

The influence of habitat, season and tidal regime in the activity of the intertidal crab *Neohelice* (= *Chasmagnathus*) *granulata*

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Abstract The activity pattern of intertidal crabs is influenced by factors that usually change rhythmically following tidal and/or diel cycles, and is often associated with the use of refuges. The movement activity of the burrowing crab *Neohelice granulata* was compared among three populations from SW Atlantic coastal areas where they face different tidal regimes, water salinities, substrata and biological factors. At each site, we examined the seasonal activity of the crabs (individuals collected in pitfall traps) in two types of habitat: mudflat and salt marsh. The working

hypothesis is that the activity would vary according to the diverse environmental conditions encountered at geographical and local scales. Crab activity varied between sites and seasons showing to be more intense when habitats were covered by water. The most active groups were large males, followed by large non-ovigerous females. Ovigerous females were almost inactive. Most crabs were near or inside burrows at low tides in Mar Chiquita and Bahía Blanca, but they were active at both low and high tides in San Antonio during spring and summer. *N. granulata* were active in a wide range of temperatures: from 10 to 37 °C at low tides and at temperatures as low as 2 °C when covered by water. Differences of activity between mudflat and salt marsh varied among sites depending on flooding frequencies. Movement activity of *N. granulata* varied both in space and in time; crabs move under very different abiotic conditions (e.g., low or high tide, daylight or night, low and high temperature) and their movement may also be prevented or elicited by biotic conditions like burrow complexity, food quality and predation pressure. The wide set of conditions under which *N. granulata* can be active may explain why this is the only semiterrestrial crab inhabiting latitudes higher than 40°S in South America.

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Introduction

The activity pattern of intertidal crabs is influenced by many different physical and biological factors that usually change rhythmically following tidal and/or diel cycles (Palmer 1995; Thurman 2004; Naylor 2005). These crabs

may be active at high tides, low tides or both, and during the day, the night or both on the basis of (1) the morphological, physiological and behavioral traits that allow them to cope with the environment (e.g., resist dehydration, construct burrows, hide under refuges, respire or move more efficiently either in the air or in the water; Wolcott 1988), and (2) the ecological context (e.g., the presence of aerial or aquatic predators that feed during low or high tide; Dumas and Witman 1993; Christy 2007; Hines 2007). Within a species, the pattern may vary at local scales: crabs may be restricted to a narrow area in the intertidal zone where all individuals experience similar conditions (e.g., Ferreira Silva et al. 2009) or the population might be spread across different tidal levels and exposed to diverse sets of conditions in each one (emersion- submersion periods; e.g., Brousseau et al. 2002). At a larger scale, in species with broad distributional ranges that are exposed to different tidal regimes, the activity pattern will change depending on the importance of tide as a factor entraining activity rhythms (e.g., Abelló et al. 1991).

The activity pattern of intertidal crabs is associated with the use of refuges (e.g., burrows, crevices) ranging from species that remain hidden for long periods, with virtually no ambulatory activity except short expeditions (from centimeters to few meters), to those that perform long journeys (from meters to kilometers) within or between different areas of the intertidal zone, staying in refuges only for very short periods (Seiple and Mueller 1992; Vannini and Cannicci 1995). However, there are also species that occupy burrows for long periods and show both types of locomotion activities; the extent of their movements is related to reproduction, foraging or habitat exploration (Goshima et al. 1978; Nakasone et al. 1982). The main forces affecting the value of refuges in intertidal crabs are predation and environmental stress (Vannini and Cannicci 1995). As a result of these selective pressures, very different patterns of activity related to the use of refuge and tidal regimes have arisen in different species.

Ocypodidae (fiddler crabs and their allies, the intertidal crabs whose activity rhythms have been more intensely studied) are a very homogeneous group regarding the construction and use of refuges. They are active outside their burrows during low tides (Vannini and Cannicci 1995; Thurman 2004). Grapsoidea, in contrast, have received much less attention and their activity patterns seem to be more heterogeneous: many species are active during high tides and hide under stones, boulders or inside burrows when tides recede, but others are active at low tide (Table 1).

Neohelice granulata Dana, 1851, formerly known as *Chasmagnathus granulatus* (Grapsoidea, Varunidae), is endemic to the warm temperate coast of the southwestern Atlantic and strictly associated with tidal flats in estuaries, bays and coastal lagoons where the halophyte grasses *Spartina* spp. form marshes in the middle and/or upper intertidal

zone (e.g., Boschi 1964; Spivak 2010). *N. granulata* digs semipermanent burrows and is active both in air and water (Iribarne et al. 1997; Halperin et al. 2000). During low tides, crabs leave burrows and perform “exploratory excursions” on mudflats between 5 and 15 cm from the entrance (Fathala et al. 2010a, b), but they hide in the presence of aerial predators (Maldonado 2002). Crabs are also active under water, carrying out longer excursions, especially during high tides, and their feeding activities rise dramatically during flooding in the vegetated habitat (D’Incao et al. 1992; Alberti et al. 2007a; Méndez Casariego et al. 2011a). Their reproduction is restricted to late spring and summer (Ituarte et al. 2004).

The habitat of these crabs includes different sets of environmental conditions at two spatial scales. Along its extensive but discontinuous geographical distribution (~22° latitude), they face different semidiurnal tide amplitudes (from few cm up to 9 m), water salinities (from near 0 up to 60), substratum (from soft bottom to cobble beaches) and biological factors as *Spartina* species (Isacch et al. 2006) and different predators (e.g., Yorio et al. 2005). In addition, they live in contrasting habitats placed at different intertidal levels (mudflats and salt marshes); in both habitats, adults of both sexes and juveniles are intermixed (Spivak et al. 1994; Bas et al. 2005). The emersion–submersion pattern, burrow size, shape and dynamics, physical and chemical characteristics of water inside them, and feeding habits vary between these habitats (e.g., Iribarne et al. 1997; Botto and Iribarne 1999; Bortolus and Iribarne 1999).

The main goal of this study is to compare the locomotory activity of *N. granulata* among three SW Atlantic coastal areas selected on the basis of their difference in tidal regime, soil characteristics, salinity and relative height of the marsh. The working hypothesis is that the activity would vary according to the diverse environmental conditions encountered at two spatial scales: geographical and local. Using bidirectional pitfall traps to quantify the movements of crabs within and between habitats, the following specific questions were examined: Does the activity pattern of this species vary throughout their geographical distribution and along the year? Is the pattern or patterns of activity affected by rhythmic phenomena like tidal cycles (that vary in predictability and amplitude), circadian cycles or seasonal cycles? Are there any other environmental conditions, such as soil, salinity and marsh position that modulate these patterns?

Materials and methods

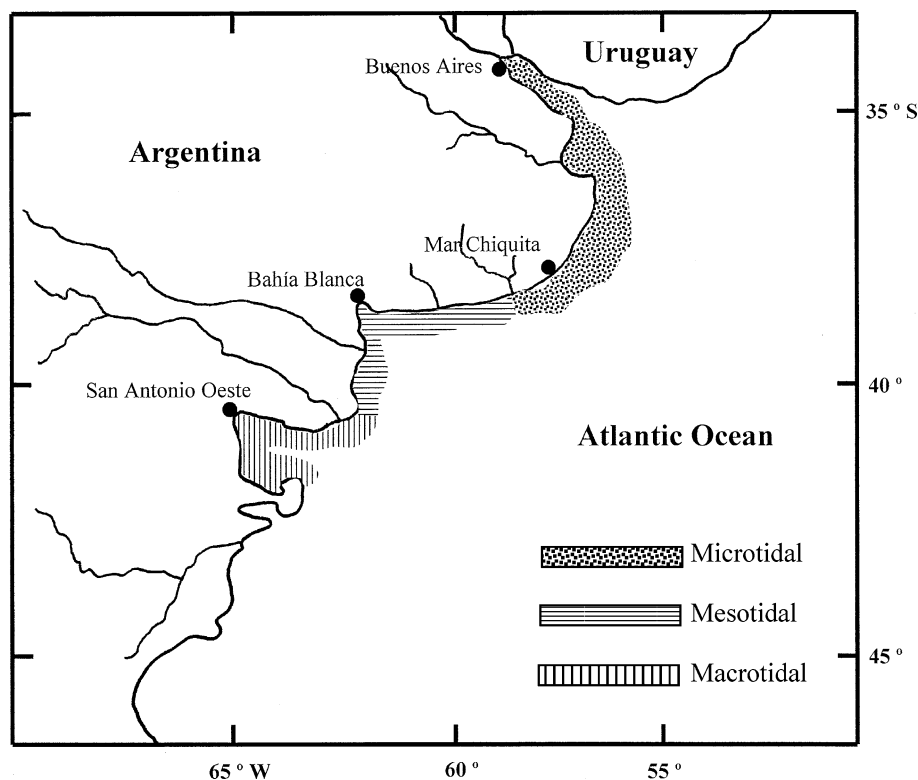
Study areas

The three selected sites form a southward gradient of increasing aridity and tidal amplitude (Fig. 1) also associated with

Table 1 Activity patterns of intertidal grapsoids (Grapsidae, Sesamidae and Varunidae)

	Time of activity	Type of refuge	References
<i>Varunidae</i>			
<i>Hemigrapsus oregonensis</i>	High tides	Inside burrows during low tide	Willason 1981; Batie 1983
<i>Hemigrapsus sanguineus</i>	High tides	Under stones or boulders during diurnal low tides	Lohrer et al. 2000; Brousseau et al. 2002
<i>Gaeitece depressus</i>	High tides	Under stones or boulders during diurnal low tides	Lohrer et al. 2000
<i>Amaeopleura parvula</i>	High tides	Under stones or boulders during diurnal low tides	Lohrer et al. 2000
<i>Cyclograpsus insularum</i>	High tides	Under stones or boulders during low tides	Brockertoff and McLay 2005
<i>Cyclograpsus lavauxi</i>	High tides	Under stones or boulders during low tides	Brockertoff and McLay 2005
<i>Helice tridens</i>	High tides	Inside burrows during low tides	Kurihara et al. 1988
<i>Helicana (=Helice) japonica</i>	High tides	Inside burrows during low tides	Omori et al. 1997
<i>Cyrtograpsus angulatus</i>	Active in the air-water boundary during both high and low tides	Under stones or boulders, inside <i>N. granulata</i> burrows if available or migration to the subtidal (low tides)	Boschi 1964; personal observations
<i>Cyrtograpsus altimanus</i>	Not observed	Under stones or boulders, or inside <i>Ficopomatus enigmaticus</i> (Polychaeta: Serpulidae) reefs (low tides)	Spivak 1999
<i>Metaplax elegans</i>	Low tides	Inside burrows	Ng and Sivasothi 2001
<i>Helograpsus haswellianus</i>	Low tides	Inside burrows during high tides	Breitfuss 2003
<i>Paragrapsus gaimardii</i>	Nocturnal low tides	Buried in sand during the day	Snow 1973
<i>Austrohelice (=Helice) crassa</i>	Low and high tides	Inside burrows	Williams et al. 1985
<i>Neohelice granulata</i>	Mainly during high tides; less frequently during low tides; diurnal or nocturnal; activity varied among sites	Inside burrows (low tides)	This paper
<i>Chasmagnathus convexus</i>	Low tides nocturnal	Inside burrows	Nakasone et al. 1982
<i>Grapsidae</i>			
<i>Pachygrapsus socius</i> (= <i>P. transversus</i>)	Diurnal and nocturnal low tides	In rock holes and crevices during high tides	Abele et al. 1986
<i>P. marmoratus</i>	Nocturnal low tides	In rock crevices during high tides	Canneci et al. 1999; Ferreira Silva et al. 2009
<i>P. crassipes</i> in salt marshes	Above and below the water line during low tides; movement changed during the tidal amplitude cycle	Inside <i>H. oregonensis</i> burrows	Willason 1981; Morgan et al. 2006
<i>P. crassipes</i> in rocky shore	Nocturnal low tides	In rock holes and crevices during high tides	Hiatt 1948
<i>Metopograpsus thukuhar</i>	Mainly at low tides but also at high tides	In crevices of mangrove roots (<i>Rhizophora mucronata</i>)	Fratini et al. 2000
<i>Grapsus grapsus</i>	Low tides	In crevices or on the surface of rocks	Romero 2003
<i>Grapsus tenuicristatus</i>	Diurnal low and high tides	In crevices at night	Eshky 1999
<i>G. adscensionis</i>	Diurnal low tides	In crevices or on the surface of rocks during nocturnal low and high tides and diurnal high tides	Hartnoll 2009
<i>Sesamidae</i>			
<i>Sesarma reticulatum</i>	Nocturnal high tides	Inside burrows during low tides	Palmer 1967; Seiple 1981
<i>Armases</i> (= <i>Sesarma</i>) <i>chireum</i>	Nocturnal	Diurnal, under boards and debris	Seiple 1979; Seiple and Mueller 1992
<i>Sesarma leptosoma</i>	Diurnal activity (tree climbing); non-tidal in the morning; related with high tides in the evening	In crevices of mangrove roots (<i>Rhizophora mucronata</i>)	Vannini et al. 1997

Fig. 1 Geographical position of sampling sites. *Shadow zones* indicates tidal regimen at each coastal region, microtidal <2 m, mesotidal >2 m <4 m, macrotidal >4 m (modified from Piccolo and Perillo 1997)



changes in the salt marsh communities (Isacch et al. 2006). From north to south, the sites were the following:

Mar Chiquita (37°45'S, 57°19'W). This coastal lagoon (46 km²) with a semidiurnal microtidal regime (0.3–1 m amplitude) is connected with the open sea by a narrow channel about 5 km long. The mean rainfall is 800 mm/year⁻¹. Tidal influence depends on the wind direction and intensity, tidal phase and freshwater runoff. The upper intertidal zone is a mixed *Spartina densiflora* and *S. perennis* marsh (Isacch et al. 2006), and the mid- and lower intertidal zones are mudflats. Sediments are fine with high penetrability and organic matter content (Fig. 2a, Spivak et al. 1994). Crabs occupy the upper- and middle intertidal zone. Burrows in the mudflat are shorter than in the salt marsh, where they reach more than 70 cm depth (Iribarne et al. 1997). In both areas, burrows reach the water table (Fanjul et al. 2008). Samples were taken in the *S. densiflora* marsh and in the mid-intertidal zone of the mudflat.

Bahía Blanca (38°45'S, 62°15'W). This is a large estuary (2,300 km², 1,550 km² of low-energy tidal flats). Rainfall is 650 mm/year⁻¹. The tidal regime is semidiurnal and mesotidal (up to 3.6 m amplitude, Servicio de Hidrografía Naval). Sediments are fine with high penetrability and organic matter content (Fig. 2b, Albano unpublished data). The intertidal area is characterized by an upper *S. perennis* marsh (Isacch et al. 2006), a mid-intertidal zone divided into a mudflat and a *S. alterniflora* marsh forming a narrow belt followed by the open low intertidal zone. Crabs are

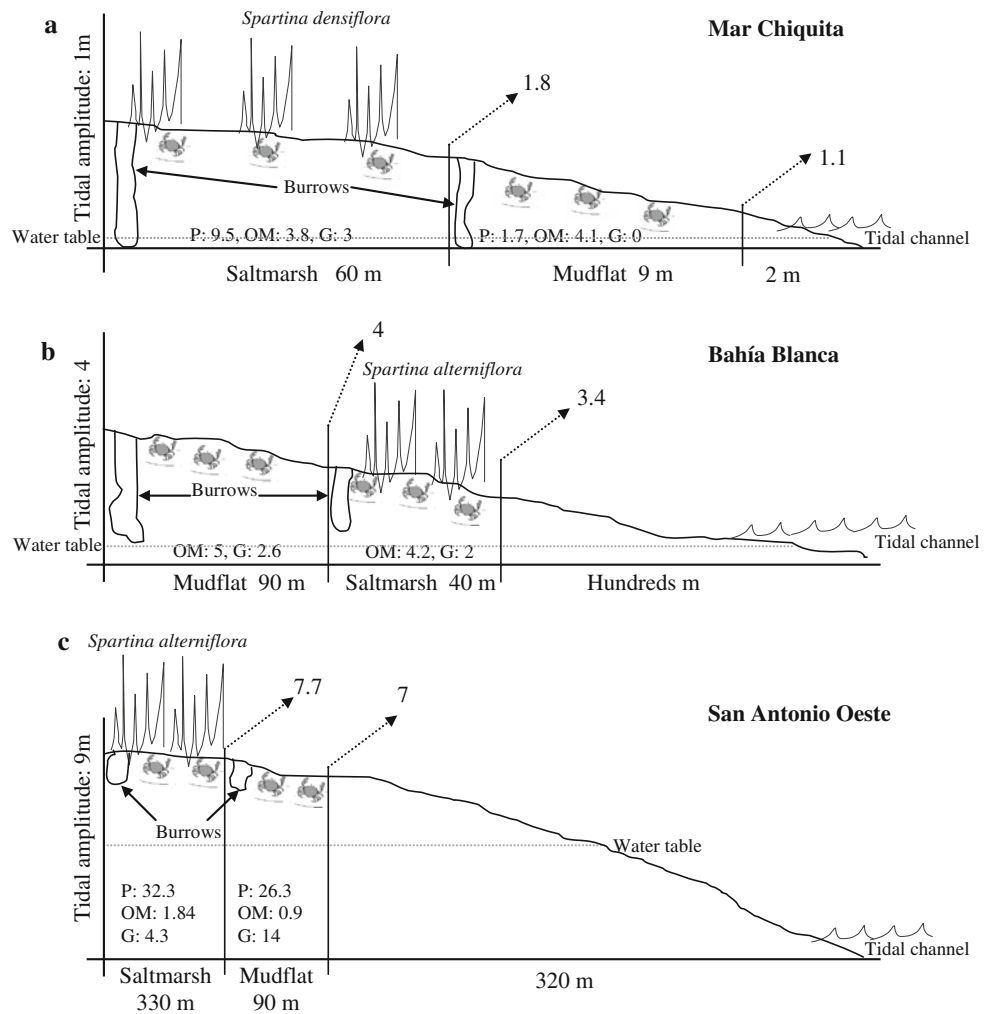
present in the upper- and mid-intertidal zones. Burrows from the mudflat range between 60 and 90 cm in length and those from the upper salt marsh are deeper, reaching 150 cm (Escapa et al. 2007); those in the *S. alterniflora* belt have not been described yet. The sampled area corresponded to the *S. alterniflora* marsh and the mudflat.

San Antonio (40°46'S, 64°50'W). This bay (80 km²) opens to the San Matías Gulf and is located in a very dry area (average rainfall: 240 mm year⁻¹) with no freshwater input. It has a semidiurnal macrotidal regime (up to 9 m amplitude, Servicio de Hidrografía Naval) (Fig. 1) with extensive sand-cobble intertidal flats. The upper intertidal zone is a *Sarcocornia perennis* marsh and the mid-intertidal zone divides into a *Spartina alterniflora* marsh (Isacch et al. 2006) and a mudflat that continues throughout the lower intertidal zone. Sediment organic matter content and penetrability are very low (Fig. 2c; Bas et al. 2005). Crab burrows occupy both the upper- and mid-intertidal zones, reaching up to 130 crabs m⁻² (Bas et al. 2005). In both areas, burrows are shallow with a maximum depth of 10.5 cm (Sal Moyano et al. in press). Samples were taken in the *S. alterniflora* marsh and in the mudflat.

Sampling program

Samplings were performed seasonally, from July 2006 (winter) to June 2007 (autumn). In each study area, two habitats were selected: one in the salt marsh and one in

Fig. 2 Schematic representation of each sampling site, **a** Mar Chiquita, **b** Bahía Blanca, **c** San Antonio. OM organic matter content (in percentage), *G* gravel (in percentage), *P* penetrability ($Kp\text{ cm}^{-2}$; not available to BB), dotted arrows with numbers indicate tidal height (in meters) necessary to cover the lower part of each mudflat and salt marsh (drawings not scaled)



the mudflat. In each site, habitats selected were extensive in relation to the area covered by traps. During each season, the ambulatory activity of *N. granulata*, air temperature and moisture, and water temperature and salinity of burrows were measured in both habitats, in the middle of flooding (3 h before high tide) and ebbing (3 h after high tide), through a 48-h period. Consequently, there were 8 sets of data per habitat and season, obtained every 6 h approximately. Additional qualitative observations were made of burrow length and water retention during a tidal cycle in San Antonio and in the lower salt marsh of Bahía Blanca in order to draw a comparison with the other sites where the information is already available (see Iribarne et al. 1997; Escapa et al. 2007).

Physical conditions of burrows, air and water

At each site and habitat, five replicates of air temperature (T_{air} ; °C, accuracy ± 1 °C) and moisture 5 cm above ground (H_{air} ; %, accuracy ± 3 % of scale), and five repli-

cates of temperature (T_{burrow} ; °C, accuracy ± 0.1 °C) and salinity (*S*; ‰, accuracy ± 0.1 ‰) of water inside burrows were taken. Measurements were made by introducing sensors inside burrow openings until water completely covered the sensitive parts. If burrows were too dry or too deep (more than 70 cm), water was not measured. Since air and water temperature and salinity varied broadly over a daily and seasonal pattern, only the range of temperature in absolute value (ΔT) and the salinity range (ΔS) were considered in comparisons. To evaluate the effect of water inside burrows in ameliorating extreme variations of temperature, ΔT from air and burrows were compared for each habitat; at the same time, ΔS of water from burrows were compared between habitats. As data from all sites and habitats together did not comply with normality and equal variance assumptions, even after transformation, comparisons were made for each site with a *t*-test for paired samples (Zar 2009).

A two-way ANOVA (Zar 2009) was used to analyze the differences in average values of moisture with habitat and

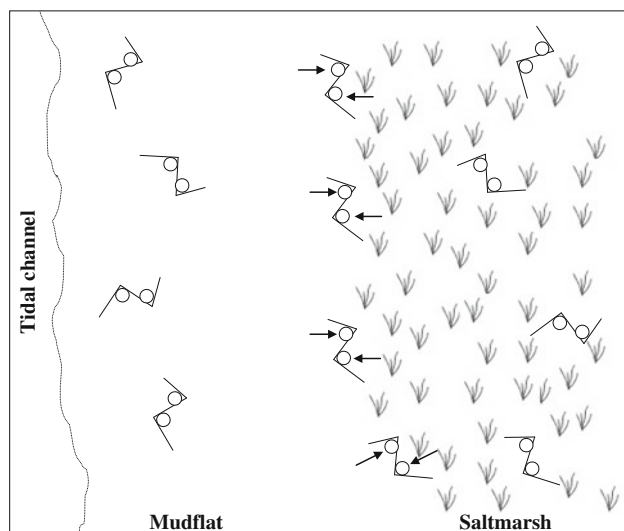


Fig. 3 Schematic representation of *trap arrays* in mudflat, salt marsh and interface between these habitats

sites as factors. Data were previously arcsin-transformed to comply with the assumptions.

Relationship of activity with season, tide, habitat, and light

Crab movements were quantified on the basis of the number of crabs caught in traps placed on mudflats, salt marshes and along the interface between both habitats. Each trap consisted of a drift fence of plastic mesh 0.30 m height and 1.5 m length, folded in three segments forming 120° angles and vertically buried a few cm into the sediment. At each angle one pitfall trap (18 cm diameter and 18 cm depth) was buried (Fig. 3). Crabs that reached the fences walked along them and fell down into the traps where they were retained. In mudflats and salt marshes, traps were oriented at any direction but at the interface between habitats, they were placed along the external edge of vegetated patches to discriminate crabs moving “into” and “out of” the marsh area (Fig. 3). Ten fences with two traps each were placed in the mudflat, ten in the salt marsh and ten in the border between the two habitats, with a minimum distance of 5 m between fences. Activity in each site was estimated as the average number of crabs per trap per tide.

Traps were checked every 6 h, that is, when they were recently uncovered or just before they were again submerged by water. Crabs collected as soon as the intertidal zone emerged during the ebb represented those active during the previous high tide, when covered by water; crabs collected just before the water covered the zone again during the flood represented those active when uncovered by water during the previous low tide.

A generalized linear model was used to compare the activity between salt marsh and mudflat areas in each site, assuming a negative binomial distribution in the response variable (with variance greater than mean, function “glm.nb()” with a log-link in library “MASS” in the R 2.10.0 package [R Development Core Team 2008]), because crab numbers showed greater variability than that allowed in a Poisson model. The generalized linear model was formulated with season and habitat as factors and diurnal phase and tide as covariates. Two tidal states were considered: emerged or submersed, independently of the tidal phase, since in many cases high tides did not cover the sampled areas. The diurnal phase also had two states: daylight and dark depending on the light conditions prevailing at the moment of high or low tide. Based on the method developed by Gerhard et al. (2007), multiple comparisons of groups were made a posteriori to estimate confidence intervals for negative binomial distributed data.

Sex and size of active crabs

Additional samples were collected to estimate the size and sex composition of the population in each study site and habitat. These samples consisted of all crabs present at the surface and in burrows in ten areas delimited by square metal frames (0.25 m²) randomly placed along transects in the salt marsh and in the mudflat, at each location and season. Once each frame was placed on the ground, crabs on the surface or escaping from burrows were rapidly collected; later, each burrow was carefully dug up to take all the crabs that remained inside. This method has been extensively used for sampling *N. granulata*, being highly efficient in retrieving all crabs from burrows (Spivak et al. 1994; Bas et al. 2005; Méndez Casariego et al. 2011b).

Crabs captured in traps and in quadrats were measured (maximum carapace width, CW) and sexed, and the presence of ovigerous females was registered. They were named “trap crabs” and “quadrat crabs,” respectively. All individuals were returned to their original area. Size frequency distributions (SFD) and sex ratio were obtained from trap crabs collected in each habitat (mudflat, salt marsh and the border between them) and from quadrat crabs collected in mudflats and salt marshes.

A χ^2 contingency table was used to compare sex ratios, a goodness of fit test of χ^2 to evaluate differences among SFDs and a Z test of comparison of proportions to evaluate the ratio ovigerous/non-ovigerous females between trap and quadrat crabs (Zar 2009). Only crabs larger than 18 mm CW (Mar Chiquita) and 14 mm CW (San Antonio and Bahía Blanca) collected in quadrats were used for comparisons; smaller crabs were discarded since they were never present in traps.

Results

Frequency of habitat submersed by tides

The observations of actual events of emersion and submersion of each habitat during a complete tidal cycle showed differences among sites. In Mar Chiquita, the salt marsh was submerged only once during the only spring high tide sampled; in winter, the mudflat remained emerged during 5 out of 16 high tides (Fig. 4). In Bahía Blanca, instead, the salt marsh remained emerged in two and the mudflat in five out of the 16 sampled high tides (Fig. 5). The highest regularity of submersion occurred in San Antonio where high tides always submerged both sampled areas (Fig. 6).

Physical conditions of burrows, air and water

In Bahía Blanca, burrows dug in the lower salt marsh had almost no structure; they frequently collapsed when the measuring instrument was introduced. Burrows in the mudflat, instead, were well structured and very deep (50 cm or more) reaching in some cases the water table. In the bare intertidal zone of San Antonio, sediment consisted of cobbles and coarse sand where water percolated easily, so burrows were dry shortly after the tide began to recede. In the salt marsh, where some fine sediment accumulated, water was retained for longer periods, and in some occasions, it persisted until the next tidal cycle.

Temperature and salinity of water in burrows varied greatly with site, season and air temperature (Tables 2 and 3). In Mar Chiquita, the daily and seasonal ranges of T_{burrow} were narrower than the range of T_{air} in both habitats, and the difference was more noticeable in the salt marsh (t test, $t = 8.11$, $p < 0.01$; t test, $t = 4.22$, $p < 0.05$, mudflat and salt marsh, respectively, Table 2). In Bahía Blanca, there were no differences between the ranges of T_{burrow} and T_{air} (t test, $t = 0.57$, $p = 0.3$; t test, $t = 0.44$, $p = 0.34$, mudflat and salt marsh, respectively, Table 2). In San Antonio, the range of T_{burrow} was narrower than the range of T_{air} in the salt marsh but not in the mudflat (t test, $t = 4.41$, $p < 0.05$ and $t = 0.67$, $p = 0.27$, respectively, Table 2).

Water salinity inside burrows differed between sites and habitats. Mar Chiquita was the only site where salinities below normal seawater were recorded (minimum value 10 ‰) and the maximum value observed (47 ‰) was lower than in the other sites (Table 3). In Bahía Blanca, it ranged between full marine and hypersaline conditions, especially in mudflat burrows (34–63 ‰, Table 3). Similar conditions were observed in San Antonio: 35–46 ‰ and 36–54 ‰ in salt marsh and mudflat, respectively (Table 3). There were no significant differences in the mean S ranges in Bahía Blanca (t test, $t = 1.19$, $p = 0.15$), and Mar Chiquita (t test,

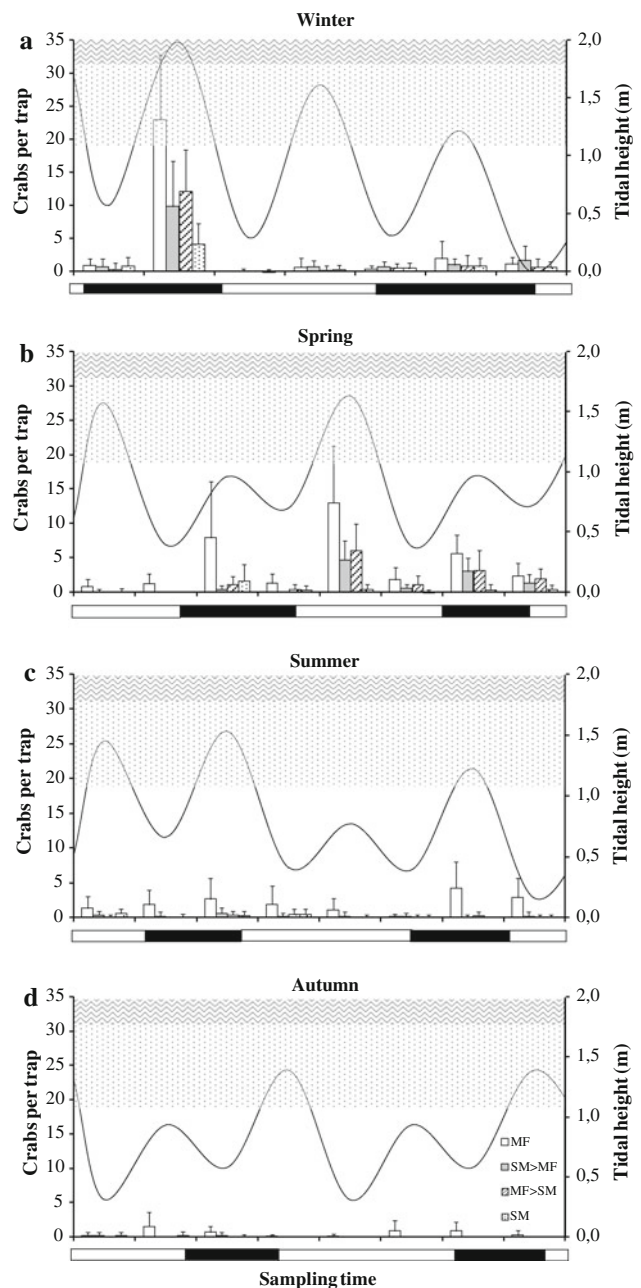


Fig. 4 Average number (\pm SD) of crabs per trap collected after each flood and ebb tide throughout 48 h in Mar Chiquita in winter (a), spring (b), summer (c) and autumn (d). Crabs trapped in mudflat (MF), salt marsh (SM) and those collected moving from salt marsh to mudflat (SM > MF) and from mudflat to salt marsh (MF > SM) are shown. Tidal height is superimposed as a continuous line. Dotted shadow indicates tidal height covering the MF; wavy shadow indicates tidal height covering the SM. Horizontal bars below each graph indicate periods of daylight (white) and darkness (black)

$t = 1.8$, $p = 0.08$) (Table 3) but they were smaller in salt marsh than in mudflat burrows in San Antonio (t test, $t = 2.97$, $p < 0.05$).

The relative humidity of the air was not different between habitats ($F_{(2,1068)} = 129.1$; $p = 0.26$) but differed

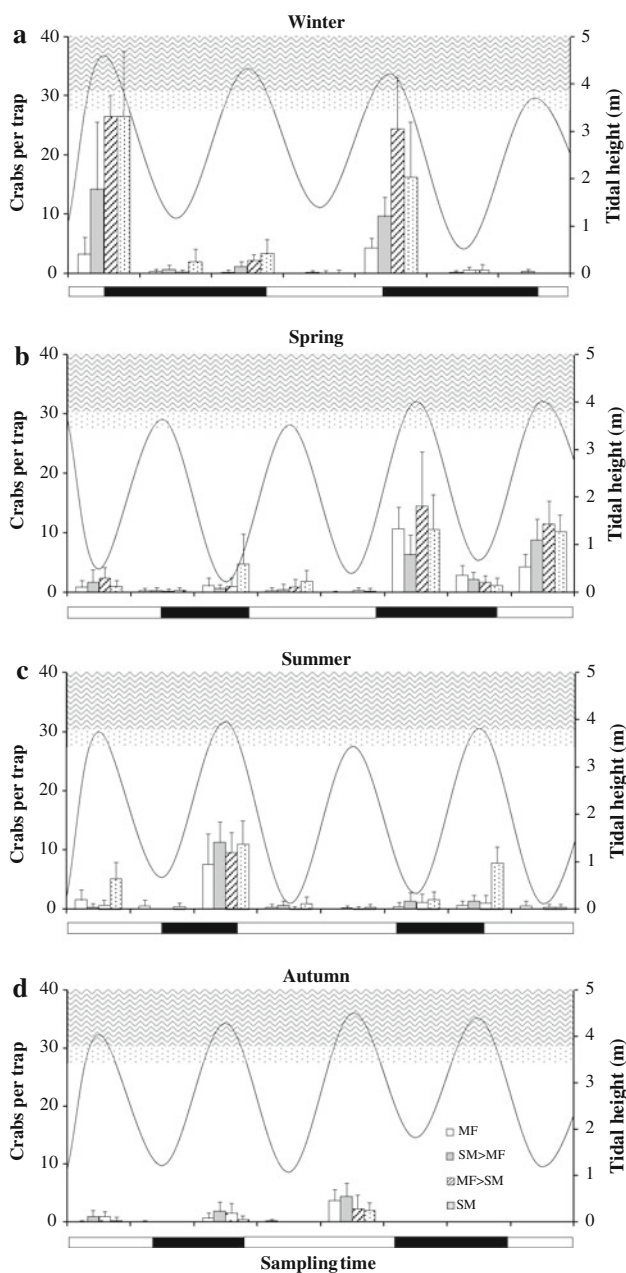


Fig. 5 Average number (\pm SD) of crabs per trap collected after each flood and ebb tide throughout 48 h in Bahía Blanca in winter (a), spring (b), summer (c) and autumn (d). See explanations in caption under Fig. 4

among sites ($F_{(2,1068)} = 1.25$; $p < 0.001$). It decreased from Mar Chiquita to San Antonio. As an example, 52 % of measurements taken after ebb tides in the mudflat of Mar Chiquita yielded values ≥ 80 % relative humidity, and only 7 % of the measured values had ≤ 60 % relative humidity. In San Antonio, the respective proportions of high and low humidity were 12.5 and 47 %. The values observed in Bahía Blanca were intermediate between both sites.

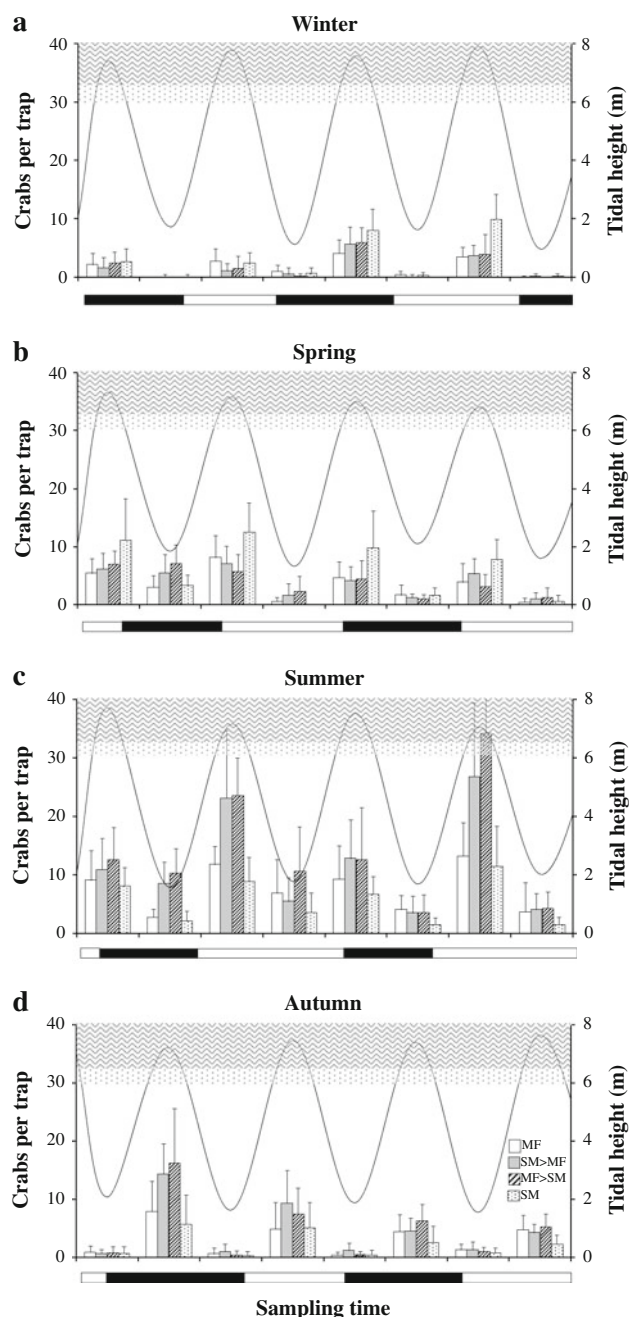


Fig. 6 Average number (\pm SD) of crabs per trap collected after each flood and ebb tide throughout 48 h in San Antonio in winter (a), spring (b), summer (c) and autumn (d). See explanations in caption under Fig. 4

General crab behavior

In winter, crabs collected from burrows during ebb tides with temperatures below 10 °C were motionless; however, when burrows or traps were covered by water, they turned active and fast moving, even at temperatures as low as 2 °C. In autumn, in Mar Chiquita and Bahía

Table 2 Range and ΔT° of air temperature (T° air) and water temperature from burrows of *Neohelice granulata* (T° burrow) in mudflat and salt marsh in three sites, Mar Chiquita, Bahía Blanca and San Antonio Bay, and four seasons (winter, spring, summer and autumn)

Site	Season	Mudflat				Salt marsh			
		T° air	ΔT°	T° burrow	ΔT°	T° air	ΔT°	T° burrow	ΔT°
Mar Chiquita	Winter	14.7–0.7	15.4	14.9–2.6	12.3	13.6–0.4	13.2	11.9–1.4	10.5
	Spring	26.1–11	15.1	24.6–14.2	10.4	28.2–12.1	16.1	21.3–16.4	4.9
	Summer	31.7–16.3	15.4	27.3–17.1	10.2	32.1–16.2	15.9		5.9
	Autumn	15.3–2.7	12.6	12.2–3	9.2	16.8–2.7	14.1	8.9–6.7	2.2
	Mean, SD		14.6, 1.3		10.5, 1.3		14.8, 1.4		5.8, 3.4
Bahía Blanca	Winter	9.8–0.6	9.2	11–0.3	10.7	9.9–0.4	9.5	10.3–0.8	9.5
	Spring	31.6–19.5	12.1	29.1–15.8	13.3	33.3–19.4	13.9	27.3–15.9	11.4
	Summer	28.5–17.6	10.9	25–15.6	9.4	30.1–18.2	11.9	31–15.9	15.1
	Autumn	15.4–1.9	13.5	13.7–4.5	9.2	15.2–3.5	11.7	14.1–5.7	8.4
	Mean, SD		11.4, 1.8		10.6, 1.8		11.7, 1.7		11.1, 2.9
San Antonio	Winter	14.8–5.4	9.4	13.7–4.2	9.5	15.2–3.8	11.4	13.1–4.4	8.7
	Spring	28.9–18.2	10.7	24.9–13.4	11.5	31.6–18.8	12.8	22.4–18.6	3.8
	Summer	35.7–18.4	17.3	32.4–15.4	17	38.5–17.5	21	30.2–19.4	10.8
	Autumn	23.2–6.1	17.1	21.1–6.6	14.5	24.8–5.1	19.7	19.1–10	9.1
	Mean, SD		13.6, 4.1		13.1, 3.3		16.2, 4.8		8.1, 3

Bold types indicate significant differences among mean ΔT° between air and burrows (*t* test, $p < 0.05$)

Table 3 Range and ΔS° of salinity of water from burrows of *Neohelice granulata* (S° burrow) in mudflat and salt marsh in three sites Mar Chiquita, Bahía Blanca and San Antonio Bay, and four seasons (winter, spring, summer and autumn)

	Mudflat		Salt marsh	
	S° burrow	ΔS	S° burrow	ΔS
Mar Chiquita				
Winter	40–27	13	40–32	8
Spring	45–32	13	47–32	15
Summer	40–10	30	40–26	14
Autumn	34–21	13	35–30	5
Mean, SD		17.2, 8.5		10.5, 4.8
Bahía Blanca				
Winter	40–34	6	40–33	7
Spring	45–35	10	51–40	11
Summer	63–50	13	57–42	15
Autumn	40–35	5	38–34	4
Mean, SD		8.5, 3.7		9.2, 4.8
San Antonio				
Winter	42–36	6	40–35	5
Spring	52–40	12	46–39	7
Summer	54–37	17	43–36	7
Autumn	50–37	13	43–36	7
Mean, SD		12, 4.5		6.5, 1

Bold types indicate significant differences among mean ΔS° between mudflat and salt marsh (*t* test, $p < 0.05$)

Blanca, the entrances of many burrows were closed with mud, and crabs inside were in pre- and post-molt. During spring and summer ebb tides in Mar Chiquita and Bahía Blanca, most crabs were near the entrances of burrows while they were full of water, moved inside as soon as they were getting drier and stayed in the burrows during the ebbing period. In San Antonio, instead, many crabs picked up and ate sediment immediately after the tide receded, not only when the sediment remained wet at night, but also during the day.

Relationship of activity with season, tide, habitat and diurnal phase

Mar Chiquita: Due to irregular flooding (see above), the tidal effect was not tested. Crab activity was almost null in autumn and thus it was not considered in the analysis afterward (Fig. 4). Crabs moved more within the mudflat (even when they were not covered by water) than between habitats or within the salt marsh, except in few winter samples with very low activity (Fig. 4). There was interaction among habitat, season and diurnal phase ($\chi^2 = 26.24$, $p < 0.001$), and the a posteriori comparisons showed that more crabs moved in the mudflat than in the salt marsh, except during the day in winter (Online Resource: Table S1 and Fig S1).

Bahía Blanca: As in Mar Chiquita, crabs were rarely active during autumn; thus, this season was not considered

in the subsequent analysis. In spring and summer, the activity was similar within and between habitats, but in winter, crabs moved more between habitats (Fig. 5). Not all diurnal phase conditions occurred at every tidal condition in both habitats so the effect of diurnal phase was not evaluated in the analysis. There was no interaction among season (winter, spring and summer), habitat and tide. Nevertheless, all pairs of factors interacted (season \times habitat, $\chi^2 = 33.87$, $p < 0.001$; season \times tide, $\chi^2 = 23.92$, $p < 0.001$; habitat \times tide, $\chi^2 = 11.79$, $p < 0.001$; Online Resource: Table S2 and Fig. S2). Crab movements were more intense during floods in both habitats. In winter, crabs were active at every other high tide instead of after each flooding, in accordance with daylight high tides, and they were significantly more active in the salt marsh.

San Antonio: Crabs were active during all seasons. Maximum activity was observed in summer and minimum in winter. More crabs were caught at the border between habitats (moving in both directions) in summer and autumn (Fig. 6). There were significant interactions among season, habitat and tide and among season, diurnal phase and tide ($\chi^2 = 10.23$, $p < 0.05$; $\chi^2 = 31.19$, $p < 0.001$, respectively; Online Resource: Table S3 and Fig. S3). In autumn and winter, the activity was always higher during flood tides in both habitats and almost null during ebb tides. In spring and summer, crabs were active even when they were uncovered by water. In spring, during low tide, the activity was higher at night. In summer, crabs moved more intensely during floods in the salt marsh while the difference between tidal phases was not significant in the mudflat.

Sex and size of active crabs

Size frequency distributions differed between traps and quadrats, except for females in the Mar Chiquita mudflat (Fig. 7; Goodness of fit test). Although only large crabs (>18 mm CW in Mar Chiquita and >14 mm CW in San Antonio and Bahía Blanca) were found in pitfall traps in all sites and habitats, small individuals represented an important part of the quadrat samples (e.g., Mar Chiquita salt marsh, Fig. 7). Sex ratios in traps were strongly biased given that at least 70 % of trapped crabs were males (excepting Bahía Blanca mudflat); they differed from the sex ratio in quadrats (1:1 or slightly male biased) excepting Bahía Blanca mudflat and Mar Chiquita salt marsh (Fig. 7, Z test, Table 4). There were no differences in size structure among crabs trapped in mudflats, salt marshes or in the interface between habitats (χ^2 contingency table, paired comparisons, all $p > 0.05$). Ovigerous females were present in spring and summer in variable proportions in different populations and were always more abundant in salt marshes. The proportion of ovigerous females in traps was

lower than in quadrats (Fig. 8); these differences were highest in San Antonio ($Z = 3.3$ and $Z = 6.9$, $p > 0.001$ mudflat and salt marsh, respectively) and also significant in the mudflat of Mar Chiquita ($Z = 2.3$, $p > 0.05$). In Bahía Blanca and in the salt marsh of Mar Chiquita, the differences were not significant; nevertheless, the power of the tests was low.

Discussion

The southwestern Atlantic burrowing crab *Neohelice granulata* has different activity patterns: the well-studied short and brief field exploratory movements (Fathala et al. 2010a, b), the movements within and between habitats (this paper), and the proposed reproductive migrations of ovigerous females that release larvae in shallow waters during high tides (Anger et al. 1994).

Movement within and between habitats was performed mainly by large crabs, predominantly males (sex ratio in traps was 5 males: 1 female) as had also been observed in *Chasmagnathus convexus* (Nakasone et al. 1982). This should represent a true difference in displacement range between sexes and size groups and not a methodological artifact (e.g., females and juveniles avoid traps more efficiently than males) because most active crabs observed in the field were large males or, to a lesser extent, large females (unpublished observations). Ovigerous females were captured much less frequently than non-ovigerous females, suggesting that activity also depends on the reproductive condition. Juveniles were not found in traps: they usually concentrate in salt marshes, protected by the higher structural complexity of this habitat and remain near the entrance of adult burrows (Spivak et al. 1994, Bas et al. 2005, Luppi et al. 2002). Similar differences between crab size and sex were observed during the intertidal migrations of *Carcinus maenas*: males moved farther than females and non-ovigerous females moved more than ovigerous ones (Hunter and Naylor 1993). In *N. granulata*, this behavioral diversity could be related to the vulnerability to predators of each sex (due to the great difference in chelae size), to the susceptibility of small crabs to be cannibalized by larger males (Luppi et al. 2001) and/or to the higher susceptibility of small crabs to extreme temperature and water loss (Willmer et al. 2000; Méndez Casariego et al. 2011a).

Neohelice granulata was active over a range of temperatures, salinity and humidity that were wider than those reported for other species with similar characteristics (Bliss et al. 1978; Goshima et al. 1978; Nakasone et al. 1982) but these variables interacted in a complex way and were also affected by other studied (e.g., tides, burrow structure) or unstudied (e.g., predation pressure) environmental factors.

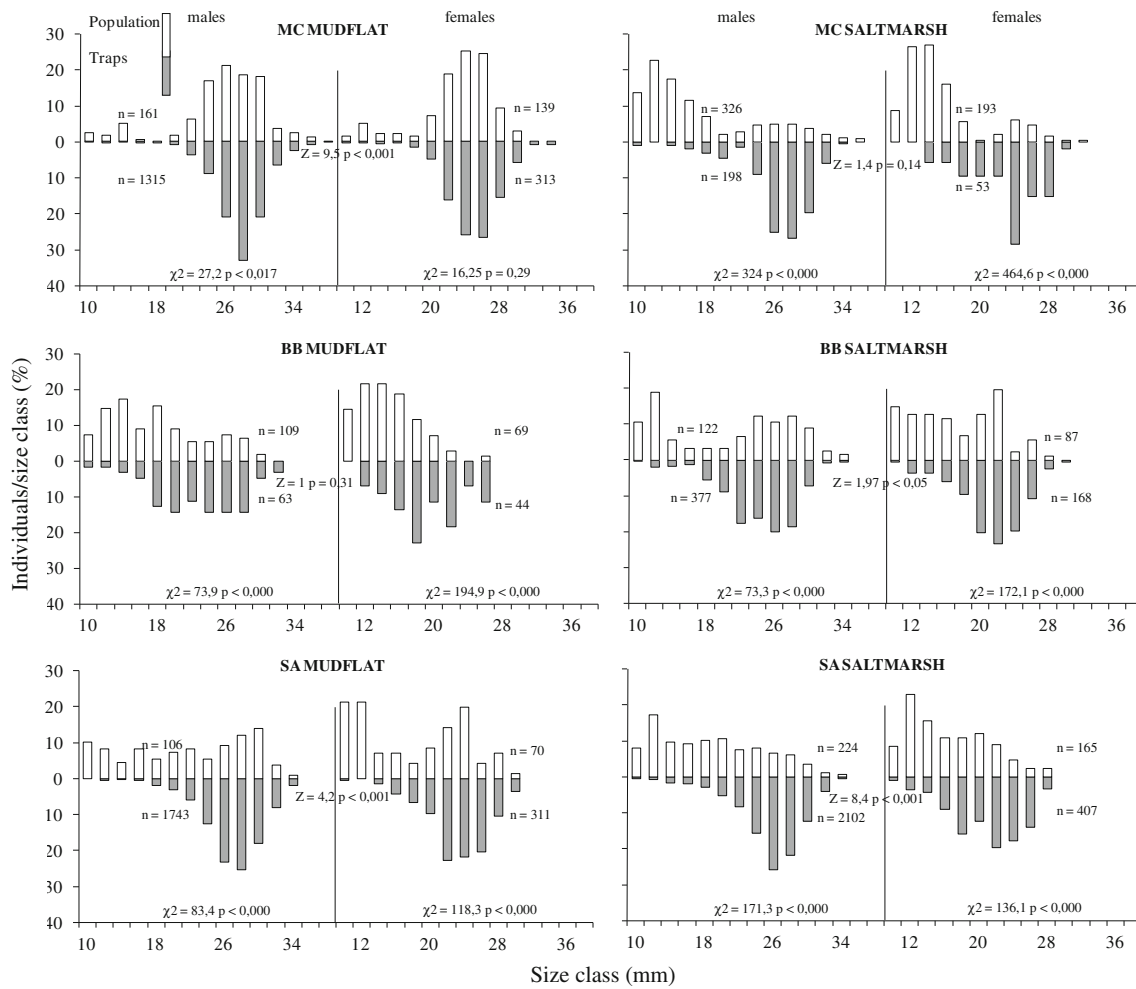


Fig. 7 Size frequency distribution (SFD) of males and females collected from quadrats (white bars, population samplings) and traps (gray bars) in salt marshes and mudflats of MC Mar Chiquita, BB Bahía Blanca and SA San Antonio (all seasons pooled). χ^2 : statistic of

Chi-square test to compare SFD of population and traps. Z: statistic of z test to compare proportions of males in populations and in traps. p: significance of tests. To compute Z test, only crabs >18 mm AC in MC and >14 mm AC in SA and BB were considered

Table 4 Numbers of males and females (carapace width >10 mm) collected in traps and in population surveys, in mudflat and salt marsh, and in three sites: Mar Chiquita, Bahía Blanca and San Antonio Bay

	Mudflat		Salt marsh			
	Males	χ^2, p	Females	Males	χ^2, p	Females
Mar Chiquita						
Traps	1,315	338.6***	315	199	46.1***	53
Population	161	0.8 ns	139	326	17.5***	193
Bahía Blanca						
Traps	63	1.5 ns	44	377	41.2***	168
Population	109	4.55*	69	122	2.7 ns	87
San Antonio						
Traps	1,743	568.2***	311	2,102	645.6***	407
Population	106	3.7 ns	70	224	4.3*	165

χ^2 : statistics of Chi-square test, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns non-significant

In addition, the activity differed among sites, tidal height and season.

The activity of crabs was, in general, higher during the high tide phase. However, crabs from San Antonio were

also collected in traps after low tides in summer, with temperatures above 31 °C and humidity below 45 %, suggesting that the underwater activity is not only related with harsh conditions at low tide. *N. granulata* was considered

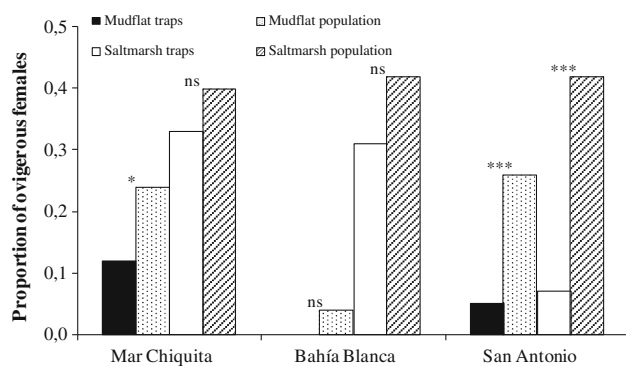


Fig. 8 Proportions of ovigerous females collected from traps and quadrats in mudflat and salt marsh, in Mar Chiquita, Bahía Blanca and San Antonio. *** $p < 0.0001$, * $p < 0.05$, *ns* non-significant for Z test

inactive during winter (D’Incao et al. 1988). This is true for crabs collected in dry burrows at temperatures of 10 °C or lower; nevertheless, they became completely active when covered by water, even at temperatures as low as 2 °C. As far as we know, this is the first report of a semiterrestrial crab active at very low temperatures (albeit under water). The available information indicates that most land crabs are restricted to the tropics and subtropics; in temperate zones, they remain in burrows during winter, and it has been suggested that the shortening of the active season may explain their absence at higher latitudes (Wolcott 1988). Consequently, the tolerance to low temperatures may help to understand why *N. granulata* is one of the few semiterrestrial crabs that reaches latitudes higher than 40°S in the southern hemisphere (at least, it is the southernmost latitude in America).

Burrowing activity, tidal pattern, and food availability may explain the differences in moving activity observed among sites. The burrowing activity is widespread among crabs from intertidal soft-bottom habitats and provides a refuge from subtidal or aerial predators (Warren 1990; Fathala et al. 2010a, b). Even when the morphology of burrows is species-specific (Griffis and Suchanek 1991), it can vary intraspecifically in relation to trophic modes, sediment type, tidal level, water table depth, and structures on and under soil (Iribarne et al. 1997; Katrak et al. 2008; Sal Moyano et al. in press). The tidal pattern of each site results from different amplitudes and regularity of submersion events. Two main food resources consumed by estuarine and salt marsh crabs such as *N. granulata* are organic matter in the sediment and live plants (Iribarne et al. 1997; Alberti et al. 2007b).

The highest activity of crabs was registered in San Antonio. The low organic matter content in the sediment implies that food is not available inside or around burrows and it could be a factor forcing crabs to use living plants of *S. alterniflora* as food, and move intensely between mudflat and

salt marsh. Burrows dug in the very coarse sediment are barely deep enough to host a crab; they get completely dry during low tide in the mudflat, although they remain humid in the salt marsh. In addition, tides that regularly (every 12 h) cover the entire intertidal zone restore the salinity and temperature conditions allowing crabs to cope with this extreme environment. The lowest activity was observed in Mar Chiquita, considering all the environmental conditions examined, in both habitats and in all seasons. Tidal cycles in this site were very irregular, and the salt marsh was rarely covered by water, but at the same time, the organic matter content of the sediment was the highest making food always available inside and around burrows. Burrows are complex, deep and well structured especially in the salt marsh (Iribarne et al. 1997); crabs have a continuous supply of water (from the table water) and experience less variation in temperature and salinity. An intermediate activity was observed in Bahía Blanca, a site with intermediate tidal regularity and burrow depth, but with high organic matter content.

In addition, it is well known that predation affects the movements of intertidal crabs (Bertness 1999; Christy 2007 and cites herein). In the laboratory, adult males of *N. granulata* are responsive to a simulated aerial predator (Oliva et al. 2007 and references therein). In Mar Chiquita, *N. granulata* face an intense predation pressure from several birds, being the main prey of *Larus atlanticus* (Biondi et al. 2005; Sánchez et al. 2008; Berón et al. 2011). In any case, these predators are a very frequent threat in this site, particularly in the mudflat, where remains of crabs eaten by birds are commonly found. No predation studies are available in Bahía Blanca, but the higher level of activity of *N. granulata* in San Antonio could be related to the fact that, in contrast with the other two sites, *L. atlanticus* is not present (Yorio et al. 2005) allowing crabs to move safer. In fact, site differences in escape response have been reported recently: crabs from San Antonio are less reactive to a visual danger stimulus than those from Mar Chiquita (Magani et al. 2011).

Seasonal changes in activity also differed among sites. Crabs were almost inactive during autumn in Mar Chiquita and Bahía Blanca, independently of the daily variation in environmental conditions; they resume their movements in winter even though burrow temperatures reached the lowest values during this period (2.6 and 0.3 °C, respectively). Interestingly, crabs were similarly active in autumn and summer in San Antonio and the decrease in activity was observed in winter, although the minimum burrow temperatures were not so extreme (4.2 °C). A relationship between inactivity and molting could be hypothesized: many pre- and post-molt crabs were found inside closed burrows in autumn in Mar Chiquita and Bahía Blanca suggesting a rather synchronized molting season; autumn, instead, was

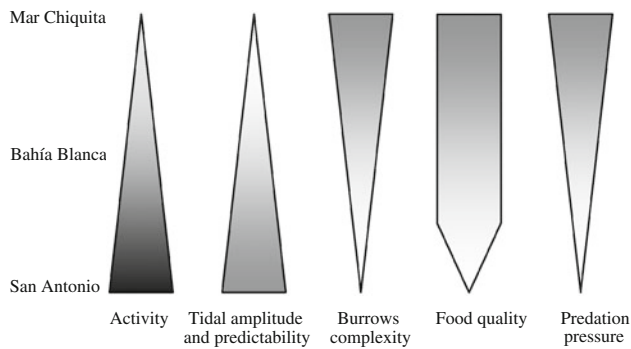


Fig. 9 Schematic representation of the combination of levels in the physical and biological factors associated with the activity level in each site

not the molting season in San Antonio (personal observations).

Summarizing, movement activity of *N. granulata* varied both in space and in time, and several environmental factors may affect them but interacting in a very complex way. In fact, a single factor could not explain all the observed patterns: crabs could move under very different conditions (e.g., low or high tide, during daylight or night, low and high temperature), and movements, instead, could be prevented or elicited by a combination of different levels of those factors and others, like burrow complexity, food quality and predation pressure (Fig. 9).

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