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Distribution and habitat preferences of two grapsid crab species in Mar Chiquita Lagoon (Province of Buenos Aires, Argentina)

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ABSTRACT: *Cyrtograpsus angulatus* and *Chasmagnathus granulata* (Grapsidae) are the two dominant decapod crustacean species in the outer parts of Mar Chiquita Lagoon, the southernmost in a series of coastal lagoons that occur along the temperate Atlantic coasts of South America. Distribution and habitat preferences (water and sediment type) in these crab species were studied in late spring. There is evidence of ontogenetic changes in habitat selection of both species. Recruitment of *C. angulatus* takes place mainly in crevices of tube-building polychaete (*Ficopomatus enigmaticus*) "reefs" and, to a lesser extent, also in other protected microhabitats (under stones). In the latter, mostly somewhat larger juveniles were found, suggesting that these are used as a refuge for growing individuals. Adults are most frequently found on unprotected muddy and sandy beaches. *C. angulatus* was found in all parts of Mar Chiquita Lagoon, including freshwater, brackish, and marine habitats. *C. granulata*, in contrast, was restricted to the lower parts of the lagoon, where brackish water predominates and freshwater or marine conditions occur only exceptionally. It showed highest population density on "dry mud" flats and in *Spartina densiflora* grassland, where it can build stable burrows and where high contents of organic matter occur in the sediment. Such habitats are characterized by mixed populations of juveniles (including newly settled recruits) and adults, males and females (including a high percentage of ovigerous). Unstable "wet mud" as well as stony sand were found to be inhabited by chiefly adult populations, with only few ovigerous females. In "dry mud" flats, the proportion of males increased vertically with increasing level in the intertidal zone, showing a significantly increasing trend also in their average body size. These observations may be explained by higher resistance of males, in particular of large individuals, to desiccation, salinity, and temperature stress occurring in the upper intertidal. However, an opposite, or no such, tendency was found in the distribution of ovigerous and non-ovigerous females, respectively. With increasing distance from the water edge, salinity increased and pH decreased significantly in *C. granulata* burrows, whereas temperature showed no consistent tendency within the intertidal gradient. A highly significant linear relationship ($r = -0.794$; $P < 0.001$) between salinity and pH in water from crab burrows is described. This regression line is significantly different from one that had been observed in water from the lagoon, indicating consistently lower pH values at any salinity level in burrow water. This is interpreted as a result of crab and/or microbial respiration.

INTRODUCTION

Salt marshes consisting of terrestrial halophytes fringe the intertidal zone of muddy and sandy shores in estuarine and protected coastal areas in temperate and cold regions.

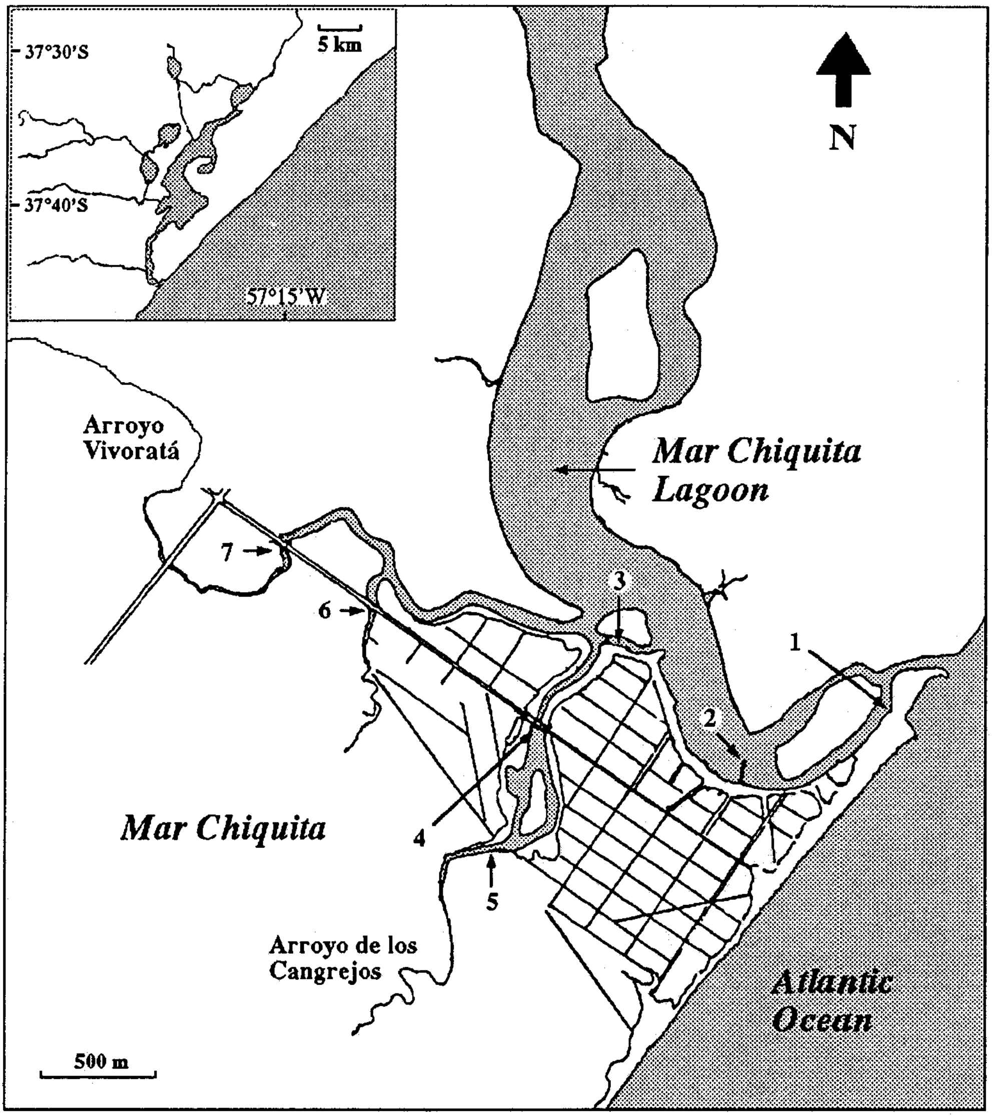

Fig. 1. Study area with sampling sites (numbers). Inset: geographical position of Mar Chiquita Lagoon

In tropical regions, they are replaced by mangroves, or they may co-occur with them in mangrove swamps. Terrestrial halophytes are restricted to the high- and mid-tide levels, whereas seagrasses may occur in deeper intertidal and subtidal zones (Valiela, 1984; Reise, 1985). Unlike in Europe, North America and South Africa, such ecosystems have scarcely been studied in temperate regions of the Atlantic coasts of South America. Along the southern parts of the Brazilian coast, *Spartina* spp. marshes cover mud flats and tidal creeks as a narrow and discontinuous belt fringing mangrove woodland (Lana et al., 1991). In contrast to these subtropical regions, in the neighbouring coasts of Uruguay and Argentina terrestrial halophytes do not coexist with mangroves or seagrasses (Boschi, 1988).

Mar Chiquita Lagoon (Province of Buenos Aires, Argentina; Fig. 1) is the southernmost in a series of temperate coastal lagoons that begins north in Santa Catarina, Brazil (28° S) and extends along the coasts of the southwestern Atlantic Ocean (southern Brazil, Uruguay, northern Argentina). It is characterized by salt marshes which are inhabited by extremely dense populations of intertidal crabs (Olivier et al., 1972a). Five species of crabs live in Mar Chiquita Lagoon: *Uca uruguayensis* (Ocypodidae), *Chasmagnathus granulata*, *Cyrtograpsus angulatus*, *Cyrtograpsus altimanus* (Grapsidae), and *Platyxanthus crenulatus* (Xanthidae). The first three species are often found together along the coasts of the Rio de la Plata as well as in other estuaries and lagoons of this region (Boschi, 1988), *U. uruguayensis* (a fiddler crab) and *C. granulata* are semi-terrestrial, burrowing species, restricted to estuarine and other brackish waters, whereas *C. angulatus* also inhabits rocky seashores (Boschi, 1964). *C. altimanus* and *P. crenulatus* are euryhaline marine species that are found exclusively near the mouth of the lagoon. Ecological and life-history traits of those abundant intertidal decapod crustaceans and other dominant salt marsh inhabitants have in general been little investigated in South America.

Even in the most dominant species in Mar Chiquita Lagoon, *Chasmagnathus granulata* and *Cyrtograpsus angulatus*, little information on their ecology and distribution has been available. Burrows of *C. granulata* are usually absent in sandy beaches near the mouth (however, adults can be found there beneath stones) and in the innermost (freshwater) parts of the lagoon. In contrast, high densities of burrows are found in tidal flats and *Spartina densiflora* grasslands of the central and outer parts of the lagoon (Olivier et al., 1972a). Unlike *C. granulata*, *C. angulatus* is found in the whole lagoon, including adjacent freshwater creeks. Its density varies from clusters of thousands of crabs near the mouth (Boschi, 1964; Spivak & Politis, 1989) to single individuals observed in Canal 7, in the inner part of the lagoon (Spivak, unpubl.). The present paper describes local distribution and habitat preference in these two dominant crab species co-occurring in the outer parts of Mar Chiquita Lagoon.

STUDY AREA, MATERIAL AND METHODS

Study area

Mar Chiquita Lagoon is a shallow lagoon that covers 46 km^2, from 37° 32′ to 37° 45′ S, and from 57° 19′ to 57° 26′ W (Fig. 1). It can be divided into a wide northern and a narrow southern part, the latter opening into the sea. Seawater enters with semidiurnal high tides, depending in its quantity on the direction and intensity of winds (maximum with strong wind from SE, minimum with winds from W or NW; Olivier et al., 1972a).

The present study was conducted in the south of the lagoon, where a small town, Mar Chiquita, is located (Fig. 1). The area is characterized by small creeks and channels with marginal flats ("upper marsh") covered by *Spartina densiflora*. At the lower end of the halophyte zone, there is a narrow tidal flat bare of macrophytes, where sediments are composed of fine sand, silt and clay. Eolic sediments originating from coastal sand dunes cover the south and east of these marginal flats, and the mouth of the lagoon is bordered by sandy beaches. At several places (e.g. the bottom of Arroyo Vivoratá), consolidated pleistocene continental sediments ("tosca") appear (Fasano et al., 1982). The substrate structure of beaches, creeks and the lagoon bottom is in general rather uniform, but it is locally modified by man-made constructions (bridges and cuarcitic stone moles) and by natural "reefs" (calcareous tubes of the polychaete *Ficopomatus enigmaticus*) (Obenat & Pezzani, 1989).

A total of seven sampling sites was chosen, based on their distance from the mouth, type of habitat, and accessibility (location: Fig. 1; further characterization: Table 1).

Field measurements

Variations in water level, temperature, salinity, and pH were measured on December 12, 1992, in order to give a rough description of the physical conditions prevailing at different sampling sites (Fig. 2). The tidal amplitude was determined as a relative difference in the water level observed at 11.00 hours (approximately high tide) and later during the course of an ebb tide, at 14.00 and 17.00 hours. These measurements were made on vertical structures (walls of a mole or bridge, respectively), where the initial water level had been marked. Since no vertical structures were available at sites 1 and 3, no determinations of the tide level were made at these sampling stations.

Temperature was measured with a laboratory thermometer (precision: ±0.1 °C), and salinity (measured as conductivity) and pH were determined by means of a calibrated Jenway 3405 portable electrochemistry analyser. Samples taken from the sediment surface were analysed as to their content of organic matter (ignition loss after 6 h at

Table 1. Sampling sites, habitat characteristics, and sampling methods

Site No.	Distance from mouth (m)	Name of location	Habitat characteristics: General	Habitat characteristics: Particular	Sampling method
1	400	Mouth	lagoon proper	sandy beach	drag net
2	850	Mole	lagoon proper	tidal flat, mole, under and between stones	drag net by hand
3	1500	Island	lagoon proper	tidal flat	drag net
4	2100	Bridge	artificial lagoon (part of Arroyo Los Cangrejos)	tidal flat *F. enigmaticus* "reefs"	drag net core sampler
5	2800	"Cangrejal"	tidal creek: Arroyo Los Cangrejos	*S. densiflora* salt marsh	by hand
6	2700	Police Station	tidal creek	narrow tidal flat *F. enigmaticus* "reefs"	drag net core sampler
7	3300	Arroyo Vivoratá	freshwater creek: Arroyo Vivoratá	"tosca" stones *F. enigmaticus* "reefs"	by hand core sampler

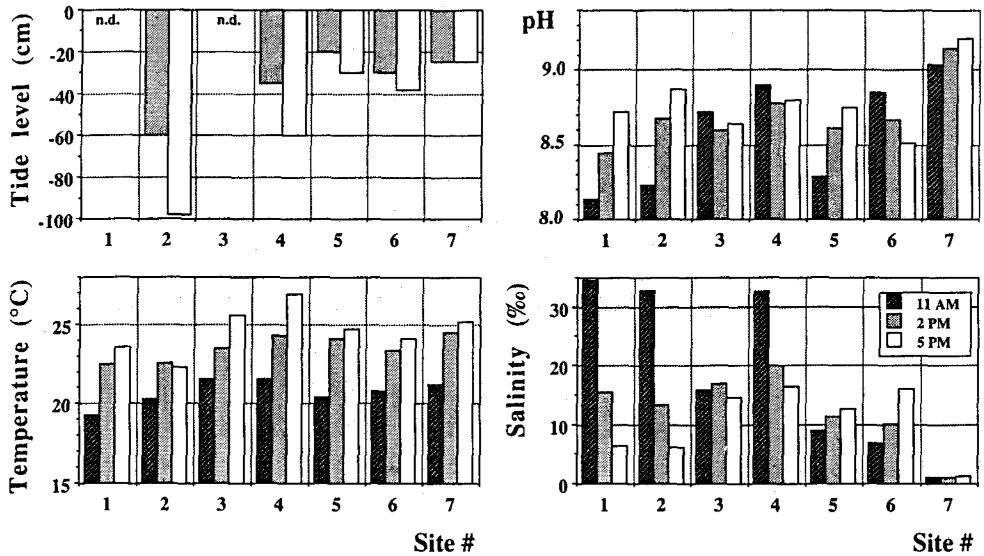

Fig. 2. Tide level (measured as difference from high tide, 11.00 hours), salinity, pH, and temperature at different sampling sites (cf. Fig. 1) during an ebb tide, on December 12, 1992, n.d.: not determined

500 °C; 3 replicate measurements; Fig. 3) and granulometric composition (Fig. 4). Sediments were sieved and sorted into three major fractions: gravel (>2.0 mm, mainly fragments of bivalve shells), sand (from 0.062 to 2 mm), and silt combined with clay (<0.062 mm). The sediment fractions were dried at 60 °C to weight constancy and then weighed. The penetrability of the substrate was measured in 5 to 10 replicates as the pressure (expressed in $kp \cdot cm^{-2}$) necessary for compressing the spring of a piston that was forced into the sediment to a standard depth (Brown & McLachlan, 1990). Since this value decreases with increasing penetrability of the sediment, low numbers indicate soft sediments (mud), whereas high numbers occur in coarser sediments such as sand.

On five days in November and December, 1992, water (siphoned out by means of a plastic tube, 5 mm inner diameter) and crabs (*Chasmagnathus granulata*) were sampled during low tide from burrows at site 3 ("dry mud" habitat) and analysed (temperature, salinity, pH, crab size, sex, and presence of eggs), with a total of 128 samples taken from burrows and 8 from the nearby tidal creek. Crabs escaped from 4 samples (no size, sex, or reproduction data available).

Field collections of crabs

Quantitative studies of crab populations proved very difficult, due to their high motility and great small-scale variability. However, rough estimates could be obtained as described below (details: see Table 1) in both *Cyrtograpsus angulatus* collected at sites 1, 2, 4, 6 and 7, on December 11, and in *Chasmagnathus granulata* collected at sites 2, 3 and 5, on December 15, 1992 (Fig. 5). *C. angulatus* found under or between stones at site 2 were taken by hand from 8 randomly chosen 0.25 m^2 areas, while crabs hidden in *Ficopomatus enigmaticus* "reefs" (sites 4, 6 and 7) were obtained from 10 replicate

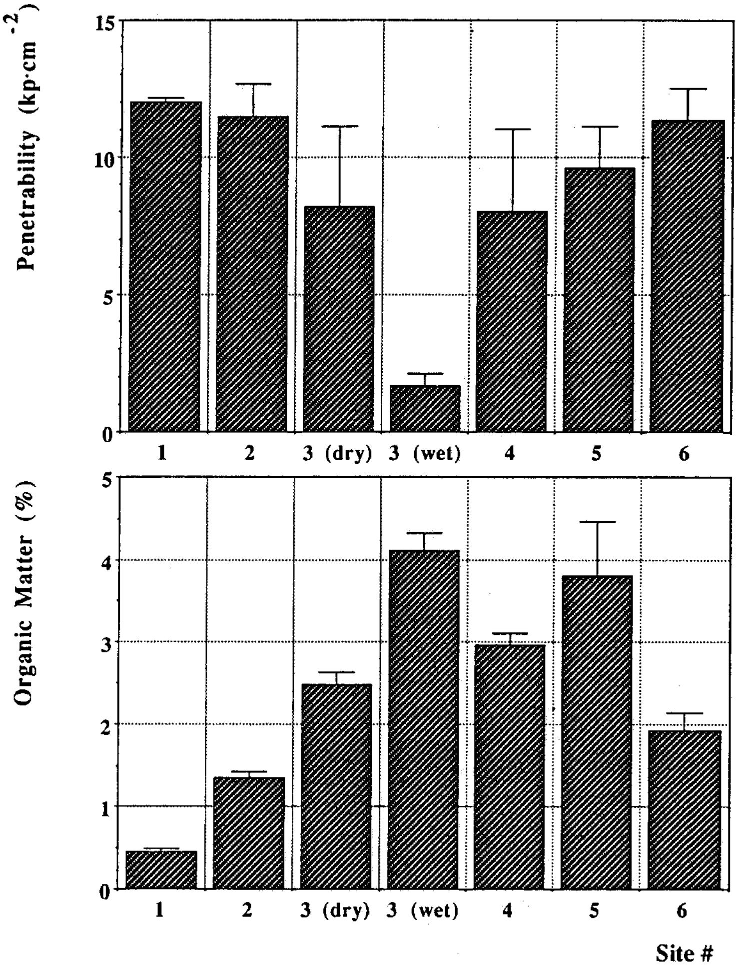

Fig. 3. Penetrability (measured after Brown & McLachlan, 1990; upper graph) and content of organic matter (measured as ignition loss; lower graph) of sediments at different sampling sites (cf. Fig. 1). Error bars: $\bar{x} \pm$ SD, with n = 5–10 (penetrability) and n = 3 (organic matter), respectively

30 cm^2 (300 cm^3) cylindrical core samples. Crabs walking in shallow water (on beaches or tidal flats; sites 1, 2, 4, 6) were caught with a dredge (opening: 10 cm height × 100 cm width) that was pulled by two persons over a defined distance (100 m). *C. angulatus* wandering on consolidated sediments (on the bottom of Arroyo Vivoratá) were taken by hand or with a small net (no quantitative density estimates possible). *C. granulata* hiding under stones of a mole at site 2 were taken by hand (no quantitative density estimates possible), whereas those from burrows in a tidal flat (site 3) or between *Spartina densiflora* plants (site 5) were obtained by digging them out from randomly chosen 0.25 m^2 sampling areas (site 3, wet mud, with 17, dry mud with 24, and site 5 with 18 replicates).

In all crabs, carapace width (CW) was measured to the nearest 0.1 mm with a Vernier

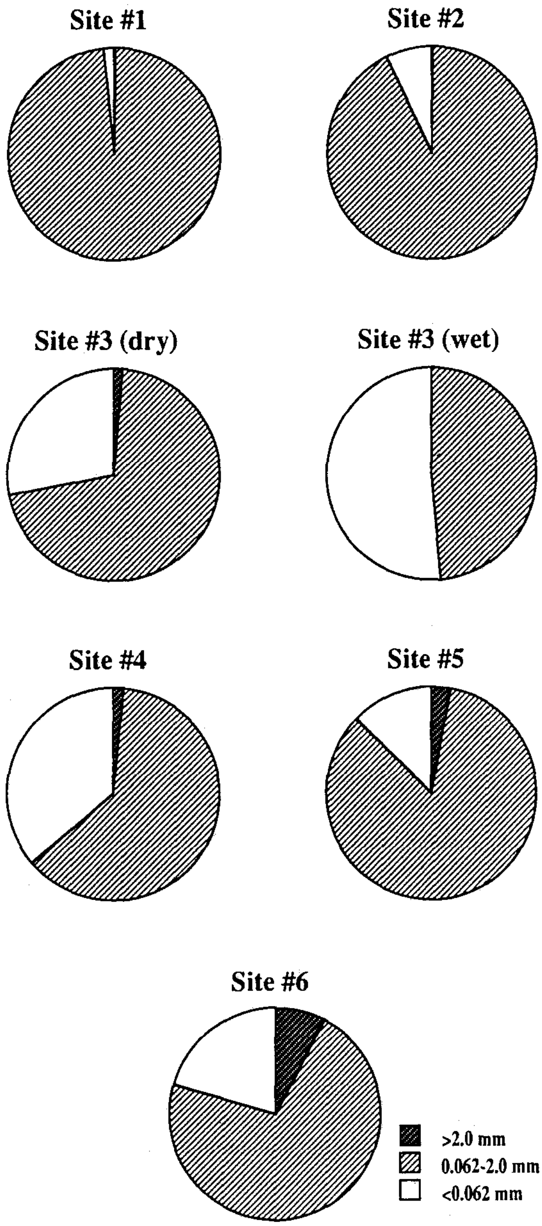

Fig. 4. Major granulometric fractions of sediments at different sampling sites (cf. Fig. 1)

caliper (large individuals) or with an 8× eye-piece micrometer under a dissecting microscope (smaller juveniles), and individuals with > 4 mm size were sexed morphologically. The number of ovigerous females was recorded, and percentage size-frequency distributions (SFD) were constructed for each site (Fig. 6). In order to include also

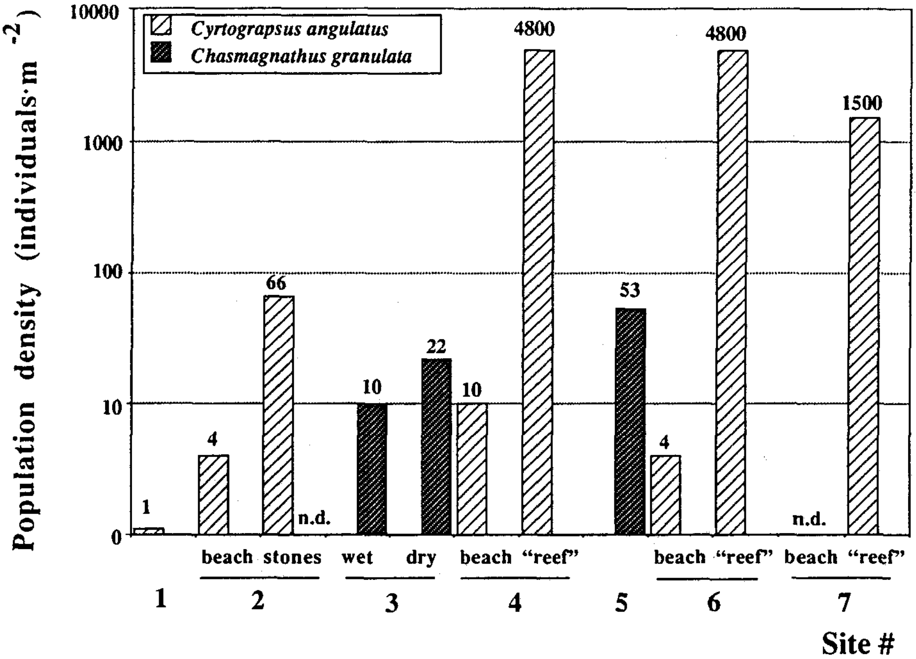

Fig. 5. Population density (numbers above columns: individuals · m^{-2}) of *Cyrtograpsus angulatus* and *Chasmagnathus granulata* at different sampling sites

sexually indeterminable individuals (< 4 mm) in SFDs, a 1:1 sex ratio was assumed, since this had been found in larger (sexable) juveniles; thus, half the number of those morphologically undifferentiated individuals was considered males, the other half females, and included in SFDs (Fig. 6).

Statistical procedures

A R×C test of independence (G test with William's correction; Sokal & Rohlf, 1981; p. 744) was applied to test the hypothesis that sex ratios or proportions of ovigerous and non-ovigerous females were independent of the sampling site. Sex ratios were tested for deviations from a hypothetical 1:1 ratio employing a goodness-of-fit test (Sokal & Rohlf, 1981; p. 692). Linear least-square regression parameters (slope, intercept of regression line with the Y-axis) were compared with tests described by Sokal & Rohlf (1981; p. 499).

RESULTS

General habitat characteristics

Sites 1, 4, 6 and 7 (Fig. 1) were dominated by *Cyrtograpsus angulatus*, with also a few *Chasmagnathus granulata* found at site 4. In contrast, sites 3 and 5 were predominantly *C. granulata* habitats, with most crabs found near the high water level, normally

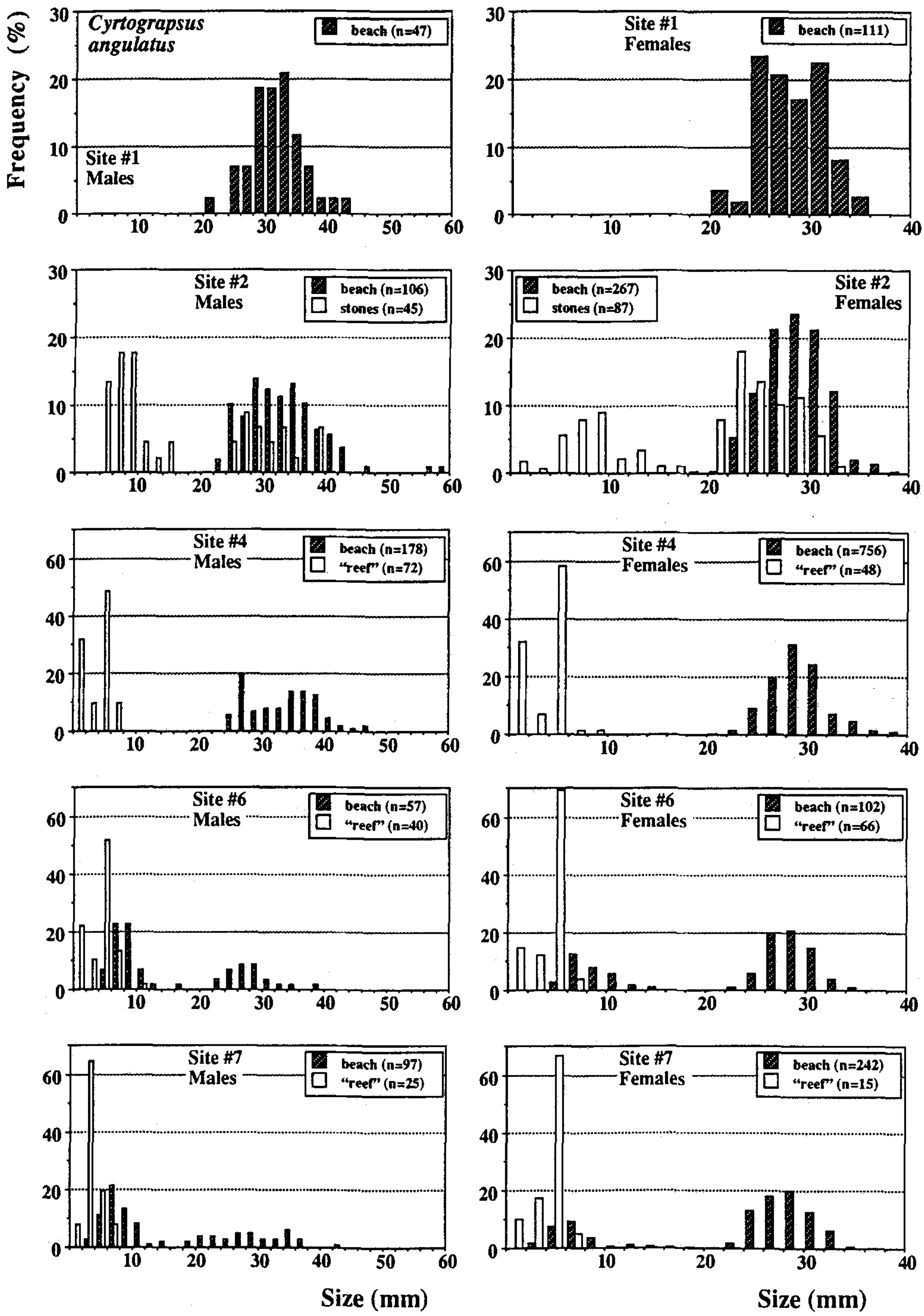

Fig. 6. Size-frequency distribution of *Cyrtograpsus angulatus* at different sampling sites

associated with burrows. At site 3, they were also collected from a soft muddy area, where burrows could not be excavated by the crabs. *C. angulatus* could be found at all sites in the lower intertidal, but they were not collected at sites 3 and 5, where only a few individuals occurred. Both species coexisted in high numbers at site 2, with *C. granulata* living mainly in the upper, and *C. angulatus* in the lower intertidal. *C. granulata* only exceptionally dug burrows at site 2; instead, most individuals occupied crevices under stones.

Tidal variations in the water level decreased gradually from sites 1 to 7 and, as a consequence, marked differences in water salinity and pH were found between the sampling sites. Figure 2 illustrates changes in water level, salinity, temperature, and pH during one ebb tide (6 h). Salinity decreased in most cases, whereas pH and temperature generally increased during this period. This pattern was particularly clear at sites 1 and 2, where salinity decreased from 33–35 to about 6 ‰, while pH and temperature increased simultaneously. Changes at site 4 were less marked. Water remained brackish (about 15 ‰) at site 3, and oligohaline (ca 2 ‰) at site 7. Only at sites 5 and 6, which are tidal creeks with no or only insignificant freshwater inflows, did salinity increase during this period (Fig. 2). This effect was probably caused by remnant salt water bodies coming from their dead ends and moving towards the mouth of the lagoon. The lowest water temperatures were registered near the mouth (19.3 to 23.9 °C), the highest at site 4 (from 21.6 to 26.9 °C).

Sediment characteristics (penetrability, granulometric composition, and content of organic matter) showed great differences between different sampling sites (Figs 3, 4). The wet mud area at site 3 showed the far highest percentage of the silt and clay fraction (52 %), together with the highest level of organic matter (4.1 %), and the highest penetrability (1.7 $kp \cdot cm^{-2}$). The opposite was observed at the beach near the mouth (site 1), where 98 % of the sediment consisted of sand, with only 0.45 % organic matter, and low penetrability (12 $kp \cdot cm^{-2}$). In the freshwater creek Arroyo Vivoratá (site 7), the substrate was found rocky ("tosca" ground), whereas at site 5 ("cangrejal") the bottom surface was partially (mean ± SD: 28.8 ± 18.5 %) covered by *Spartina densiflora* plants.

Cyrtograpsus angulatus

Population density in this crab species was found to vary greatly, not only between different sampling sites, but also in different microhabitats (Fig. 5). *C. angulatus* was very common on all open beaches, but only occurred in relatively small numbers (1–10 $individuals \cdot m^{-2}$). Much higher density was observed between stones of a mole (site 2; 66 $individuals \cdot m^{-2}$), and extremely high numbers (1500–4800 $individuals \cdot m^{-2}$) in *Ficopomatus* "reefs". Size-frequency distribution (Fig. 6) shows that such high abundance figures were almost exclusively caused by the occurrence of numerous juveniles.

Our results suggest that recruitment takes place mainly in the protected microhabitats of polychaete "reefs", where small individuals remain until they reach ca 7 to 11 mm in size. Larger juvenile individuals could be found hidden under stones (site 2) or exposed in tidal or freshwater creeks (sites 6 and 7), while adult crabs of both sexes (>20 mm CW) were most frequent on open muddy or sandy beaches. Adult and juvenile crabs were observed coexisting in almost equal proportions (56 and 44 %, respectively) at site 2, living on and beneath stones.

The sex ratio of *C. angulatus* was in general approximately 50:50 in small crabs (4 to 11 mm CW; living in "reefs"), but it was significantly biased towards females in all larger individuals, with only 19 to 35 % males (Fig. 7). The proportion of ovigerous females (as a percentage of all females) varied greatly among sites, from only 12 % on the beach of a freshwater creek (site 7) to 86 % in a brackish tidal creek (site 4). High numbers of ovigerous females were found also on beaches near the mouth of the lagoon, i.e. at sites 1 and 2 (Fig. 7).

Chasmagnathus granulata

Maximum population density of *C. granulata* was found on a tidal flat whose upper zone was covered by *Spartina densiflora* grassland (site 5; 53 individuals$\cdot$m^{-2}; however, no quantitative estimate could be made at site 2, where this species also occurred in high numbers. At site 3 (bare mud flats), two different microhabitats could be distinguished within only a few meters distance from each other: on relatively dry mud, where stable burrows could be excavated, *C. granulata* was twice as abundant as on soft wet mud, where excavation was not possible (Fig. 5).

Size frequency distribution and sex ratio varied between the three sites at which *C. granulata* was sampled (Figs 7 and 8). Crabs of all sizes were found together in samples from the most densely populated habitat, site 5. Deep and interconnected burrows, placed among plants, were found to be occupied by juveniles, adult males, and both ovigerous and non-ovigerous females. A similar pattern was observed in burrows at site 3 (dry mud). Both populations (more pronounced at site 3) showed a bimodal size-frequency-distribution, with juveniles <10 mm and adults >25 mm CW dominating (Fig. 8). At site 2 (mole), only larger juvenile and adult individuals were found.

The sex ratio of *C. granulata* was approximately 50:50 at site 2. A slight but statistically significant ($P < 0.05$) deviation occurred at the "cangrejal" (site 5), with 56 % males and 44 % females, whereas the population at site 3 was strongly biased towards females, in particular in the dry mud habitat (Fig. 8). The latter showed also the highest proportion of ovigerous females, where 67 % of all females carried eggs, followed by site 5 (Fig. 8). It is interesting to note that only very few females in wet mud (site 3) and between stones (site 2) were ovigerous (Fig. 8).

Burrow study

Burrows inhabited by adult *Chasmagnathus granulata* at site 3 (dry mud) were studied on five days as to their physical conditions during low tide. During the first sampling (24 November), the distance of burrows from the edge of the tidal creek was grouped and recorded only in three classes (zones); no correlation analyses were carried out with these data. Four individuals escaped during sampling, so that no data are available for them. Six burrows contained more than one individual (three burrows with pairs of 1 male and 1 non-ovigerous female each, and one each with 2 males, 2 ovigerous females, or a pair of 1 male and 1 ovigerous female). These cases of double occupancy had obviously a random nature. In all other cases (118 samples), one individual was present in each burrow.

Crab size did not show a very clear tendency in relation to the position of the burrow within the intertidal mud flat (Fig. 9). While males tended to be bigger in the upper intertidal zone (significant positive correlation between carapace width and distance of the burrow from the water edge; $r = 0.329$; $P < 0.01$), ovigerous females showed a weak but statistically significant opposite trend ($r = -0.341$; $P < 0.05$). No tendency was visible in non-ovigerous females (Fig. 9).

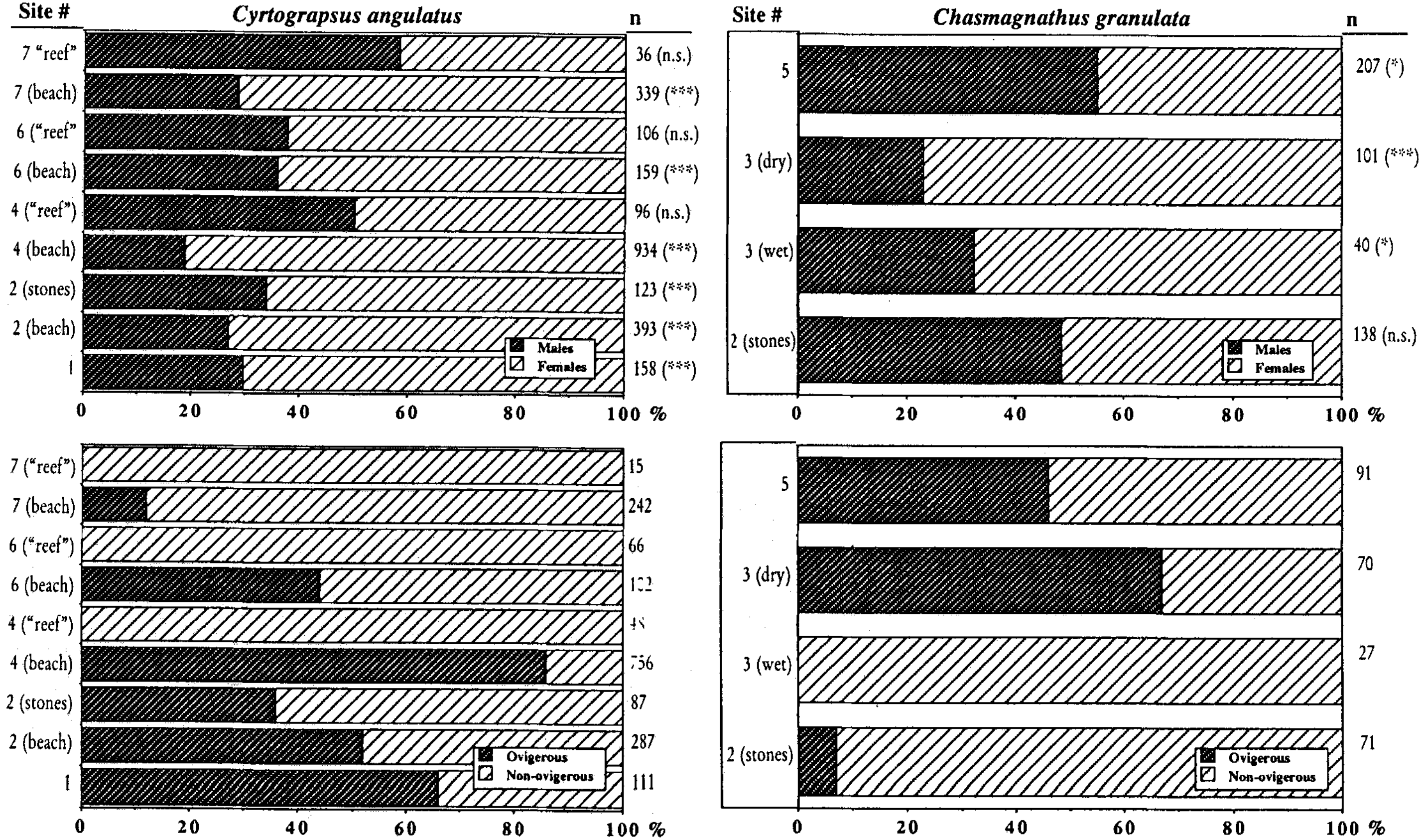

Fig. 7. Sex ratio (in % of total population; upper graphs) and percentage of ovigerous females (in % of females; lower graphs) in *Cyrtograpsus angulatus* and *Chasmagnathus granulata* at different sampling sites; n: number of crabs. Significance of deviations froms a hypothetical 1:1 sex ratio: *: $0.1 > P > 0.01$; ***: $P < 0.001$; n.s.: not significant

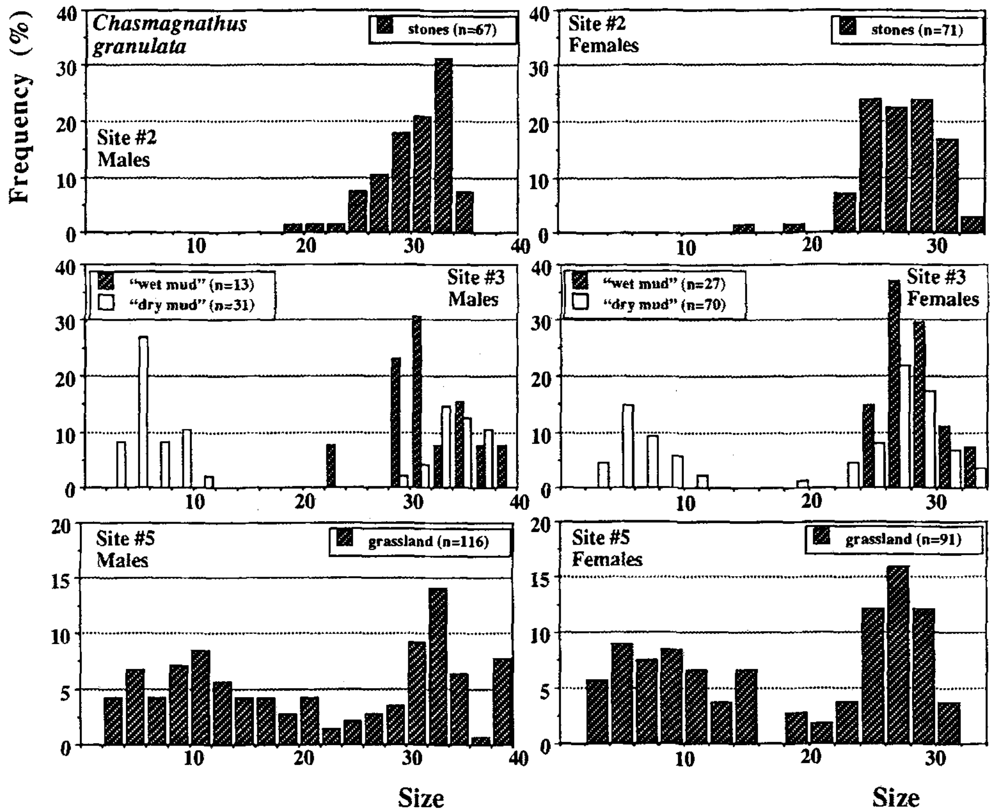

Fig. 8. Size-frequency distribution of *Chasmagnathus granulata* at different sampling sites

When all data from this study were pooled, an overall sex ratio of 50:50 was obtained (66 males, 64 females). However, significantly different ratios were found in the lower and in the upper zones of the intertidal gradient (in both $P < 0.01$). While females clearly dominated in the lower part of the intertidal (31 out of 44 individuals, or 70 %), males dominated as clearly in the uppermost zone (30 out of 44, or 68 %); the transitional zone had an intermediate composition, with a sex ratio close to one of 50:50 (Fig. 10).

The ratio of ovigerous to non-ovigerous females showed a clear shift within the intertidal gradient. While only 14 out of 31 females (45 %) carried eggs in the lowest zone, about 80–90 % were ovigerous in the upper parts (Fig. 10).

This intertidal zonation in population structure of *C. granulata* co-occurred with gradual changes in physical factors (Fig. 11). Variations in water temperature of crab burrows did not show a consistent relationship with their position in the intertidal, since short-term changes of air temperature (for instance during periods of clouded sky) had stronger effects than the time of exposure since the last high tide. Only on two relatively cold days (25 November and 14 December) were significantly decreasing trends with increasing distance from the water edge (i.e. with increasing exposure time) observed (Fig. 11).

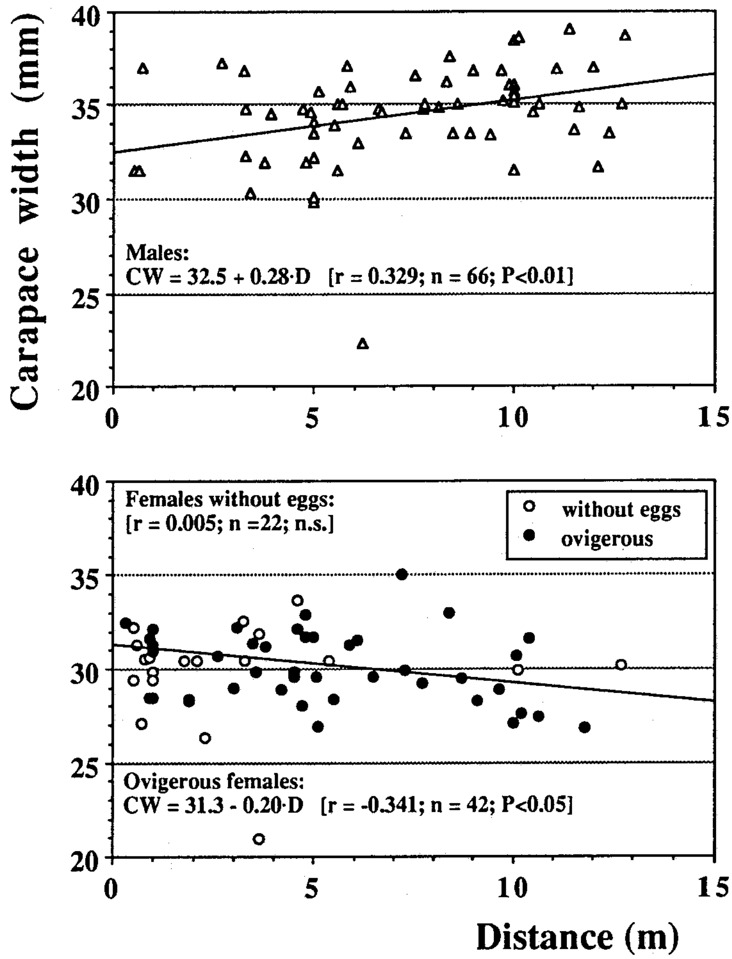

Fig. 9. Size (carapace width, CW) of *Chasmagnathus granulata* (upper graph: males; lower: ovigerous and non-ovigerous females) in relation to the position of their burrows (distance, D, from tidal creek at low tide), within an intertidal mud flat, site 3. r: correlation coefficient; n: number of measurements; P: probability of error for rejecting H_0 ($r = 0$); n.s.: not significant

Salinity showed, on all sampling dates, a significantly increasing trend with increasing height in the intertidal, whereas pH consistently showed the opposite tendency (Fig. 11). Besides such vertical variation of physical factors within the intertidal habitat, our data document the minimum overall range of temporal variation that may occur here. Salinity values varied during the sampling period between 2 and 28 ‰S in the tidal creek, and between 4 and 34 ‰S in crab burrows, with increments of about 10–15 ‰S within the tidal zonation. The pH varied relatively little in the tidal creek (8.2–8.7), but clearly more in crab burrows distributed over the intertidal mud flat (7.5–8.4). Most pH values

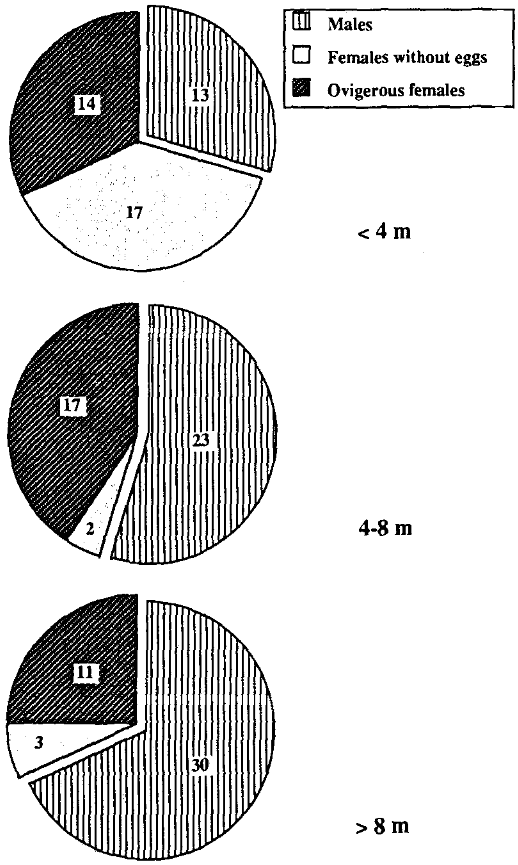

Fig. 10. Proportions of males, ovigerous and non-ovigerous females of *Chasmagnathus granulata* in three different zones (grouped by horizontal distance of burrows from the edge of a tidal creek at low tide), within an intertidal mud flat, site 3. Numbers: number of individuals in each group

measured within about 3 m distance from the creek were above 8, while those in the upper parts of the intertidal were generally lower (Fig. 11).

As a consequence of these opposite tendencies in salinity and pH, a highly significant negative correlation was found between these two variables ($r = -0.794$; $P<0.001$; Fig. 11). A similar linear relationship between salinity and pH had been found also in water samples taken from different parts of Mar Chiquita Lagoon (Anger et al., 1994); however, the present regression line differs significantly in both the slope and intercept values ($P<0.01$; Fig. 11). As a result of these differences, 125 out of 136 pH measurements that were made in the present "burrow" study were below those predicted by the regression line obtained from water samples in the lagoon. Thus, water chemistry in crab burrows shows significant differences from that in the adjacent lagoon, with consistently lower pH values at any salinity level.

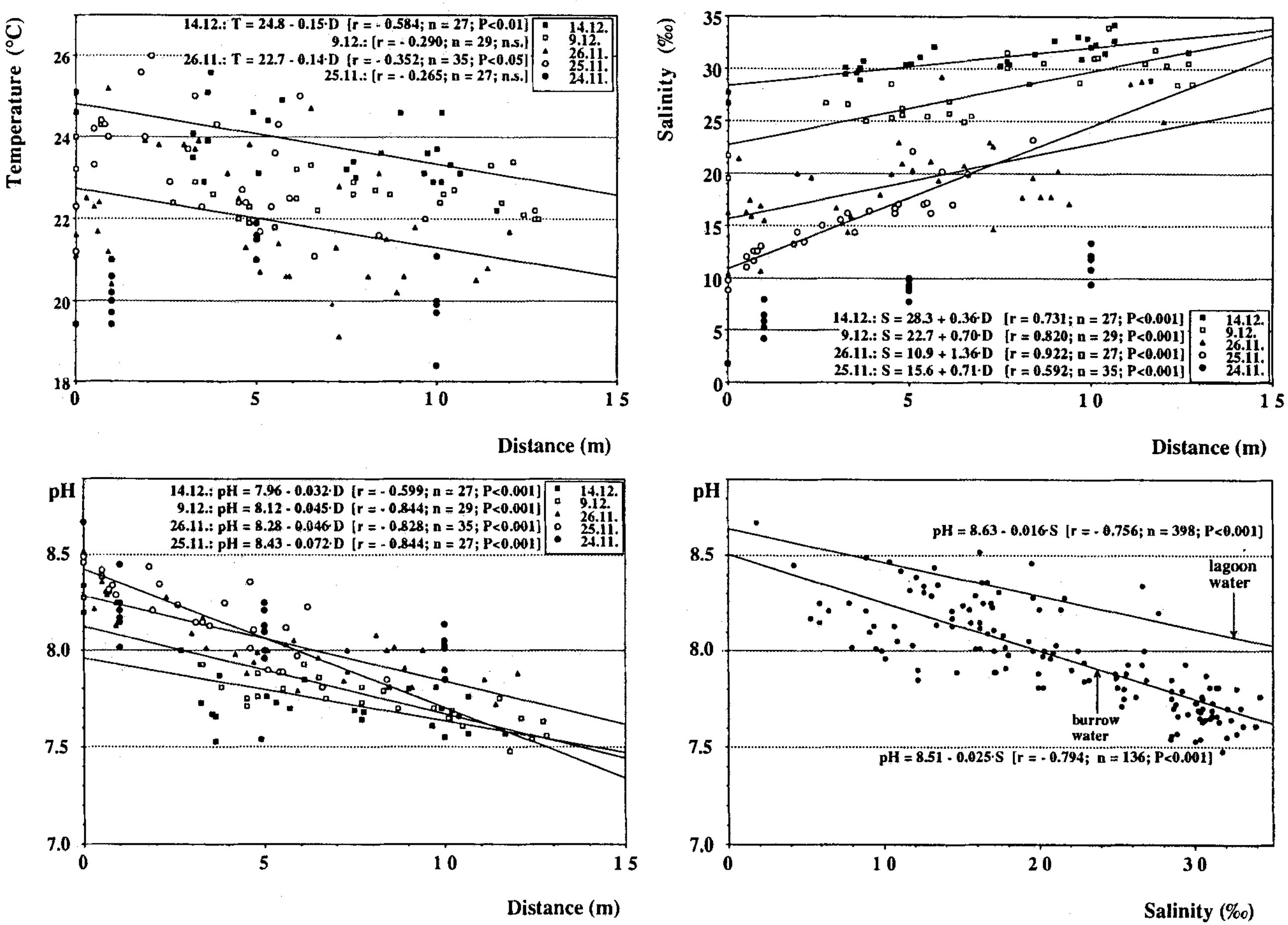

Fig. 11. Relationships between the distance (D) of *Chasmagnathus granulata* burrows from the edge of a tidal creek (site 3) at low tide, and temperature (T), salinity (S), and pH, respectively, in water taken from these burrows on different sampling dates. Lower right graph: relationship between pH and salinity within crab burrows (this study; pooled data) and in water taken from the lagoon (Anger et al., 1994); r: correlation coefficient; n: number of measurements; P: probability of error for rejecting H_o (r = 0); n.s.: not significant

DISCUSSION

Limitations imposed by salinity (problems of osmoregulation), moisture (desiccation and respiration), availability of food, and suitability of the sediment for burrowing had been identified as important cues determining the habitat choice in estuarine grapsid crabs (Seiple, 1979). Moreover, ontogenetic changes in osmoregulatory ability, air exposure resistance, feeding, and predator-avoiding mechanisms, as well as reproductive behaviour, may cause variations in habitat use during the life cycle of estuarine and littoral crabs. The range of environmental conditions allowing reproduction is much narrower than that for survival and growth of a species (Sastry, 1983).

The study area shows great small-scale variation in tidal amplitude and the nature of substrata. Three physically different types of habitat can be distinguished on the basis of tidal height, water salinity, and pH (Fig. 2): (a) the uppermost, basically freshwater parts of the lagoon, which are little, or not at all, influenced by tides (site 7); (b) upper estuarine areas with irregular salinity changes (sites 3, 5 and 6); and (c) lower estuarine areas with more or less regular salinity changes during tidal cycles (sites 1, 2 and 4). In the second habitat type, water that enters or leaves the lagoon with tidal currents often mixes with residual bodies of fresh, brackish or salt water. The organic matter, silt and clay contents, and the penetrability of the sediments ranged from low (sand, site 1) to high values ("wet mud", site 3; grassland, site 5). Sites 2, 6, 3 ("dry mud"), and 4 showed intermediate values, in general increasing with increasing distance from the mouth of the lagoon. Only site 5 showed a high content of organic matter with low penetrability, indicating soil consolidation by *Spartina densiflora* plants and organic enrichment by dying root parts.

Adult *Cyrtograpsus angulatus* live in the whole lagoon, mostly on sandy or muddy beaches, where they feed upon polychaetes and detritus particles (Olivier et al., 1972b). Highest density, together with the highest percentage of ovigerous females, were in the present study recorded on bare mud flats at site 4. This suggests that such lower estuarine habitats, which are physically relatively predictable and have sediments rich in organic matter, may be preferred by adult individuals of this species. They were found in habitats with all salinities varying from fresh to seawater, indicating an extremely high degree of osmoregulatory capacity.

Both adults and half-grown juveniles were found in high numbers on and under stones at site 2, where water conditions were similar to those at site 4 but the sediment contained less organic matter. High population density was probably related here to the existence of refuge spaces between stones, where young crabs can hide from their predators, mainly sea birds (Olivier et al., 1972b). The smallest juvenile individuals were found in protected microhabitats, namely in crevices of tube-building polychaete (*Ficopomatus enigmaticus*) "reefs", where recruitment of this species takes place (sites 4, 6 and 7), and where population densities of up to 4800 individuals per m^2 were estimated. Polychaete "reefs" are also, in other crab species, an important refuge habitat where predation pressure is significantly reduced (Heck & Hambrook, 1991). Ontogenetic changes in habitat preference of *C. angulatus* had been observed also by Obenat & Pezzani (1989) and Spivak & Politis (1989). Interestingly, both "reefs" and stones represent relatively new structures in the lagoon system, with *F. enigmaticus* colonizing them only a few years ago (Obenat & Pezzani, 1989), and stones being introduced recently, when a number of moles and bridges were built. Hence, these new habitats should have contributed to the establishment of a dense and stable *C. angulatus* population in Mar Chiquita Lagoon.

Chasmagnathus granulata is known as an omnivorous deposit-feeder (Olivier et al., 1972b) and, consequently, was found most frequently on sediments that were rich in organic matter. It reached its highest population density at site 5, in the upper intertidal zone of a brackish creek that shows irregular salinity changes. Highest proportions of juveniles and ovigerous females were observed in this habitat, where *C. granulata* may be found throughout the year, showing a complex spatial organization related to the presence of *Spartina densiflora* and the distance from the creek (Rivero d'Andrea, 1989). Its lack in freshwater parts of the lagoon indicates a somewhat lower osmoregulatory capacity in *C. granulata* as compared with *Cyrtograpsus angulatus*. On the other hand, *C. granulata* is extremely well adapted to exposure to atmospheric air, showing a particularly great gill area in comparison to other semiterrestrial crab species (Santos et al., 1987). This enables this species to occupy the uppermost parts of the intertidal, and it even occurs frequently at large distance (several hundred metres) from the water's edge in the supratidal zone, where *C. angulatus* would not survive (pers. observ.).

Small-scale distribution patterns in *Chasmagnathus granulata* were particularly obvious at site 3, where two physically different microhabitats occurred at only a few meters distance from each other. Marked differences were observed here in size-frequency distribution, sex ratio, and proportion of ovigerous females, with juvenile crabs and ovigerous females living mainly in "dry mud", but only adults (including only few ovigerous females) in "wet mud". These differences in population structure may be related to different preconditions for digging of burrows, varying from only superficial, simple holes in "wet mud", to deep, sinuous, sometimes ramified and intercommunicated tube systems in "dry mud" and *Spartina* grassland (Goya, 1988). Site 2, in contrast, appears to be a marginal habitat for this species, colonized only by adults (again, with only a few ovigerous females present) that can hide there between stones but do not excavate burrows in the sandy ground (Rivero d'Andrea, 1989). Thus, the present study suggests that "dry mud" and *Spartina* grassland habitats are optimum for *C. granulata*, where crabs of all sizes can dig stable burrows, and females may incubate their eggs.

When a vertical intertidal gradient within a "dry mud" microhabitat is considered, further ecological characteristics of *Chasmagnathus granulata* may be discerned. Our burrow study showed a significant increase in average carapace size in males with increasing distance from the water's edge. This tendency coincides with a seemingly increasing burrow size towards the uppermost intertidal zone. It could be explained with an increasing resistance against desiccation, temperature, and salinity stress in larger individuals of this semiterrestrial crab species (Powers & Bliss, 1983; Burggren & McMahon, 1988). However, such a tendency was not found in females, where a homogeneous size-distribution within the intertidal gradient was found, or even a slightly opposite trend, with decreasing average body size toward the upper zone (in ovigerous individuals). The latter trend, which was statistically significant on the 0.05 level, cannot be explained at present, and it should be reinvestigated.

A rather clear zonation was found in the sex ratio of *Chasmagnathus granulata*, with a strong increase in the proportion of males in the upper part of the intertidal mud flat. Again, this might be explained with a higher resistance of males to harsh environmental conditions. Ovigerous females were most frequently found in the lower and intermediate zones, where physical conditions are relatively stable; however, not much less occurred in the upper zone. Non-ovigerous females were most numerous near the edge of the water. This suggests that hatching of the larvae may take place outside the burrows, in the tidal creek, or the females leave their burrows after hatching in order to mate. Future behavioural studies may solve this question.

The physical conditions inside the burrows show clear vertical gradients, with normally increasing salinity and decreasing pH values toward the upper intertidal, while temperature varies more randomly. The increase in salinity reflects mainly a tidal pattern, with high values at high tide, and low figures at low tide. It may be enhanced, particularly on warm days, by partial evaporation of water from the burrows. Since pH shows, in the lagoon water, a general negative relationship with salinity, the decrease in pH is partly explained by the salinity increase. However, the pH level in water from crab burrows was, at any salinity, consistently lower than in water from the lagoon. This can only be explained by enhanced respiration processes (both in crabs and microbial activity), with increased production of CO_2 in burrows. Future ecophysiological studies should quantify the share of these two major causes of changing water chemistry within the intertidal gradient.

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