SIZE STRUCTURE, SEX RATIO, AND BREEDING SEASON IN TWO INTERTIDAL GRAPSID CRAB SPECIES FROM MAR CHIQUITA LAGOON, ARGENTINA

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INTRODUCTION

Brachyuran crabs are typical epibenthic invertebrates inhabiting estuarine and protected coastal areas world-wide. In the intertidal and supratidal zones of such areas, frequently several species of Grapsidae or Ocypodidae may be found (Willason, 1981; Pillay & Ono, 1978; Seiple, 1979; Seiple & Salmon,1987; Jones & Simons, 1982). Crabs belonging to these families form in general a typical and quantitatively important component of the fauna of tropical and temperate coastal lagoons (Barnes, 1980). They are also key species in "cangrejal" ecosystems (from spanish: cangrejo = crab); a particular brackish salt marsh ecosystem of eastern South America (Boschi, 1964, 1988).

Studies on ecological and life history traits of dominant species from "cangrejales" have become available only recently, including aspects of their population structure (Spivak & Politis, 1989; Spivak *et al.*, 1991; Gavio & Spivak, 1994a), their role as a prey for birds (Spivak & Sánchez, 1992), distribution and habitat preferences (Spivak *et al.*, 1994), fecundity, relative growth, and sexual dimorphism (Luppi *et al.*, 1994; Gavio & Spivak, 1994b; Gavio *et al.*, 1994), and the occurrence of their larvae in a coastal lagoon (Anger *et al.*, 1994). In other intertidal habitats, interspecific comparisons of life history patterns were made between intertidal crabs living at high

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or low tide levels, respectively (Pillay & Ono, 1978; Seiple, 1979; Seiple & Salmon, 1987), or between estuarine and marine species (Jones & Simons, 1982).

In the present study, adult population structure and reproductive patterns were investigated in two grapsid crabs, *Chasmagnathus granulata* and *Cyrtograpsus angulatus*. They are the dominant species in Mar Chiquita Lagoon, Argentina, the southernmost in a series of brackish coastal lagoons extending along the coasts of the southwestern Atlantic Ocean. *C. granulata*, which forms dense populations in "cangrejales" and other estuarine environments, coexists frequently with a fiddler crab, *Uca uruguayensis*. Both are a burrowing species which are widely restricted to fine sediment substrates in the upper intertidal fringe of brackish water zones. *C. angulatus* is predominantly found at the lower intertidal level and in the adjacent subtidal, but frequently also on rocky sea shores (Boschi, 1964; Spivak *et al.*, 1994).

STUDY AREA

Mar Chiquita is a shallow lagoon that covers 46 km^2, from 37° 32' to 37° 45'S and from 57° 19' to 57° 26'W. It is divided into a wide northern and a narrow southern part, the latter opens to the sea. A few small rivers feed it constantly with freshwater, while seawater enters and leaves it periodically with semidiurnal high tides, passing over a shallow sandbar in the mouth of the lagoon. The extent of water exchange depends on the tidal amplitude and the direction and speed of winds. The lagoon is characterized, at least in spring, by highly variable physical conditions and oligohaline waters frequently predominating over extended periods (Anger *et al.*, 1994).

This study was conducted in the southern part of the lagoon (Fig. 1). The area is bordered by marginal flats that are covered by *Spartina densiflora*; however, this plant has disappeared in most urban areas. Downwards the halophyte zone, there is a narrow tidal flat, bare of macrophytes, whose sediments are composed of fine sand, silt and clay carried by creeks and channels. The south and east of the marginal flats are covered by eolic sediments from coastal dunes, and sandy beaches border the mouth of the lagoon. At several places, consolidated pleistocene continenta sediments appear (Fasano et al., 1982).

Only scarce data are available about the climatic conditions at Mar Chiquita. Fig. 2 shows a few available measurements on monthly mean surface water temperature in the lagoon (only March to Sepember; Alvarez et al., 1983), and average maximum and minimum air temperatures at Mar del Plata Harbour, 35 Km south of it. July and January are the coldest and warmest months, respectively. Frosts occur occasionally during winter (June to September, rarely in May or October), with a maximum frequency (3 to 7) in July.

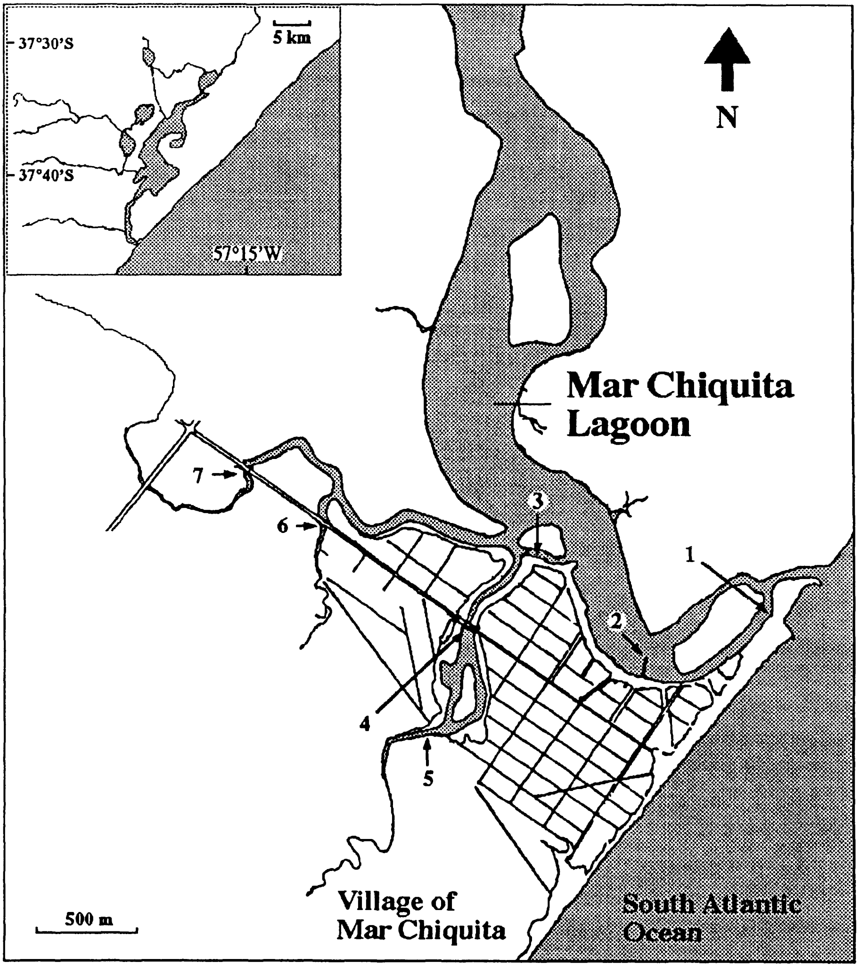

Fig. 1
Mar Chiquita lagoon, Argentina: study area and sampling sites (1 to 7)

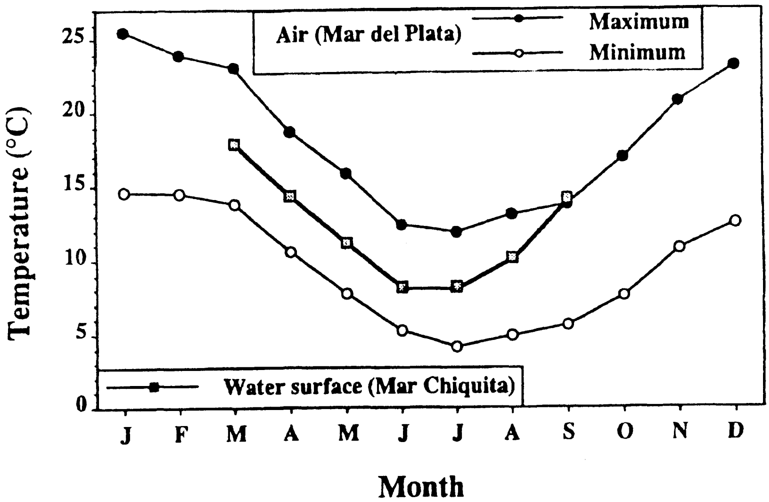

Fig. 2
Average maximum and minimum monthly air temperatures at Mar del Plata Harbour (1951-1960; data from: Anonymous, 1980); mean surface water temperature at Mar Chiquita (from Alvarezal et al., 1982).

MATERIAL AND METHODS

A total of 7 sampling sites was chosen differing in their distance from the mouth and in habitat type (Fig. 1). Sites 1 (mouth), 2, and 3 are located in the lagoon proper, sites 4, 5, and 6 at the margins of a tidal creek, and 7 at a freshwater creek. Sites 5 (a typical "cangrejal" and 7 are farthest (2.8 and 3.3 km) from the mouth. A more detailed description of sediment characteristics and hydrographical conditions at these sampling sites was recently given by Spivak *et al.* (1994).

Collection of crabs

Cyrtograpsus angulatus and *Chasmagnathus granulata* co-exist in high numbers at site 2, while at all other sites only one species was frequent enough to allow for sampling (*C. angulatus* at sites 1, 4, 6, and 7; *C. granulata* at sites 3 and 5). Since in both species juveniles (< 20 mm) co-exist only rarely with conspecific adults (spatial segregation in different microhabitats; Spivak et al., 1994), we examined exclusively adult stages.

We considered a minimum carapace size of 18 mm as an appropriate lower size limit for the definition of adults, because (1) we never observed males below this size in copulation, and (2) it represents the approximate lower size limit for ovigerous females. Juveniles <18 mm occurred only occasionally in our samples and were disregarded.

In November 18, 1991, and in February 3, April 2, and September 29, 1992, a total of 4270 adult *Cyrtograpsus angulatus* was collected at sites 1, 2, 4 and 6. At sites 2, 3 and 5, a total of 3088 *Chasmagnathus granulata* were collected (November 19, 1991, January 31, April 2 and September 29, 1992). At each of these collecting dates, the highest possible number of crabs was collected by hand during one ebb tide. All individuals were sexed, measured with a Vernier caliper (carapace width, CW, to the nearest 0.1 mm), and females were examined for the presence of eggs. Size frequency distribution (SFD; 2 mm size intervals), and total and operative sex-ratios (male:female, male:non ovigerous females, respectively) were determined for each species, sampling date, and site.

From November 1991 to April 1992 (spring to autumn), females were collected at all sites, at intervals of approximately 15 days. Due to bad weather conditions and a high water level in the lagoon, only site 1 was sampled in May, and no samples were obtained in June and July. Sampling continued, on a monthly basis, from August to November 1992. At site 3, females were collected separately from two different microhabitats ("wet mud" and "dry mud"), near to and far from the water edge, respectively. Each sample consisted of the highest possible number of females accessible during one low tide (22 to 337 individuals). Each female was examined for presence of eggs, and the percentage of ovigerous females within the total number of females (POF) was calculated for each site and species. A sample of eggs was taken from each ovigerous female for later microscopical examination of the embryonic stage, before the crabs were released.

Embryonic staging

Three embryonic stages were defined on the basis of microscopical examination. Eggs belonging to stage 1 were undifferenciated, the vitellum occupying from 70 to 100 % of their volume; stage 2 eggs showed chromatophores and evidence of segmentation, the vitellum occupying from 40 to 70 %; stage 3 eggs contained embryos with well-developed eyes and heart beat, the vitellum occupying less than 40 % of the egg volume.

Statistical procedures

Size-frequency distributions were analyzed for dominating size groups using the procedure described by MacDonald & Pitcher (1979). Size differences were compared by means of Kruskal-Wallis or Mann-Whitney U-tests. A Tukey-type nonparametric multiple comparison test (Zar, 1984, pp. 199-200) was used to determine between which of the sites there were significant differences. Sex ratios were tested for deviations from a hypothetical 1:1 ratio employing a goodness-of-fit test (Chi-square test; Zar, 1984; p. 40). Mann-Whitney U-tests were used to ascertain the significance of size differences between ovigerous and non-ovigerous adult females.

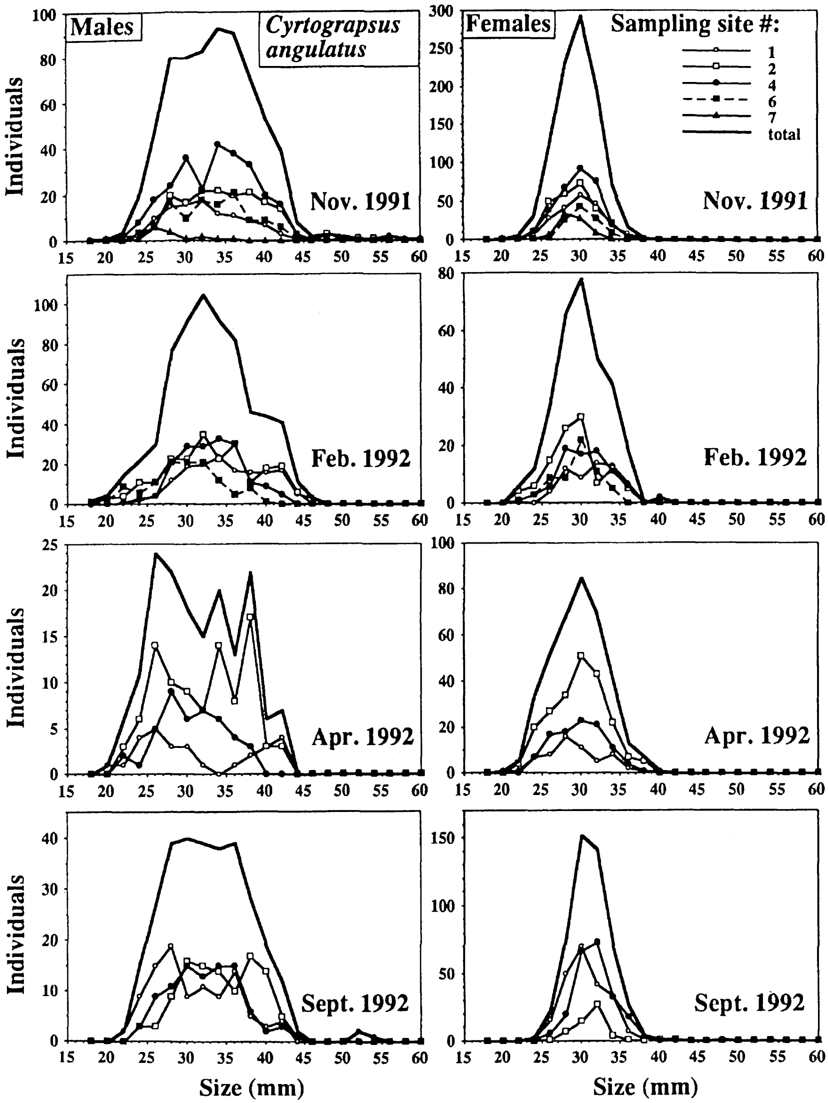

Fig. 3
Seasonal changes in size-frequency distribution (SFD) of males and females of *Cytograpsus angulatus* at different sampling sites.

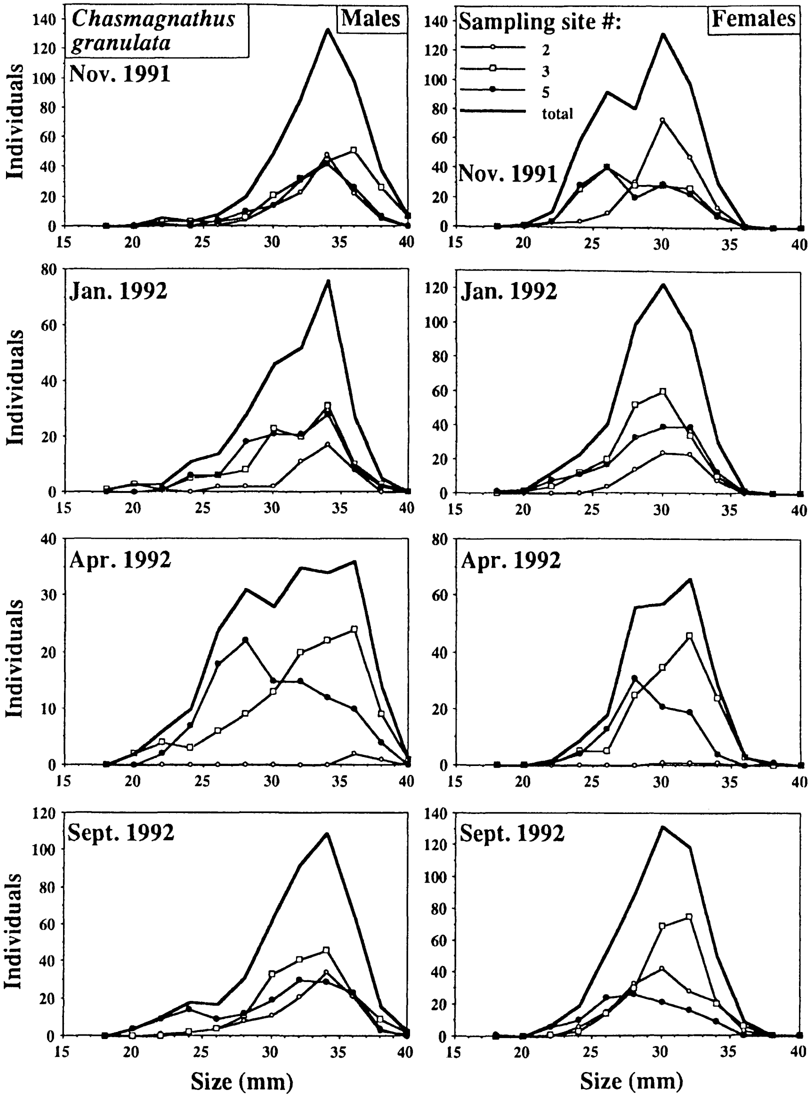

Fig. 4
Seasonal changes in size-frequency distribuitions (SFD) in males and females of *Chasmagnatus granulata* at different sampling sites.

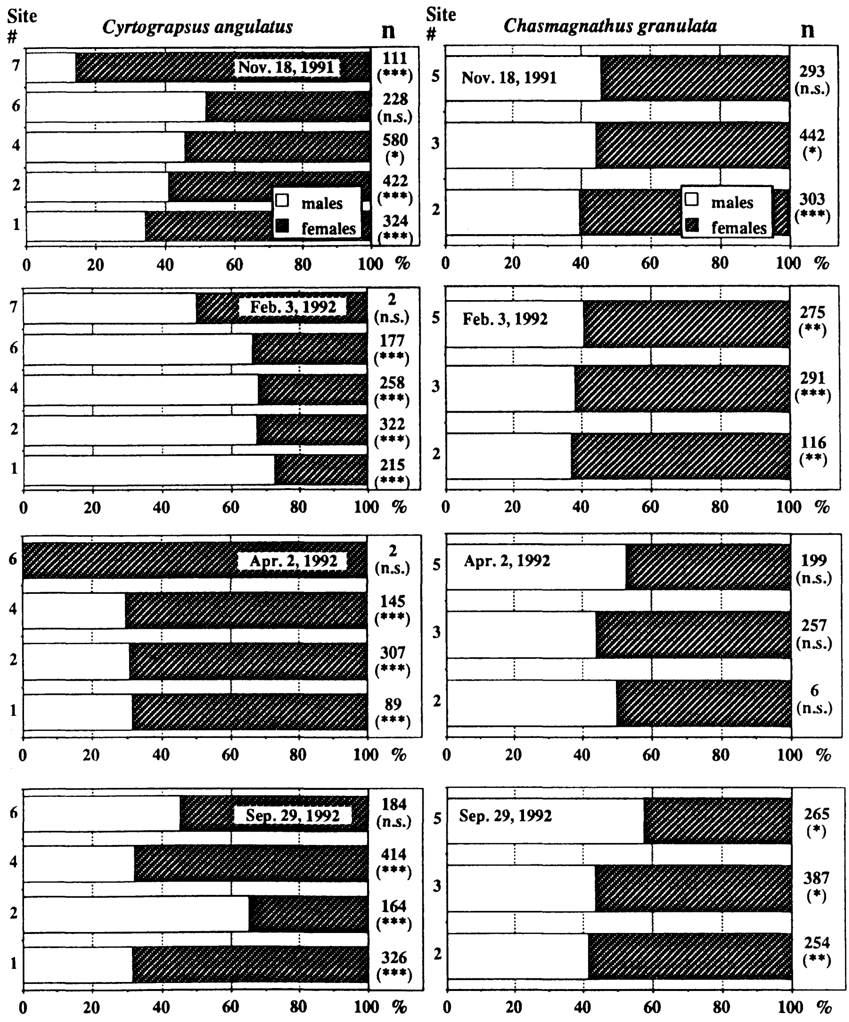

Fig. 5

Seasonal changes in sex ratio of *Cytograpsus angulatus* and *Chasmagnatus granulata* at different sampling sites. Tests for deviations from a hyponetical 1:1 ratio: goodness-of-fit test; n = number of observations; P=level of significance. with n.s. = not significant, *, **, ***: P<0.05, <0.01, and <0.001, respectively).

RESULTS

Adult population structure

Cyrtograpsus angulatus was found at sites 1, 2, and 4 during all seasons, but at site 6 only in November 1991 and February 1992, and at site 7 only in November 1991 (size-frequency distribution, SFD, shown in Fig. 3). The total number of crabs collected in the intertidal zone was highest in late spring (November) and summer (February), minimum in autumn (April), and intermediate in early spring (end of September). SFD of males varied in spring and summer significantly among sites (Kruskall-Wallis test: $P<0.001$), but not in autumn. A Tukey-type nonparametric test showed that crabs collected at site 7 and 6 were significantly smaller than those collected at all other sites in November 1991 and in February 1992, respectively. Three groups of crabs were identified in the SFD of males and further analysed statistically (MacDonald & Pitcher, 1979). In spring, mean carapace widths (CW) of these groups were calculated as 29, 37 and 53 mm, respectively. The latter group represented crabs near the maximum size of the species; they constituted less than 4% of the adult population (>18 mm CW) at sites 1 and 2 in November 1991 and at site 1 in September 1992. In summer and autumn, again three groups were identified, with mean sizes of ca. 24-26, 32-30 and 39-37 mm, respectively, and no individuals with > 46 mm CW were found. As in males, SFD of females differed significantly among sites in spring and summer ($P<0.001$), but not in autumn ($P>0.1$). Among the significantly different SFD, the Tukey test did not allow for recognizing a clear pattern in relation to sampling sites. Female size structure was dominated throughout the year by a single size group (CW 30-32 mm). A few exceptionally large females were collected in September 1992 at sites 1 and 2 (maximum CW: 47.6 mm).

Chasmagnathus granulata was collected exclusively at sites 2, 3 and 5. Crabs were found at all three sites in spring and summer, but in autumn only at sites 3 and 5 (SFD: Fig. 4). The SFD varied in all seasons significantly among sites (Kruskall-Wallis and Mann-Whitney U tests; $P<0.001$). The total number of crabs showed the same pattern as in *Cyrtograpsus angulatus*, with maximum numbers in spring and summer, and a minimum in autumn. The size structure of adult males (all sites pooled) was in general characterized by two groups, with mean CW of 24-27 and 34 mm, respectively (calculation method: MacDonald & Pitcher, 1979). Large crabs were mostly predominating; maximum CW was 39.5 mm. The size structure at site 5 changed dramatically in April, when smaller crabs (25-29 mm) became relatively more abundant; larger crabs remained predominant at site 3, but became scarce at site 2. In the following spring, two size groups (22-25 mm and 29-36 mm) were identified at site 5, while only one group (large crabs) was found at sites 2 and 3. Two size groups could in general be distinguished in SFD of adult females, especially in November 1991, with CW 24-27 and about 31 mm, respectively. Both size groups were present at site 3 and, more markedly, at site 5, where smaller females predominated. At site 2, we found in general

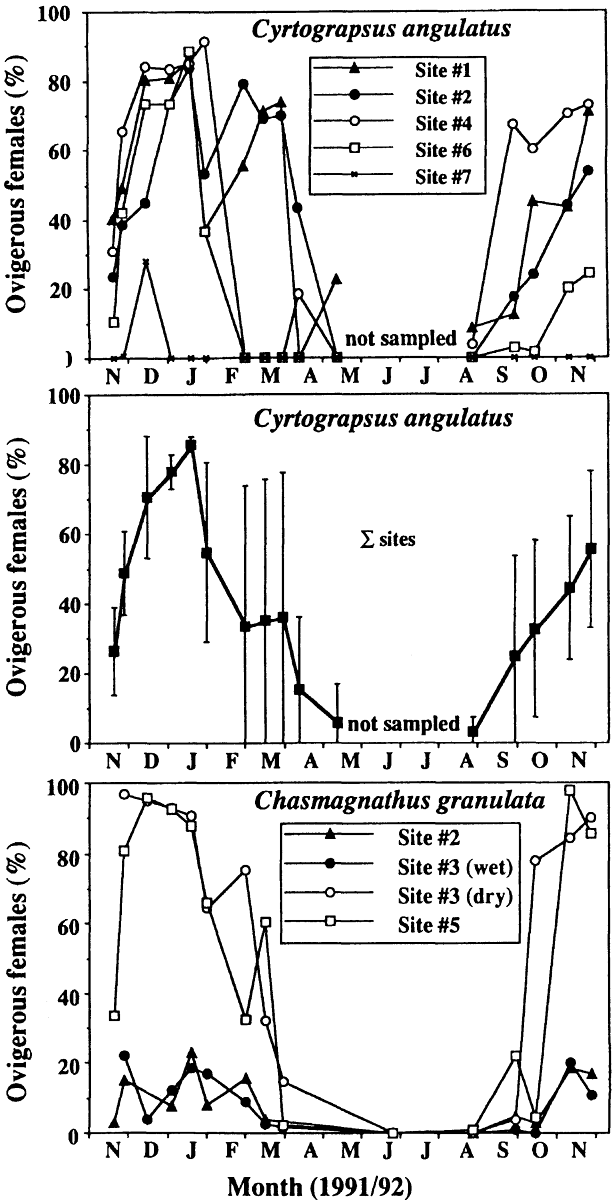

Fig. 6
Seasonal changes in the percentage of ovigerous females (% of all females) of *Cytograpsus angulatus* and *Chasmagnthus granulata* at different sampling sites. Error bars: $\bar{x}\pm SD$, with n=5.

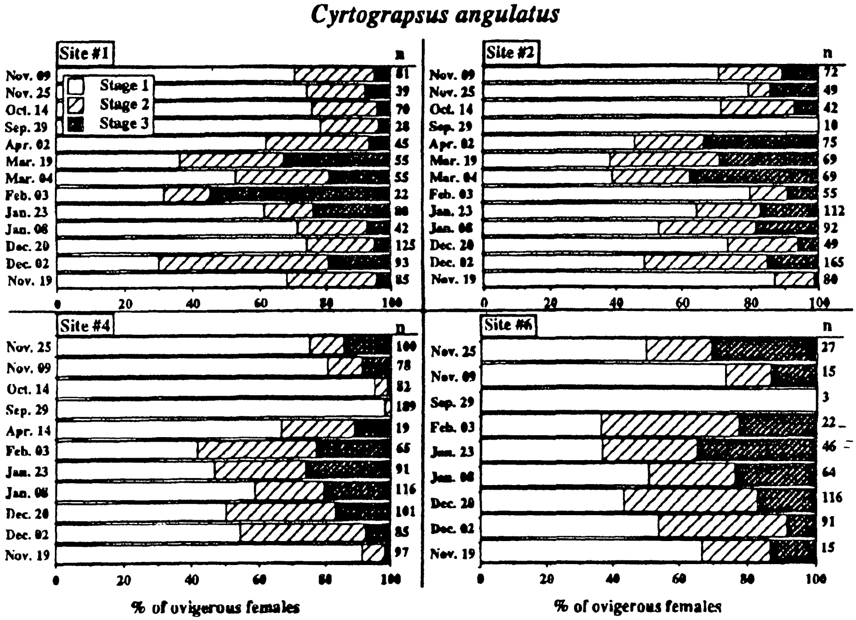

Fig. 7
Seasonal changes in the proportion of embryos Cyrtograpsus angulatus in different stages of developement at different sampling sites. Stage 1: eggs indifferenciate: 2: with chromatophores and segmentation; stage 3: well developed embryos with eyes (see text for further details)

most exclusively large females which, in summer, predominated also at all other sampling sites. In autumn, until the following spring, site 3 was characterised by large females, whereas numerous small females were found at site 5.

Sex-ratio

In *Cyrtograpsus angulatus*, the sex ratio varied both in space (among sites) and time (seasonally). In most samples it differed significantly from 1:1 (Fig. 5). The operative sex-ratio (OSR = ratio of males:non ovigerous females, expressed in %) includes only those adult females that should be ready for mating (Orensanz and Gallucci, 1988). The OSR showed variation both in space and time that did not always follow the patterns of the overall sex-ratio (all females considered; Fig. 5). On November 18 the OSR varied from 47 to 55% (sites 1-6), differing significantly from 1:1 at

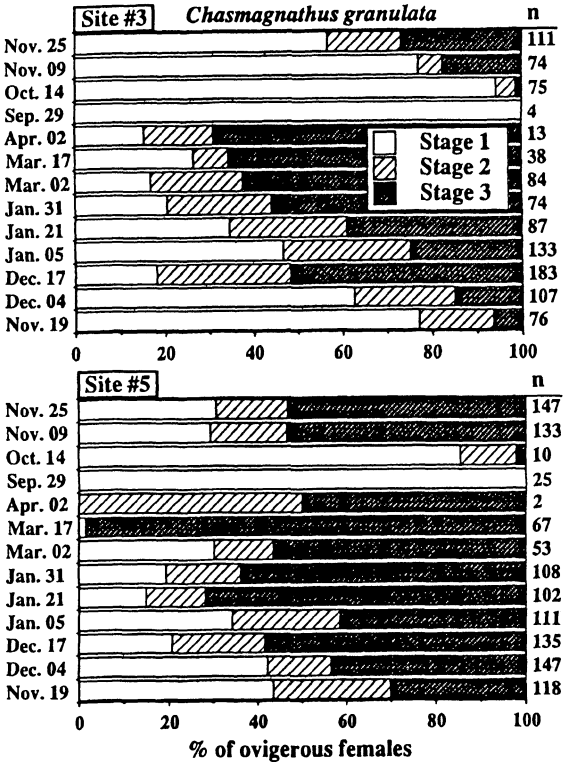

Fig. 8

Seasonal changes in the proportion of embryos *Chasmagnatus granulata* in different stages of developementat different sampling sites. Stage 1: eggs indifferenciated; stage 2; with chromatophores and segmentation; stage 3: well developed embryos with eyes (see text for further details)

site 4 (X^2Test, P<0.05). At site 7, none of the 95 collected females had embryos under their pleon. In February 3, males predominated at all sites; the OSR varied between 82 and 75% (significantly different from 1:1; P<0.001). In April 2, the OSR did not differ significantly from 1:1 at sites 1 and 2 (64 and 46%, respectively) but at site 4 (34%; P<0.001). In September 29, the OSR differed significantly from 1:1 at sites 1, 2 and 4, with females predominating at site 1 (35%; P<0.001), but males at sites 2 (69%; P<0.001) and (59%;P<0.01). At site 6, only 3 out of 101 collected females were ovigerous.

In *Chasmagnathus granulata*, temporal and spatial changes of the sex-ratio were less conspicuous than in *Cyrtograpsus angulatus*. Females predominated in general in spring and summer (Fig. 5). In November 18, there were significantly more females than males at sites 2 and 3, but not at site 5. In January 31, females predominated significantly at all sites. In April 2, however, the sex-ratio did not differ at any site from 1:1. In September 29, significantly more females than males were collected at sites 2 and 3, but the opposite occured at site 5.

When the OSR is considered, males were in spring and summer significantly more frequent at site 5 than non-ovigerous females, with 56, 67 and 64% (Chi-square tests: P<0.05, <0.001, and <0.001, in November 18, January 31 and September respectively), but the opposite was observed at site 2, with 40, 39 and 43% (Chi-square test: P<0.001, <0 .05, and <0.05, respectively). At site 3, significant differences from 1:1 were detected only on September 29 (OSR 44%; Chi-square test: P<0.05).

Breeding period

Cyrtograpsus angulatus females were collected from November 1991 to May 1992, and from August to November 1992. During these sampling periods, ovigerous females were always found at sites 1 and 2, but less frequently at sites 4 and 6, and only occasionally at site 7. No crabs were found in the intertidal during winter (June, July, most of August). The percentage of ovigerous females (POF) varied both in time and space, showing similar seasonal patterns at all sites (Fig. 6). POF values increased in general from the end of spring to the middle of summer, then they decreased (February) and levelled off in autumn. Locally (at sites 1 and 2) a second smaller peak was observed at the end of summer (March).

At site 1, POF values increased from November to January (40 to 86%), decreased in February, increased again in April, and finally decreased in May. By the end of August, only 10% of the few collected females were ovigerous. POF increased continuously again during the following spring. POF had similar patterns at sites 2, 4 and 6 during spring and most of summer. However, a second peak occurred early at site 2 (early March). The maximum POF value (92%) was registered at site 4 in February, while it was decreasing at all other sites. Ovigerous females were not found from March to August at sites 4 and 6. They rarely occurred at site 7 throughout the sampling period; at this site, the maximum POF (28%) was registered in December.

Chasmagnathus granulata females were collected from November 1991 to November 1992, but no data were obtained in April, May, and July 1992. Ovigerous females were frequently found during spring and summer, practically disapeared at the beginning of autumn, and apparently remained absent during winter. The POF varied both in time and space (Fig. 6), with similar seasonal patterns of change at all sites: it increased rapidly in late spring and reached a maximum in mid-summer, then decreased toward autumn. As in *Cyrtograpsus angulatus*, a second smaller peak was observed at the end of summer, before the frequency of ovigerous females decreased sharply in autumn.

At site 2, POF values were in general low, reaching maximum values of 20% only in November and January. Two separate samples were obtained at site 3, beginning in December 1991: "wet mud" (near the water edge) and "dry mud" (upper intertidal).

In wet mud, POF values were similarly low as at site 2. Crabs sampled in the upper intertidal, in contrast, showed much higher POF values. Here, most females (90%) were ovigerous from December to January. The POF decreased later in January, increased again (early March), before it decreased toward autumn. During the following spring, POF figures increased from the end of September to the end of November (from 4 to 90%), with similar figures in a "cangrejal" habitat (site 5) and site 3 (dry mud).

Embryonic stages

Ovigerous female *Cyrtograpsus angulatus* were collected during spring, summer and autumn at all sampling sites. Females with newly laid eggs predominated in most of the samples (Fig. 7). The percentage of females with well developed embryos (stage 3; short before hatching of larvae) varied during the reproductive season and among sites. At site 1, the frequency of embryonic stage 3 was mostly low during spring, but increasing by the end of the season. After a decrease at the beginning of summer, the figures reached another maximum in early February (up to 54%). A third, but smaller peak was reached at the end of summer (March), followed by a sharp decrease. At site 2, also three peaks were observed in the frequency of late embryonic stages: in early December, January and March-April. At sites 4 and 6, two peaks in the frequency of occurrence of stage 3 embryos could be clearly distinguished: in late November and late January.

Ovigerous female *Chasmagnathus granulata* were collected at sites 3 and 5 from spring to early autumn (Fig. 8); only a few were found at site 2. At site 3 (pooled wet and dry mud data), the frequency of females with late (stage 3) embryos showed a first peak in December, another from mid-summer to early autumn (January-April). Three peaks may be distinguished at site 5: mid-December, late January, and the highest (98%) in mid-March.

DISCUSSION

Adult population structure

The analysis of size-frequency distributions (SFD) allows to separate year classes in crustaceans, if several prerequisites are met: there must be a limited breeding season, significant growth from year to year and no changes in the stock due to migration (Hartnoll, 1982). The SFD of crabs belonging to a single year class shows approximately a normal distribution (Hartnoll & Bryant, 1990). When year classes are not well differenciated, they can sometimes be separated by graphical or other analytical methods (Hartnoll, 1982). In populations that produce several clutches per individual or a single brood per individual, but out of phase, a year class can reveal several size groups (Sastry, 1982).

Cyrtograpsus angulatus did not continuously occur at sites 6 and 7, and when present, the crabs were on average smaller here. The wide size range observed in most samples can be explained by long breeding and recruitment seasons, in combination with quite variable, temperature and size-dependent growth rates (Hartnoll, 1982). Moreover, migration of young adults from juvenile to adult habitat should be a continuous process. Hence, the number of male year classes in *C. angulatus* must remain open, in spite of the apparent persistence of three size-groups throughout the year. The mean size in the two smaller groups that were found in spring differed by 20%, and similar figures appeared in summer and autumn. Crabs belonging to the third group were in spring more than 50% larger than those of the second. No evidence allowed for deciding whether the first two size-groups found in spring represented two separate year classes or different cohorts belonging to the same year class. However, the largest male crabs, which were close to the maximum size of this species (sites 1 and 2) should represent a definite year class. Their disappearance in the following summer may be caused by increased death rates in larger crabs observed in particular during hot days (Gavio & Spivak, 1994). Also a few very large females found in early spring suggest that there were two distinct year classes in *C. angulatus*.

Differences in SFD among sampling sites were consistent with previous findings of small-scale distribution patterns in *Chasmagnathus granulata* (Spivak et al., 1994). This species has a shorter reproductive period and probably a more restricted growth season than *Cyrtograpsus angulatus. C. granulata* is a semiterrestrial species that is active from spring through most of autumn, but remains dug in its burrows during winter. Consequently, the time available for feeding and growth should be limited by cold periods (Wolcott, 1988). These facts, together with a narrower size range in adult *C. granulata*, allowed to detect growth from SFDs, in spite of possible ontogenetic migrations. For instance, females probably grew conspicuously in late spring and early summer at sites 3 and 5 (Fig. 4), whereas no growth was detected during the course of winter.

SFDs suggested that two year classes appear in both male and female *Chasmagnathus granulata*. They were more evident at site 5 in November (females) and September (males). The decrease in the proportion of older crabs registered at sites 2 and 5, from November to April (at site 3 from November to January; Fig. 4), may be due to mortality. An incorporation of juvenile crabs into the adult group is suggested by two well-defined size groups in males at site 5 (September 1992), and by the presence of smaller females at site 5 in autumn as compared with summer (Fig. 4).

Site 2, where large males and females live throughout spring and summer, appeared to be a marginal habitat for *Chasmagnathus granulata* (Spivak et al., 1994). Large crabs of another burrowing shore crab, the ocypodid *Macrophthalmus japonicus*, were also observed to live in less typical habitats, probably because of a reduced competition at low densities (Henmi, 1992).

Sex-ratio

The average sex-ratio of juvenile crabs does not differ from 1:1 in both species studied here (Spivak et al., 1994), but that of adults, especially in *Cyrtograpsus angulatus*, does frequently. It may vary both in time and space as a consequence of specific environmental requirements for mating and larval release, probably leading to migrations over relatively long distances. *C. angulatus* is a very mobile species, whose spatial distribution shows great small-scale variability. Clusters of males with a few females, or pairs of crabs in precopula or copula, have been observed in shallow waters in early spring and late summer suggesting a "male encounter" mating system (Boschi, 1964; Gavio & Spivak, 1994a). Females may choose their mates from a dense transitory aggregation of males on the basis of their body size and sexually dimorphic traits (Christy, 1987). On the other hand, dense patches of ovigerous female *C. angulatus* were found at site 4, almost completely buried in the mud (Spivak, unpublished). A strongly male biased sex-ratio one week later suggests that most females migrated from the intertidal to deeper water to release their larvae.

Variations in the sex-ratio and other population parameters did not show a clear pattern, since reproductive phenomena have a short transient existence, and possible tidal, daily or seasonal migrations to deeper waters were not investigated. Such migrations were suggested to occur in both marine and estuarine populations of *Cyrtograpsus angulatus* (Mar del Plata Harbour: Spivak, 1986; Tramanda estuary: Cracco, 1994). They were intensively studied also in *Carcinus maenas* (Klein Breteler, 1975), which shows remarkable similarities with *C. angulatus* in its habitat, behaviour and life history.

Chasmagnathus granulata builds elaborated and rather stable burrows. Consequently, this species shows a more steady spatial distribution, in spite of significant small-scale variation occurring also in this species (Spivak et al., 1994). Deviations from a 1:1 sex-ratio are weaker, in particular at site 5, which is a typical "cangrejal" habitat. Mating couples have been observed both in burrows and in shallow waters; on the other hand, one male and several non-ovigerous females were often found together in shallow pitches at site 3 ("wet mud"; Spivak et al., 1994). Other burrowing grapsids, which inhabit similar salt-marsh habitats, have a polyginic mating system: males attract females to their burrows for mating (Christy, 1987). Hence, the operative sex-ratio of polyginic species should be female-biased. In contrast to site 5, however, non-ovigerous female *C. granulata* predominated during the whole reproductive season at site 2, where digging of burrows is more difficult and thus, many crabs remain under stones during ebb tide.

Reproductive cycles

Both species studied have a seasonal cycle of reproductive activity, with females breeding from spring to the beginning of autumn, most probably producing several egg clutches per season. In general, this period is longer in species living in the low intertidal as compared with those from the high intertidal zone (Sastry, 1982; Emmerson, 1994). Ovigerous females of *Cyrtograpsus angulatus*, which lives in the lower intertidal, were present over a longer period (September-May; a few remained even in winter), whereas those of *Chasmagnathus granulata*, which is more terrestrial, were found only from October to March. Differences in the length of the breeding season may be a consequence of sometimes low temperatures in terrestrial habitats (Wolcott, 1988). On the sea coast near Mar Chiquita, ovigerous *C. angulatus* were found during the whole year, with a clear minimum during winter (Spivak, 1986). A similar seasonal breeding cycle was observed in this species also in the Tramandaí estuary (southern Brazil; Cracco, 1994).

Similar differences between the breeding periods of grapsid crabs with different degrees of terrestrial adaptation were found also in estuarine crabs in Japan (Pillay & Ono, 1978) and South Africa (Emmerson, 1994). Differences may be related to differential exposure to seasonal and daily changes in temperature, light, and food availability. A comparison of water and air temperatures near Mar Chiquita (Fig. 2) showed that an increase from 7 to 14° C takes place in the water by the end of winter (August-September), but only two months later in the air. This may explain why *Cyrtograpsus angulatus* reproduces earlier in the season, while low air temperatures might cause a prolonged dormancy in *Chasmagnathus granulata*, with reduced feeding activity and delayed gonad growth.

It has been suggested that larvae of both species do not develop in this lagoon but exhibit an export strategy, probably based upon exogenously coordinated egg hatching rhythms (Anger et al., 1994). Both species show during the reproductive season various peaks in the percentage of ovigerous females, with highest values at the beginning of summer. The study of embryonic stages provided further evidence for discontinuous hatching patterns during the course of the reproductive cycle. Peak frequencies of females carrying late embryonic stages (near hatching) suggest a synchronous larval hatching in *Chasmagnathus granulata* (Fig. 7). In contrast, several, apparently uncoordinated peaks were observed in *Cyrtograpsus angulatus* (Fig. 6), probably indicating a more continuous release of larvae in this species.

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ABSTRACT

Life history patterns of two grapsid crab species were studied in Mar Chiquita, a brackish coastal lagoon in Argentina. *Chasmagnathus granulata* is a burrowing crab living in the upper intertidal, whereas *Cyrtograpsus angulatus* lives predominantly in the lower intertidal and subtidal. *C. granulata* is active (i.e. foraging and reproducing) during spring, summer and most of autumn, but remains mostly hidden inside its burrows during winter. Two dominant size groups each were found in the size-frequency distributions of males and females. Since this species builds elaborated and rather stable burrows, we found a rather uniform spatial distribution and a stable sex ratio, with only weak local deviations from a 1:1 ratio. In *C. angulatus*, which is a very mobile species, the sex ratio varied greatly in time and space, indicating local migrations with differential intensities or directions in males and females. Adult size structure in this species was similar at different sampling sites, with size frequency distribution of males revealing three dominant size groups, but that of females only one or two. In late autumn, most individuals of this species leave the intertidal zone and stay during winter in deeper water. Both species show a pronounced seasonal reproductive activity pattern, with a maximum percentage of ovigerous females found in the beginning of summer, and both appear to produce several subsequent egg clutches until late summer. The reproductive season is longer in *C. angulatus* (September-May; a few ovigerous females were found also in winter) than in *C. granulata* (October-March). In the intertidal, a low percentage of *C. angulatus* was observed to carry eggs in late embryonic stages. This suggests that ovigerous females of this species may migrate to the subtidal to release their larvae in deeper water.

Key words: Grapsid crabs, intertidal, life history, reproduction, sex ratio

RESUMEN

En Mar Chiquita, una laguna costera de Argentina, fueron estudiados los patrones de historia de vida de dos especies de cangrejos grápsidos. *Chasmagnathus granulata* es un cangrejo excavador que vive en el intermareal superior mientras que *Cyrtograpsus angulatus* vive predominantemente en el intermareal inferior y en el submareal. *C. granulata* está activo (se alimenta y reproduce) durante la primavera, el verano y la mayor parte del otoño, pero durante el invierno permanece casi siempre oculto en sus cuevas. En las distribuciones de frecuencias de tallas se encontraron dos grupos de tallas dominantes. Esta especie construye cuevas elaboradas y bastante estables; coincidentemente, se encontró una distribución espacial bastante uniforme y una proporción de sexos estable, con solo pequeñas desviaciones de la proporción 1:1. La proporción de sexos de *C. angulatus*, una especie muy móvil, vara mucho en el tiempo y el espacio, indicando migraciones locales con intensidades y direcciones diferenciales en machos y hembras. La estructura de tallas de los adultos de esta especie fue similar en diferentes sitios de muestreo; las distribuciones de frecuencia de tallas revelan tres grupos de tallas dominantes en los machos y sólo uno o dos en las hembras. Al avanzar el otoño, la mayora de los individuos de esta especie abandonan el intermareal y permanecen durante el invierno en aguas más profundas. Ambas especies muestran un patrón de actividad reproductiva marcadamente estacional, con un porcentaje máximo de hembras ovígeras al comienzo del verano, y ambas parecen producir varias camadas sucesivas de huevos hasta el fin del verano. La estación reproductiva es más larga en *C. angulatus* (Septiembre-Mayo; unas pocas hembras ovígeras fueron encontradas también en invierno) que en *C. granulata* (Octubre-Marzo). Un bajo porcentaje de *C. angulatus* llevando huevos en estados embrionarios

avanzados fue observado en el intermareal. Esto sugiere que las hembras ovígeras de esta especie pueden migrar hacia el submareal y liberan sus larvas en aguas más profundas.

Palabras clave: cangrejos grápsidos, intermareal, historia de vida, reproducción, proporción de sexos

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