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Research Article

Population structure of the burrowing crab *Neohelice granulata* (Brachyura, Varunidae) in a southwestern Atlantic salt marsh

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ABSTRACT. *Neohelice granulata* inhabits estuarine and protected coastal areas in temperate regions and is the most dominant decapod crustacean in the Bahía Blanca Estuary, Argentina. The population structure was studied during a year in a SW Atlantic salt marsh located in the Bahía Blanca Estuary. Crabs were sampled monthly from August 2010 to July 2011. The maximum observed density was 30 crabs m^{-2} in February and 70 burrows m^{-2} in May. The maximum carapace width (CW) was 32 and 27.5 mm in males and females respectively. Medium size crabs were between 16 and 20 mm CW. Significantly smaller sized crabs were observed at the lower intertidal regions ($P < 0.05$). The sex ratio was favorable for males and was significantly different from the expected 1:1 ($P < 0.05$). The recruitment of unsexed juveniles crabs (CW <6.5 mm) was observed throughout the year and the presence of ovigerous females from October to February indicated seasonal reproduction. The average size of ovigerous females was CW = 20.8 mm and the smallest ovigerous female measured was 16 mm CW. For the first time, the population structure of the most important macro-invertebrate is analyzed in the Bahía Blanca Estuary. This study may help to make decisions in the area, where anthropic action is progressing day by day.

Keywords: *Neohelice granulata*, crabs, population structure, salt marsh, estuary, southwestern Atlantic.

Estructura poblacional del cangrejo cavador *Neohelice granulata* (Brachyura, Varunidae) en una marisma del Atlántico sudoccidental

RESUMEN. *Neohelice granulata* habita áreas estuarinas y costeras en regiones templadas y es el crustáceo decápodo más predominante en el estuario de Bahía Blanca, Argentina. Su estructura poblacional fue estudiada durante un año en una marisma del sudoeste Atlántico localizada en el estuario de Bahía Blanca. Los cangrejos fueron muestreados mensualmente desde agosto de 2010 hasta julio de 2011. La densidad máxima observada fue de 30 cangrejos m^{-2} en febrero y 70 cuevas m^{-2} en mayo. El ancho de caparazón (AC) máximo fue de 32 y 27,5 mm en machos y hembras, respectivamente. La longitud promedio de los cangrejos se situó entre 16 y 20 mm de AC. Cangrejos significativamente más pequeños se observaron en las regiones intermareales más bajas ($P < 0{,}05$). La proporción de sexos favoreció a los machos y fue significativamente diferente de la esperada 1:1 ($P < 0{,}05$). El reclutamiento de cangrejos juveniles asexuados (AC <6,5 mm) ocurrió todo el año y la presencia de hembras ovígeras de octubre a febrero, lo que indica una reproducción estacional. El tamaño promedio de las hembras ovígeras fue de 20,8 mm de AC y la hembra ovígeras más pequeña fue de 16 mm AC. Por primera vez se ha analizado la estructura poblacional del más importante macroinvertebrado del estuario de Bahía Blanca. Este estudio podría ayudar a tomar decisiones en el área, donde la actividad antrópica está avanzando día a día.

Keywords: *Neohelice granulata*, cangrejos, estructura poblacional, marismas, estuario, Atlántico sudoccidental.

INTRODUCTION

The salt marshes and mud flats are ecosystems which characterize the intertidal zone of estuarine and coastal areas in temperate regions. Brachyura crabs are the most abundant and ecologically important macro invertebrates inhabiting vegetated and unvegetated salt marshes areas. They are a key species in "cangrejal" eco-

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systems a particular brackish salt marsh ecosystem of eastern South America (Boschi, 1964; Spivak, 2010).

Neohelice granulata (Dana, 1851) (=*Chasmagnathus granulatus*) is a semiterrestrial burrowing crab endemic from a tropical and subtropical estuaries in South America. These species occur in the southwestern Atlantic Ocean in Brazil (from Río de Janeiro 22°57'S, 52°32'W, to Rio Grande do Sul, Uruguay and San José Gulf, Northern Patagonia, Argentina 42°25'S, 64°36'W) (Spivak, 2010). Dense populations of *N. granulata* inhabit almost all zones of the intertidal, the soft bare sediments flats and areas with the cordgrass *Spartina densiflora*, *Spartina alterniflora* and *Sarcocornia perennis* (formerly known as *Salicornia ambigua*) (Botto *et al.*, 2005; Bortolus, 2006). This crab constructs vertical burrows of up to 10 cm of diameter that can reach up to 1 m depth in vegetated marshes. The burrows remain open during high tide periods and generally remain full of water during low tide. Furthermore, these burrows act as passive traps of sediment and detritus in open mud flats. Burrowing activity may also change sediment characteristics (Botto *et al.*, 2006; Mendez-Casariego *et al.*, 2011).

The structure of *N. granulata* populations (their life-history, reproduction, feeding and ecological role), have been studied in numerous locations characterized by low or fluctuating salinity, such as Dos Patos Lagoon, southern Brazil (31°04′18″S, 51°28′35″W; D'Incao *et al*., 1992; Ruffino *et al.*, 1994); Jabaquara Paraty, Brazil (23°12'26"S, 44°43'18"W; Gregati & Negreiros-Fransozo, 2007, 2009); Santa Lucía Wetlands, Uruguay (34°47'S, 56°20'W; Merentiel Ferreyra, 2014); Samborombón Bay, Buenos Aires province, Argentina (35°27'S, 56°45'W; Botto & Irigoyen, 1979; López & Rodríguez, 1998; César *et al.*, 2005); Mar Chiquita Lagoon, Buenos Aires province, Argentina (36°09'26″S, 60°34′11″W; Anger *et al.*, 1994; Spivak *et al*., 1994, 1996; Iribarne *et al*., 1997; Luppi *et al*., 1997, 2002; Bortolus & Iribarne, 1999; Iribarne, 2001; Ituarte *et al*., 2004); and San Antonio Bay, Río Negro province, Argentina, (40°44′51.43″S, 64°52′5.10″W; Bas *et al*., 2005). In Bahía Blanca, the burrowing crab activities in the estuary intertidal habitat has been extensively studied (Menone *et al.*, 2004; Botto *et al.*, 2005; Minkoff *et al.*, 2006; Alberti *et al*., 2008; Escapa *et al.*, 2008). However, available information on its population structure (abundance, composition, sex rate, size frequency) in Bahía Blanca Estuary ecosystem is null.

A structural characterization of populations is essential for the preservation of natural resources. Such data can be employed in ecological studies concerning spawning, mortality, growth and migration, for example. Thus, the main objective of this paper is to study the population structure, habitat use, seasonal variation and reproductive biology of *N. granulata* in a SW Atlantic salt marsh.

MATERIALS AND METHODS

Study area

The Bahía Blanca Estuary (38°50'S, 62°30'W) is located in the southwest of Buenos Aires Province, Argentina and is characterized by a series of major NW-SE tidal channels that separate extensive tidal flats, salt marshes and islands (2.300 km^2). It is a mesotidal coastal plain estuary with a semidiurnal tidal regimen. The mean tidal amplitude ranges from 2.2 to 3.5 m and the spring tidal amplitude ranges from 3 to 4 m, with highest tidal amplitudes taking place near the head of the estuary. The estuary is characterized by low depth (between 3 and 22 m from head to mouth) and the presence of various channels and fine sand and silt-clay sediments. The main energy into the Bahía Blanca system is produced by standing and semidiurnal tides. The freshwater input to the estuary is weak, and comes mainly from two tributaries on the northern shore of the interior of the system: the Sauce Chico River and the Napostá Grande creek. The mean annual runoffs of the Sauce Chico River and Napostá Grande creek are 1.5-1.9 and 0.5-0.9 m^3 s^{-1}, respectively. The seawater salinity in the middle portion of the estuary is about 33.98 (annual mean), while the inner zone becomes hypersaline during dry summers because of the high rate of evaporation. Several ports, towns and industries are located on the northern boundaries of the estuary, discharging their processing residues into streams or directly into the estuary (Piccolo *et al.*, 2008).

The study site is located in the north coast of the Bahía Blanca Estuary; near Villa del Mar a coastal town located in the middle-outer reach of the Canal Principal where the mean tidal range is 3.5 m. A peculiar feature of this area is the total absence of tidal creeks and channels, with the exchange of tidal water and suspended sediments taking place across the entire saltmarsh front (Negrin *et al*., 2011). The substrate is composed by a mixture of 87% mud and 13% sand, showing no evidence of net sediment accumulation, rather there may be mild erosion (Pratolongo *et al.*, 2010). Salt marshes have both *Spartina* species: *S. alterniflora* that dominates the lower marsh and *S. densiflora* along with *Sarcocornia perennis* dominating the upper marsh area. The very extensive intertidal is dominated by the burrowing crab *N. granulata* (Bortolus, 2006; Isacch *et al.*, 2006) (Fig. 1).

Field measurements

Sampling was conducted monthly in the intertidal zone, between August 2010 and July 2011. Four micro-habitats subject to different hydrodynamic and ecological

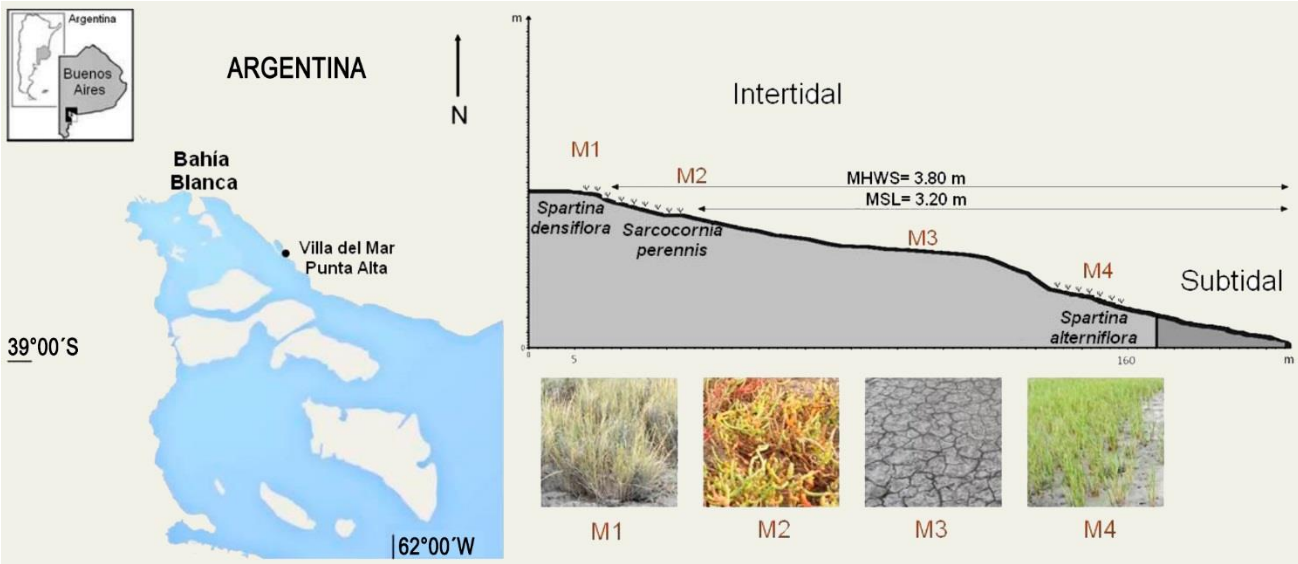

Figure 1. Study area with sampling sites (M1, M2, M3 and M4).

conditions were preselected: two vegetated saltmarshes in the upper intertidal; one dominated by *S. densiflora* (M1) and the other dominated by *S. perennis* (M2), a middle non-vegetated open mudflat (M3) and a low vegetated saltmarshes dominated by *S. alterniflora* (M4). Burrows and crabs densities were calculated using quadrats (0.5x0.5 m side) which were randomly allocated in each microhabitats during low tides, when the area was exposed (n = 4 samples in each site), counting burrows and collecting all crabs present inside the squares. Crabs were kept in 4% formaldehyde for morphometric analysis and transported to the laboratory.

Laboratory measurements and data analysis

Once in the laboratory, crabs were counted and classified as male, female or undifferentiated (those which did not present secondary sexual characters). Ovigerous females were registered. The following somatic parts of each crab were measured: maximum carapace width (CW; was always measured behind the third cephalothoracic spine), abdomen width for females (AW; obtained from the 5^{th} to 6^{th} abdominal somite) and gonopod length for males (GL) to the nearest 0.1 mm using a Vernier caliper. Only crabs in intermoult stages and complete, without any defective appendages, were used in this analysis.

Densities were compared among sites and dates by a two-way ANOVA with equal proportional replication (Zar, 1996), applied to detect differences between mean densities of all crabs and their burrows. Data were also checked for homoscedasticity. Crabs collected in all quadrats of each site were pooled and a size frequency distribution was constructed for each microhabitat and for the whole intertidal zone; size intervals used for grouping individuals were 4 mm. Size differences were compared by means of Kruskal-Wallis test. Spatial variations in sex ratio were tested using X^2 tests. We compared some life history traits between Bahía Blanca Estuary and other *N. granulata*'s populations in South America.

RESULTS

The 434 *N. granulata* crabs captured included 259 males, 142 females and 33 undifferentiated. All of them were found inside and around the burrows. Crabs, lived both in vegetated and un-vegetated areas and were mostly distributed in the upper and lower tide level, but density varied between zones and between different sampling dates. Maximum density of the year was 30 crabs m^{-2} in February, in M4. *N. granulata* was found at M1, M2 and M4 during all seasons but never in M3. M1 shows more number of crabs in spring (September and November), while M2 shows more crabs in summer and autumn (January and February, May and June respectively) and M4 in summer (December and February) (Fig. 2). Density of crabs showed no significant variations among months ($F_{2.25}$ = 1.39; $P >$ 0.24) neither among sampling sites ($F_{3.44}$ = 2.13; $P >$ 0.14).

A total of 893 burrows were registered, the maximum observed density was 70 burrows m^{-2} in May, in M2. Few burrows were recorded in M3 in autumn, but they were absent the rest of the year (Fig. 3).

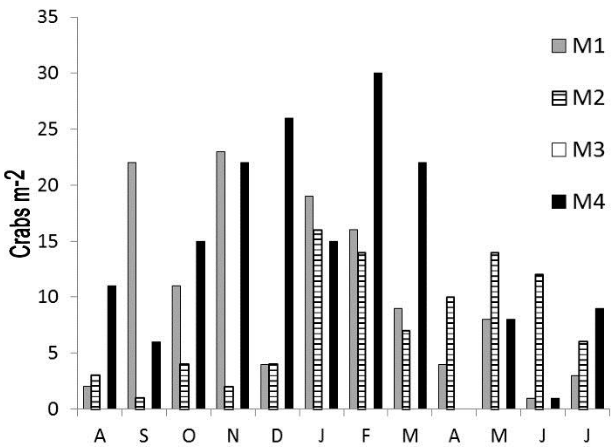

Figure 2. Population density (crabs m^{-2}) of *N. granulata* monthly at different sampling sites.

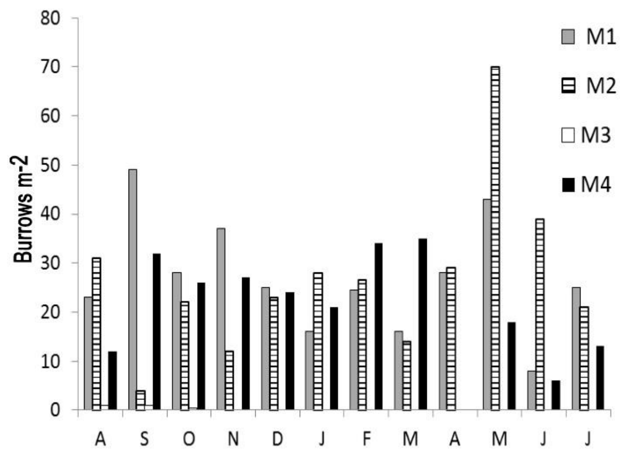

Figure 3. Burrows density (burrows m^{-2}) of *N. granulata* monthly at different sampling sites.

The density of the crab's burrows showed no significant variations among months ($F_{2.26}$ = 0.72; P > 0.70) nor among sampling sites ($F_{3.44}$ = 0.76; P > 0.48). Burrows' densities show similar variations with crab's densities: M1 shows more number of burrows in spring (September), M2 in autumn (May) and M4 in summer (February). While the absence in M4 of burrows and crabs, in April, may be due to the estuary's high dynamic for that period, where the sample area was not defined.

N. granulata was recorded in all class intervals for the distribution of sizes. The crab population in the whole intertidal zone (all sites polled) through the year showed a unimodal size-frequency-distribution (one size group was identified) and skewed to the right. Medium size crabs were mostly predominating (between 16-20 mm CW). Maximum CW was 32 mm and 3.5 mm minimum. In smaller than 6.5 mm crabs no external morphological differences between sexes were observed and were considered sexually undiffe-rentiated. The maximum and minimum size reached was 32 and 6.5 mm respectively for males, and 27.5 and 7.5 mm for females (Fig. 4).

When we analyzed the size-frequency-distribution (SFD) of each microhabitat, the histograms showed differences between them. In M1, medium size crabs registered in this study were predominating too, but it was characterized by two main modes or size groups; the mayor frequencies were between 8-12 mm and between 16-20 mm CW. M2 showed the presence of only one mode which was approximately 16-20 mm CW. Moreover in M4 small size crabs were predominating; between 4-8 mm CW (Fig. 5). The SFD varied significantly among sites (Kruskal-Wallis test); the assumption of equality among samples was not met (H = 15.6337; P < 0.05).

For population biology analysis, the crabs were distributed in two categories: unsexed crabs (undifferentiated) and sexed crabs (juveniles and adults). The smaller crabs (undifferentiated) were more abundant in M4 than in M1 and M2. There were more males than females in the whole intertidal area studied. The sex ratio varied in space (among sites) and differed significantly from 1:1 (Fig. 6). The Chi-square tests for difference in male and female sex ratios showed significant differences along the coast of Bahía Blanca estuary. In M1 ratio = 1.8:1, in M2 ratio = 2:1 and in M4 ratio = 1.7:1 (P < 0.05).

Ovigerous females (n = 11) were only found at M4 during spring and summer (from October to February), practically disappeared at the beginning of autumn, and apparently remained absent during winter. The average size of ovigerous females was CW = 20.8 mm and AW = 12.1 mm. The biggest ovigerous female measured was 23.5 mm CW and 14.5 mm AW (in January) and the smallest ovigerous female measured was 16 mm CW and 10 mm AW (in February). In M4, the proportion of ovigerous females was 50% (October, n = 5) and 5% (February, n = 1). Females from M1 and M2 were always non-ovigerous.

DISCUSSION

The Bahía Blanca Estuary is a temperate zone with well distinct thermal seasons; mean temperatures vary from 14°C in winter to 20°C in summer, this means that summers and winters are rigorous, and the intermediate seasons are more benign. The annual mean rainfall is 630 mm, with maximum values in March and October (90.9 and 80.9 mm respectively) and lowest values in winter (June; 16.5 mm). Salinity ranges from 15.84 in winter to 40.91 in summer with an annual mean of 33.98.

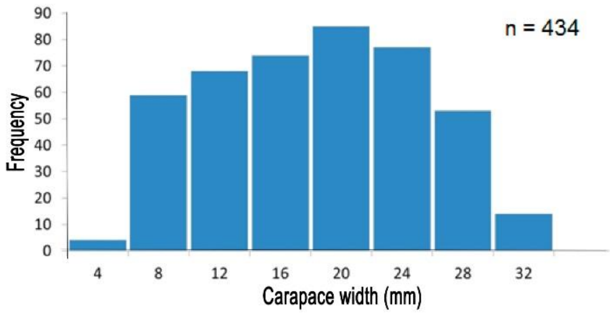

Figure 4. Size-frequency distribution of *N. granulata* (n = 434) in the whole intertidal zone through the year.

Due to the system high dynamics, dissolved oxygen is always near saturation levels and the pH is near neutrality (Piccolo & Hoffmeyer, 2004). The predominant sediments vary from mud to sands (Angeletti *et al*., 2014). Based on this previous information, these crabs would have a wide range of tolerance to the environmental factors cited for this estuary.

The density of *N. granulata* in Bahía Blanca estuary is the lowest compared with other populations. However, *N. granulata* density does not decrease along with increasing latitude, and the abundant center hypothesis along a wide latitudinal range cannot be applied (Sagarin & Gaines, 2002). Values registered in San Antonio Bay, near the southern limit of its geographical distribution (136 ind m^{-2}, Bas *et al*., 2005), were higher than the maximum reported for Mar Chiquita Lagoon (53 ind m^{-2}, Spivak *et al*., 1994) and for Samborombón Bay (52 ind m^{-2}, César *et al*., 2005). Intermediate values were found in the northernmost populations studied (98 ind m^{-2}, Dos Patos Lagoon; D'Incao *et al*., 1992).

Although there is scarce previous information about the number of burrows, our data indicates that the maximum burrow's density is less compared with the observed in Santa Lucia Wetlands, Uruguay (95 burrows m^{-2}; Merentiel-Ferreyra, 2014). Both populations have the maximum number of burrows in May. This curious feature is not related to the maximum density of crabs neither with environmental factors, such as temperature. So, further samplings are needed to analyze this phenomenon.

N. granulata is a semi-terrestrial species, active from spring throughout most autumn, but remains inactive or hidden inside their burrows during winter. Consequently, the time available for feeding and growth should be limited by cold periods (Bas *et al*., 2005). So, the fact that M1 and M2 showed more number of crabs in spring and autumn respectively, would respond to the crab's needs to feed with halophytes species *S. densiflora* and *S. perennis*, and in this way to face and recover (before and after) the cold season. They would take advantage of the shelter and food provided by these plants present in the intertidal highest areas. On the other hand, M4 presented more crabs in summer and this correspond to a mainly fact for mating and larvae eclosion, because the proximity to the water allows the successful development of these. According to Mantelatto & Biagi-García (1999) this move would be associated with reproductive strategies. Movements among microhabitats through the year could be a kind of migration in the intertidal, responding to the crabs needs. On the other hand, it is known that the colonization of intertidal by *N. granulata* is facilitated by the presence of halophyte plants that generate shaded areas where the sediment stays moist, soft and more likely to be excavated (Bortolus *et al*., 2002). Therefore, we assumed that the almost total absence of burrows and crabs in M3 could be due to both cohesive nature of sediment and the lack of plants (Angeletti *et al*., 2014).

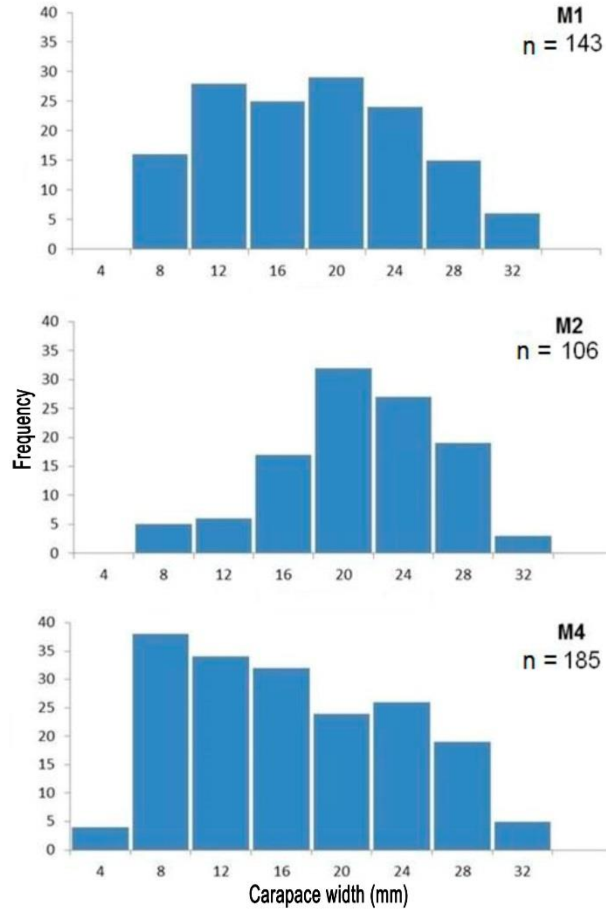

Figure 5. Size-frequency distribution of *N. granulata* at different sampling sites.

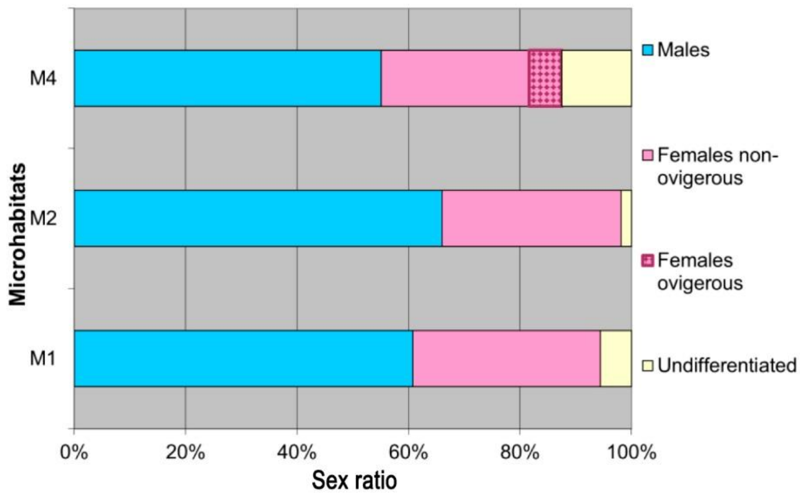

Figure 6. Sex ratio (in % of total population) of *N. granulata* at different sampling sites.

The maximum size of males and females of *N. granulata* in Bahía Blanca Estuary (32 and 27.5 mm CW, respectively) was smaller than in Mar Chiquita (39.5 and 35 mm CW; Spivak *et al.*, 1996) and Jabaquara Paraty, RJ, Brasil (39.5 and 36.8 mm CW; Gregati & Negreiros-Fransozo, 2007). However, quite similar to San Antonio Bay (32 and 29.8 mm CW; Bas *et al.*, 2005); Samborombón Bay (33.2 mm CW for males; César *et al.*, 2005); and Santa Lucía Wetlands (32.9 and 29.8 mm CW; Merentiel Ferreyra, 2014). Size variations are common likely due to the phenotypic plasticity of the organisms, a consequence of a reduced growth per molt or influenced by environmental factors (as photoperiod, temperature and rainfall) that also affect the food availability (Gregati & Negreiros-Fransozo, 2007). Such environmental factors can explain the larger size of *N. granulate* specimens from Mar Chiquita and Jabaquara Paraty RJ, when compared with these populations of Bahía Blanca. The availability and the quality of the food, besides an adequate substratum in the environment are the main factors that influence the growth and size of the crabs (Colpo & Negreiros-Fransozo, 2002).

The fact that males are larger than females, this differential growth between sexes can be explained by processes related to reproductive events. When females reach maturity, they grow more slowly because of energy allocation to egg production. As in this study, it is very common to find males reaching larger sizes than females (Gregati & Negreiros-Fransozo, 2007). Even though the variation in maximum size, the minimum size of ovigerous females observed in Bahía Blanca estuary (16 mm CW) is similar to that reported for Dos Patos Lagoon (16.5 mm CW; Ruffino *et al.*, 1994), San Antonio Bay (17 mm CW; Bas *et al.*, 2005); Jabaquara Paraty (17.5 mm CW; Gregati & Negreiros-Fransozo, 2009), so a modification in maturity size is not evident.

A unimodal and asymmetrical frequency-distribution pattern is very common among Decapoda species from tropical regions without abrupt climatic variations, which suggests that the population is in equilibrium, with continuous recruitment and constant mortality rate (Hartnoll & Bryant, 1990). Moreover, the spatial and temporal variations in size frequency distributions among microhabitats suggest that the structure of this population is dynamic (due to migration, growth and recruitment) and that there is a clear spatial segregation of sizes. The ovigerous females were recorded between October to February, which confirmed that *N. granulata* spawning in Bahía Blanca Estuary occurs in almost spring and summer (Cervellini, 2001). This coincides with months of higher environmental temperature. The reproductive period, in Mar Chiquita Lagoon and San Antonio Bay, was recorded from November to February (Spivak *et al.*, 1994; Bas *et al.*, 2005); in Santa Lucia Wetlands from October to March (Merentiel-Ferreyra, 2014) and in Samborombón only in the summer months (César *et al.*, 2005). In the tropical mangrove population of Brazil the females had continuous reproductive periods and were found throughout the year (Gregati & Negreiros-Fransozo, 2009). While to determine the reproductive period of a species, the percentage of ovigerous females over the year is the most common technique used, the gonadal activity should be consider for a better estimation. It is important to say that in Elías *et al.* (2011), embryos were found inside females in the state prior to maturity. This critical topic needs more research.

The population structure of the most important macro-invertebrate in a region of such importance as Bahia Blanca Estuary has been analyzed for the first time. The comparative analysis of the population structure of *N. granulata* with other populations of South America reveals that latitudinal range is not a valid response for the considerable variations between them. Despite *N. granulata* has been investigated by many research group, studies of local physical and biological conditions (type of substratum, salinity, competition, predation) are needed to understand the variations and environmental influences concerning the latitudinal and environmental aspects of this population in the Bahía Blanca Estuary. We are working on this area and we hope to solve these questions.

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