the use of the *Ch. granulatus* bed by *C. angulatus* in winter (JUN 01, JUL 01 in Fig. 4B,C), when activity of *Ch. granulatus* decreased (Spivak et al., 1996). However, a sample obtained during the summer 2001–2002 (since DEC 01 in Fig. 4C) shows an increment of density of *C. angulatus* inside crab beds.

C. angulatus of both sexes were larger in the *Ch. granulatus* beds than outside (males: inside = 25.29 mm, S.D. = 7.14, $n = 113$; outside = 22.45 mm, S.D. = 7.07, $n = 133$; $t_c = 3.12$, $P < 0.01$; females: inside = 24.86 mm, S.D. = 4.4, $n = 134$; outside = 19.14 mm, S.D. = 2.7, $n = 276$; $t_c = 13.81$, $P < 0.01$). Soft molting and mating pairs of *C. angulatus* were never found in these areas.

3.3. Field experiments

Juveniles of the crab *C. angulatus* were found only in the cages that excluded adult crabs (density: $x = 165$ ind m^{-2}, S.D. $= 46.7$, $n = 10$). They constructed a network of superficial burrows (up to 2 cm deep) covering the entire surface of the caged substrata. This pattern of burrow construction has never been observed before in any part of the mudflat and is different from burrows built by juveniles *Ch. granulatus*.

The field inclusion experiment showed that 40% ($n = 60$) of the adult *C. angulatus* crabs constructed burrows that were similar in shape to those found in the *R. maritima* patch. The result of the inclusion of *Ch. granulatus* in burrowing beds of *C. angulatus* showed that *Ch. granulatus* always ($n = 10$) displaced *C. angulatus* from their burrows.

Burrow colonization in areas with *Ch. granulatus* was always by *Ch. granulatus*; however, outside their beds first colonizers were *C. angulatus* (80%) although they were replaced soon by *Ch. granulatus* (60% in 24 hours; $P < 0.05$). Three days after starting the experiment, all crabs inhabiting burrows were *Ch. granulatus*.

3.4. Location and characterization of beds of C. angulatus south of the distributional limit of Ch. granulatus

Large intertidal burrow assemblages were found at the end of the Caleta Valdez (Valdez Peninsula) and in Caleta Sara (Fig. 1), both areas have low wave energy. Sediments from Caleta Valdez (K–S, $D = 32.8$; $P < 0.05$) and Caleta Sara (K–S, $D = 28.8$; $P < 0.05$) were silty clay similar to the *Ch. granulatus* beds at Mar Chiquita (see Botto and Iribarne, 2000). Density of burrows was 46.3 burrows m^{-2} (S.D. $= 15.6$, $n = 60$) covering a total area of more than 6 ha in Caleta Valdez, and 33.01 burrows m^{-2} (S.D. $= 2.7$, $n = 60$) in Caleta Sara covering a total area of more than 3 ha. In both sites, burrows showed mainly one entrance (96%). These entrances were in general a simple straight tunnel (not a funnel shape) and 32% of them (S.D. $= 4\%$, $n = 150$) showed a chimney shape structure extending above the sediment up to 10 cm. Similar crab beds were found at the estuary of Puerto Deseado (PD in Fig. 1). In all these sites, there were also individuals of *C. altimanus* living in similar burrows.

Carapace width of crabs was not correlated with burrow diameter ($r^2 = 0.07$, $n = 99$, $P > 0.05$) or depth ($r^2 = 0.01$, $n = 99$, $P > 0.05$, Fig. 2) in Caleta Valdez, likely due to the small range of sizes. However, at Caleta Sara crab carapace width was positively correlated with burrow diameter ($r^2 = 0.24$, $n = 77$, $P < 0.0001$) and with burrow depth ($r^2 = 0.33$, $n = 77$, $P < 0.0001$, Fig. 2).

4. Discussion

Sympatric occurrence of brachyuran crabs, usually involving members of the families Grapsoid and/or Ocypodidae, are common (e.g. Snelling, 1959; Boschi, 2000; Bacon, 1971; Bright and Hogue, 1972; Abele, 1973; Crane, 1975; Zucker, 1978; Spivak et al., 1994; Omori et al., 1997). *Ch. granulatus* and *C. angulatus* are also sympatric over much of their geographic distributions and occur in the same general habitats but rarely co-occur

on a microhabitat scale. However, a strong shift in microhabitat use when species are sympatric like the one described here has never been reported before and is consistent with those predicted by interspecific competition.

If the resource is limited, accepting resource partitioning, as evidence for competition may be circular given that, partitioning must occur to allow similar species to coexist (Peters, 1976; Connor and Simberloff, 1979; Dunham, 1980). In any case, habitat segregation is one of the most important means by which ecologically similar species partition resources (Schoener, 1974). As a result, shifts in habitat use by species when similar forms are absent provide some of the strongest evidence for the action of competition in structuring communities (Connell, 1983; Schoener, 1983). Based on our observations (i.e., comparison of habitat use between areas of sympatry and allopatry), there is strong evidence that *Ch. granulatus* displaces *C. angulatus* from soft-bottom habitats. Contrary to the common belief (see Iribarne et al., 1991; Spivak et al., 1994), the mud crab *C. angulatus* constructs burrows and, in areas where *Ch. granulatus* is absent, generates dense burrowing assemblages in soft-bottom intertidal otherwise used by *Ch. granulatus*. These burrows are very similar in shape and size to those of *Ch. granulatus* (see Iribarne et al., 1997). This pattern suggests that *Ch. granulatus* displaces *C. angulatus* from soft bottom areas located within the Argentine Province.

Where both species coexist, small patches of burrows of *C. angulatus* are restricted to coarser sediments, as happens in Mar Chiquita coastal lagoon (MCh) and San Blas (SB). However, when *Ch. granulatus* are excluded, new settlers and adults construct burrows. The success of new settlers of *C. angulatus* is affected by adults of both species (Botto and Iribarne, 1999). The smallest juveniles of *C. angulatus* have always been reported to reach higher densities in highly structured habitats, such as the reefs of the polychaete *Ficopomatus enigmaticus* Fauvel with recruitments of up to 4800 individuals m^{-2} (Spivak et al., 1994; Schwindt and Iribarne, 2000). However, our results here and elsewhere (Botto and Iribarne, 1999) show that when adult crabs are excluded, new settlers successfully recruit in bare soft-bottom habitats.

Why does *Ch. granulatus* displace *C. angulatus*? Our results show that competition for burrows, or habitat for their construction, is dominated by *Ch. granulatus*. Only in habitats where *Ch. granulatus* were not present, outside of their distribution range or in areas of low wave energy but with relatively coarser sediment, were *C. angulatus* burrowing beds constructed. The ultimate mechanism of competition is unknown, but based on our results we infer that *Ch. granulatus* have territorial behavior. Indeed the seine sampling showed that only rarely does *C. angulatus* venture inside *Ch. granulatus* beds. Those that venture were always the larger crabs of their sex. However, when activity of *Ch. granulatus* decreases during the winter period, *C. angulatus* used their area more frequently. Moreover, samples obtained after a long rainy winter–spring season showed that the crab beds have been reduced to very low density of *Ch. granulatus* with individuals moving into the marsh (Martinetto, personal observation). Thus, the area usually dominated by a bed of *Ch. granulatus* became a bare intertidal flat and there was a notorious increase in the use of these areas by *C. angulatus*. *Ch. granulatus* was always restricted to the burrowing bed, being their densities outside very low. Moreover, in the different experiments where burrows were offered as limiting resources, the winner was always *Ch. granulatus*.

It is generally agreed that in intertidal habitats where space is limited, dominant competitors displace competitive subordinates to refuge habitats (Connell, 1972). This is a robust description of spatial competition among seaweed and sessile invertebrates on rocky shores, mainly at low intertidal heights and in subtidal habitats (i.e. Connell, 1972; Lubchenco and Gaines, 1981; Buss, 1986; Keddy, 1989; Goldberg and Barton, 1992). However, most evidence to date has shown that organisms that live in three-dimensional soft-sediments habitats are an exception to this rule, mainly because other factors, such as disturbance and predation, limit these organisms (Peterson, 1979, 1991). Benthic infaunal species living in soft sediments posses enough mobility to reduce the intensity of local competition. This mobility difference with sessile epifauna of rocky shores may even help to demonstrate that space is the potential limited resource in rocky shores, while it is difficult to distinguish space from food in soft-bottom interactions (Peterson and Andre, 1980). Nevertheless, there are cases of competitive interaction among soft-bottom organisms that affect spatial distribution, and the best examples involve organisms that share access to the sediment surface (see Woodin, 1976). These species are not strongly influenced by the three-dimensional nature of soft sediments. The homogeneous spatial distribution of polychaetes that share the access to the sediment surface has been shown to be the result of density-dependent migration (Levin, 1981; Ambrose, 1984). These individuals feed with their tentacles on the surface, and the regular spacing is due to the avoidance of being in contact one with another (Levin, 1981). There are also examples of habitat shifts over geographic scales. One good example is the mud snail *Hydrobia totteni* Morrison that occurs at both high and low intertidal in Europe, but is restricted to high intertidal on the Atlantic coast of North America, where the low intertidal is occupied by another mud snail *Ilyanassa obsoleta* Say (Levinton, 1981, 1985). The interaction between *Ch. granulatus* and *C. angulatus* is additional evidence of a competitive exclusion when the shared resource is the access to the sediment surface, a two-dimensional well-defined resource.

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