



## Temperature influences the reproduction of fiddler crabs at the southern edge of their distribution

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**Abstract.** Understanding the spatial patterns of reproductive biology might provide predictions about fitness and population stability in different locations within the geographical range of a particular species. *Leptuca uruguayensis* is a fiddler crab that breeds year round in tropical estuaries but only in summer months in temperate salt marshes. In this study, we examined several reproductive attributes of the southernmost population of *L. uruguayensis*, including the proportion of ovigerous females, the proportion of surface-active crabs, the developmental status of the gonads and hepatopancreas, and the fullness of seminal receptacles, and related them to environmental factors such as temperature, photoperiod, and sediment organic matter content. We found that temperature was the environmental factor that was most correlated with the reproductive process of the southernmost fiddler crab, since this environmental factor was related to ovarian development, to the fullness of seminal receptacles, and to the hepatosomatic index. At the southern edge of its distribution, the low temperatures of winter restricted reproduction in *L. uruguayensis*. These winter temperatures might represent the lower limit of the thermal window of this fiddler crab, limiting its extension toward higher latitudes.

*Additional key words:* gonadal development, seasonality, seminal receptacles, surface active crabs, temperate estuary

The reproductive output of marine species is often associated with latitudinal clines. The breeding season, for example, tends to be continuous or prolonged in tropical populations, and restricted to warmer months in temperate ones (Clarke 1987; Hines 1989; Bauer 1992; Defeo & Cardoso 2002; Hartnoll 2006; Luppi et al. 2013; Stocks et al. 2015; Bi et al. 2016). Other traits that influence reproduction and can be affected by variation in climatic conditions (e.g., temperature, photoperiod) or availability of resources along the latitudinal gradient include size at the onset of sexual maturity, ovary maturation, synthesis of vitellogenin, and the number and size of broods (Pörtner et al. 2007; Hirose et al. 2013; Bronstein & Loya 2014; Thongda et al. 2015; Thatje & Hall 2016). Understanding the spatial patterns of reproductive biology might allow prediction of species fitness and population stability

in different locations within the geographical range of a particular species (Lester et al. 2007; Pörtner et al. 2007; Stocks et al. 2015). Such information can also facilitate understanding of the consequences of global warming, since the thermal window of a species can be affected by climate change (Helmuth et al. 2002; Cumillaf et al. 2016).

Fiddler crabs usually inhabit tropical and subtropical estuaries (Crane 1975). In such areas, these crabs usually exhibit continuous reproduction, probably due to the constancy of environmental conditions and resource availability throughout the year (Colpo & Negreiros-Fransozo 2004; Litulo 2005; Benetti et al. 2007; Costa & Soares-Gomes 2009; Martins & Masunari 2013a). However, some fiddler crabs have extended their distribution and are able to inhabit temperate estuaries, but the conspicuous seasonality in these areas seems to shorten their reproductive period (Wolfrath 1992; Rodríguez et al. 1997; Yamaguchi 2004; Hartnoll 2006; César et al. 2007; Boa & Guerra-Garcia 2015). One of

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these eurythermal fiddler crabs is *Leptuca uruguayensis* NOBILI 1901. This species is common in the southwestern Atlantic coast, and can be found from tropical estuaries in Rio de Janeiro, Brazil (22°S) to temperate salt marshes in Buenos Aires, Argentina (37°S) (Melo 1996; Bezerra 2012). Studies on the frequency of ovigerous females or juvenile recruitment during the year in populations near the extremes of the species' geographical distribution have shown that, in tropical estuaries, breeding individuals of *L. uruguayensis* are present all the year round whereas, in temperate salt marshes, ovigerous females are found only in summer months (Spivak et al. 1991; Torres-Jordá & Roccatagliata 2002; César et al. 2005; Costa et al. 2006; Hirose et al. 2013; Martins & Masunari 2013a; Ribeiro et al. 2016).

The thermal window in tropical crustaceans is wider than that of temperate ones, and intertidal crabs are more tolerant to high temperatures than to low ones (Cumillaf et al. 2016). Therefore, although the reproductive effort tends to be lower in areas close to the edges of the species distribution range (Wehrmann et al. 2012), reproduction in *L. uruguayensis* could be more limited at the species' southern edge of distribution than at the tropical edge, because in temperate estuaries individuals of this species would spend more energy to cope with minimal temperatures in winter. Therefore, our objective was to examine several reproductive attributes of the southernmost population of fiddler crabs, and relate them to environmental variation throughout the year, identifying the consequences of seasonality on their reproduction. Moreover, based on changes in these reproductive attributes, we aimed to characterize the periods of the annual reproductive cycle of *L. uruguayensis* at the southern edge of its distribution.

## Methods

The study was carried out in Samborombón Bay, in the Río de la Plata estuary, Argentina, where the southernmost stable population of *Leptuca uruguayensis* is found (Spivak et al. 1991). Other occurrences of this species at 37°S and 38°S are intermittent and limited by wind conditions, which affect larval settlement (Bogazzi et al. 2001). The field work was performed in a muddy sand area of approximately 3500 m<sup>2</sup> of the intertidal zone of the Saladero canal (36°25'0.3"S, 65°57'11"W), in the locality of General Lavalle, Buenos Aires province. Sampling was carried out during low tides, monthly from February 2014 to January 2015, with a

periodicity of 29±3 d (mean±standard deviation). Data of air temperature and photoperiod of the sample months were obtained from the Agricultural Experimental Station of Cuenca del Salado (National Institute of Agricultural Technology–INTA, Argentina). Three samples of the upper 3–5 mm of the sediment were obtained to determine organic matter content, by ash-free dry weight, because this information can be indicative of the availability of food for fiddler crabs (Colpo & Negreiros-Fransozo 2011; Sayão-Aguiar et al. 2012).

The reproductive attributes evaluated in this study included: the proportion of ovigerous females, the proportion of surface-active crabs, the developmental status of the gonads and hepatopancreas, and the fullness of seminal receptacles. To evaluate these attributes, in each sampling month, we estimated the population density of *L. uruguayensis*, using two sampling techniques (excavation of crabs in the substrate or filming of active crabs on the surface) in five randomly selected quadrats of 0.25 m<sup>2</sup> in the study area. Each quadrat area was excavated to 30 cm depth, because this is the average depth of the crab burrows in the area. The sediment removed from the quadrats was carefully examined to search for fiddler crabs. All crabs found were sexed, measured by means of a caliper (carapace width [CW] in mm), and the ovigerous condition recorded in the field. In each sample month, we also recorded the density of active fiddler crabs on the substrate surface. For this, five random quadrats of 0.25 m<sup>2</sup> were delineated with cotton line placed at the same level as the substrate to minimize avoidance by the crabs. Each quadrat was photographed and filmed for 1 min, between 1 h before and 1 h after the time of low tide, from a minimum distance of 6 m to prevent observer interference on the behavior of crabs. Afterward, the images were analyzed and the total number of crabs (males+females) outside the burrows, performing any sort of activity (e.g., feeding, waving, fighting, walking, self-cleaning), was recorded. A two-way analysis of variance (ANOVA) was used to model the variation in fiddler crabs densities: sampling technique was a fixed and orthogonal factor with two levels (excavation and filming); and the sampling month was a fixed and orthogonal factor with twelve levels (February 2014 to January 2015). *Post hoc* Student–Newman–Keuls tests were applied for multiple comparisons. The data were log-transformed to fulfill the requirements of the ANOVA.

In each month, about 80 adult fiddler crabs (>10 mm CW), in a proportion of 1 female: 1 male were transported alive to the laboratory. The fiddler

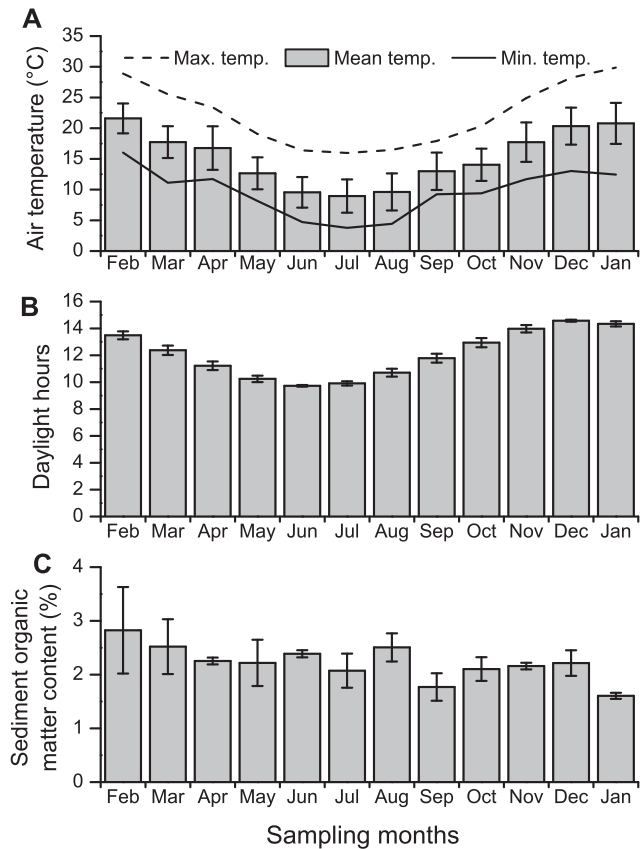
crabs were anesthetized by holding them in cold temperatures, and dried with paper towels. Afterward, they were measured (CW in mm) and weighed (mg). Under a stereomicroscope, the hepatopancreas and the gonads of both sexes and the seminal receptacles of females were removed, and their wet weights (mg) recorded separately. These data were used to estimate the wet gonadosomatic index ( $GSI=100 \times \text{wet weight of gonad} / \text{wet body weight}$ ), and the wet hepatosomatic index ( $HSI=100 \times \text{wet weight of hepatopancreas} / \text{wet body weight}$ ). We also calculated the relative weight of seminal receptacles for females ( $RWSR=100 \times \text{wet weight of both seminal receptacles} / \text{body weight}$ ). These indices indicate, respectively, the developmental status of gonads and hepatopancreas for each sex, and the fullness of seminal receptacles.

To investigate whether the reproductive cycle of *L. uruguayensis* was related to the seasonal variation in environmental factors throughout the year, we performed multiple regression analyses (GLM), including data from the twelve sample months. We tested the effects of air temperature ( $^{\circ}\text{C}$ ), daylight hours, and sediment organic matter content (%) (predictor variables) on the reproductive attributes of this fiddler crab population (dependent variables: proportion of ovigerous females, proportion of surface-active crabs, GSI, HSI and relative weight of seminal receptacles).

Based on changes in the reproductive attributes throughout the months, we attempted to recognize the annual reproductive cycle of *L. uruguayensis*, determining different periods throughout the year. To confirm differences between these periods, we clustered data from gonads, hepatopancreas, and seminal receptacles to each reproductive period and compared them by one-way ANOVA. *Post hoc* Student–Newman–Keuls tests were applied for multiple comparisons. The Cochran test was used for testing homogeneity of variances, and the data were log-transformed to fulfill the requirements of the ANOVA.

## Results

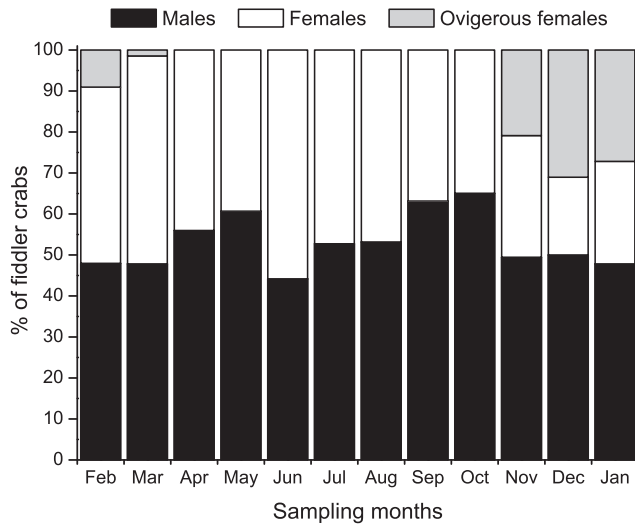
During the sampling period, the air temperature ranged from  $4 \pm 1^{\circ}\text{C}$  (mean  $\pm$  standard deviation) in winter to  $30 \pm 2^{\circ}\text{C}$  in summer, and the photoperiod fluctuated from 9.7 h of daylight in June to 14.6 h of daylight in December (Fig. 1A,B). The studied period showed ENSO-neutral conditions (El Niño Southern Oscillation, National Oceanic and Atmospheric Administration, National Weather Service, USA), suggesting that recorded temperatures were



**Fig. 1.** Environmental factors recorded in the study region during the sampling months. **A.** Minimum, maximum, mean, and standard deviation of air temperature. **B.** Mean and standard deviation of light hours. **C.** Mean and standard deviation of sediment organic matter content.

typical for the area. The sediment contained  $2.2 \pm 0.3\%$  (mean  $\pm$  standard deviation) organic matter, with little variation throughout the year (Fig. 1C).

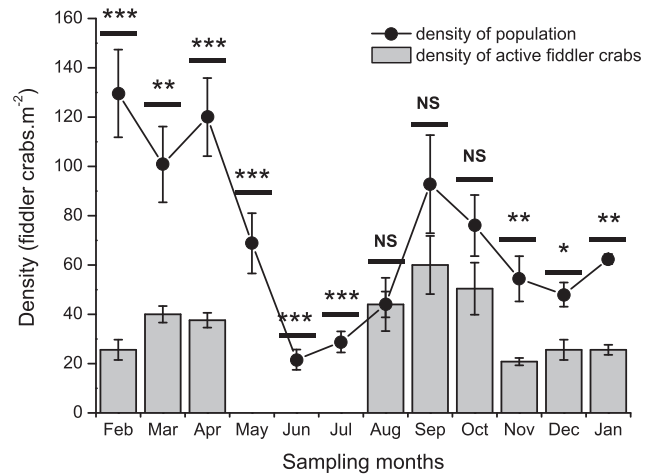
At the end of the sampling year, we had collected 1308 individuals of *Leptuca uruguayensis* in the excavated quadrats. The size of the fiddler crabs sampled ranged 5.8–14.9 mm CW (mean  $\pm$  standard deviation:  $10.7 \pm 1.5$  mm). Of the total crabs sampled, 703 were males, 521 were females, and 84 were ovigerous females. Ovigerous females were found in the five warmest months with longest daylight periods, from November to March (Figs. 1, 2). In November, December, and January, ovigerous females represented more than 40% of the females sampled, suggesting a peak in the reproductive process of the population. The density of fiddler crabs recorded by excavation of quadrats was greater than that of active crabs on the substrate surface in most of the months studied, except in August, September,



**Fig. 2.** Proportion of males, females, and ovigerous females of *Leptuca uruguayensis* in each sampling month.

and October, when the densities were similar (Table 1, Fig. 3). This result suggests that the proportion of surface-active crabs is greater in this period. During May, June, and July the activity rate was nil, since no fiddler crab was recorded on the surface (Fig. 3). Throughout the year, the GSI and HSI showed more variation in females (Fig. 4A,C) than in males (Fig. 4B,D). The most conspicuous change was observed in the female gonadal development. The volume of ovaries started to increase from September, reached a peak in November, and decreased until depletion in February (Fig. 4A). The relative weight of the female seminal receptacles also showed variation throughout the year, showing lower values from June to September (Fig. 4E).

Although we found ovigerous females in the months of higher temperatures and longer daylight period, and no active crabs in the months of lower temperatures and fewer hours of daylight, these environmental variables showed no relationship with the proportion of ovigerous females or to the



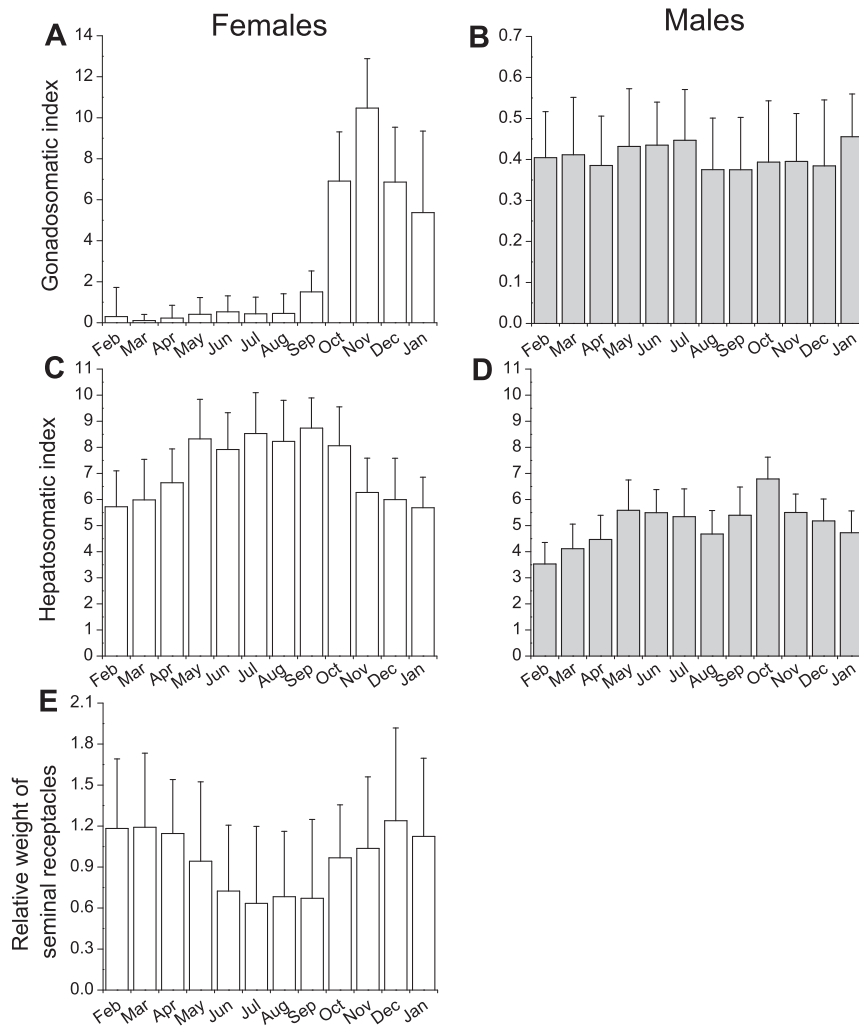
**Fig. 3.** Comparison between density of population (obtained by excavation sampling technique) and density of active crabs on the substrate surface (obtained by filming sampling technique), in each sampling month. Mean and standard deviation. NS, not significant; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

proportion of surface-active fiddler crabs (Table 2). Nevertheless, the seasonal variations in temperature and photoperiod seemed to positively affect the development of female gonads and the degree of fullness of the seminal receptacles (Table 2). Also, the temperature was negatively related to the HSI of both sexes (Table 2). However, the GSI of males showed no relationship with the environmental factors evaluated (Table 2). The organic matter content of sediments did not affect any of the dependent variables tested (Table 2).

Based on the proportion of ovigerous females, the proportion of surface active crabs, and ovarian development, we determined the annual reproductive cycle of *L. uruguayensis* (Table 3). We considered May, June, and July as a period of low activity (LA), since the proportion of active crabs outside burrows was nil (Fig. 3). In the following months—August, September, and October—the rate of

**Table 1.** Summary of the two-way ANOVA, testing the variation in the density of individuals of *Leptuca uruguayensis* measured by excavation and filming techniques throughout the sampling months (February 2014 to January 2015).

	Cochran C = 0.172328		p = 0.247793	
	df	MS	F	p
Techniques	1	11.772	543.73	<0.001
Months	11	1.910	88.22	<0.001
Techniques × Months	11	0.852	39.39	<0.001
Error	96	0.021	—	—



**Fig. 4.** Variation in gonads, hepatopancreas, and seminal receptacles in *Leptuca uruguayensis* throughout the sampling months. Mean and standard deviation. **A.** Developmental status of female gonads. **B.** Developmental status of male gonads. **C.** Hepatosomatic index of females. **D.** Hepatosomatic index of males. **E.** Fullness condition of seminal receptacles.

activity increased, and the density of active crabs was similar to the population density (Fig. 3). Also, in these months, the female gonads began to develop (Fig. 4A). Therefore, we considered this time as the pre-reproductive period (Pre-R). In November, December, and January, more than 40% of the females sampled were ovigerous (Fig. 2) and ovarian development reached its maximum (Fig. 4A). Therefore, we determined these months as the reproductive period (R). In February and March, we recorded few ovigerous females but the female gonads were depleted (Fig. 4A). Therefore, we considered these months and April as the post-reproductive period (Post-R).

In Post-R and LA, the ovaries of most females were empty, resulting in a lower GSI in these periods. Intermediate values of GSI in Pre-R suggest

preparation of females for the reproduction period. In the R period, the ovary reached its maximum development (Fig. 5A). However, the male GSI showed no conspicuous variation throughout the annual reproductive cycle of *L. uruguayensis* (Fig. 5B). The HSI of females was greater in LA and Pre-R than in R and Post-R (Fig. 5C). The HSI of males was lower in the Post-R period (Fig. 5D). The seminal receptacles of females were more filled in R and Post-R than in LA and Pre-R (Fig. 5E).

### Discussion

At the southern edge of the *Leptuca uruguayensis* distribution range, the temperature was the environmental factor that most affected reproductive



**Table 2.** Summary results of the multiple regression analysis (GLM), testing the relationship between environmental factors (predictor variables)—mean air temperature (°C), daylight hours, and sediment organic matter content (%)—and reproductive attributes of *Leptuca uruguayensis* (dependent variables)—proportion of ovigerous females, proportion of active crabs (%), development index of gonads and hepatopancreas for females and males, and the relative weight of seminal receptacles in females. The symbols in the effect column indicate how each environmental factor affects the dependent variables: 0, no effect; +, positive effect; −, negative effect.

Predictor variables	df	Summary results of the multiple regression analysis (GLM)							
		MS	F	p	Effect	MS	F	p	Effect
		Proportion of ovigerous females				Proportion of active crabs			
Air temperature	1	3.90	0.017	0.899	0	2930.4	3.665	0.092	0
Daylight hours	1	636.78	2.785	0.134	0	4080.6	5.104	0.054	0
Organic matter	1	124.92	0.546	0.481	0	271.13	0.339	0.576	0
Error	8	228.67	—	—	—	799.49	—	—	—
R <sup>2</sup>		0.581	—	—	—	0.398	—	—	—
		Female gonadosomatic index				Male gonadosomatic index			
Air temperature	1	24.279	5.890	0.0413	+	0.001	1.029	0.340	0
Daylight hours	1	63.259	15.347	0.0044	+	0.001	1.571	0.245	0
Organic matter	1	1.390	0.337	0.5774	0	0.001	1.440	0.264	0
Error	8	4.122	—	—	—	0.001	—	—	—
R <sup>2</sup>		0.682	—	—	—	0.217	—	—	—
		Female hepatosomatic index				Male hepatosomatic index			
Air temperature	1	2.919	10.399	0.012	−	2.408	6.281	0.037	−
Daylight hours	1	0.009	0.033	0.861	0	1.254	3.271	0.108	0
Organic matter	1	0.316	1.127	0.319	0	0.564	1.470	0.260	0
Error	8	0.281	—	—	—	0.383	—	—	—
R <sup>2</sup>		0.810	—	—	—	0.602	—	—	—
		Seminal receptacles							
Air temperature	1	0.139	15.191	0.005	+	—	—	—	—
Daylight hours	1	0.006	0.643	0.446	0	—	—	—	—
Organic matter	1	0.007	0.739	0.415	0	—	—	—	—
Error	8	0.009	—	—	—	—	—	—	—
R <sup>2</sup>		0.824	—	—	—	—	—	—	—

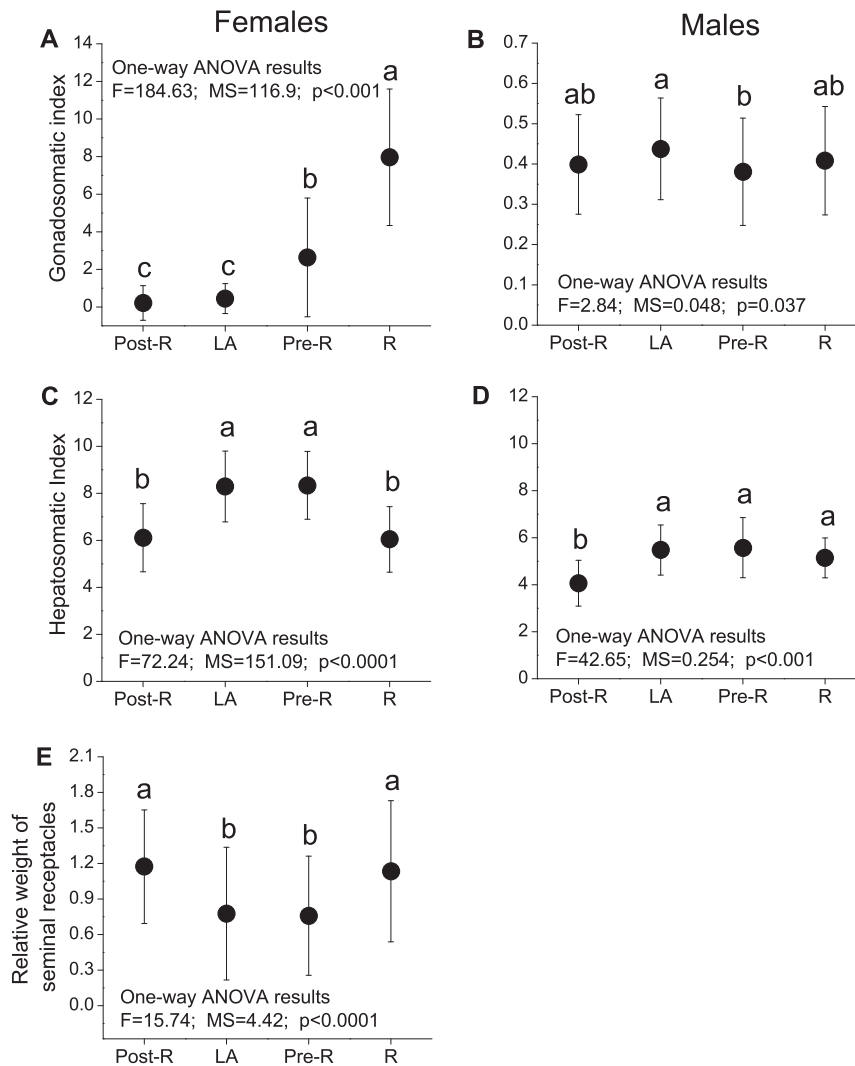
**Table 3.** Periods of the annual reproductive cycle of *Leptuca uruguayensis* based on the proportion of ovigerous females, the proportion of active crabs, and ovarian development observed throughout the sampling months.

Period	Sampling months	Reproductive attribute	Status
Low activity (LA)	May, June, and July	Proportion of active crabs	Null
Pre-reproductive (Pre-R)	August, September, and October	Proportion of active crabs	High
Reproductive (R)	November, December, and January	Ovarian development	Begins to develop
		Proportion of ovigerous females	More than 40% of females
Post-reproductive (Post-R)	February, March, and April	Ovarian development	Reaches the maximum development
		Ovarian development	Depleted

processes. Ovarian development, the fullness of the seminal receptacles, and the hepatosomatic index were related to temperature. Moreover, the conspicuous variations in the proportion of surface active crabs and in the reproductive condition, mainly in

females, allowed us to define four periods (LA, Pre-R, R, and Post-R) in the annual cycle of the southernmost stable population of fiddler crabs.

Only a few studies have evaluated reproductive traits of *L. uruguayensis* (e.g., breeding season) such



**Fig. 5.** Comparison of gonads, hepatopancreas, and seminal receptacles in *Leptuca uruguayensis* between the periods of its annual reproductive cycle (Post-R, post-reproductive; LA, low activity; Pre-R, pre-reproductive; R, reproductive). **A.** Developmental status of female gonads. **B.** Developmental status of male gonads. **C.** Hepatosomatic index of females. **D.** Hepatosomatic index of males. **E.** Fullness of seminal receptacles. Mean and standard deviation. Different letters indicate statistically significant differences between means ( $p<0.05$ ).

as the presence of ovigerous females (Spivak et al. 1991; Torres-Jordá & Roccatagliata 2002; César et al. 2005; Costa et al. 2006; Martins & Masunari 2013a), fecundity (Bogazzi et al. 2001; Costa et al. 2006; César et al. 2007), formation of gametes (Cuartas & Petriella 2007), the size at the onset of sexual maturity (Hirose et al. 2013; Martins & Masunari 2013b), and the mating mode and hood-building (Ribeiro et al. 2010, 2016). Most of these studies were carried out near the northern and southern edges of the geographical distribution of *L. uruguayensis*. Northernmost populations experience low thermal and photoperiod amplitudes throughout the year (annual mean and standard

deviation of air temperature  $23\pm4^{\circ}\text{C}$ ; day length from 10.8 h in June, to 13.5 h in December; database available at the Center for Weather Forecasting and Climate Studies [CPTEC], <http://bancodedados.cptec.inpe.br/Brazil>). In these populations, fiddler crabs are active year-round and have a continuous reproductive cycle, since ovigerous females and juvenile recruits are found throughout the year (Costa et al. 2006; Hirose et al. 2013; Martins & Masunari 2013a). However, the southernmost populations live under greater variations of temperatures (annual mean and standard deviation  $17\pm9^{\circ}\text{C}$ ) and day length (about 5 h difference between summer and winter). In this study, we found that individuals of

*L. uruguayensis* interrupted their activity in winter and that ovigerous females were present only in the warmer months. Other studies in the Argentine coast have suggested a similar pattern (Spivak et al. 1991; Bogazzi et al. 2001; Torres-Jordá & Roccatagliata 2002; César et al. 2005, 2007; Ribeiro et al. 2016). Such large-scale differences in the duration of the reproduction season could be explained by the latitudinal influence of the temperature (Defeo & Cardoso 2002).

Interpopulation variability in the reproductive traits along latitudinal gradients is usually recorded in decapods with wide geographical distributions (Defeo & Cardoso 2002; Castilho et al. 2007; Wehrmann et al. 2012). This plasticity ensures the reproductive performance required for maintenance of populations facing different environmental conditions. Temperature affects physiological process (Winwood-Smith et al. 2015) and hence, the reproductive biology of species. *Leptuca uruguayensis* shows reproductive plasticity, probably to cope with the different thermal conditions at each edge of its distribution range. Although the breeding season is shorter at the southern edge than at the northern edge, temperate females are larger and produce more eggs than tropical ones (Costa et al. 2006; César et al. 2007; Hirose et al. 2013). Such different strategies could compensate for differences in reproductive performance at each edge of the geographical range of *L. uruguayensis*. However, the current available knowledge of the reproductive biology of *L. uruguayensis* is not enough to suitably estimate the equivalence of the reproductive effort at both edges of its distribution.

Low temperature is an environmental stress that affects the energetic balance of ectotherms (Pörtner et al. 2007; Cumillaf et al. 2016). The energy budget for activity, growth, and reproduction is reduced to cover the increased maintenance costs during the stress period (Sokolova et al. 2012). In temperate estuaries, the minimal temperatures of winter are probably below the optimal range for fiddler crabs, representing a source of stress. Usually, when the temperatures are low, no fiddler crabs are found active on the surface. During winter, individuals of *Afruca tangeri* in European salt marshes (Wolfrath 1993; Rodríguez et al. 1997; Boa & Guerra-García 2015) and of *Astruca lactea* in Japan (Yamaguchi 2004) remain inside their burrows. This behavior saves a fiddler crab's activity costs, preserving energy during the stressful period of lower environmental temperatures. In this study, the proportion of surface active crabs was not explained by environmental factors (Table 2), probably because the period of greatest activity (in Pre-R) coincided with

intermediate values of temperature and photoperiod. Despite the lack of statistical relationship between the proportion of surface-active crabs and environmental factors, individuals of *L. uruguayensis* also remained underground when the temperatures decreased substantially. This reduction in activity on the surface seems to be a strategy to cope with the stressful low temperatures of winter in Samborombón Bay. After the LA period, when the sediment temperature reached 20°C (KDC, unpubl. data), individuals of *L. uruguayensis* emerged from their burrows and showed high activity rates on the surface. In European salt marshes, when the sediment temperature exceeds 18°C, after the winter, individuals of *A. tangeri* also leave their burrows, and a great number of these fiddler crabs can be observed on the surface, performing several behaviors (Wolfrath 1993; Boa & Guerra-García 2015).

In this study, the proportion of ovigerous females had no relationship with environmental factors, but the female GSI showed a remarkable variation throughout the year, and this ovarian maturation cycle was correlated with temperature and daylight hours in Samborombón Bay. These two factors are important regulators of reproduction in decapods (Carmona-Osalde et al. 2004; Hamasaki et al. 2004). The GSI in females of *L. uruguayensis* started to increase as the temperature and photoperiod increased, in the Pre-R period. The greatest ovary indices were recorded when these environmental factors reached their maxima, in R. Afterwards, the GSI decreased until depletion, even as the temperature and photoperiod decreased, in Post-R. The start of ovarian development would be controlled by temperature, whereas the increasing photoperiod stimulates maturation (Daniels et al. 1994; Liu et al. 2013). In addition, high temperatures increase metabolic rates, reducing the ovarian maturation time (Vázquez et al. 2013). During the LA period, the GSI was minimal. Probably, the temperatures of winter in Samborombón Bay were below the optimal range for *L. uruguayensis*, representing an environmental stress. At this time, the females might use most of their energy to cover the high maintenance costs caused by stress and save little energy to invest in ovary maturation (Sokolova et al. 2012). The male gonads showed similar volume and aspect in the four periods of the annual reproductive cycle. This constancy in the male GSI throughout the year has also been recorded in other Decapoda in tropical and temperate habitats (Pillay & Nair 1973; Kyomo 1988; Omori et al. 1997; Yamaguchi 2001; Sokolowicz et al. 2006; Magalhães et al. 2012). This pattern can be explained by the low requirement of



dietary nutrients to ensure the gonadal development of male crabs (Wu et al. 2010). This suggests that males of *L. uruguayensis* maintain sperm production during the year, independently of the environmental conditions, thereby guarding against sperm limitation (MacDiarmid & Butler 1999).

In crabs, the hepatopancreas is the principal organ for nutrient storage (Harrison 1990; Jones & Obst 2000). During R and Pre-R periods, the HSI in *L. uruguayensis* decreased, especially in females, indicating the high-energy requirement of reproduction and the role of the hepatopancreas in supporting this demand. Such a pattern has also been recognized in other crabs (Pillay & Nair 1973; Yamaguchi 2004; Wu et al. 2010; Spivak et al. 2012). A large hepatopancreas mass (high HSI) usually indicates good nutritional and physiological conditions in Decapoda (Wang & McGaw 2014; Han et al. 2015; Sacristán et al. 2016). During stress periods (e.g., hypothermia, starvation), energy demands are probably met by hepatopancreas lipolysis (Vinagre & Chung 2016), usually reducing the HSI. During the LA period, individuals of *L. uruguayensis* remained inside their burrows, probably to escape the low environmental temperatures. In this period, no fiddler crabs were recorded on the surface feeding around the burrows. This change in feeding behavior was not related to food availability (organic matter content) on the upper layer of sediment, since this environmental factor showed no significant variation throughout the year. Therefore, we consider that LA is a stressful period for individuals of *L. uruguayensis*, and that crabs could starve inside the burrows during these cold months. Certainly, the activity reduction conserves energy and the rate of utilization of hepatopancreas reserves can be delayed in low temperatures (Jones & Obst 2000), but the starvation would promote some decrease in HSI, to ensure somatic maintenance (Sokolova et al. 2012). However, we found the greatest values of HSI during the LA period, in an inverse relationship with temperature. This increase in HSI when temperatures are lower was an unexpected finding, and could be a consequence of a reabsorption of nutrient reserves from other tissues (Jones & Obst 2000; Calvo et al. 2012), a response to stress conditions (Figueiredo-Fernandes et al. 2006), or it suggests that individuals of *L. uruguayensis* preserve some energetic intake during LA. In fiddler crabs, mating and egg incubation have been recorded as underground activities (Christy 1988; Koga et al. 2000; Henmi 2003; Ribeiro et al. 2016), but there is no report of feeding inside the burrows. Nonetheless, underground food

consumption has been suggested in other semi-terrestrial crabs (Kyomo 1988; Nordhaus et al. 2009). Therefore, the high HSI values during the LA period suggest that individuals of *L. uruguayensis* can feed inside their burrows and avoid the low ambient temperatures. As deposit feeders, these crabs could forage on sediments from the burrow wall to obtain quality food because the organic carbon and nitrogen contents are greater in deeper layers of the sediment (Wang et al. 2010). Because the beginning of gametogenesis requires energy (Olive 1995), restarting the activities in Pre-R with reserves (high HSI) can be an important strategy, especially in females who need greater energy investment to develop the ovary in a short time (Yamaguchi 2004).

The seminal receptacles provide females with the opportunity to store sperm from different males, which could result in multiple paternity (Orr & Brennan 2015). The relative weight of seminal receptacles in individuals of *L. uruguayensis* varied with temperature. In the colder months, during the non-reproductive periods, the seminal receptacles were less full, while fullness of the seminal receptacles increased in R, confirming mating. Usually, at the end of the annual breeding cycle, the fullness of the seminal receptacles decreased (González-Gurriarán et al. 1998). However, in *L. uruguayensis*, the receptacles remained filled in the post-R period, probably because females did not have mature gonads to use the stored sperm in a new spawning. Pardo et al. (2013) suggest that in the course of time, the sperm stored in receptacles can use the seminal fluid as a nutritional source, promoting a volume decrease in receptacles. This hypothesis could explain the low values of the relative weight of seminal receptacles in females of *L. uruguayensis* in LA and Pre-R. Females with empty seminal receptacles are more receptive to copulations, to (re)load them (Moyano et al. 2012). Therefore, females starting a new breeding season with high mating receptivity can favor accumulation of sperm from several males in the discharged seminal receptacles, promoting sperm competition and a genetically diverse progeny.

A species usually occurs in a geographical range where abiotic and biotic factors are suitable to ensure population sustainability (Caughley et al. 1988; Gaston 2003). In the center of this range, environmental conditions are often optimal and a species reaches its maximum performance, but toward the boundaries, habitat quality can decline, reducing survival and reproduction (Gaston 2003; Wehrmann et al. 2012; Hargreaves et al. 2014). In this study, we showed that at the southern edge of the species' distribution, temperature is likely to be

an important regulator of activity and reproduction in *L. uruguayensis*. The winter temperatures recorded in the study area might represent the lower limit of the thermal window of the southernmost fiddler crabs. Three populations of *L. uruguayensis* can be found further south of Samborombón Bay. However, the density of those populations decreases significantly as latitude increases (Bogazzi et al. 2001), suggesting a decrease in fitness. Furthermore, the maintenance of those populations seems to be more related to allochthonous recruitment (larvae imported from the Samborombón population) than to self-recruitment (Laurenzano et al. 2012). For this reason, populations further south of Samborombón Bay are probably beyond the fundamental niche limits of *L. uruguayensis* (Hargreaves et al. 2014). Therefore, considering that temperature plays an essential role in reproduction at the south edge of the distribution of *L. uruguayensis* and that reproductive output can set species range boundaries (Lester et al. 2007), we suggest that low temperature is probably the single most important environmental factor limiting the advancement of *L. uruguayensis* toward higher latitudes.

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