



Biogeomorphically driven salt pan formation in *Sarcocornia*-dominated salt-marshes



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ABSTRACT

Salt-marshes are under increasing threat, particularly from sea-level rise and increased wave action associated with climate change. The development and stability of these valuable habitats largely depend on complex interactions between biotic and abiotic processes operating at different scales. Also, interactions between biotic and abiotic processes drive internal morphological change in salt-marshes. In this paper we used a biogeomorphological approach to assess the impact of biological activities and interactions on salt pan formation in *Sarcocornia*-dominated salt marshes. Salt pans represent a key physiographic feature of salt-marshes and recent studies hypothesized that biogeomorphic processes could be related to salt pan formation in SW Atlantic salt-marshes. The glasswort *Sarcocornia perennis* is one of the dominant plants in the salt-marshes of the Bahía Blanca Estuary (Argentina) where they form patches up to 8 m in diameter. These salt-marshes are also inhabited in great densities by the burrowing crab *Neohelice (Chasmagnathus) granulata* whose bioturbation rates are among the highest reported for salt-marshes worldwide. A set of biological interactions between *N. granulata* and *S. perennis* appears to be responsible for salt pan development in these areas which has not been described elsewhere. The main objective of this work was to determine the ecological interactions occurring between plants and crabs that lead to salt pan formation by using field-based sampling and manipulative experiments. Our results showed that *S. perennis* facilitated crab colonization of the salt-marsh by buffering otherwise stressful physical conditions (e.g., temperature, desiccation). Crabs preferred to construct burrows underneath plants and, once they reach high densities (up to 40 burrows m⁻²), the sediment reworking caused plant die-off in the central area of patches. At this state, the patches lose elevation and become depressed due to the continuous bioturbation by crabs. Thus, salt pans are generated in this case by a set of biogeomorphic processes that include pure ecological interactions such as plant facilitation of crab settlement and also indirect negative effects of crabs on plant survival. Furthermore, crab bioturbation affects sediment structure due to concentration of burrowing activity under plant canopies promoting elevation loss and leading, after a few years, to salt pan formation in a previously vegetated substrate.

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1. Introduction

Salt-marshes play an essential role in overall intertidal morphodynamics (Perillo et al., 2009; Mariotti and Fagherazzi, 2010; Fagherazzi et al., 2013). It is increasingly noted that interactions among geomorphological, physical and biotic processes shape many ecosystems, including coastal salt-marshes (D'Alpaos, 2011; Townend et al., 2011). In particular, the effects of biota on salt-marsh geomorphology have been addressed through different methodologies including numerical and conceptual models, field measurements and observations, and a few field-based experiments. Salt-marshes are

ideal systems for studies on ecomorphodynamics because they are subjected to intense morphodynamic processes and their ecological functioning is relatively simple (Adam, 1990; Allen, 2000). There are many examples of salt-marsh plants and animals affecting the hydrodynamics, sediment dynamics and geomorphology of these environments (Reed, 2000; Neumeir, 2007; Temmerman et al., 2007; Fagherazzi et al., 2012). Plants reduce current velocities, promoting an increase in suspended sediment deposition (Leonard and Croft, 2006); they also trap sediment in their tissues (Li and Yang, 2009) and they can increase the stability of the substrate by binding sediments with roots (Reed, 2000). However, burrowing animals often destabilize salt-marsh sediments and promote localized erosion mainly when they occur at high densities (Talley et al., 2001; Escapa et al., 2007; Smith and Green, in press). Sediment stabilizers (e.g., salt-marsh plants) and destabilizers

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(e.g., burrowing fauna) often coexist and interact on these environments; the net effect of such interactions on salt-marsh morphodynamics seems to be complex but initial assessments have been made using field-based experiments (e.g., Paramor and Hughes, 2004; Escapa et al., 2007; Wilson et al., 2012). In salt-marsh environments, tidal creeks and salt pans are often considered key physiographic features and, as such, are discussed by most authors dealing with salt-marsh geomorphology (Allen, 2000), ecology (Mallin and Lewitus, 2004) and biogeomorphology (Escapa et al., 2007; Wilson et al., 2012).

Salt pans, often referred to as ponds or pools, are distinctive physiographic features present in most salt-marshes (Allen, 2000; Minkoff et al., 2006; Wilson et al., 2009; Goudie, 2013). These pans are non-vegetated shallow depressions that retain standing water at low tide (Reidenbaugh and Banta, 1980; Wilson et al., 2009, 2010; Goudie, 2013). The process of salt pan formation was first described by Yapp et al. (1917), who distinguished between primary pans, which are roughly circular flat-bottomed pools, and channel or secondary pans. Primary pans often originate in the first stages of salt-marsh development, as zones of incomplete colonization of bare surfaces by vegetation (Steers, 1960; Pestrong, 1965; Verger, 1968). Secondary pans develop on mature salt-marshes (Pethick, 1974; Perillo and Iribarne, 2003; Wilson et al., 2009, 2010) and their formation has been mostly related to physical processes, such as water-logging of minor depressions (Redfield, 1972), snow patches (Chapman, 1938), ice-scouring in cold-climate salt-marshes (Dionne, 1968), sub-surface drainage (Kesel and Smith, 1978), and surface erosion by wind-generated waves (Perillo et al., 1996). However, some evidence suggests that biological processes may also play an important role in salt pan formation. For instance, plant retreat in topographically low areas and surface accumulation of tidal wrack promote vegetation die-off and surface layers to subside (Ranwell, 1964). Also, herbivory and grubbing by snow geese may shape salt pans by producing unvegetated soil patches (McLaren and Jefferies, 2004), which over time may suffer localized erosion (Kirwan et al., 2008). Moreover, salt-marsh crabs may induce elevation loss of marsh surface when sediments are intensely bioturbated (Smith and Green, in press). Although bioturbation was not directly related to salt pan generation until now, it could produce and maintain bare areas due to reduction of plant recolonization by disturbance and also due to reduced seedling establishment and success (e.g., Alberti et al., 2010; Smith and Tyrrell, 2012; Smith and Green, in press).

SW Atlantic salt-marshes are mainly dominated by *Spartina densiflora*, *Spartina alterniflora* and *Sarcocornia perennis* (Costa and Davy, 1992; Isacch et al., 2006). *S. perennis* is a perennial macrophyte acting as pioneer species on intermediate and high levels of tidal salt-marshes in the SW Atlantic (Daleo et al., 2014), it is considered an 'extreme halophyte' that often grows in bare sediments where it forms roughly circular patches (Escapa et al., 2007; Alberti et al., 2008). This plant is characterized by succulent, articulated and leafless stems. They can form mats up to 30 cm high, the main branches are prostrated and rooting often occurs at the stem nodes (Adams and Bate, 1994; Davy et al., 2006). These salt-marshes are also inhabited by the burrowing crab *Neohelice (Chasmagnathus) granulata* (Iribarne et al., 1997; Escapa et al., 2007, 2008; Alberti et al., 2008). This species potentially inhabits the whole intertidal zone, from mudflats to salt-marshes vegetated by *S. densiflora* and *S. perennis* (Iribarne et al., 1997), where the crabs excavate and maintain semi-permanent open burrows causing zones of high density and bioturbation intensity. Those zones of high crab densities are generally associated with salt-marsh vegetated matrix (i.e., *Spartina* spp. dominated marshes), plant patches (both in *Spartina*- and *Sarcocornia*-dominated salt-marshes) and creek banks (Iribarne et al., 1997; Fanjul et al., 2007; Escapa et al., 2008). As in other salt-marsh systems (e.g., Bertness and Miller, 1984), colonization by the crabs is strongly dependent on plant presence. Plants facilitate crab colonization of salt-marshes by buffering stressful conditions for burrowing species (e.g., increase in sediment stability due to rooting, desiccation stress reduction as a result of

increased shading; Bertness and Miller, 1984; Bortolus et al., 2002). Bioturbation by crabs has distinct effects on these intertidal systems, as it oxygenates salt-marsh soil, enhances soil drainage, influences sedimentary balance and geomorphology, and impacts on infaunal abundance (Escapa et al., 2004; Daleo et al., 2007; Escapa et al., 2008; Fanjul et al., 2008). In particular, when crabs excavate *Sarcocornia*-dominated salt-marshes their burrows may reach up to 10 cm in diameter, its average depth reaches 50 cm, and their density is roughly 60–80 burrows m^{-2} under plant canopies (Iribarne et al., 1997; Escapa et al., 2007, 2008). Moreover, burrowing activity in these salt-marshes has been positively related to creek inland growth (i.e., creek extension), when crabs were excluded from creek basins the rate of creek growth was drastically reduced (Escapa et al., 2007). A combination of direct sediment removal (Escapa et al., 2008) and indirect changes in sediment geotechnical properties (Escapa et al., 2007) appears to be responsible for the erosive effect of crab activities in SW Atlantic *Sarcocornia*-dominated salt-marshes.

The Bahía Blanca Estuary (Argentina, 38° 50' S, and 62° 30' W, Fig. 1) is an area with low freshwater input, it is characterized by the presence of very extensive intertidal flats and large salt-marshes dominated by monospecific stands of *S. alterniflora*, *S. densiflora* and *S. perennis* (Isacch et al., 2006). The later species often grows in middle and high marsh levels, forming circular clonal mats with stems growing with a centrifugal pattern (Perillo and Iribarne, 2003). As the clones increase in size (i.e., diameter) there is a significant die-off of vegetation in the central part, while the living green stems become restricted to the external borders. The central-depressed part of the clones often appears as an unvegetated salt pan intensely excavated by crabs. Due to the close association between the two species, and the known effects of the crabs on sediment dynamics, it is plausible to hypothesize that these biotic interactions drive biogeomorphic processes further resulting in salt pan formation (Perillo and Iribarne, 2003; Minkoff et al., 2006). This paper aims to examine this hypothesis. With this aim we assessed three particular objectives: 1) the description of salt pan morphology, distribution and dynamics in the salt-marsh, 2) to evaluate how plants facilitate salt-marsh colonization by burrowing crabs, and 3) to evaluate how crabs are affecting plant survival and growth, which further leads to salt pan formation on the salt-marsh surface.

2. Materials and methods

2.1. Study site

The study was performed in the Bahía Blanca Estuary, a large embayment habitat (2300 km²) affected by up to 4 m semi-diurnal tides (Perillo and Piccolo, 1991), and characterized by a series of major NW–SE tidal channels separated by extensive tidal flats, salt-marshes and islands which constitute a mesotidal coastal plain system (Perillo and Piccolo, 1999; Perillo et al., 2005). Salt-marshes are mostly dominated by species of *Spartina* (mainly *S. densiflora* and *S. alterniflora*) and by *S. perennis* as in most of the SW Atlantic salt-marshes (Isacch et al., 2006). The estuary has a negative sedimentary balance due to its geological history (Melo et al., 2003). Although it does not mean that all environments are suffering from erosion, *Sarcocornia*-dominated marshes are losing area rapidly (Pratolongo et al., 2013) as they experience very high erosion rates (Escapa et al., 2008; Pratolongo et al., 2013). Thereby, these are valuable areas to study biogeomorphic processes and their importance on eroding salt-marshes. The perennial plant acts as pioneer species colonizing middle and high salt-marsh levels, and their establishment facilitates other salt-marsh species such as *S. densiflora* (Alberti et al., 2008). Upper zones of mudflats, creek banks and most of the inner salt-marsh area are dominated by the burrowing crab *N. granulata* (Iribarne et al., 1997; Botto et al., 2006; Escapa et al., 2008). *S. perennis* and *N. granulata* seem to live in close association, generating ring-shaped patches (hereafter referred to as "salt pans"; Perillo and Iribarne, 2003) that accumulate standing

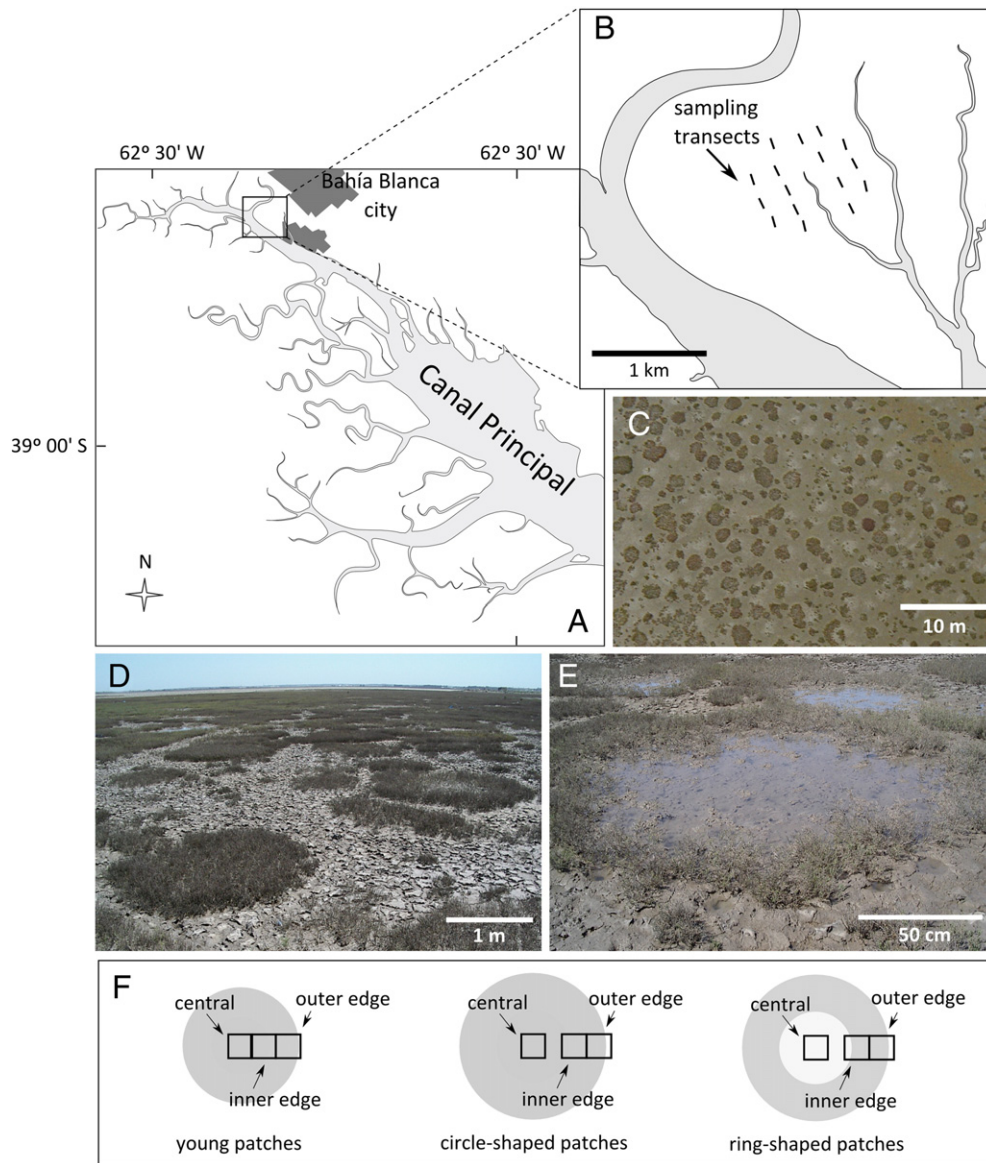


Fig. 1. Maps of the study site at NW Bahía Blanca Estuary showing sampling transects (A and B). Aerial (C), ground (D), and close (E) views of *Sarcocornia perennis* patches on the salt-marsh surface. Bottom panel (F) shows inner patch sampling areas (i.e., outer edge, inner edge and central areas) for young, circle-shaped and ring-shaped patches.

water during low tide (Fig. 1). These characteristic salt pans have not been described elsewhere, even in other areas of the same estuary where the two species coexist.

2.2. Distribution, dynamics and morphology of *Sarcocornia*–*Neohelice* patches

Previous surveys revealed that *S. perennis* is distributed forming circular mats and different stages of patch development have been recognized (Perillo and Iribarne, 2003; Minkoff et al., 2006). Based on this information, bimonthly sampling was conducted from April 2002 to April 2007 to determine the distribution and occurrence of patches of *S. perennis*. Patch type (i.e., different stages of development), the occurrence of new patches (i.e., seedlings of *S. perennis*), presence/absence of crabs and colonization of patches by crabs were surveyed by measuring active burrow densities at each sampling time. Sampling was conducted at 16 fixed transects (10 m wide, 100 m long). Eight transects were located near the salt-marsh edge (within 20 m from the salt-marsh edge) and the other eight were distributed on the inner zones of the salt-marshes. Three *Sarcocornia* patch types were distinguished:

(a) young patches without crabs, (b) patches with crab burrows and full vegetation coverage (i.e., circle-shaped patches), and (c) patches with crab burrows and with living plants only at patch edges (i.e., ring-shaped patches, Fig. 1). The null hypotheses of no difference in the total number of patches of each type, and the rate of occurrence of new patches between the edge and inner salt-marsh zones were assessed with a *t*-test (Zar, 1999).

Patch growth and topographic dynamics were also surveyed over 5 years; thirty patches of each type were randomly selected and flagged. Their major diameter was measured and marked with two steel stakes located far enough from the edge to avoid indirect effects of semi-permanent structures (i.e., stakes) on plant growth and hydrodynamic conditions. The patches were surveyed monthly (from June 2002 to July 2007) and the stakes were relocated if necessary to determine the new diameter. The null hypothesis of no difference in growth rate (cm month^{-1}) among patch types was evaluated using an ANOVA test (Zar, 1999). The topographic dynamics of those patches was also determined for each type ($n = 20$) using markers consisting of two iron posts inserted about 0.8 m in the sediment (~ 1.3 m tall and 1.5 cm diameter), located at a distance of 1 m from the outer patch

edge. A horizontally-leveled crossbar was then installed joining the two posts at 40 cm of height; the vertical distance from the crossbar to the substrate was then measured at intervals of 20 cm, crossing each patch by its major diameter. This method was developed following previous guidelines to establish salt-marsh elevation dynamics (see Perillo et al., 2003) and their estimated vertical error was ± 3 mm. Sampling was performed bimonthly for three years. The mean patch elevation (hereafter 'relative elevation') was calculated and compared among patch types using ANOVA (Zar, 1999). The rate of change (cm month^{-1}) in relative elevation was also estimated and compared among patch types using ANOVA (Zar, 1999). Also, a correlation analysis (Zar, 1999) was used to assess if there was a relationship between patch size and its mean relative elevation.

Additional samplings were conducted to determine intra-patch biotic and topographic features. Plant condition, crab burrow density and activity, and relative elevation were assessed in different areas within the patches. Ten patches of each type were randomly selected, and three areas were defined to account for the intra-patch variation: outer edge (i.e., external zone of the vegetated border), inner edge (internal zone of the vegetated border) and central areas. Vegetation cover was surveyed in squares ($25 \text{ cm} \times 25 \text{ cm}$) randomly assigned and marked on each area. Stem density was also recorded in these squares discriminating between green (i.e., photosynthetically active) and woody-stems. In addition, burrow density, burrow activity (i.e., density of burrows with recently removed sediment, fresh crab prints or crab presence, see Escapa et al., 2008) and relative elevation (as previously described) were also estimated for each intra-patch area. The null hypothesis of no difference in vegetation cover, stem number, density and activity of burrows, and relative elevation in different intra-patch areas and for each patch type were evaluated using a two-way ANOVA (Zar, 1999), with areas and patch type as fixed factors.

2.3. Effect of *S. perennis* on crab colonization and permanency

The presence of *S. perennis* and *S. densiflora* could alter surface sediment physical characteristics that are crucial for the establishment and survival of *N. granulata* in salt-marshes vegetated by both species (Bortolus et al., 2002). In particular, surficial and shallow sub-surface sediment features mostly affect the initiation of burrowing by the crab. Sediment features were then measured for three consecutive summers to determine whether the presence of patches of *S. perennis* engineers salt-marsh abiotic conditions favoring crab colonization. Surface sediment characteristics examined were: penetrability, shear strength; and shallow sub-surface features were: water content, organic matter content, and below-ground biomass. These features were determined for bare sediments (i.e., inter-patch substrate) and for the different vegetated patch types described previously in Section 2.2 (i.e., young, circle-shaped and ring-shaped patches). Ten patches of each type and ten bare areas (1 m^2) were randomly selected and flagged. Three parameter readings and/or samples for each variable were taken in those selected patches and bare areas; these three values were then averaged to obtain a single value for each replicate and sampling date. Penetrability was measured using a hand penetrometer, and it was calculated as the inverse of the pressure (N cm^{-2}) needed to introduce a piston into the sediment to a standard depth (2 cm) (Brown and McLachlan, 1990). A Torvane shear strength meter was used for measuring the torsional strength (i.e., the amount of torsional force required to shear the top 1 cm of sediment, kg cm^{-2}). Sediment water content was evaluated by coring (corers of 5 cm diameter, 10 cm deep). Corers were carried to the lab where wet and dry weight of sediment was determined (precision: $\pm 0.1 \text{ mg}$) and then water content was calculated as the difference between the two weights. A sub-sample ($\sim 10 \text{ g}$) of sediment was extracted from corers to determine organic matter content, the samples were incinerated at $550 \text{ }^\circ\text{C}$ for 8 h and weighed to obtain a percentage of ash-free dry weight as an estimate of organic matter content. Below-ground biomass was measured

by coring (corers of 20 cm diameter, 15 cm deep). Core material was sieved (2 mm mesh) to extract roots and rhizomes, which were then dried and weighed to estimate below-ground biomass (g m^{-2}). The null hypothesis of no difference in the mean values of these variables among patch types and bare areas was evaluated using ANOVA (Zar, 1999). The different patch types and bare areas were also used to evaluate diurnal temperature variation. Atmospheric temperature was measured at the surface (0.5 cm above ground level) of each replicate at intervals of 1 h (16 h per day) using a digital thermometer. Temperature measures were taken only during summer days when salt-marshes were not flooded by tides. The null hypothesis of no difference daytime temperature among hours and type of patch was evaluated with a two-way ANOVA (Zar, 1999).

Additionally, a field experiment was conducted to assess the role of vegetation on crab colonization and permanency (i.e., facilitation) between August 2003 and September 2006. Forty experimental plots were marked (using four steel stakes to delimit 50 cm side squares) in bare areas (i.e., inter-patch areas) of the salt-marsh without crabs or burrows. Four treatments were set up: (a) Shade addition: shades (neutral plastic mesh) were placed 20 cm above the ground surface; (b) Structural addition: *S. perennis* stems were inserted into the sediment to an average depth of 20 cm up to 1 cm above substrate level in order to increase sediment structural complexity; (c) Shade + Structure: shading added as in (a) and structures added to sediment as in (b); and (d) Control: squares ($50 \text{ cm} \times 50 \text{ cm}$) marked in the salt-marsh without shade or structure additions. Each treatment consisted of ten randomly-distributed replicates. The occurrence of burrows was monitored monthly to determine colonization rate (expressed as burrows month^{-1}), and burrow activity was also registered to determine permanence of crabs (total number of active burrows at the end of experiment). The null hypothesis of no difference in colonization rate and crab permanency among treatments were evaluated using ANOVA (Zar, 1999).

2.4. Effect of *N. granulata* activities on *S. perennis* and patch elevation

Due to the effect of crabs on sediment dynamics (Escapa et al., 2008) it is expected that crabs produce geomorphic changes when they occur in high densities. A field experiment was deployed to assess the effect of crab bioturbation on plant performance and the evolution of patch topography. The experiment ran from September 2002 to April 2005. Twenty young *Sarcocornia* patches without the presence of crabs were randomly selected across the salt-marsh; all selected patches had a minimum diameter of 0.6 m. These patches were surrounded with plastic mesh (hereafter referred to as 'experimental units': 50 cm high over the salt-marsh surface, 1 cm aperture mesh, inserted 30 cm into the substrate). Crabs were added to half (10) of the experimental units at the beginning of the experiment (September 2002). To accomplish this, adults of *N. granulata* were collected in the salt-marsh ($\sim 25 \text{ mm}$ of carapace width) and added in the experimental units until reaching densities of 40 crabs per m^2 (similar to the mean marsh crab density). The remaining experimental units (10) served as controls without crab inclusion (controls were maintained without crabs until the end of the experiment). In March 2003, 2004 and 2005 we recorded the number and length of all stems of 5 randomly selected plants in each experimental unit. Canopy index ($[\text{mean total length} / \text{maximum total length}] + [\text{mean number of stems} / \text{maximum number of stems}]$) was estimated using plant stem data. This method allows setting parameters to evaluate the relative plant states, their robustness and architecture. The above-ground parts of plants within the experimental units were carefully removed at the end of the experiment, washed out and weighed (after drying at $60 \text{ }^\circ\text{C}$ to constant weight), discriminating into green and woody stems. Also, the relative elevation of experimental units was bimonthly determined (see methodology previously described in Section 2.2), by measuring the elevation in one fixed point located in the central zone of each experimental unit, to assess whether the presence of crabs affects patch topography. The null

hypothesis of no difference in canopy index and relative elevation between treatments and years were analyzed using repeated measures ANOVA (Zar, 1999). The null hypothesis of no effect of crab inclusion in above-ground plant biomass was evaluated with a *t*-test (Zar, 1999).

3. Results

3.1. Distribution, morphology and dynamics of *Sarcocornia*–*Neohelice* patches

The distribution of the different patch types did not differ for transects located on the edge or inner zones of the salt-marsh, the less abundant patch type were young *Sarcocornia* patches without crabs (salt-marsh edge: *mean* = 16.2%, *sd* = 2.68; inner marsh: *mean* = 15.6, *sd* = 1.58, *t* = 0.55, *df* = 14, *p* > 0.05); circle-shaped patches represented roughly 36% of all patches and there was no difference in their percentage of occurrence between salt-marsh zones (salt-marsh edge: *mean* = 35.6%, *sd* = 1.51; inner salt-marsh: *mean* = 37, *sd* = 1.8, *t* = 1.6, *df* = 14, *p* > 0.05); finally ring-shaped patches were the most abundant and they were also homogeneously distributed in both salt-marsh zones (salt-marsh edge: *mean* = 49.52%, *sd* = 1.21; inner salt-marsh: *mean* = 47.84, *sd* = 2.71; *t_c* = 1.59, *df* = 13, *p* > 0.05). The total number of patches did not differ between salt-marsh zones (salt-marsh edge: *mean* = 2100 patches ha⁻¹, *sd* = 151; inner salt-marsh: *mean* = 2047 patches ha⁻¹, *sd* = 340; *t_c* = 0.79, *df* = 43, *p* > 0.05). For all cases, new patches were formed from seedlings that germinated in the spring season, and the post-germination success of seedlings mostly occurred in empty spaces between patches; we never observed new seedling growth within patches. The rate of appearance of new patches was higher in transects located at salt-marsh edge zones (salt-marsh edge: *mean* = 52 patches ha⁻¹ yr⁻¹, *sd* = 20.1; inner salt-marsh: *mean* = 25 patches ha⁻¹ yr⁻¹, *sd* = 10.3, *t_c* = 3.29, *df* = 11, *p* < 0.05). A small percentage of these new patches was colonized by crabs during the first year (<3%, *n* = 128). For the second year the percentage of those new patches colonized by crabs reached 60% (*n* = 119), and 90% of the patches were colonized after three growing seasons (*n* = 112). The mean minimum size of patches that started to be colonized by crabs varied between transects located at the edge and inner zones of the salt-marsh (salt-marsh edge: *mean* = 25 cm, *sd* = 7.6; inner salt-marsh: *mean* = 34 cm, *sd* = 10.1; *t* = -4.5, *df* = 98, *p* < 0.05).

Patch growth rates did not differ among patch types (ANOVA: *F*_{2, 267} = 0.80, *p* > 0.05) during the growing season (September to March, pers. obs.). It reached maximum growth rates of 16 cm per month (*mean* = 5.1 cm month⁻¹, *sd* = 4.5). After the appearance of seed-bearing flowers (i.e., in March), vegetative growth was near zero until the following spring (*mean* = 0.5 cm month⁻¹, *sd* = 1.1). Relative elevation was different for each patch type. Young patches and circle-shaped patches exist at higher relative elevation with respect to the surrounding salt-marsh level (*mean* = 2.8 cm, *sd* = 3.1, *n* = 60), while ring-shaped patches were depressed with respect to that level (*mean* = -4.3 cm, *sd* = 4.4; ANOVA: *F*_{2, 87} = 24.18, *p* < 0.05; Fig. 2A). Rates of elevation change were different among patch types (Kruskal–Wallis: *H*_{2, 60} = 8.67, *p* < 0.05, Fig. 2B): values near zero occurred for young *Sarcocornia* patches without crabs, these rates were more variable for circle-shaped patches but most of the cases showed negative values indicating net elevation loss, and the ring-shaped patches also mostly presented negative rates indicating elevation loss (young: *mean*_{young} = -0.05 cm, *sd* = 0.16; *mean*_{circle} = -0.95 cm, *sd* = 1.75; *mean*_{ring} = -0.96 cm, *sd* = 0.86; Fig. 2B). Overall, a negative correlation was found (*r* = -0.84, *n* = 80, *p* < 0.05) between the relative patch elevation and patch diameter (Fig. 3).

Plant cover within patches remained constant in different areas of *Sarcocornia* patches without crabs. However, circle-shaped patches presented a reduction in plant cover in the central areas. Ring-shaped patches had drastically reduced plant coverage in the central area

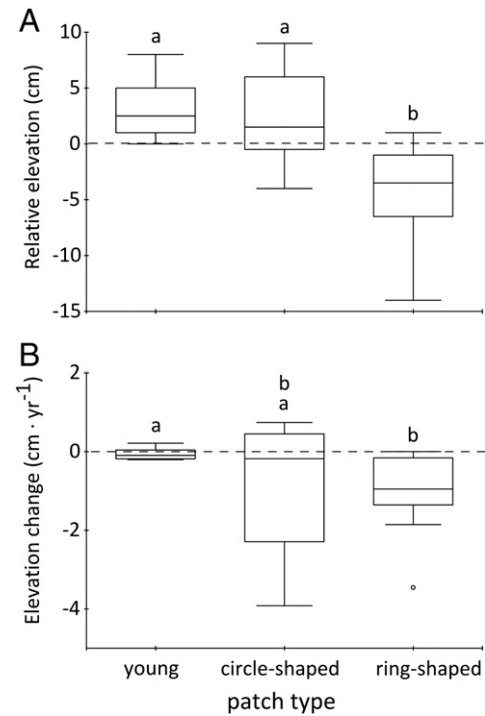


Fig. 2. (A) Relative elevation (cm) with respect to surrounding salt-marsh, and (B) elevation change (cm yr⁻¹) for young *Sarcocornia perennis* patches (without crabs), circle-shaped patches (with crabs), and ring-shaped patches (with crabs). Box limits represent the 75th and 25th percentiles of data, lines out of the boxes are the 1st and 99th percentiles, and lines inside the boxes represent the median, circles outside the boxes represent outliers. Different letters above boxes indicate significant differences detected among groups with a posteriori multiple comparison test after ANOVA (Tukey test, $\alpha = 0.05$).

(Table 1; Fig. 4A). The ratio between green and woody stems was always greater in the outer-edge areas than in the inner-edge and central areas for all patch types. This ratio was low in the central area of circle-shaped patches, but the lowest value was found in the central area of ring-shaped patches (Table 1; Fig. 4B). Crab burrow density and activity did not change among different areas of circle-shaped patches (Table 1, Fig. 4C–D); but it significantly decreased in the central areas of ring-shaped patches. In these patches, burrow density in the central area decreased as much as four times from those registered in the edge areas, and active burrows in the central area were an order of magnitude lower than in edges (Fig. 4C–D). All patch types showed super-elevation with respect to surrounding salt-marsh level in their vegetated-edge areas (*mean* = 2.53 cm, *sd* = 1.86 in both outer edges and inner edges, Table 1; Fig. 4E). Young patches without crabs and circle-shaped patches were more elevated in the central areas (Fig. 4E) than in the outer (i.e., inter-patch) area. The central areas of

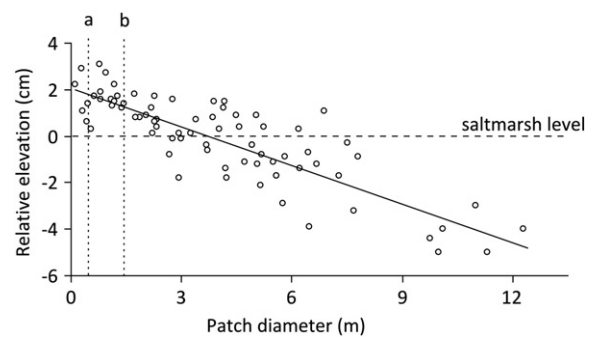


Fig. 3. Relationship between patch diameter and patch relative elevation. Vertical dotted lines indicate (a) the minimum diameter for colonization by crabs, and (b) the diameter for which 95% of the patches were colonized by crabs.

Table 1

Two-way ANOVA summary for patch characteristics among patch types (i.e., young, circle-shaped and ring-shaped) and inner patch areas (i.e., outer edge, inner edge and center areas) ns = non-significant differences.

	df_{effect}	df_{error}	MS_{effect}	F
<i>Plant cover</i>				
Patch type	2	81	11736.1	84.4
Patch area	2	81	6101.0	43.9
Type \times area	4	81	3871.8	28.6
<i>Green/woody ratio</i>				
Patch type	2	81	48.3	6.4
Patch area	2	81	103.2	13.6
Type \times area	4	81	6.4	0.85 ^{ns}
<i>Burrow density</i>				
Patch type	2	54	129.8	8.7
Patch area	1	54	74.8	5.0
Type \times area	2	54	300.3	20.1
<i>Active burrow density†</i>				
Patch type	2	54	146.0	11.5
Patch area	1	54	170.0	13.4
Type \times area	2	54	341.8	26.9
<i>Relative elevation</i>				
Patch type	2	81	18.0	9.4
Patch area	2	81	72.2	37.6
Type \times area	4	81	106.5	55.5

the ring-shaped patches always showed negative values, reaching values of up to 6 cm below the mean elevation in the surrounding salt-marsh (Fig. 4E).

3.2. Effect of *S. perennis* on crab colonization and permanency

Sediment water content was higher in circle-shaped patches and ring-shaped patches than in young patches without crabs and sediment outside patches (ANOVA: $F_{3, 36} = 7.35, p < 0.05$; Fig. 5A), in these latter sites mean water content was 10.42% ($sd = 4.1, n = 10$), a value almost three times lower than in the ring-shaped patches ($mean = 30.3\%, sd = 12.1, n = 10$). Sediment penetrability was greater in patches inhabited by crabs (i.e., circle-shaped and ring-shaped patches) than in bare sediments and young *Sarcocornia* patches without crabs (Kruskal–Wallis: $H_{3, 36} = 23.09, p < 0.05$; Fig. 5B). The inverse pattern was observed for sediment torsional strength, being more than three times lower in circle- and ring-shaped patches ($mean = 0.32 \text{ kg cm}^{-2}, sd = 0.17, n = 20$) than bare areas and young *Sarcocornia* patches ($mean = 1.19 \text{ kg cm}^{-2}, sd = 0.33, n = 20$; Kruskal–Wallis: $H_{3, 36} = 27.83, p < 0.05$, Fig. 5C). Organic matter content was similar among different patch types and bare areas (ANOVA: $F_{3, 36} = 2.05, p > 0.05$, Fig. 5D) with mean values for pooled data of ~3% ($sd = 1.2, n = 40$). The highest below-ground biomass occurred in young patches ($mean = 103.3 \text{ g m}^{-2}, sd = 34.2$), and the lowest in ring-shaped patches ($mean = 17.7 \text{ g m}^{-2}, sd = 9.9$). Circle-shaped patches showed intermediate values ($mean = 60.2 \text{ g m}^{-2}, sd = 40.1$; ANOVA: $F_{2, 27} = 19.6, p < 0.05$, Fig. 5E). The patterns of variation in daytime temperature were different for each patch type (Fig. 6). Also temperature was similar among patch types when minimum values were registered (i.e., morning vs. night), but as temperature rises it reached higher values in bare areas and inside ring-shaped patches (ANOVA interaction: $F_{48, 612} = 5.1, p < 0.05$, Fig. 6). Overall, the maximum temperatures recorded during the day were higher in patches devoid of vegetation (i.e., sediment bare areas and ring-shaped patches, $mean = 37.98 \text{ }^\circ\text{C}, sd = 3.1, n = 40$) than in vegetated patches (i.e., young *Sarcocornia* patches and circle-shaped patches $mean = 29.2 \text{ }^\circ\text{C}, sd = 4.1, n = 40, t_c = 12.3, df = 78, p < 0.05$).

Experimental results revealed that initial colonization by crabs was higher for shade and shade + structure treatments than for the structure treatment, while the lowest colonization rate was recorded in the controls (ANOVA: $F_{3, 36} = 18.34, p < 0.05$; Fig. 7A). At the end

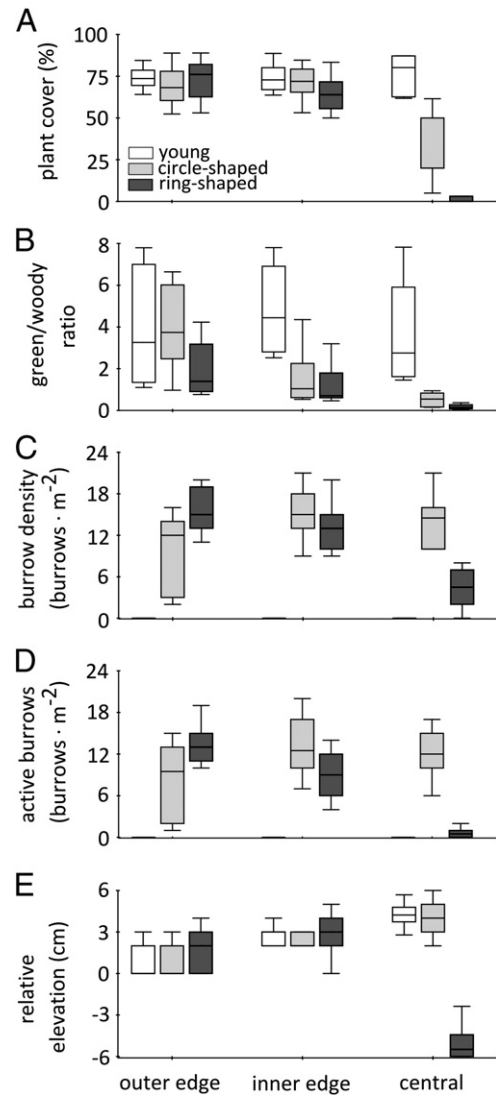


Fig. 4. (A) Plant cover, (B) green to woody biomass ratio, (C) total number of burrows, (D) number of active burrows, and (E) relative patch elevation, discriminating the outer edge of the patches (outer), the inner edge (inner), and central areas (central) for each patch type.

of the experiment, the permanence of burrows showed a pattern similar to the colonization rates. Maximum burrow permanency occurred in both shaded treatments (i.e., shade and shade + structure). The few burrows established in experimental controls did not remain and the same pattern occurred for burrows that colonized structure treatment plots (ANOVA: $F_{3, 36} = 29.85, p < 0.05$; Fig. 7B).

3.3. Effect of *N. granulata* activities on *S. perennis* and patch elevation

Plant health, represented by the canopy index, was approximately the same between treatments after one year of the beginning of the field experiment. Starting in the second year, the values of this index declined in the crab-inclusion treatment, a trend that continued until the end of the experiment (ANOVA: $F_{2, 27} = 44.42, p < 0.05$; Fig. 8A). In contrast, plants inhabiting crab-exclusion treatments did not experience a reduction in their canopy indexes (Fig. 8A). In addition, at the end of the experiment the total biomass of woody stems was on average two times lower in the crab-inclusion treatment ($mean = 64.3 \text{ g plot}^{-1}, sd = 47.1$) than crab-exclusion treatment ($mean = 112.6 \text{ g plot}^{-1}, sd = 51.1; t_c = -2.19, df = 18, p < 0.05$). Also, there was a reduction in the final biomass for green stems for crab-inclusion treatment

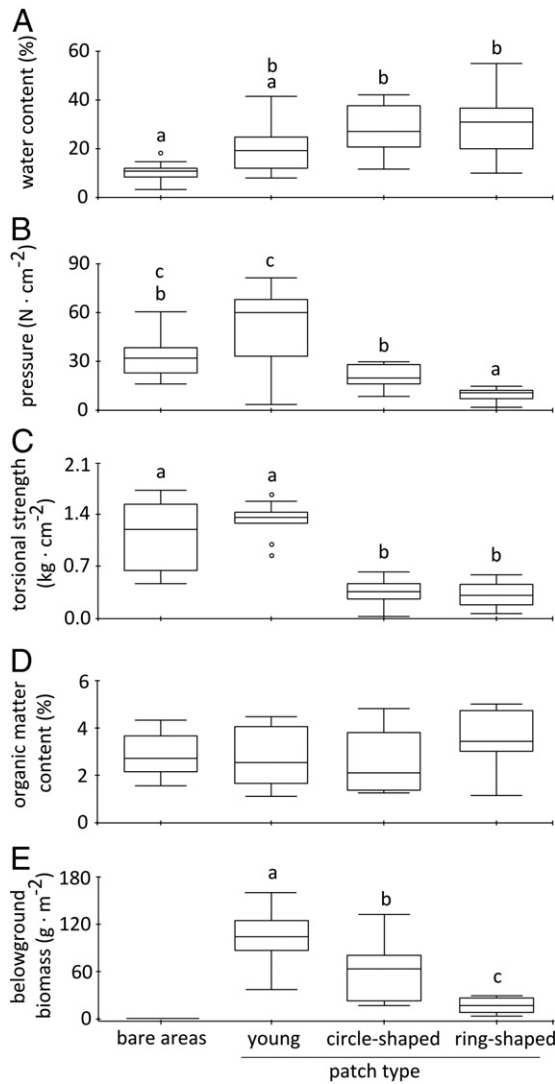


Fig. 5. (A) Sediment water content, (B) sediment penetrability, (C) torsional strength, (D) organic matter content, and (E) below-ground biomass at inter-patch areas (bare areas), young *S. perennis* patches (young), circle-shaped patches (circle-shaped), and ring-shaped patches (ring-shaped). Notice that sediment penetrability and torsional strength are superficial features, and water content, organic matter content and below-ground biomass are shallow sub-surface features. Box limits represent the 75th and 25th percentiles of data, lines out of the boxes are the 1st and 99th percentiles, and lines inside the boxes represent the median, circles outside the boxes represent outliers. Different letters above boxes indicate significant differences detected among groups with a posteriori multiple comparisons test after ANOVA (Tukey test, $\alpha = 0.05$).

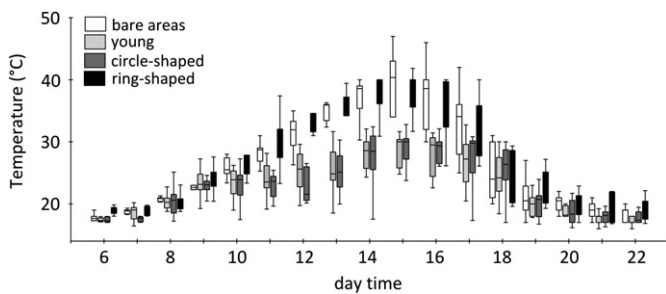


Fig. 6. Daytime temperature variation at 0.5 cm above sediment surface for bare areas (unvegetated) and the different patch types (young: vegetated without crabs, circle-shaped: vegetated with crabs, and ring-shaped: unvegetated with crabs).

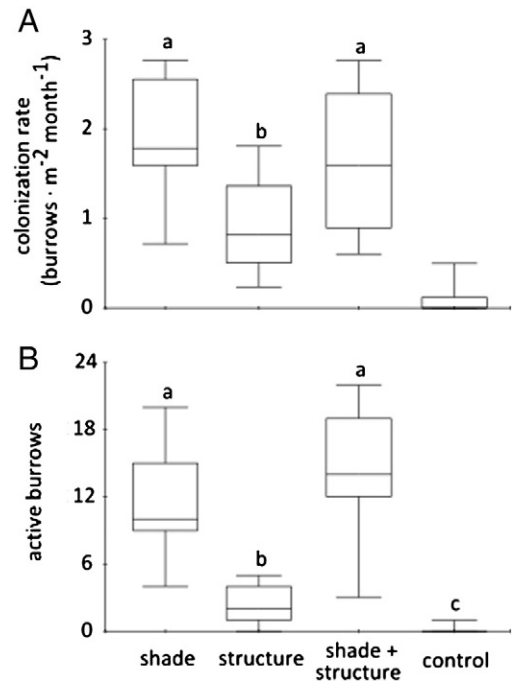


Fig. 7. (A) Rate of colonization by crabs ($\text{burrows m}^{-2} \text{ month}^{-1}$) and (B) final permanence of crab burrows estimated as number of active burrows (burrows m^{-2}) for experimental treatments with shade addition (shade), structure addition in sediment (structure), addition of both shade and structure (shade + structure), and controls (control). Box limits represent the 75th and 25th percentiles of data, lines out of the boxes are the 1st and 99th percentiles, and lines inside the boxes represent the median, circles outside the boxes represent outliers. Different letters above boxes indicate significant differences detected among groups with a posteriori multiple comparison test after ANOVA (Tukey test, $\alpha = 0.05$).

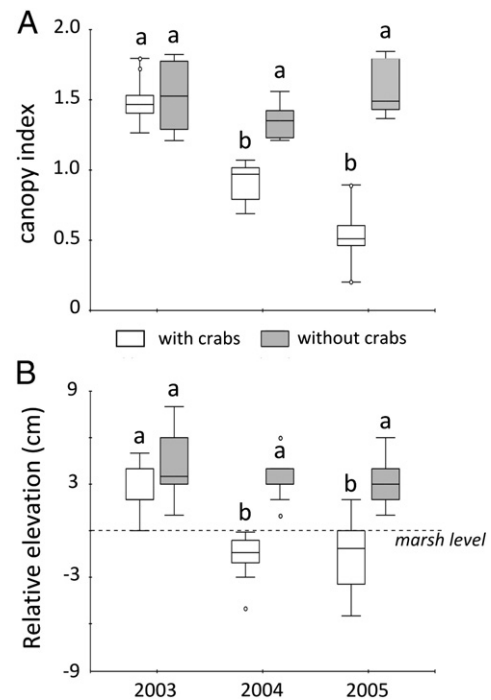


Fig. 8. Temporal variation of (A) *S. perennis* canopy index and (B) relative elevation for experimental treatments with and without crabs. Box limits represent the 75th and 25th percentiles of data, lines out of the boxes are the 1st and 99th percentiles, and lines inside the boxes represent the median, circles outside the boxes represent outliers. Different letters above boxes indicate significant differences detected between groups after the *t*-test ($\alpha = 0.05$).

($t_c = -5.25$, $df = 18$, $p < 0.05$) but, in this case, the reduction was much more pronounced: green stem biomass was on average four times lower in crab-inclusion ($mean = 27.2 \text{ g plot}^{-1}$, $sd = 9.4$) than in crab-exclusion treatments ($mean = 27.2 \text{ g plot}^{-1}$, $sd = 9.4$). The ratio between green and woody biomass was also different for the two treatments, being higher for crab-exclusion treatments (green to woody biomass ratio = 3.43, $sd = 3.93$, $n = 10$) than in crab-inclusion treatment (green to woody biomass ratio = 1.06, $sd = 0.65$, $n = 10$; $t_c = 1.85$, $df = 18$, $p < 0.05$). Relative elevation in experimental units remained constant throughout the experiment for crab-exclusion treatment (Fig. 8B), registering roughly a super-elevation of 3 cm when it was compared with the adjacent salt-marsh substrate. For crab-inclusion treatment the relative elevation remained at the same level (~3 cm above salt-marsh level) during the first year, but it decreased significantly from the second year (ANOVA: $F_{2, 27} = 7.01$, $p < 0.05$, Fig. 8B).

4. Discussion

The results presented here reveal a set of biogeomorphological interactions among pioneer salt-marsh plants, burrowing crabs and elevation dynamics that lead to the formation of salt pans over a high salt-marsh surface. The origin of these salt pans, since they appear in the earlier stages of salt-marsh succession, differs from explanations that reported primary salt pans as a result of incomplete colonization of salt-marsh surface (Yapp et al., 1917; Allen, 2000; Wilson et al., 2009). Actually, the salt pans investigated here are secondary geomorphic features that develop from pre-established vegetation patches which are later colonized by burrowing crabs. *S. perennis* colonizes bare sediment and forms clonal patches which were homogeneously distributed in the studied salt-marshes occupying approximately 50% of the surface (see Minkoff et al., 2006). Different stages of patch development could be recognized: from small clones of *S. perennis* without crab presence to large patches where central areas become depressed after being excavated by *N. granulata*. These different patch types were also homogeneously distributed over the salt-marsh, the same proportion of each patch type was found on the salt-marsh edge and on inner salt-marsh zones. Once established, *S. perennis* engineers salt-marsh substrate and favors crab colonization and their permanency over time, by damping stressful environmental conditions (i.e., alleviation of extreme temperature, reduction in desiccation stress) coupled to an increase in the structural complexity of the substrate (i.e., increased sediment stability due to rooting). Once patches become colonized by crabs, and the patches grow in size (i.e., centrifugally), the central plants die because of the effect of crabs on green tissues (i.e., photosynthetically active tissues). Also, this intense bioturbation promotes sediment instability that makes the soil unstable for the roots to sustain the plant (i.e., plant roots become unanchored after intense bioturbation, M.E. unpublished data). It seems that both the loss of vegetation and the removal of sediment by crabs lead to localized deflation, and these processes further promote the formation of salt pans.

The establishment of *S. perennis* patches facilitates crab colonization and burrow permanence. Sampling of these salt-marshes revealed that the spatial distribution of crab burrows was always biased and restricted to vegetated areas regardless of the patch type analyzed. Abiotic changes promoted by plant presence are actually buffering stressful conditions for crab habitation and it appears to be the mechanism at work here. There is evidence that the distribution and survival of intertidal species is often regulated by heat and desiccation stresses (Bertness, 1999). Below *Sarcocornia* canopies, maximum temperatures reached were lower than in non-vegetated areas, and it is known that crabs can die quickly when exposed to elevated air temperatures (Bortolus et al., 2002). In those salt-marshes, as in the one studied here, the damping of extreme temperatures and the consequent reduction in the evaporation of water contained in the sediment appear to be responsible for the higher rates of colonization registered under plant canopies (Bortolus et al., 2002). The method used here to measure

sediment water content eventually includes water trapped in below-ground plant tissues. Thus, such results should be interpreted taking this into account, because of increased humidity in sediment below plant canopies could be overestimated given the method used. Moreover, crabs also preferred to settle in sites with structural aggregates (such as roots) in the sediment, which are independent of plant canopies. This structural complexity may also be a determinant for the distribution of benthic organisms; in the Northern Hemisphere salt-marshes (i.e., Atlantic Coast of the USA) the presence of roots and rhizomes that provide structure to the ground may facilitate salt-marsh colonization by crabs (Bertness, 1985, 1999). However, the burrows established in areas with increased structural complexity showed lower permanence in areas without vegetation cover than vegetated areas. In other environments, only the construction of the burrows has been favored by the vegetation and, once established, the refuge that burrows offer is enough to mitigate the stressful environmental conditions (Bortolus et al., 2002). In the salt-marsh investigated here, the burrows located outside shaded areas become non-functional and were mostly abandoned after a short time. Thus, in these systems the vegetation could be the determining factor for successful crab colonization and permanency.

After substrate colonization by *S. perennis*, the sediment level below the plants rises a few centimeters. This is probably due to the plant capability for retaining sediment being transported by the tides and also for binding the substrate by rooting. Since the salt-marsh considered is a high salt-marsh, covered by the tides only about 40 times a year (Minkoff et al., 2005), tidal currents are small (Pratolongo et al., 2010) and the transported suspended sediments are easily retained by the plant patches. Castellanos et al. (1994) described this topographical effect for the same plant species in Northern Hemisphere salt-marshes and indicated that it is strictly restricted to the area of the plant canopy (Pethick et al., 1990; Castellanos et al., 1994). *Sarcocornia* patches in SW Atlantic salt-marshes are further colonized by burrowing crabs when they reach a minimum diameter (approximately 0.6 m). Over time, crab bioturbation negatively affects plant performance and, after a few years, all plants die or become unanchored in the central area of patches. High bioturbation intensity by *N. granulata* could be responsible for these patterns in the temporal evolution of the patches. The experimental results obtained here demonstrate that the presence of crabs negatively affects plant growth by reducing the total biomass of green stems (i.e., photosynthetically active) and it also produces the collapse of the central part of the patches. The crabs relocate large amounts of sediment during excavation and maintenance of burrows (up to $5 \text{ kg m}^{-2} \text{ day}^{-1}$; Iribarne et al., 1997; Escapa et al., 2008) transporting sediments from the deeper levels to the surface (i.e., 'regenerative bioturbation', sensu Kristensen et al., 2012). Sediment relocated by the crabs is deposited in the surface forming large mounds (up to 10 cm in height and 20 cm in diameter; Escapa et al., 2008) that lead to the transformation of photosynthetically active stems to woody stems due to burial (pers. obs.). Moreover, crab activity reduces sediment hardness (i.e., bioturbation activity increases penetrability and reduces sediment torsional strength; Botto and Iribarne, 2000; Escapa et al., 2004, 2007) which affects the binding capacity of new rooting stems. However, plants that occur at patch edges can anchor in the outer-patch areas where there are no crabs. This process could explain the centrifugal growth of patches and also their ring-shaped form, where plants survive only in the patch edges, in particular for the biggest and consequently oldest patches. Furthermore, mature plants of *S. perennis* can tolerate high sediment salinity (Waisel, 1972) only when they occur in well-drained sediments with high redox potential (Castellanos et al., 1994; Davy et al., 2006). Thus, the almost permanently waterlogged conditions in the central areas of the patches due to surface elevation loss could eventually result in death of the plants because of decreased sediment redox potential.

The losses of the plants coupled with crab bioturbation are highly likely to be the processes that explain the elevation loss in the central part of the patches and the formation of salt pans. In other salt-

marshes there are multiple factors that could affect elevation dynamics, such as peat decomposition or sediment compaction (Allen, 2000). These *Sarcocornia*-dominated salt-marshes are mostly minerogenic and this plant species does not produce significant amounts of litter/peat, as reflected by the low organic matter content of the sediments. *S. perennis* has also low sediment trapping capacity compared with other common salt-marsh plants such as *Spartina* spp. (Leonard and Luther, 1995; Townend et al., 2011). However, Davy et al. (2006) mentioned that *S. perennis* increases sediment deposition and also binds substrate with its roots, leading to an increase in relative elevation (Boorman et al., 2000). Furthermore, the net effect of the plants on flow attenuation and the consequent increase in sediment deposition will be increased for denser and taller plants (Leonard and Croft, 2006). Thus, the decrease in vegetation cover due to the activity of crabs could lead to lower rates of sediment trapping, producing contrasting sedimentation patterns between areas with varying plant coverage (e.g., patch edges vs. central areas of patches). Furthermore, plant roots can increase sediment resistance to erosion (Reed, 2000), so the death of the plants in the central areas of the patches could generate more easily erodible areas. Crab activity within the patches reduced sediment hardness, affecting sediment geotechnical properties which are strongly related with sediment erodibility (Grabowski et al., 2011). Also, crabs expose burrow-removed sediment to direct erosion by currents and waves when they form mounds around burrow entrances (Escapa et al., 2008). It is well known that salt-marsh crabs affect sediment geotechnical and geochemical properties and processes (e.g., Escapa et al., 2007; Needham et al., 2011; Wilson et al., 2012; Fanjul et al., 2014), but their effect on geomorphologic features seems to be significant when the biogeomorphologic agent reaches high densities – or ‘concentrate’ – in discrete areas within a system (Jones, 2012). Distinct crab effects on these salt-marshes, such as the death of the plants in the patch central area, the decrease in sediment hardness and the continuous removal of sediment promote localized erosion. Fig. 9 illustrates a conceptual model for the evolution of the interactions between plants and crabs and also the evolution of topographic dynamics of the patches. Sediments are first colonized by plants that produce small (but detectable) elevation gains just under canopy. Once patches increase in size, plant presence facilitates the colonization by burrowing crabs. Later, the bioturbation by crabs negatively affects plant performance and the patches start to lose elevation. Finally, there is a complete die-off of plants in the central part of the patches and at the same time the patches become depressed due to loss in elevation. Thus, this set of processes leads to biogeomorphologically driven salt pan formation after a few years from initial plant colonization.

5. Conclusions

Coastal salt-marshes offer the opportunity to test hypothesis about the interplay between biology and geomorphology as they are highly dynamic systems, which increasingly provide attractive examples of biogeomorphic controls on morphodynamics. Since the ecological, geomorphological and hydrological domains in salt-marshes are closely linked, a comprehensive and interdisciplinary understanding of feedback processes among these domains is increasingly required to address management strategies currently applied for these threatened environments. While the interplays between salt-marsh plants and morphodynamics are well-known, the impact of salt-marsh fauna and their interaction with vegetation remains largely unknown. By using manipulative field-based experiments we demonstrate the effect of ecological interactions between salt-marsh plants and burrowing crabs on the formation of a discrete physiographic salt-marsh structure such as salt pans. These biogeomorphic interactions have not been reported as generators of salt pans until now. However, salt-marsh crabs – usually burrowing species – occur in many salt-marshes worldwide, and their effect on salt-marsh morphology will depend on the intensity of their activity and on the system context (i.e., biotic and abiotic). The Bahía Blanca Estuary has a negative sedimentary balance, and crab bioturbation seems to exacerbate erosion of some environments within the estuary, such as *Sarcocornia*-dominated salt-marshes where the activity of the crab increases erosion due to creek extension (Escapa et al., 2007), and also promotes salt pan formation due to its interaction with *Sarcocornia* patches.

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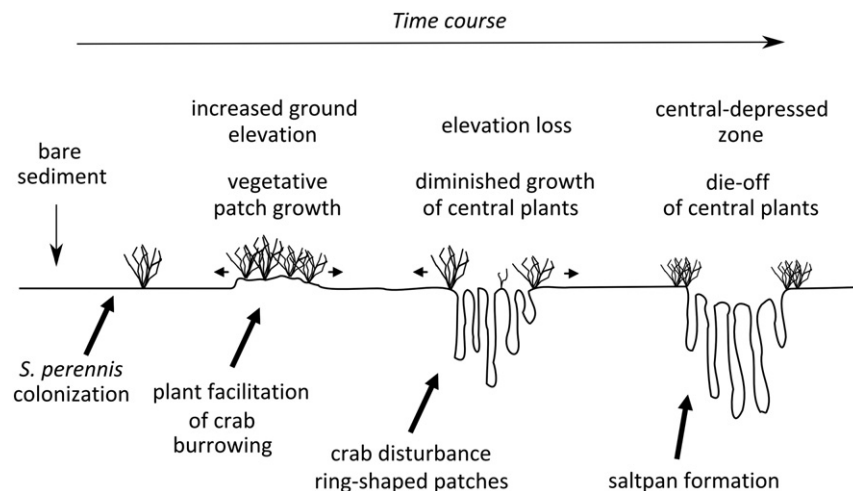


Fig. 9. Conceptual model showing the time evolution that leads to salt pan formation.

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