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Changes in rainfall pattern affect crab herbivory rates in a SW Atlantic salt marsh

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Abstract

Climatic fluctuations usually change the intensity of existing interactions. Thus, in the context of the global climate change, it is important to consider new potential interactions or changes that may appear. Heavy rainy periods (one of the consequences of global climate change in eastern-central Argentina) can promote flooding in some estuaries (mainly on coastal lagoons), and thus, affect interactions between species. In this work we investigate if climatic fluctuations can affect *Spartina densiflora* Brong. (dominant marsh plant) survival through a chain of biotic and abiotic interactions in a SW Atlantic costal lagoon (37° 40′S, 57° 23′W; Mar Chiquita, Argentina). To achieve this, the long-term rainfall behavior of this region, and the effect of rainy periods on submergence of estuarine marsh areas (using satellite images) were analyzed. Then, the effect of flooding on the activity of the dominant herbivore of this system, the burrowing crab *Neohelice granulata* (= *Chasmagnathus granulatus*), was studied using pitfall traps. Finally, the effect of flooding on crab herbivory rates and plant survival were analyzed using transplants, stem-marking and flooding experiments. Long-term rainfall behavior showed that mean annual rainfall has increased during the last century, with the occurrence of more rainy years, and increases in cumulative monthly rainfall increased the submerged area of the *S. densiflora* marsh. Also, crab activity in the marsh largely increased during periods of flooding, associated with more than 100% increments in herbivory rates and stem mortality. These results reveal that increments in rainfall regime can trigger a cascade of abiotic and biotic interactions leading to increased marsh mortality, and stresses the importance of considering both, biotic and abiotic factors, together to predict changes in community organization.

Keywords: Cascade of interactions; Climate change; Crab herbivory; *Neohelice granulata*; *Spartina densiflora* marsh

1. Introduction

Habitat use by species can be affected by many different biotic and/or abiotic factors (Karr and Freemark, 1983). Among biotic factors, we can find examples of competition (e.g., Robertson and Gaines, 1986), predation (e.g., Werner et al., 1983) and indirect interactions (e.g., Wootton, 1993). On the other hand, abiotic factors include temperature (e.g., Garner et al., 1998), rainfall (e.g., Stenseth et al., 2002) and flooding (e.g., Bodmer, 1990; Gasith and Resh, 1999). However, they do not act in isolation; biotic and abiotic factors, commonly operate together to influence habitat use (e.g., Gasith and Resh,

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1999; Martin, 2001; Lima et al., 2002). In fact, both factors need to be considered together when analyzing community organization and function (Dunson and Travis, 1991). At the same time, there is a wealth of information on species habitat selection and use, which may be produced by large-scale environmental changes. Even more, there is a necessity of considering new potential biotic interactions or changes in the existing ones when analyzing global change (abiotic factors; Martin, 2001; Klanderud, 2005).

One of the consequences of global climate change in some regions, is a significant increment in heavy rainfall episodes (e.g., Argentina: Viglizzo et al., 1995; Berbery et al., 2006; Australia and New Zeland: Suppiah and Hennessy, 1998; Plummer et al., 1999; Brazil: Collischonn et al., 2001), which can potentially have strong ecosystem impacts (e.g., Carpenter et al., 1992; Cornelissen et al., 2001). Rainfall is one of those abiotic factors that, either directly or indirectly, can strongly affect habitat use (e.g., Vickery and Rivest, 1992; Fritz et al., 1996; Martin, 2001). Indirectly, it can affect species by promoting flooding, especially in wetlands (e.g., Gasith and Resh, 1999; Garcia et al., 2001; Roshier et al., 2001), having positive or negative effects on a wide variety of organisms (e.g., Bodmer, 1990; Leidy et al., 1992; Golladay et al., 1997; Canepuccia et al., in press).

During the last four decades in eastern-central Argentina, “the Pampas” region, the rainfall regime has been higher than the historic mean (Viglizzo et al., 1995; Berbery et al., 2006), with 10 to 30% increases over the last 50 years, and an associated increase in the occurrence of heavy rainy periods (Berbery et al., 2006). In this area, rainfall regime is cyclically affected by another phenomenon: the El Niño Southern Oscillations (ENSO) which cause an increase in precipitation from southern Brazil to central Argentina (Viles and Goudie, 2003) that can lead to higher water levels in estuaries associated with lagoons like the Mar Chiquita coastal lagoon (Argentina, 37° 40′S; Reta et al., 2001; Canepuccia et al., in press) and the Patos Lagoon (Brazil, 32° 09′ S; Garcia et al., 2001). In this region, estuarine marshes associated with high fresh water input (like coastal lagoons and rivers) that can potentially be affected by rainfall and flooding are dominated by the plant *Spartina densiflora* Brong. (see Isacch et al., 2006).

These marshes and the tidal flats next to them are also inhabited by the burrowing crab *Neohelice granulata* Dana (= *Chasmagnathus granulatus*; for recent taxonomic revision see Sakai et al., 2006. See also Spivak et al., 1994; Iribarne et al., 1997). This relatively large crab (up to 40 mm carapace width; Spivak et al., 1994) is distributed from southern Brazil (23°S) to the northern Argentinean Patagonia (San Matías Gulf, 41°S; Iribarne et al., 2003), in salinity conditions from freshwater (i.e. upper reach of the Samborombom Bay) to hyper-saline environments (i.e., Bahia Blanca; Iribarne et al., 2005). Crabs are primarily deposit feeders in mud flats and herbivorous–detritivorous in the salt marsh (Iribarne et al., 1997, Bortolus & Iribarne 1999, Botto et al., 2005). Field observations and gut content analysis indicate that *N. granulata* is a herbivore–detritivore in the vegetated salt marsh (e.g., Iribarne et al., 1997; Bortolus and Iribarne, 1999) that concentrates its herbivore impacts in the low marsh (Alberti et al., in press). Stable isotopic analyses confirmed that *Spartina* spp. are their primary food source (Botto et al., 2005). Herbivory by *N. granulata* can decrease the aerial biomass of *S. densiflora* by up to 87% (Bortolus and Iribarne, 1999). However, preliminary observations suggest that these crabs use the marsh mainly when it is flooded (A. Méndez Casariego, pers. obs.). Hence, the questions to answer in this study were: 1) has long-term rainfall behavior changed in the Mar Chiquita area?, 2) how do changes in rainfall pattern affect the degree of submergence of *S. densiflora* marshes?, 3) does flooding (abiotic factor) affect the use of the marsh by *N. granulata*?, 4) does flooding promote a change to a more herbivorous behavior?, 5) does crab herbivory affect plant survival?

2. Material and methods

2.1. Study site

The study was performed at the estuary of the Mar Chiquita Coastal Lagoon (37° 40′S, 57° 23′W; an UNESCO Man and the Biosphere Reserve), Argentina during the summers of 2006 and 2007. This is a body of brackish water (46 km^2) of low tidal amplitude (~1 m) permanently connected to the sea (Reta et al., 2001), with a wide salinity range (2 to 35 PSU; Spivak et al., 1994). The main habitats around the lagoon are intertidal mudflats and large plains irregularly flooded (10 to 15 times per month) dominated by the cordgrass *S. densiflora* (Isacch et al., 2006). *N. granulata* crabs are distributed in both the *S. densiflora* salt marsh and the intertidal mudflats generating large burrowing beds (Spivak et al., 1994; Iribarne et al., 1997; Botto et al., 2005).

2.2. Has long-term rainfall behavior changed in the Mar Chiquita area?

Given that global climate change can affect rainfall regime in this region (Viglizzo et al., 1995; Berbery et al., 2006), the long-term behavior of rainfall regime in the study area was analyzed. To evaluate this, we conducted a simple linear regression analysis (Zar, 1999) between cumulative annual rainfall (log-transformed) and years. Data of the cumulative annual rainfall of the last century (1900–2006) were obtained from the U. S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), National Environmental Satellite, Data, and Information Service Office, National Climatic Data Center (http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html) from Mar del Plata city station (37° 56′ S; 57° 35′ W). This city is also located in the same coastal area, but 25 km south of our study site. Thus their information is a good proxy for the rainfall regime at the study site.

2.3. How do changes in rainfall pattern affect the degree of submergence of S. densiflora marshes?

As heavy rainy periods can lead to higher water levels in the estuary of the Mar Chiquita coastal lagoon (Reta et al., 2001), we evaluated if the flooded area of the *S. densiflora* marsh was related to the occurrence of heavy rainy months. To achieve this, marsh area covered with water was calculated by analyzing Landsat satellite images. Images analyzed were two from the ETM + sensor of Landsat (path-row 223-86: 19 August 2001, 9 December 2001) and six from the TM sensor (path-row 223-86: 25 March 1997, 6 October 1998, 11 January 2000, 16 February 2001, 3 February 2002; path-row 224-86: 24 March 2000). To determine marsh area flooded using the images, we masked the uplands and the area always covered by water. Then, we applied a supervised classification to the masked images, selecting three classes: water, mudflat and vegetation (dominated by *S. densiflora*). A maximum likelihood algorithm, based on the probability density function associated with a particular training site signature in the classification procedure was then used. After that, we analyzed the spectral signature for each class and confirmed that reflectance ranges were never superposed among classes in at least one band of Landsat (i.e. habitats were consistently separated). After having all these variables evaluated, we determined the area of each of the three classes. Thus, we assessed the flooded area of *S. densiflora* marsh by subtracting the lagoon and mudflat area during a non-flooding period to the lagoon area expanded by the flood in the other periods. Simple linear regression (Zar, 1999) was used to assess the relationship between monthly cumulative rainfalls and the area flooded (log-transformed) of the *S. densiflora* marsh.

2.4. Does flooding (abiotic factor) affect the use of the marsh by N. granulata?

Given that flooding can strongly affect species (e.g., Gasith and Resh, 1999), we evaluated if flooding affected crab activity in the marsh by using a field trapping experiment, during November 2005, December 2005 and February 2006. We buried 18 5-liter empty bottles into the low-marsh ground to surface level, two weeks before collecting data for the first time. The tops of the bottles were removed and were replaced with funnels to ease crab trapping and to prevent crabs from escaping once caught. Small holes were drilled in the bottle wall to stop them from floating during high tides. The day before each sampling date, all crabs inside the bottles were removed. Then, the number of crabs per trap was counted (as an estimation of crab activity) the day after the lowest neap high tide of the month (the low marsh was not flooded) and the day after the highest spring high tide of the month (the low marsh was flooded for more than 7 h). Crab activity in the marsh between days with maximum (flooding) and minimum tides (not flooding) were compared using the Mann–Whitney *U* test (due to lack of normality, Conover, 1980) for November and December 2005 and using a *t*-test (log-transformed; Zar, 1999) for February 2006.

2.5. Does flooding promote crab herbivory?

Plants in the low marsh remain under water during longer periods than those from the middle marsh, and at the same time, the *Spartina* spp. (dominant plants in SW Atlantic marshes; see Isacch et al., 2006) are more consumed by crabs (Alberti et al., in press). Hence, we evaluated the hypothesis that flooding increases crab herbivory rates. To study this, we first evaluated if herbivory rates differed between marsh heights, and then we contrasted this pattern using transplants to diminish the possibility of confounding effects. Finally, we conducted an experiment to detect if differences in submergence time affected crab herbivory.

2.5.1. Do herbivory rates differ with marsh elevation?

First, we conducted a survey to establish if crab herbivory rates differed with marsh elevation (i.e., mid and low). Hereafter, herbivory was estimated as the percent of leaves grazed per stem (see Rand, 1999, 2002, 2004), and leaves were considered to be consumed by crabs when their tips were lacking (crab herbivory removes, in average, more than 20% of leaf biomass; J. Alberti, unpubl. data). We marked 50 stems without signs of herbivory at each marsh height, and the next day we recorded percent leaves damaged per stem. Data from the same marsh elevation

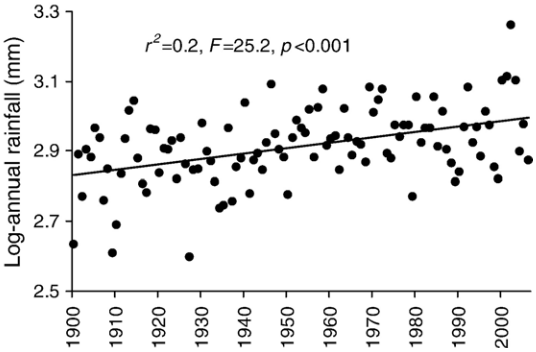

Fig. 1. Annual rainfall behavior over the last century (1900–2006). Regression between annual rainfall (in mm; log-transformed) and years.

(i.e., mid or low) were averaged ($n=50$) to avoid pseudoreplication (Hulbert, 1984, obtaining one single datum per day and per low-marsh elevation. We repeated this procedure 19 different days during the summer of 2006 and considered values of different days as replicates. Then, mean herbivory rates between these two marsh elevations ($n=19$ per marsh elevation) were compared using a paired t-test (log-transformed; Zar, 1999; results from the same day were considered a pair).

To experimentally evaluate this pattern, 20 *S. densiflora* units (10×10×30 cm; which compromises most of the belowground system of this plant in this marsh, P. Daleo, unpubl. data) were transplanted to two low-marsh elevations and herbivory on one stem per unit was registered after 20 days ($n=10$ per zone). Transplants were obtained from the middle marsh and preliminary results showed no significant differences in herbivory between un-manipulated plants and transplant controls (J. Alberti, unpubl. data). Due to lack of normality, differences in herbivory between the two zones were contrasted using the Mann–Whitney U test (Conover, 1980).

2.5.2. Do differences in submergence time affect crab herbivory?

To evaluate if differences in herbivory between the two zones were the product of different submergence periods (which affected the rates of crab herbivory), and not the result of different local abiotic factors or crab densities, a second experiment with two treatments was conducted: 1) submerged plants, 2) not submerged plants. New *S. densiflora* units (30 cm diameter×30 cm height) were transplanted into two plastic enclosures (40 cm diameter×70 cm high; one unit per enclosure). In both cases, empty surface in the bottom of the enclosures was filled with mud up to the height of the sediment (30 cm) from the transplants, and then 8 crabs randomly chosen from the marsh were left inside each enclosure to achieve similar densities than those commonly found in the marsh (Iribarne et al., 1997; Botto et al., 2005). Ten stems per transplant (without signs of herbivory) were marked, and after 4 days the percent of leaves grazed per stem was quantified and averaged to avoid pseudoreplication. The enclosure from the submerged treatment was then filled to the top with water from the closest tidal channel; the one from the not submerged treatment was filled with water just to cover the entire belowground system. This process was repeated every 4 days during an entire month (8 times) and each 4-day period was considered as a replicate. During the entire experiment recipients were left in the field to ground level and next to undisturbed marsh plants. Finally, mean percent of leaves grazed per stem between the two treatments (i.e. submerged and not submerged; $n=8$ per treatment) was compared using a paired t-test (Zar, 1999).

2.6. Does crab herbivory affect plant survival?

Given that *N. granulata* herbivory can strongly affect *S. densiflora* survival (Bortolus and Iribarne, 1999), using transplants (as described above), we experimentally evaluated if increased crab herbivory associated with increased inundation frequency can affect plant survival. Ten live stems randomly chosen were marked in each of the five units moved to each of the two low-marsh elevations, and after two months, the number of dead stems per group was counted. Differences in the mean number of dead stems between heights were evaluated using a t-test (Zar, 1999). A preliminary experiment revealed no differences in mortality between

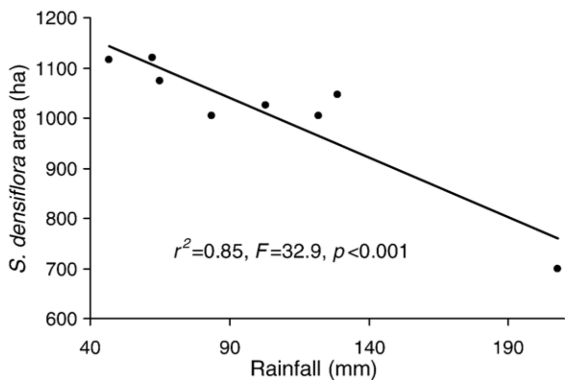

Fig. 2. Regression between monthly cumulative rainfalls (in mm) and *Spartina densiflora* marsh area not flooded (in ha).

the transplanted and un-manipulated plants ($U=10$, $Z=0.52$, $n=10$, $p>0.6$).

3. Results

3.1. Has rainfall long-term behavior changed in the Mar Chiquita area?

During the last century, annual rainfalls have increased in the study area, thus generating a positive relationship between annual rainfall and years ($r^2=0.2$, $F=24.6$, $p<0.001$, $n=106$, Fig. 1), with a high interannual variability. The cumulative annual rainfall of this region has increased from an annual average of 751 (SD=173) mm during the period 1900 to 1950 to an average of 934 (SD=213) mm during the period 1951 to 2006. Even though the range of annual rainfall remained similar between the two halves of the last century; it exhibited an increase in its minimum (from 396 mm to 588 mm) and maximum values (from 1231 mm to 1826 mm) showing the occurrence of more rainy periods.

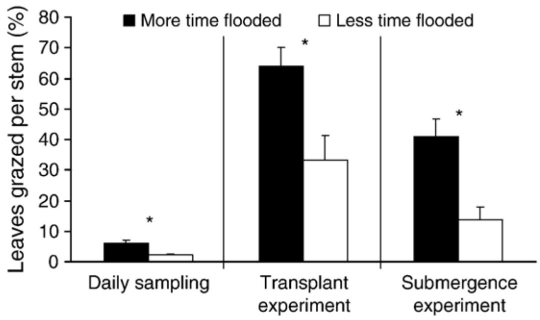

Fig. 3. Percent of leaves grazed per *Spartina densiflora* stem (i.e. estimation of herbivory) in two different flooding frequencies and three different surveys. Daily sampling: daily herbivory rate in two low-marsh elevations (low = more time flooded; mid = less time flooded). Transplant experiment: data on herbivory collected after 20 days, from transplants moved to those two low-marsh elevations. Submergence experiment: data on herbivory obtained after 4-day cycles, from transplants moved to recipients with (more time flooded) or without water (less time flooded). Bars show means + SE, data are presented prior to transformations and asterisks denote significant differences between the two different flooding conditions.

3.2. How do changes in rainfall pattern affect the degree of submergence of S. densiflora marshes?

As cumulative monthly rainfalls increased, the area of the *S. densiflora* marsh flooded also increased ($r^2=0.84$, $F=32.9$, $p<0.05$, $n=8$; Fig. 2).

3.3. Does flooding (abiotic factor) affect the use of the marsh by N. granulata?

During the day with the highest spring high tide of the month, the mean number of trapped crabs (an estimation of crab activity; in November: 14, SE=2.58; in December: 4.83, SE=1.14; in February: 4, SE=1.06) was almost 23, 29 and 2.7 times higher (in November, December and February, respectively) than during the day with the lowest neap high tide of the month (November: 0.61, SE=0.2, $Z=5.15$, $n=36$, $p<0.001$; December: 0.17, SE=0.04, $Z=5.03$, $n=36$, $p<0.001$; February: 1.5, SE=0.33, $t=2.52$, df=34, $p<0.05$).

3.4. Does flooding promote crab herbivory?

3.4.1. Do herbivory rates differ with marsh elevation?

Daily herbivory rates in the low marsh were 2.5 higher at lower than at higher elevations (paired $t=4.75$, df=18, $p<0.001$; Fig. 3). When transplants were used to contrast this pattern, after 20 days, those moved to the lowest marsh zones were almost two times more consumed than those moved to higher elevations ($Z=2.89$, $n=40$, $p<0.01$; Fig. 3).

3.4.2. Do differences in submergence time affect crab herbivory?

The submergence experiment showed that when crabs were 4 days under water with plants, they consumed *S. densiflora* up to three times the values of crabs that were not under water (paired $t=6.95$, df=7, $p<0.001$; Fig. 3).

3.5. Does crab herbivory affect plant survival?

As with herbivory rates, stem mortality in the lower zones (mean=5, SE=0.71) was almost two times higher than in the mid zones (mean=2.6, SE=0.51; $t=2.75$, df=8, $p<0.05$).

4. Discussion

Our results show that the annual precipitation in the northern coastal area of Argentina is increasing with the subsequent occurrence of more rainy years. Rainy episodes promote longer submerged periods in the *S. densiflora* marsh at Mar Chiquita. These inundations affect marsh use by crabs, because they are more active in the marsh when under water, which leads to greater herbivory rates, and increased marsh plant mortality.

4.1. Climate change can promote a cascade of interactions

One of the consequences of global climate change is an alteration of the rainfall regime, with a significant decrease in some regions (e.g., some regions of Australia: Suppiah and Hennessy, 1998; Spain: de Luís et al., 2000; Roshier et al., 2001), and a significant increase in others including Argentina and Brazil (e.g., Argentina: Viglizzo et al., 1995; Berbery et al., 2006; Australia and New Zeland: Suppiah and Hennessy, 1998; Plummer et al., 1999; Brazil: Collischonn et al., 2001). Over the last 40 years, annual rainfall in the Argentinean pampas region have increased above the historic mean (Viglizzo et al., 1995; Berbery et al., 2006; this study), and this pattern is closely associated with the occurrence of heavy rainy episodes (see Fig. 5.6 in Berbery et al., 2006). These rainy episodes promote flooding in coastal marshes (e.g. Canepuccia et al., in press; this study), mainly in those with discharge of freshwater like our study site. The "El Niño Southern Oscillation" (ENSO) events also affect rainfall regime by causing cyclic rises and drops in precipitation from southern Brazil to central Argentina (Viles and Goudie, 2003; Berbery et al., 2006). Whatever the cause of increased rainfall, our results also show that wet periods are associated with higher water levels in certain estuarine marsh areas (i.e., Mar Chiquita coastal lagoon). This pattern was also observed in other wetlands (e.g., Gasith and Resh, 1999; Collischonn et al., 2001; Garcia et al., 2001; Roshier et al., 2001).

However, effects of changes in rainfall regime are not restricted to direct effects that cause variations in the water level; there are also several indirect effects on biotic interactions. Flooding (whether periodical or not) can affect species in very different ways such as increasing the importance of biotic interactions like competition and predation (e.g., Gasith and Resh, 1999), habitat use (e.g., Bodmer, 1990; Garcia et al., 2001), diet selection (e.g., Bodmer, 1990), species diversity (e.g., Leidy et al., 1992), population size (e.g., Golladay et al., 1997), and zonation limits (e.g., Connell, 1972; Lenssen and de Kroon, 2005) among others. Flooding can also affect diversity and promote canopy-tree mortality in forest through a cascade of biotic interactions (Terborgh et al., 2001, 2006; these results were recently questioned by White, 2007). Our survey and experimental results show that flooding affects habitat used by *N. granulata*, given that during un-flooded periods crab activity in the marsh remains very low, but when the water covers the marsh, crab movement dramatically increases. This increase in crab activity is associated with an increase in its herbivorous behavior, with a much higher rate of consumption of the dominant marsh plant, *S. densiflora*. As a consequence of higher consumption rates, there is a subsequent increase in *S. densiflora* mortality, as previously noted (e.g., Bortolus and Iribarne, 1999; Bortolus et al., 2004; Alberti et al., in press). Flooding can also increase *S. densiflora* mortality through increased anoxic conditions over a one-year period (Castillo et al., 2000). However, coupling our short-term results (i.e., two months) with the fact that rainfall is not constant through the year (Berbery et al., 2006), suggests a more important role of herbivory on *S. densiflora* mortality over anoxia.

4.2. The importance of considering both biotic and abiotic factors

Climate change is predicted to cause shifts in distribution of species along climatic gradients given that species are expected to track climate as a function of their physiological tolerances (e.g., Harte and Shaw, 1995; Root and Schneider, 1995). However, abiotic and biotic factors can strongly interact to influence micro-habitat choice, and thus, consideration should be given to new potential biotic interactions or changes in the existing interactions when analyzing global climate change (Martin, 2001; Klanderud, 2005). Altogether, our results reveal that increments in rainfall regime can potentially trigger a cascade of abiotic and biotic interactions leading to increased marsh mortality. These results provide further evidence supporting the fact that abiotic and biotic factors commonly operate together, and that considering both is fundamental to accurately predict the consequences of changes in the conditions that control community organization (e.g., Gasith and Resh, 1999; Martin, 2001; Lima et al., 2002; Klanderud, 2005).

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