



# Effects of climate on the mole crab *Emerita brasiliensis* on a dissipative beach in Uruguay

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**ABSTRACT:** Climate change is expected to have considerable impacts on sandy beach ecosystems through the loss of intertidal area and changes in physical properties. These changes may affect demography and life history traits of macrofaunal species. We evaluated the role of climate in explaining variations in population traits of the mole crab *Emerita brasiliensis* over 20 yr on a sandy beach in Uruguay, based on a set of predictive hypotheses recently developed from studies of beach and climate-change ecology. Population abundance increased with sea surface temperature (SST), reproductive and recruitment periods were more extended, and recruitment was higher during warm years, when population structure showed a multi-modal structure. Decreasing asymptotic sizes and increasing growth rates were also observed concurrently with increasing SST. La Niña events, which in coastal Uruguayan waters are characterized by a higher influence of tropical oceanic waters (warm and salty), had marked positive impacts on abundance and individual growth. In a climate change scenario, an increasing frequency of extreme La Niña events is expected and therefore our results have strong implications. In a space-for-time substitution context, our long-term trends are reinforced by macroscale results that reported an increase in growth rates and in reproduction and recruitment periods, together with a decrease in female individual sizes, from temperate to tropical beaches of the Atlantic coast of South America. Space-for-time substitution is highlighted as an alternative approach to analyze potential population changes resulting from climate change in these data-poor ecosystems.

**KEY WORDS:** Population traits · Long term study · Climate change · Sea surface temperature · La Niña · Space-for-time substitution

## INTRODUCTION

Sandy beaches dominate open coasts worldwide, and their position between the sea and land make them highly vulnerable to climate change (Schoeman et al. 2014). These ecosystems are at risk of significant habitat loss and ecological impacts, acidification and erosion caused by sea level rise, as well as more frequent storms induced by warmer air and sea surface temperatures (SST) (Dugan et al. 2010, IPCC 2014). Increasing SST, storminess, and velocity, periodicity, and frequency of onshore winds have significantly altered the physical properties of sandy beaches (Ortega et al. 2013). Indeed, increased water

depth caused by higher tidal velocity (Pethick 1993) has led to a shift in sediment composition towards coarser particles and an increase in the steepness of beach profiles and in wave exposure (Goss-Custard et al. 1990, Ortega et al. 2013). These climate change issues are also expected to have considerable impacts on sandy beach macrofauna through the loss of intertidal area (Schoeman et al. 2014), impacting ecosystem functioning and species richness and abundance (Yamanaka et al. 2010). A narrow (i.e. meters) intertidal fringe defines a restricted habitat with absence of spatial refuges for resident benthic fauna with a very limited dispersal capacity. This is of utmost importance, considering that macrofaunal

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species richness is positively correlated with the extent of the intertidal area (McLachlan & Dorvlo 2005, Defeo & McLachlan 2013). In particular, dissipative beaches, which are defined by fine sands, gentle slopes, low substrate penetrability and high water content, host the greatest biodiversity among all beach types (Defeo & McLachlan 2013, Barboza & Defeo 2015). These systems are at major risk due to their erosive nature and the much greater run-up and backwash of waves on gentle slopes (Defeo et al. 2009, Ortega et al. 2013).

Ecological responses of intertidal macrofauna to climate variability encompass factors such as changes in the timing of reproduction, population dynamics, abundance, spatial distribution, and interspecific interactions (Sagarin et al. 1999, Riascos 2006, Riascos et al. 2009, Revell et al. 2011, Ortega et al. 2012). Hence, time series of biological and physical variables are crucial to understand how sandy beach macrofauna and its habitat respond to changes in climatic conditions (Brown et al. 2011, Bessa et al. 2014). Few long-term studies have assessed the effects of climate change on sandy beach macrofauna (Revell et al. 2011, Ortega et al. 2012, Defeo et al. 2013), and therefore many of the predictions of the likely impacts on these species are derived from other systems (Defeo et al. 2009, Dugan et al. 2010). This paucity of sandy beach studies related to global warming is partially due to the lack of multiyear, large-scale data sets which assess the effects of critical stressors on patterns and processes. In this context, the space-for-time substitution modeling approach could be a useful alternative to infer temporal trends from spatial variations in population features and ecological processes across sites that vary in environmental conditions (Pickett 1989, Fukami & Wardle 2005, Blois et al. 2013, Lester et al. 2014).

In South America, intertidal suspension feeders of the genera *Donax*, *Emerita*, and *Mesodesma* dominate the biomass of invertebrate assemblages in dissipative sandy beaches (Defeo & de Alava 1995, Defeo 2003). Among them, the cold-water species of the genus *Mesodesma* have been particularly affected by climate change and concurrent changes in physical conditions of the habitat, both in the Atlantic (Ortega et al. 2012, 2016, Defeo et al. 2013) and the Pacific (Arntz et al. 1987, Riascos et al. 2009). An increase in SST over the past 3 decades along the Atlantic coast has drastically affected the abundance and individual size of the yellow clam *M. mactroides* (Ortega et al. 2012, 2016). Other indirect and unpredictable effects on this species included changes in phytoplankton composition and abundance (Odebrecht et al. 2014), which

markedly diminished its food availability (Bergamino et al. 2011). While these results are restricted to a few species, they nevertheless indicate a direct link between regional climate change and changes in population structure and abundance.

The genus *Emerita* (Crustacea: Anomura: Hippidae) constitutes one of the most conspicuous components of sandy beach ecosystems. These suspension feeders are well-adapted to live in the intertidal of exposed, high-energy sandy beaches around the world (Dugan et al. 1994, Subramoniam & Gunamalai 2003). On the Atlantic coast of South America, the mole crab *E. brasiliensis* is commonly found on reflective and dissipative sandy beaches from Venezuela to Uruguay. This species has shown clear latitudinal gradients in life history traits, population dynamics, and demographic features from tropical to temperate beaches, including (Defeo & Cardoso 2002, 2004) (1) an exponential decrease in abundance and natural mortality and an increase in body size and life span; (2) a shift from continuous to seasonal reproduction and recruitment; and (3) a sex ratio strongly biased towards females, which have significantly lower growth and mortality rates. These large-scale patterns follow variations in SST and could be attributed to an extreme sensitivity of the species to environmental variations and to its biogeographic affinity to the tropics (Defeo & Cardoso 2004). Moreover, *E. brasiliensis* is particularly abundant on dissipative beaches (Celentano & Defeo 2006), which constitute the main source habitats in a metapopulation context (Celentano et al. 2010).

We assessed long-term trends in *E. brasiliensis* on a dissipative sandy beach in Uruguay. We evaluated the role of climate in explaining variations in mole crab abundance, population structure, and individual growth over a 20 yr period. To this end, we combined theory from beach ecology and climate-change ecology to evaluate a set of predictive hypotheses recently developed by Schoeman et al. (2014) regarding climate impacts on beaches. Taking into account the systematic increase in SST observed in recent decades in the region (Ortega et al. 2016) and the fact that *E. brasiliensis* is a species with tropical affinities, we predict that the mole crab on a dissipative beach in Uruguay experienced a long-term (1) increase in population abundance and in the number of size classes represented; (2) extension of its reproduction and recruitment seasons; and (3) increase in individual growth rates and decrease in individual sizes. In a space-for-time substitution context, if these predictions hold, long-term patterns in mole crab life history traits will follow the latitudinal patterns detailed above.

**MATERIALS AND METHODS**

The study was conducted at Barra del Chuy, a dissipative microtidal (tidal range = 0.5 m) oceanic sandy beach in Uruguay (33° 84' S, 53° 27' W), with a wide surf zone, fine to very fine well-sorted sands, as well as exposure to strong wave action and a gentle slope, both of which make this beach particularly vulnerable to sea level rise (Ortega et al. 2013). The beach was sampled mostly on a monthly or seasonal (at least 4 times a year) basis from March 1988 to March 2010 (year 1992 was not sampled). Three transects spaced 8 m apart were made perpendicular to the shoreline, with sampling units (SUs) starting at the base of the dunes and continuing seaward at 4 m intervals, until 2 consecutive SUs yielded no mole crabs (Celentano & Defeo 2006). In each SU, a sheet metal cylinder 27 cm in diameter was used to remove the sediment up to a depth of 40 cm. Mole crabs retained after sieving through a 0.5 mm mesh were fixed and, in the laboratory, measured to the nearest 0.01 mm from the tip of the rostrum to the distal scoop of the cephalothorax (carapace length: CL). Mole crabs were classified as megalopae (non-adults) or adults. Megalopae were those with an undeveloped ocular peduncle and with plumose pleopods (Velooso & Cardoso 1999). Adults were sorted into males with and without spermatophores, females without eggs, and ovigerous females.

Species abundance (total and by population component: megalopae and adults) was estimated by the number per strip transect (ind.m<sup>-1</sup>) following Defeo (1996). Reproductive and recruitment periods were inferred from the months with occurrence of reproductive (ovigerous females and males with spermatophores) and recruitment (megalopae) components in the total number of sampling events performed in 5 periods with monthly sampling periodicity (1988–1989, 1996–1997, 1999–2001, 2002–2004, 2008–2010).

To assess long-term changes in population structure, an index of recurrence of size classes (IRSC, Celentano et al. 2010) was estimated as follows:

$$IRSC = \frac{N_L}{NT_L} \tag{1}$$

where  $N_L$  defines the number of size classes ( $L_i$ ; grouped in 1 mm bins) in a given month, and  $NT_L$  is the total number of size classes observed for the species throughout the study period. The IRSC is derived from the index of recurrence in recruitment (Caddy & Defeo 2003) and ranges between 0 and 1 (all size classes present). IRSC values close to 1

suggest periodic recruitment patterns, whereas values approaching 0 suggest irregular/spasmodic recruitment.

Individual growth patterns of female mole crabs were determined by analyzing monthly length-frequency distributions (LFDs) in those time intervals with high sampling frequency (1988–1989, 1996–1997, 1999–2001, 2002–2004, and 2008–2010). We followed the procedure detailed by Gómez & Defeo (1999), summarized as follows: (1) for each month, we separated normally distributed components of size frequencies by maximum likelihood, through the application of the routine NORMSEP (Gayaniilo & Pauly 1997); (2) as we followed each cohort through its entire life span, we were able to assign absolute ages to relative ones (lengths) and thus to build an age-length key. Time 0 (month of birth) was defined on the basis of the size at recruitment of a mole crab to the beach (CL close to 2 mm). Subsequent ages were assigned from time 0, taking into account the date of the  $i^{\text{th}}$  sample, measured as a portion of the year; (3) the age-length key obtained in (2) was used to fit the generalized von Bertalanffy growth function (VBGF, Eq. 2) that allows for the estimation of growth seasonality as follows (Gayaniilo & Pauly 1997):

$$L_t = L_\infty \left[ 1 - e^{-K(t-t_0) + \left(\frac{KC}{2\pi}\right)\sin 2\pi(t-t_s) - \left(\frac{KC}{2\pi}\right)\sin 2\pi(t_0-t_s)} \right] \tag{2}$$

where  $L_t$  is the length at time  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is the curvature parameter that measures the rate at which the organisms reach the asymptotic length,  $t_0$  is the theoretical length at age 0,  $C$  is the amplitude of the seasonal growth oscillation, and  $t_s$   $-0.05$  is the winter point (WP), defined as the time of year in which growth is minimal or stopped and is expressed as a decimal fraction of the year. A quasi-Newton method was used to estimate the parameters (mean  $\pm$  SE). Growth curves of mole crabs were compared by likelihood ratio tests, under different null hypotheses (Kimura 1980, Cerrato 1990). First, we simultaneously compared the 3 main parameters of the VBGF ( $L_\infty$ ,  $K$ , and  $t_0$ ) from the 5 specific time periods considered under the general null hypothesis to be constant through time ( $C$  was assumed constant in all analyses). Following this, the model selection process was performed by sequentially altering the number of parameters under comparison (Haddon 2001). We also used the growth indices:  $\phi'$  ( $= 2 \times \log L_\infty + \log K$ ) to assess female growth performance (Pauly & Munro 1984); and  $\omega$  ( $= K \times L_\infty$ ), defined as the instantaneous growth rate near to the point at which the mole crab length is 0 (Gallucci & Quinn 1979). Growth parameters of male mole crabs were

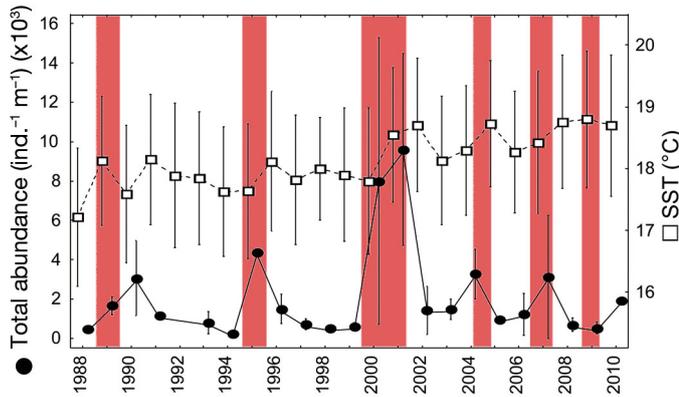


Fig. 1. Long-term fluctuations (mean  $\pm$  SE) of total annual abundance (all population components pooled, black circles) of *Emerita brasiliensis* and sea surface temperature (SST, white squares) for the period 1988 to 2010 at Barra del Chuy beach, Uruguay. SST values are from Reynolds et al. (2002). Periods in which La Niña episodes were registered (Niedzielski 2014) are highlighted in red

not estimated due to their very low abundance, which precluded the progression of modes through time.

SST and the corresponding anomalies (SSTA) were calculated based on the data series in Reynolds et al. (2002) by averaging SSTA from  $48^\circ \times 3^\circ$  grid cells of the shelf and the adjacent oceanic region in the Southwestern Atlantic Ocean (SAO). SSTA data for empirical orthogonal function analysis were obtained

from the Extended Reconstructed Sea Surface Temperature, version 3 (ERSST\_V3) dataset based on the International Research Institute/Lamont-Doherty Earth Observatory Climate Data Library (IRI/LDEO 2013). Previous exploratory multivariate studies relating mole crab features and environmental variables that could be relevant in a climate change context (e.g. wind speed, grain size, beach width, beach slope) showed that SST was the relevant explanatory variable for long-term trends (Celentano 2014), and therefore SST was used here for model fitting. Relationships between population descriptors (abundance, biomass, reproductive and recruitment periods, IRSC, and individual growth) and SST were modeled by linear or nonlinear fitting. In all cases, the model that best explained the relationship between biological and physical variables was selected based on  $R^2$ .

## RESULTS

### First prediction: abundance and size class representation increase with SST

Abundance of *Emerita brasiliensis* varied markedly through time (Fig. 1) and increased exponentially with SST (Fig. 2). Abundance was especially higher in the summers of the warmest years, which in most

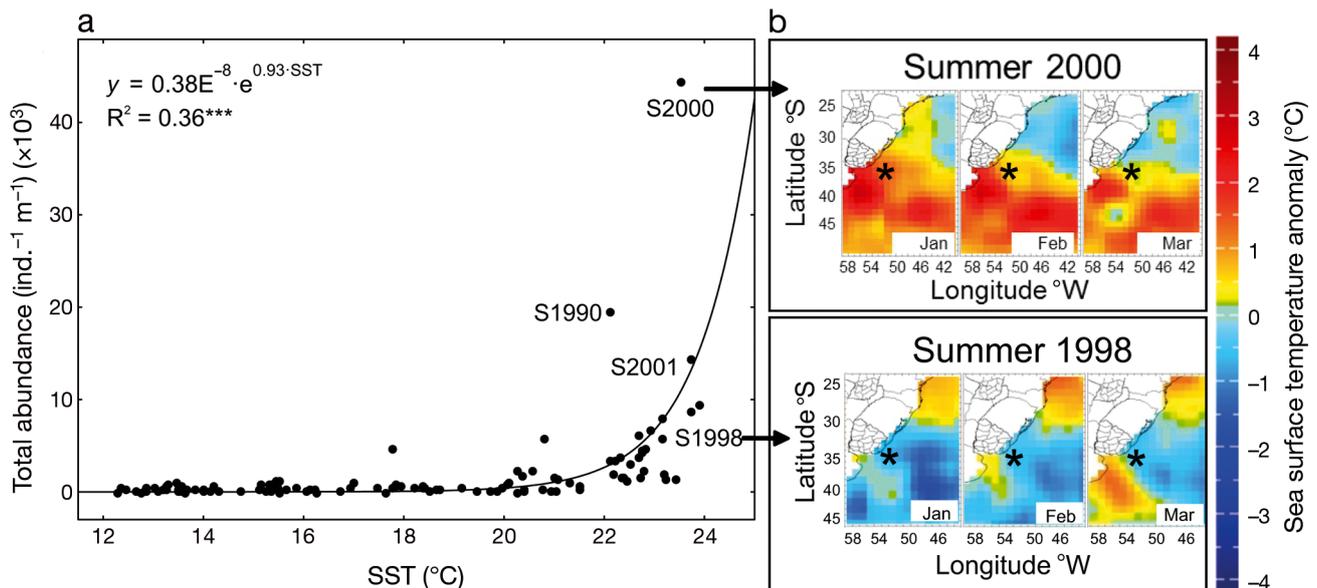


Fig. 2. (a) Exponential relationship between seasonal abundance of *Emerita brasiliensis* and sea surface temperature (SST) at Barra del Chuy beach, Uruguay, between 1988 and 2010. \*\*\* $p < 0.001$ . (b) Isotherm maps in the Uruguayan waters of the southwestern Atlantic Ocean ( $\star$ ) for a cold summer (1998) with low mole crab abundance and a warm one (2000) where the highest abundance was recorded. SST values are from Reynolds et al. (2002)

cases coincided with La Niña episodes (Niedzielski 2014; our Fig. 1), defined by positive SST anomalies (Fig. 2). The lowest mole crab abundance was registered in the summer of 1998, the coldest summer recorded throughout the study period (Fig. 2).

Mole crab recruitment (estimated by megalopae abundance in the recruitment season) showed large fluctuations through time that were significantly related to changes in SST (Fig. 3a). Megalopae abundance peaked in 1990, 2000–2001, 2004, and 2007 (Fig. 3b), which in most cases coincided with La Niña episodes (Fig. 1). The highest recruitment abundance was obtained in 2007, close to the end of the study period, concurrently with the highest SST value.

The relationship between abundance of adults (*A*) and recruits (*R*) was significantly explained by linear ( $F_{1,17} = 9.51$ ;  $R^2 = 0.36$ ,  $p < 0.01$ ) and exponential ( $F_{2,17} = 10.68$ ;  $R^2 = 0.33$ ,  $p < 0.05$ ) models. However, the best fit was obtained when SST was incorporated as a predictor of recruitment abundance in the exponential model of the form ( $F_{2,17} = 12.07$ ;  $R^2 = 0.38$ ,  $p < 0.001$ ):

$$R = e^{-bA + cSST} \quad (3)$$

where  $b = 2.89 \times 10^{-4}$  and  $c = 0.32$  were significant parameters ( $p < 0.001$  in both cases).

Concerning the population structure of the mole crab, higher *E. brasiliensis* recruitment in La Niña years promoted a wider representation of the full range size of classes, i.e. 2 to 26 mm, which influenced the population structure in subsequent years (Fig. 4). Consequently, monthly IRSC values were significantly correlated with SST ( $R^2 = 0.11$ ,  $p < 0.05$ ; Fig. 5).

### Second prediction: duration of reproductive and recruitment periods increases over time

The reproductive season of the mole crab, inferred from the number of months with occurrence of breeding adults (ovigerous females and males with spermatophores), was concentrated between December and May in 1988–1989, representing 50% of the months sampled. In 2008–2010, breeding adults also occurred in November and July, accounting for 80% of the months sampled (Fig. 6).

The recruitment period of the mole crab, inferred from the occurrence of megalopae, increased over time from 1996 onwards. In 1996–1997, megalopae occurred in austral autumn months (i.e. May to June), whereas in 2008–2010, this population component also occurred in late spring and summer (from November onwards), indicating a more extended recruitment season in recent years (Fig. 6).

### Third prediction: growth increases with SST

Growth curves of female mole crabs significantly explained 96 to 99% of the variance in the data, and most growth parameters of the VBGF were highly significant ( $p < 0.001$ ) for the 5 analyzed periods ( $p < 0.001$ ) for the 5 analyzed periods (Table 1, Fig. 7). Likelihood ratio tests indicated highly significant differences in mole crab growth between time periods. Of the 10 comparisons, 8 showed significant differences in the combination of growth parameters, and in 4 cases, the combination given by  $K$  and  $L_{\infty}$ , which defines the growth index  $\omega$ , significantly differed among growth curves ( $p < 0.005$ , Table 2). The observed long-term differences

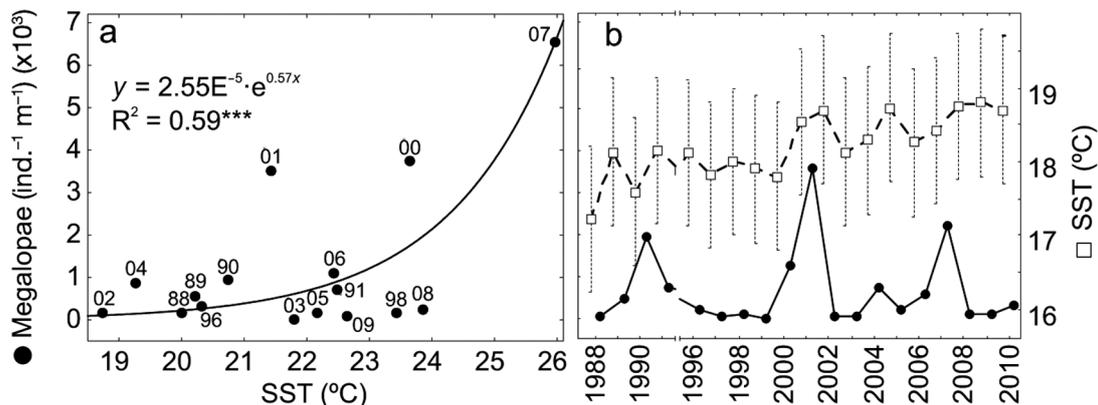


Fig. 3. (a) Relationship ( $***p < 0.001$ ) between *Emerita brasiliensis* megalopae abundance (recruitment period) and sea surface temperature (SST). (b) Annual fluctuations (mean  $\pm$  SE) in megalopae abundance (black circles) and SST (white squares) at Barra del Chuy beach, Uruguay, between 1988 and 2010. SST values are from Reynolds et al. (2002)

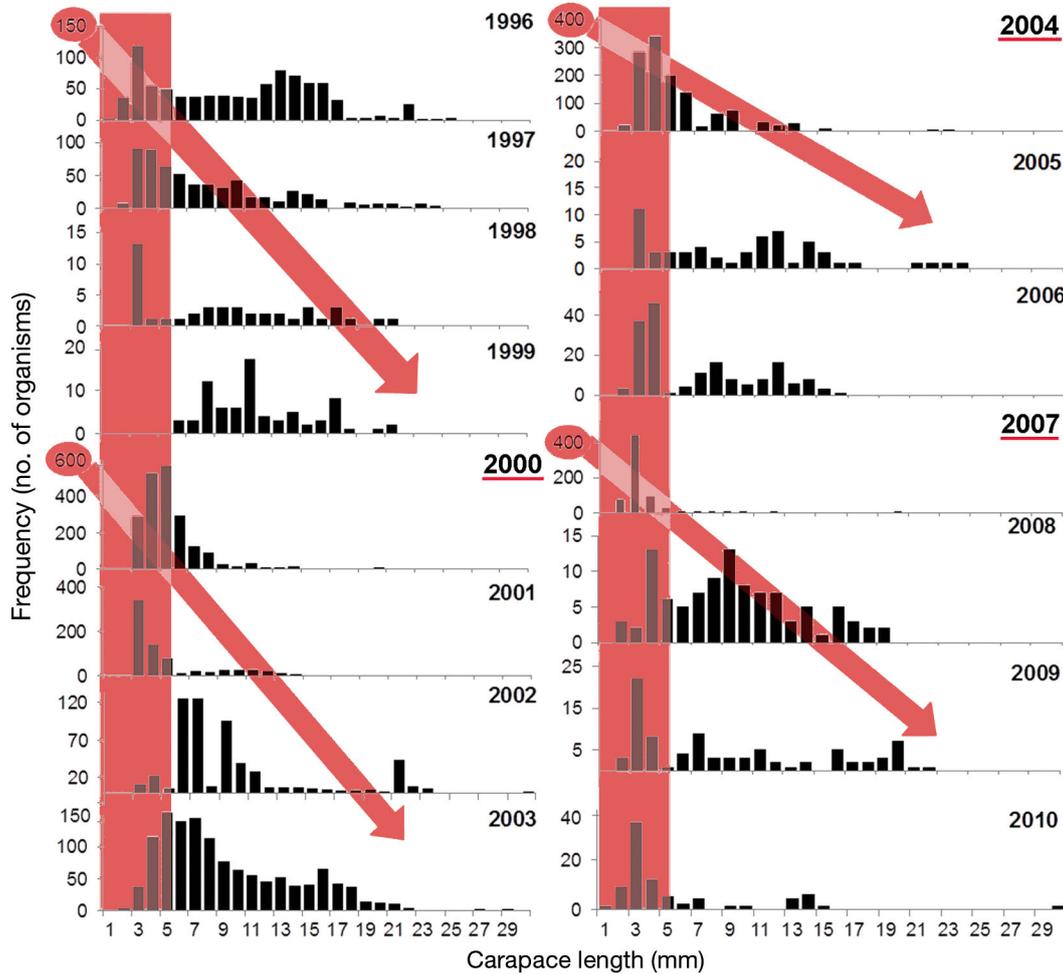


Fig. 4. Length-frequency distributions of *Emerita brasiliensis* (sexes pooled) for the period 1996 to 2010 at Barra del Chuy beach, Uruguay. Body size of megalopae (carapace length < 5 mm) and high frequency during La Niña episodes (encircled) are highlighted, and their influence on the number of adults in subsequent years is indicated by red arrows. La Niña years promoted a wider representation of the full range size of classes, which influenced the population structure in subsequent years; La Niña events occurred in the years 2000, 2004, and 2007 (underlined) and 1995 (no samples taken, thus not shown)

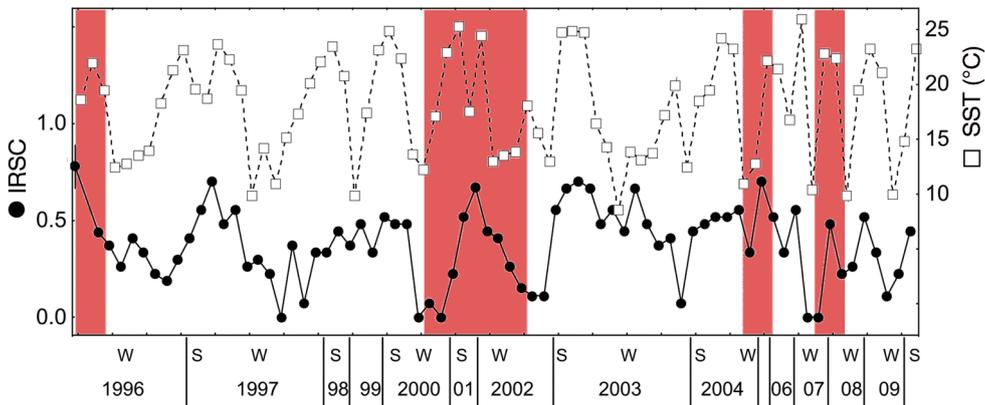


Fig. 5. Monthly variations in the index of recurrence of size classes (IRSC, black circles) of *Emerita brasiliensis* and sea surface temperature (SST, white squares), for the period 1996 to 2010 (S: summer; W: winter). Both variables were significantly correlated ( $R^2 = 0.11$ ,  $p < 0.05$ ). SST values are from Reynolds et al. (2002). La Niña episodes are highlighted in red

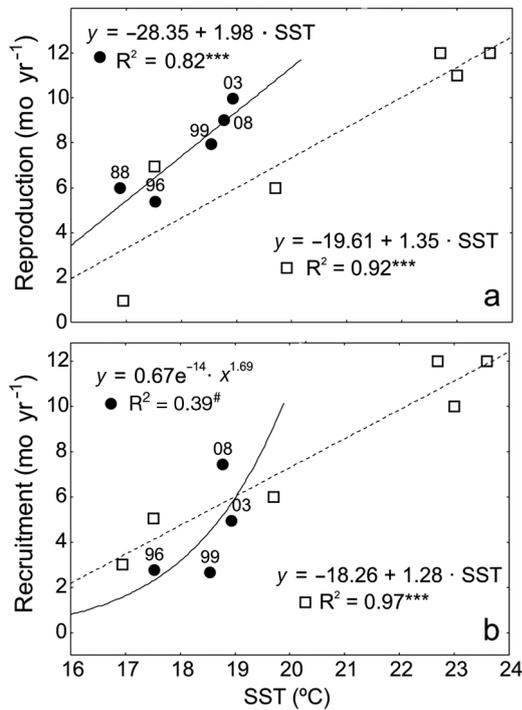


Fig. 6. Long-term relationships between sea surface temperature (SST; values are from Reynolds et al. 2002) and annual duration of (a) reproductive and (b) recruitment events of *Emerita brasiliensis* at Barra del Chuy beach, Uruguay (black circles). The first year of each analyzed period is indicated. Macroscale results reported by Defeo & Cardoso (2002) are included for comparative purposes (white squares). \*\*\* $p < 0.001$ ; # $0.05 < p < 0.1$

in *E. brasiliensis* growth can therefore be attributed primarily to variations in growth rates ( $\text{mm yr}^{-1}$ ) instead of differences in individual growth parameters. Female mole crabs showed a reduction in  $L_{\infty}$  and an increase in the curvature parameter  $K$  with increasing SST (Fig. 8). Moreover,  $\omega$  was almost 2 times higher at the end of the study period (2008–2010;  $\omega = 71.25$ ), followed by the growth curve

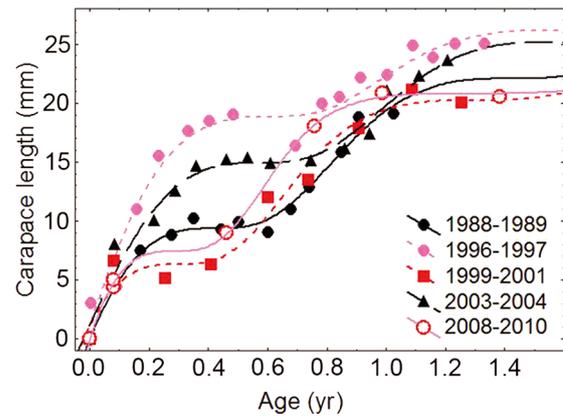


Fig. 7. von Bertalanffy growth curves for female mole crabs *Emerita brasiliensis* at Barra del Chuy beach, Uruguay, for 5 periods spanning 2 decades of data

fitted for 1999–2001 ( $\omega = 43.43$ ), with both cases coinciding with La Niña episodes (Table 1). The period 1996–1997, which immediately followed the La Niña episode of 1995, also showed high growth rates (Fig. 7), concurrently with a wide representation of size classes (see Fig. 4).

## DISCUSSION

Our 20 yr population study of *Emerita brasiliensis* on a Uruguayan sandy beach showed that population abundance increased with SST, the reproductive and recruitment periods were more extended, and recruitment was particularly successful during warm years, when the mole crab population showed a multi-modal structure. Moreover, decreasing asymptotic sizes and increasing growth rates were observed concurrently with increasing SST. Thus, demographic and biological traits of the mole crab changed in ways consistent with expectations under

Table 1. Results of the von Bertalanffy growth models fitted by nonlinear least squares for female mole crabs *Emerita brasiliensis* at Barra del Chuy beach, Uruguay (in all cases,  $p < 0.001$ ). The parameter of growth oscillation was set constant ( $C = 1$ ) for fitting. Mean ( $\pm$ SE) estimates of the parameters defined in Eq. (2) are shown.  $L_{\infty}$ : asymptotic length;  $K$ : curvature parameter that measures the rate at which the organisms reach the asymptotic length;  $t_0$ : theoretical length at age 0; WP: winter point. The growth indices  $\phi'$  and  $\omega$  are also included (see 'Materials and methods' for details)

Parameter	1988–1989	1996–1997	1999–2001	2003–2004	2008–2010
$L_{\infty}$ (mm)	27.16 (4.74)	28.22 (1.98)	22.62 (2.83)	31.69 (5.68)	21.27(0.42)
$K$ ( $\text{yr}^{-1}$ )	1.25 (0.38)	1.52 (0.31)	1.92 (0.66)	0.94 (0.32)	3.35 (0.29)
$t_0$ (yr)	0.001 (0.01)	-0.01 (0.02)	-0.02 (0.03)	-0.02 (0.02)	0.001 (0.004)
WP	0.42 (0.02)	0.39 (0.04)	0.29 (0.04)	0.43 (0.03)	0.28 (0.01)
$R^2$	0.98	0.96	0.96	0.97	0.99
$\omega$ ( $\text{mm yr}^{-1}$ )	33.95	42.89	43.43	29.79	71.25
$\phi'$	2.96	3.08	2.99	2.97	3.18

Table 2. Results of the likelihood ratio tests comparing von Bertalanffy growth parameters in *Emerita brasiliensis* females at Barra del Chuy beach, Uruguay, under different null hypotheses. Significant parameters or combinations (experiment-wise Bonferroni significance level = 0.005) are listed. ns: no significant differences between growth curves. See Table 1 for parameter definitions

Time period	1988–1989	1996–1997	1999–2001	2003–2004
1996–1997	$L_{\infty}$ $K$ $t_0$ $L_{\infty}K$ $K t_0$			
1999–2001	ns	$L_{\infty}$ $K$ $t_0$ $L_{\infty} t_0$ $K t_0$		
2003–2004	$L_{\infty}$ $K$ $t_0$ $L_{\infty}K$ $L_{\infty} t_0$ $K t_0$	$L_{\infty}$ $K$ $t_0$ $L_{\infty}K$ $L_{\infty} t_0$	$L_{\infty}$ $t_0$ $L_{\infty}K$ $K t_0$	
2008–2010	$L_{\infty}$ $K$ $t_0$ $L_{\infty} t_0$ $K t_0$	$L_{\infty}$ $K$ $t_0$ $L_{\infty} t_0$	$L_{\infty}$ $K$	ns

climate change, the latter reflected in the monotonic and systematic long-term increase in SST observed in the SAO in recent decades (Ortega et al. 2012, 2013).

SST was an important explanatory variable in mole crab abundance throughout the 20 yr analyzed. Total abundance increased exponentially with SST, particularly in years when La Niña events occurred. This trend driven by SST was also meaningful to explain long-term recruitment patterns. Even though SST could not be singled out as the only variable driving the patterns, it could be considered as an aggregate variable that has various simultaneous effects on the nearshore beach environment and in the resident fauna (Ortega et al. 2013, 2016). Diaz et al. (1998) also found a strong correlation between the SSTA associated with El Niño-Southern Oscillation events in the SAO and precipitation anomalies for Uruguay. In particular, strong La Niña events that occurred in 1988–1989 and 1999–2000 (Baethgen & Giménez 2001, Grimm 2011) led to low precipitation and a higher incidence of the Brazil Current, which is associated with warm and salty tropical water in the area (SST > 20°C and salinity > 36; Ortega & Martínez 2007). Thus, our results reinforce the notion that species with complex life cycles and high fertility like *E. brasiliensis* are extremely labile to environmental fluctuations. Furthermore,

the long-term correlation found here between mole crab population traits and SST highlights the importance that favorable years (not captured in a short-term study) can have for the dynamics of marginal populations (Sexton et al. 2009), especially in a context of climate variability. In this vein, the Uruguayan coast constitutes the leading (southernmost or poleward) edge of the *E. brasiliensis* distribution, and the trends reported here are in agreement with responses of various species to recent climate change, particularly at their poleward distributions (e.g. Parmesan & Yohe 2003, Chen et al. 2011). Our results also reinforce the notion that climate change effects are expected to be strongest at the edges of species' ranges (Poloczanska et al. 2013).

The effect of climate change elicits opposite responses in species with different biogeographic

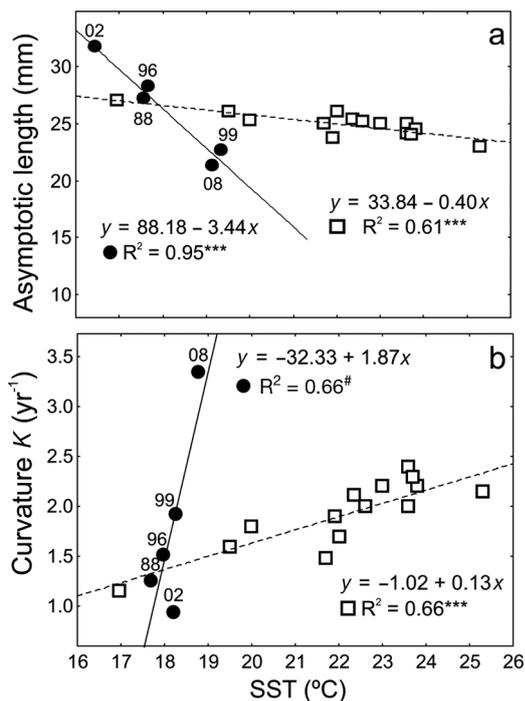


Fig. 8. Relationships between sea surface temperature (SST) of the swash zone and von Bertalanffy growth parameters for female *Emerita brasiliensis* in Barra del Chuy beach, Uruguay (black circles): (a) asymptotic length  $L_{\infty}$ ; and (b) curvature parameter  $K$ . The first year of each analyzed period is indicated. Macroscale results (white squares) reported by Defeo & Cardoso (2002) and Veloso & Cardoso (1999) are included for comparative purposes. \*\*\* $p < 0.001$  and # $0.05 < p < 0.10$

origins, defined as diagnostic fingerprints (Parmesan & Yohe 2003, Poloczanska et al. 2013). At Barra del Chuy, abundance and individual size of the yellow clam *Mesodesma mactroides*, a cold-water species that integrates the intertidal guild of suspension feeders with *E. brasiliensis* on sandy beaches of the SAO, has drastically decreased in the last 30 yr (Ortega et al. 2012, 2016). Indeed, mass mortalities have decimated yellow clam populations throughout the species' distribution range (Brazil, Uruguay, and Argentina), mostly during austral summers (Odebrecht et al. 1995, Fiori et al. 2004), after a shift from a cold to a warm phase during the 1990s (Ortega et al. 2012, 2016). The drastic and opposite changes observed in cold and warm water sandy beach species in the course of long-term observations suggest that regional warming could have triggered changes in the structure of the guild of suspension feeders at Barra del Chuy beach, reducing the *M. mactroides* population and enhancing populations of *E. brasiliensis* and the sympatric wedge clam *Donax hanleyanus*, which have tropical affinities and are subordinate competitors for space and food (Defeo & de Alava 1995, Defeo 2003, Schoeman et al. 2014). This supports the perception that climate change, through the direct effects of temperature on survival, can affect the abundance and distribution of species, thus changing the competitive balance in closely related populations (Ottersen et al. 2001, Poloczanska et al. 2008, 2014).

The observed increase in the extent of reproductive and recruitment periods of *E. brasiliensis* supports our predictions and indicates a positive response of species with tropical affinities to increasing temperatures at the cold edge of their range. Warming has advanced and extended the occurrence of population processes in *E. brasiliensis*, notably the breeding and recruitment seasons, and these long-term trends agree with phenological responses to global warming (Parmesan 2007, Chambers et al. 2013, Schwartz 2013). In a space-for-time substitution context, our results were consistent with macroscale (2700 km of the species distribution) findings that reported continuous reproduction in tropical and subtropical mole crab populations and marked seasonality in temperate populations (Fig. 6), thus following latitudinal variations in water temperature (Defeo & Cardoso 2002, 2004).

LFDs and IRSC estimated for *E. brasiliensis* gave additional support to the first prediction about population structure and abundance. In La Niña years and those immediately following La Niña episodes, high recruitment abundance and a full representation of

individual sizes were observed (Figs. 4 & 5). Riascos (2006) also reported positive effects of La Niña on growth and reproduction of another conspicuous filter feeder with tropical affinities, the bivalve *D. dentifer*, which inhabits South American Pacific sandy beaches. These trends were attributed to higher food availability during La Niña episodes. Body size is a major determinant of life histories, demography, nutrient turnover rate, and food-web structure (Edeline et al. 2013), and decreasing body size has been observed as a universal response to increasing temperatures (Angilletta 2009, Gardner et al. 2011). In this sense, mole crab asymptotic length ( $L_{\infty}$ ) linearly decreased with SST (Fig. 8), concurrently with higher growth rates. Therefore, current warming can potentially disrupt ecosystem function and services by altering body sizes through the magnification of competitive asymmetry in favor of smaller organisms (Edeline et al. 2013). Under a climate change scenario, expected warming and consequent body downsizing should drive the architecture of temperate food webs towards structures more consistent with the tropics (Edeline et al. 2013). These issues are in agreement with the observed changes in the sandy beach ecosystem analyzed here, where body downsizing was observed for the guild of intertidal suspension feeders *M. mactroides*, *E. brasiliensis*, and the wedge clam *D. hanleyanus* (Ortega et al. 2012, 2016, present study).

The space-for-time substitution approach also holds when looking at the relationship between SST and individual growth of the mole crab population. Indeed, a decrease in the asymptotic length ( $L_{\infty}$ ) and an increase in the curvature parameter  $K$  with increasing SST were detected across a period of warming (Fig. 8). This is consistent with the significant correlation found between female growth parameters and SST (inverse with  $L_{\infty}$  and direct with  $K$ ) at a macroscale, along the Atlantic coast of South America (Defeo & Cardoso 2002, 2004) (Fig. 8). Moreover, Veloso & Cardoso (1999) found increased  $K$  and decreased  $L_{\infty}$  values (both sexes) with increasing temperatures in a subtropical Brazilian beach (Fora beach: 22° 57' S, 43° 10' W), which is comparable to the results obtained here for the same species (Fig. 8). Therefore, this space-for-time substitution modeling approach (Fukami & Wardle 2005, Blois et al. 2013, Lester et al. 2014) could be useful for predicting responses of sandy beach populations for which long-term records are scarce (Lima et al. 2000, Revell et al. 2011).

In summary, the long-term variations in abundance, population structure, and individual growth

of *E. brasiliensis* were influenced by SST. Given the steady increase in SSTA in the study area (Ortega et al. 2012) and the tropical origin of the mole crab, the species is expected to expand its range poleward as a pioneer or colonizer ('leading edge' sensu Poloczanska et al. 2013) over time. This expansion could be more feasible during La Niña years, when the effect of the physical barrier given by the Rio de la Plata estuary is weakened and the incidence of the warm and salty waters driven by the tropical Brazil Current markedly increases (Ortega & Martínez 2007). Potential increases in SST could increase fertility and reproductive periodicity of the mole crab on Uruguayan beaches at the southernmost end of its geographic distribution. We suggest considering biogeographic affinity and mode of development of sandy beach species to assess long term effects of climate variability. Finally, the space-for-time substitution has proven useful in understanding long-term responses of the mole crab population and is highlighted as a future research venue in addressing potential changes in population processes resulting from climate change in these data-poor ecosystems.

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