

Accepted Manuscript

---

This is an Accepted Manuscript of the following article:

Jonathann Yukio Arakaki, Fernando Rafael De Grande, Alexandre Luiz Arvigo, Juan Carlos Farias Pardo, Bruno Rafael Fogo, Fábio H.C. Sanches, Caio Akira Miyai, Murilo Zanetti Marochi, Tânia Marcia Costa. Battle of the borders: Is a range-extending fiddler crab affecting the spatial niche of a congener species?  
Journal of Experimental Marine Biology and Ecology.  
Volume 532, 2020, 151445, 0022-0981.

The article has been published in final form by Elsevier at  
<https://doi.org/10.1016/j.jembe.2020.151445>

© 2020. This manuscript version is made available under the

CC-BY-NC-ND 4.0 license

<http://creativecommons.org/licenses/by-nc-nd/4.0/>

---

1 **Battle of the borders: is a range-extending fiddler crab affecting the spatial niche**  
2 **of a congener species?**

3 Jonathann Yukio Arakaki<sup>a</sup>, Fernando Rafael De Grande<sup>a,b\*</sup>, Alexandre Luiz Arvigo<sup>a,b</sup>

4 Juan Carlos Farias Pardo<sup>a,b,c,d</sup>, Bruno Rafael Fogo<sup>a,b</sup>, Fábio H. C. Sanches<sup>b,e</sup>, Caio Akira

5 Miyai<sup>a,f</sup>, Murilo Zanetti Marochi<sup>a</sup>, Tânia Marcia Costa<sup>a,b,f</sup>

6

7 <sup>a</sup> Biosciences Institute, São Paulo State University (UNESP), Coastal Campus, 11330-  
8 900, São Vicente, SP, Brazil.

9 <sup>b</sup> Postgraduate Program in Biological Sciences (Zoology), Biosciences Institute, São  
10 Paulo State University (UNESP), 18618-000, Botucatu, SP, Brazil.

11 <sup>c</sup> University of Agder (UiA), Center for Coastal Research, NO-4604 Kristiansand,  
12 Norway

13 <sup>d</sup> Norwegian Institute for Water Research (NIVA), Jon Lilletuns vei 3, 4879, Grimstad,  
14 Norway

15 <sup>e</sup> Institute of Marine Science, Federal University of São Paulo (IMar/UNIFESP), 11070-  
16 102, Santos, SP, Brazil.

17 <sup>f</sup> Aquaculture Center (CAUNESP), São Paulo State University (UNESP), Jaboticabal, SP,  
18 14884-900, Brazil.

19 \*Corresponding author: Biosciences Institute, São Paulo State University (UNESP),  
20 Coastal Campus, Praça Infante Dom Henrique, S/N, Parque Bitarú. ZIP code: 11330-900,  
21 São Vicente, SP, Brazil. Phone: +55 13 3569 7116. E-mail address:  
22 frdegrande@gmail.com

23

24

25

26 **Abstract**

27 Climate change is drastically altering environmental conditions and resource  
28 availability. Many organisms are shifting their distribution boundaries. Fiddler crabs,  
29 for instance, are important ecosystem engineers in coastal environments that have been  
30 extending their distribution range poleward. In this study, we evaluated the influence of  
31 a range-extending species, *Leptuca cumulanta*, which has recently overlapped the  
32 distribution of the resident species *Leptuca uruguayensis*. Through a set of field and  
33 laboratory experiments, we characterised the degree of territorial overlap between *L.*  
34 *cumulanta* and *L. uruguayensis* from the lower to upper intertidal zone in a mangrove  
35 area. We also analysed whether the presence of *L. cumulanta* prevents habitat  
36 choosiness or influences agonistic behaviours in *L. uruguayensis* in territorial fights. We  
37 found that both species overlap territories at the same level in the intertidal zone.  
38 However, we observed that both habitat choice and agonistic behaviours of *L.*  
39 *uruguayensis* were unresponsive to the presence of *L. cumulanta*. The low interference  
40 between recent heterospecific neighbours sharing the same space supports coexistence  
41 of fiddler crabs *L. uruguayensis* and *L. cumulanta* in the early stage of overlapping.

42

43 **Keywords:** *Leptuca uruguayensis*, *Leptuca cumulanta*, interspecific interactions,

44 distribution, territory overlap

## 45 1. Introduction

46 Climate change and associated changes in temperature, hydrological regime, and  
47 sea-level are altering global habitats and resources available for many living species  
48 (Poff et al., 2002; Parmesan and Yohe, 2003; Ernakovich et al., 2014). One of the  
49 consequences of these phenomena is the change in the distribution of organisms (Dukes  
50 and Mooney, 1999; Poff et al., 2002; Rahel and Olden, 2008). In response to global  
51 warming, various species have spread their distribution to higher latitudes as conditions  
52 become favourable for survival in these areas (Chen et al., 2011), including fishes  
53 (Mandrak, 1989; Eaton and Scheller, 1996; Sharma et al., 2007), copepods (Rombouts  
54 et al., 2009), polychaetes (Maximov, 2011), corals (Yamano et al., 2011), and fiddler  
55 crabs (Rosenberg, 2018). All shifts in the distribution of taxa encounter established  
56 niches and environmental conditions which in turn may determine winners and losers  
57 (Somero, 2010).

58 The presence of a new species may change an established community structure  
59 shifting species abundance and composition (Duckworth and Badyaev, 2007; Hejda et  
60 al., 2009; Scheffel et al., 2018). One important factor in the context of territorial  
61 expansion is the degree of phylogenetic proximity between range-extending species and  
62 native species. The congener species are potentially more critical competitors for native  
63 species since both tend to present a high niche overlap (Brown et al., 2002; Skálová et  
64 al., 2013). For example, between congener bluebird species, the success of colonisation  
65 by the range-extending *Sialia mexicana* was related to a higher degree of aggressiveness  
66 over the native species *S. currucoides* (Duckworth and Badyaev, 2007). The population  
67 of *S. mexicana* increased due to aggressiveness, whereas *S. currucoides* population  
68 decreased over time, indicating that aggressiveness contributed to the successful  
69 establishment of the arriving species in extending its territory (Duckworth and Badyaev,

70 2007). The degree of aggressiveness in range-extending species can determine success  
71 over native species in obtaining resources (e.g., food or territory), which promotes  
72 growth, survival, and reproduction in the establishment of territory (Hudina et al.,  
73 2014). The intensity of agonistic interactions may force submissive competitors to  
74 occupy less preferred habitats (Orians, 2000; Hudina et al., 2014). Thus, competitive  
75 processes are important predictors to understand how species interactions will be  
76 affected under a climate change scenario.

77 Fiddler crabs are a key group in estuaries due to their bioturbation activities  
78 (McCraith et al., 2003; Reinsel, 2004; Smith et al., 2009; Natálio et al., 2017) and are  
79 considered ecosystem engineers, modifying the environment and affecting the  
80 availability of resources to other organisms (Jones et al., 1994; Reinsel, 2004; Smith et  
81 al., 2009). Species from this group have the potential to be affected by alterations in  
82 their habitat related to climate change (Sanches et al., 2018), spreading their distribution  
83 borders and extending their territory range to higher latitudes (Johnson, 2014;  
84 Rosenberg, 2018). For example, *Uca princeps*, originally found from Peru to Mexico,  
85 recently extended their range into the state of California, USA (Rosenberg, 2018). The  
86 main factor limiting distribution of the fiddler crab *Minuca pugnax* are cold water  
87 temperatures, which negatively affect larval development (Sanford et al., 2006). An  
88 increase of 1.3 °C in the mean oceanic water temperature from 2012 to 2013 was  
89 accompanied by expansion of *M. pugnax* distribution 80 km to the north (Johnson,  
90 2014). Thus, it is plausible to suppose that global warming may allow other fiddler crab  
91 species to extend their occurrence, likely resulting in territorial overlap between  
92 congener species.

93 Fiddler crab burrows are one of the most valuable resources for this group, and  
94 crabs will aggressively defend it against floaters (individuals that have lost or

95 abandoned their burrows) (Crane, 1975). Losing a burrow will impose several costs to  
96 the evicted tenant associated with mating success, exposure to predation, and increasing  
97 dehydration (Munguia et al., 2017). Fiddler crab males have one major claw, which is  
98 used in reproductive displays to court females or in agonistic behaviours towards other  
99 males. In this case, agonistic movements are categorised by intensity level (e.g.,  
100 touching/pushing, grabbing, or throwing an opponent) and are employed in fights  
101 according to the type of opponent (neighbour/floaters) or motivation to fight  
102 (Booksmythe et al., 2010a, Fogo et al., 2019). Under competitive pressure from a  
103 newly-settled fiddler crab congener, we expected that native species would increase  
104 their investment in agonistic behaviours, which would decrease the amount of time  
105 invested in feeding and reproduction.

106         The fiddler crab *L. cumulanta* is widespread in the western Atlantic Ocean  
107 (Thurman et al., 2013). Its occurrence was originally reported from Venezuela to the  
108 northeastern coast of Brazil (Paraíba, 6°46'S, 34°56'W) (Crane, 1975), and then  
109 extended to the Brazilian southeastern coast (Rio de Janeiro, 23°13'S, 44°43'W) (Fig.  
110 1); thus, it is already considered an extended species (Thurman et al., 2013). Recently,  
111 *L. cumulanta* was observed at low density (0.14 ind./m<sup>2</sup>) at higher latitudes in the  
112 southeast of Brazil, reaching into Santos/São Vicente estuary, São Paulo state (23°59'S,  
113 46°24'W) (Checon and Costa, 2017). One possible explanation is that the sea surface  
114 temperatures off the southeast coast of Brazil are influenced by the Brazilian Current, a  
115 western boundary current responsible for transferring warm tropical waters to the mid-  
116 latitudes, which showed a warming trend of  $1.93 \pm 0.28$  °C between 1950 and 2008  
117 (Wu et al., 2012).

118         Concurrent with the expansion of *L. cumulanta* due to increasing temperatures,  
119 we have observed an increase in its density in Santos/São Vicente estuary. This newly-

120 colonised mangrove area was already inhabited by several fiddler crab species,  
121 including the congener species *Leptuca uruguayensis*, whose distribution in the  
122 intertidal zone would be overlapped by *L. cumulanta* (Checon and Costa, 2017).  
123 *Leptuca uruguayensis* occurs from Rio de Janeiro on the southeast coast of Brazil  
124 (22°51'S, 42°02'W) to Buenos Aires in Argentina (37°45'S, 57°28'W) (Spivak et al.,  
125 1991; Thurman et al., 2013; Truchet et al., 2019). The southern distribution range of *L.*  
126 *cumulanta* now overlaps the northern boundary of *L. uruguayensis* in Rio de Janeiro  
127 and São Paulo state. However, there is no information about the competitive potential  
128 between these two species. Considering they are congener species (Shih et al., 2016)  
129 and show pronounced agonistic interactions (Fogo et al., 2019), we aimed to investigate  
130 whether the presence of *L. cumulanta* has affected the intertidal distribution of the  
131 resident species *L. uruguayensis*. If the range-extending species is a strong competitor  
132 and overlaps the territories of resident species at the same level in the intertidal zone, we  
133 expect that *L. uruguayensis* will avoid, or be excluded from habitats where *L. cumulanta*  
134 are present due to the potential agonistic behaviour of *L. cumulanta*. Based on the above  
135 statement, we evaluated the distribution of *L. uruguayensis* and *L. cumulanta* in the  
136 same level of intertidal zone to test the following hypotheses: (1) the presence of *L.*  
137 *cumulanta* prevents the selection of habitat by *L. uruguayensis* and (2) the presence of  
138 *L. cumulanta* increases the number of agonistic interactions of *L. uruguayensis*.

139

## 140 **2. Material and Methods**

### 141 **2.1 Experimental sites and study species**

142 Both *L. uruguayensis* and *L. cumulanta* were observed and manually collected in  
143 the Santos/São Vicente estuary, city of Praia Grande – SP, Brazil (Fig. 1), where they  
144 occur in the intertidal zone along the edges of estuarine systems. *Leptuca cumulanta*  
145 occurs predominantly in the intertidal region on sand/clay banks, whereas *L.*

146 *uruguayensis* inhabits sandy banks (Thurman et al., 2013; Checon and Costa, 2017).  
147 The vegetation of this area is a typically Brazilian southwestern mangrove forest,  
148 mainly composed of *Rhizophora mangle* Linnaeus (1753), *Laguncularia racemosa* (L.)  
149 Gaertn (1807) and *Avicennia schaueriana* Stapf & Leechm (Cordeiro and Costa, 2010).  
150 Tides are semi-diurnal, flooding the crabs' assembly during spring high tides.

151 We tested our hypotheses using both field and laboratory approaches. We chose  
152 an area in Santos/São Vicente estuary (23°59'S, 46°24'W) and sampled three different  
153 sites (approximately 100 m<sup>2</sup> each and 25-m distant from each other) from the same crab  
154 population. We selected three different sites to ensure independence among experiments  
155 (Fig. 1). Only males were used in the manipulative experiments to standardise the  
156 response variables (proportion of choice between habitat and agonistic behaviour) since  
157 agonistic interactions between male fiddler crabs are better described and more  
158 noticeable (De Grande et al., 2018; Sanches et al., 2018; Fogo et al., 2019). Field  
159 surveys were conducted in September 2017 and laboratory trials between July and  
160 August 2018. Since this is the southernmost population of *L. cumulanta* reported,  
161 individuals were deposited under museum collection numbers MZUSP 36438 to  
162 MZUSP 36441 at the Museum of Zoology of the University of São Paulo, São Paulo,  
163 Brazil.

## 164 **2.2 Experimental design**

165 In the first part of the study, we evaluated if the range-extending species *L.*  
166 *cumulanta* overlap the territorial areas of the resident species *L. uruguayensis*. First, we  
167 described the density of both species along the edges of different levels in the intertidal  
168 zone. If the range-extending species overlapped the niche of resident species, it presents  
169 a strong competitive potential, and we predicted that the presence of *L. cumulanta*  
170 would cause negative effects on *L. uruguayensis*.



171 In the second part of the study, we set up an experiment in the laboratory, based  
172 on Olabarria et al. (2002), Underwood (2004), and De Grande et al. (2018), to verify if  
173 *L. uruguayensis* would avoid choosing habitats occupied by *L. cumulanta*. Individuals  
174 of *L. uruguayensis* were allowed to choose between two microhabitats, and their choice  
175 was observed. Microhabitats offered included: an empty microhabitat, a microhabitat  
176 occupied by *L. cumulanta*, and a microhabitat occupied by a conspecific competitor.  
177 Since each focal crab could only choose between two options, left or right side of the  
178 terrarium, we expect that they would always avoid the microhabitat occupied by any  
179 species if there is an empty option due the lack of competitors. In addition, we also  
180 expect they would always avoid the microhabitat occupied by *L. cumulanta*,  
181 irrespectively of the other option. Thus, the choice of *L. uruguayensis* for the  
182 microhabitats occupied by *L. cumulanta* could be explained if *L. cumulanta* is not able  
183 to displace the resident species from its territory or limit access to resources.

184 In the third experiment, we evaluated the aggressiveness between the resident  
185 and range-extending species in their natural habitat. For this, we measured the agonistic  
186 interactions between pairs composed of conspecific and heterospecific opponents. If *L.*  
187 *cumulanta* presents a high degree of aggressiveness, they may shift the resident *L.*  
188 *uruguayensis* to a less preferred territory.

### 189 **2.3 Description of the territorial distribution of *Leptuca uruguayensis* and *Leptuca*** 190 ***cumulanta***

191 To describe whether *L. cumulanta* share their territory with *L. uruguayensis* in  
192 the same level of the intertidal zone, we observed their distribution during spring low  
193 tides. We traced five transects in the intertidal region (site 1; Fig. 1), parallel to the  
194 water line and separated by a distance of one metre. Transect 1 was made at the inferior  
195 limit of the intertidal zone (close to the water at low tide); the other transects were  
196 subsequently positioned at one-metre intervals toward land. Each transect was

197 composed of 10 quadrants of 70 x 70 cm distributed on the same topographic horizon,  
198 with a distance of 15 cm between them. Every crab assembly was sampled from the  
199 lower to the upper intertidal region encompassing the entire intertidal zone. We  
200 excavated all burrows in each quadrant (sample units) and counted all *L. uruguayensis*  
201 and *L. cumulanta* individuals to estimate their density.

#### 202 **2.4 Habitat selection by *Leptuca uruguayensis***

203 To evaluate if the presence of *L. cumulanta* modifies the habitat selection of *L.*  
204 *uruguayensis*, we conducted a manipulative habitat-choice experiment in the laboratory.  
205 The experiment consisted of presenting a combination of two options (on both sides of a  
206 terrarium) from three microhabitats with different visual stimuli for a focal *L.*  
207 *uruguayensis* male: (1) empty microhabitat, (2) microhabitat occupied by *L.*  
208 *uruguayensis*, or (3) microhabitat occupied by *L. cumulanta*. We chose one reference  
209 side from each combinations expecting the following hypothesis: 1) No preference  
210 when the two sides present the same stimulus (0.5 of choice; Fig. 2: T1, T2, and T3); 2)  
211 Preference for the reference side when it is empty (irrespectively of the competitor on  
212 the other side) or when the reference side contains a conspecific and the other side  
213 contain *L. cumulanta* (>0.5 of choice for the reference side; Fig. 2: T4, T5 and T6); 3)  
214 Avoidance for the reference side when the opposite side is empty (irrespectively of the  
215 competitor on the reference side), or when the reference side is compound by a  
216 heterospecific stimulus and with conspecifics on the other side (<0.5 of choice for the  
217 reference side; Fig. 2: T7, T8 and T9). As we always had a reference side, we presented  
218 the same two microhabitats possibilities combined for the same terrarium to ensure the  
219 independence of predictive variables, dividing into two treatments to compare crabs'  
220 choice for each habitat separately (Olabarria et al., 2002; Underwood, 2004). For each  
221 replicate stimuli was tested a group composed by four differently *L. uruguayensis*

222 males. We used as response variable both initial (when we released the focal crab in the  
223 terrarium) and final proportion of microhabitat choices (15 minutes after the focal crab  
224 was released in the terrarium) by *L. uruguayensis* groups. Thus, our experimental design  
225 was composed by 76 males per treatment and 684 male crabs for all treatments (9  
226 treatments x 19 replicates per treatment x 4 males per replicate).

227 We selected only adult males with carapace width (CW) 7–10 mm (Pralon and  
228 Negreiros-Fransozo, 2008; Hirose et al., 2013) for both species (mean  $\pm$  SD; *L.*  
229 *uruguayensis*:  $8.89 \pm 1.00$  mm, *L. cumulanta*  $9.23 \pm 0.61$  mm). Regarding the major  
230 claw length, *L. uruguayensis* was  $14.45 \pm 2.59$  mm and *L. cumulanta* was  $14.49 \pm 1.91$   
231 mm. We standardised the size of crabs since males with larger carapaces and chelipeds  
232 present advantages in combat over individuals with smaller features (Jennions and  
233 Backwell, 1996; Jaroensutasinee and Tantichodok, 2002).

234 Crabs were collected (site 2; Fig. 1) and kept for 12 h in individual containers  
235 containing 10 ml of water (salinity 27) at  $25.7 \pm 0.21$  °C and fed with macerated  
236 aquarium fish feed. We used a terrarium (40 x 10 x 20 cm in length, width, and height,  
237 respectively) separated by a glass plate (10 x 10 cm, width and height) which created  
238 two microhabitats (20 x 10 x 20 cm). The microhabitat area was based on the maximum  
239 field density for *L. uruguayensis*, and thus each compartment was sufficient for each  
240 crab establish its territory (De Grande et al., 2018). The terrarium was filled with 10 cm  
241 of sediment (mean height of *L. uruguayensis*' burrows; Machado et al., 2013) from the  
242 natural environment of both species. In total, we collected 360 litres of sediment from  
243 the superficial region of overlap of both species' territories. We used a 1 mm mesh to  
244 sift the sediment, removing coarse debris and benthic organisms. Then, we mixed and  
245 homogenised the sediment for 15 min to prevent bias in granulometric composition as a  
246 potential interference factor in choice. Based on Suguio's (1973) classification, a

247 granulometric analysis showed that the mean sediment composition used in the  
248 experiments was 0.03% coarse sand, 0.98% medium sand, 53.94% fine sand, 41.03%  
249 very fine sand, and 4.09% mud.

250       Individuals used as visual stimuli remained in the predetermined microhabitat  
251 and visible above the sediment surface. To prevent crabs used as visual stimuli from  
252 digging into their burrows, we glued a line to the carapace and attached it to a wooden  
253 shaft (12 cm long) to be inserted in the substrate (Booksmythe et al., 2010b). Thus,  
254 focal *L. uruguayensis* males could indeed recognise microhabitats occupied by a  
255 conspecific or a heterospecific stimulus. We placed the crabs used as visual stimuli into  
256 the microhabitats as described and acclimated them to the experimental conditions for  
257 10 min. Males of *L. uruguayensis* were then reallocated in the terrarium for behavioural  
258 analysis where they were able to observe both habitats and identify the visual stimulus.  
259 For this, a PVC plate (6 x 6 cm) was placed in the centre of the terrarium, and to keep  
260 the crab above the plate, we used a translucent plastic container (4 cm diameter) as a  
261 barrier to prevent burrowing behaviour. Males were kept under these experimental  
262 conditions for 10 min. After this step, we obtained the initial selection by removing the  
263 barrier and observing ( $\approx$  1 minute) which side *L. uruguayensis* moved toward (when  
264 their body was 100% on one side of the terrarium, away from the PVC plate). Then,  
265 after 15 min, we obtained the final selection by determining which side *L. uruguayensis*  
266 chose to inhabit (crab usually dug burrows in the selected habitat). Lastly, the focal  
267 male was removed from the terrarium, the sediment was rearranged, and another *L.*  
268 *uruguayensis* male was inserted until the complete the group of four individuals were  
269 tested.

## 270 **2.5 Agonistic interaction**

271 To test whether the agonist interactions of *L. uruguayensis* increase as a result of  
272 the presence of *L. cumulanta*, we performed a field experiment where both species were  
273 found and shared neighbouring territories (site 3; Fig. 1). We created three experimental  
274 groups, each one composed of two male individuals in the following combinations: (1)  
275 *L. uruguayensis* x *L. uruguayensis* (n = 23), (2) *L. uruguayensis* x *L. cumulanta* (n = 20)  
276 and (3) *L. cumulanta* x *L. cumulanta* (n = 19). We chose only neighbouring pairs where  
277 there was no other crab between them to avoid direct interference from other  
278 individuals.

279 To evaluate whether the number of agonistic interactions differs between  
280 neighbouring pairs, we selected an agonistic behaviour characteristic of fiddler crab  
281 interactions (Booksmythe et al., 2010a; Fogo et al., 2019): touch/push (using the surface  
282 of the cheliped to touch/push the opponent). We selected only this behaviour because it  
283 was the most representative agonistic interaction observed during fights. We also  
284 observed grapple and flick/dig out behaviours, but we excluded them from analysis due  
285 to low frequency or absence of these interactions. After selecting our focal crabs, we  
286 positioned ourselves about one metre away, waited five minutes until activity resumed  
287 and then evaluated their agonistic behaviour. We observed and recorded the number of  
288 touch/push behaviours for 10 minutes. At the end of each observation, we captured the  
289 individuals and measured their major claw length and the distance between their  
290 burrows.

## 291 **2.6 Statistical analyses**

292 We used Generalized Linear Models (GLM) in all analyses performed to test our  
293 hypotheses. Models were performed in R (R Core Team, 2018) using the package *MASS*  
294 (Venables and Ripley, 2002). To evaluate whether the habitat selection of *L.*  
295 *uruguayensis* is biased by the presence of *L. cumulanta*, we compared the average

296 proportion in which the *L. uruguayensis* males selected one microhabitat-side of the  
297 terrarium according to the treatment type. We used the choice proportion of a group of  
298 *L. uruguayensis* (four males) at the beginning (initial choice) and the end of the  
299 experiment (final choice). The proportion was expressed as the success of choosing the  
300 terrarium side expected out of the total number of choices (i.e.,  $\frac{\text{choice in the}}{\text{expected side, number total of choices}}$  in R function. The treatment type (nine levels:  
301 T1 to T9) was fitted as a fixed factor. Proportion data were fitted to a binomial  
302 distribution with a logit link function.  
303

304 To test whether the presence of the range-extending species *L. cumulanta* affects  
305 the frequency that agonistic interactions were employed in fights, we used the count  
306 data of touch/push movements as a response variable. The fighting group (three levels:  
307 *L. uruguayensis* vs *L. uruguayensis*, *L. uruguayensis* vs *L. cumulanta*, and *L. cumulanta*  
308 vs *L. cumulanta*) was fitted as a fixed factor. Size is an important trait determinant of  
309 fight intensity in animal contests (Morrell et al., 2005). The distance between opponents  
310 may also be indicative of territory size or foraging area, and due to that, may increase  
311 animal territorial defense postures (Di Virgilio and Ribeiro, 2013). We used the claw  
312 size difference (CSD) between opponents and the distance between the resident burrows  
313 (DRB) as covariates in the models (both continuous variables). Counting data were  
314 overdispersed (Zuur et al., 2013). We used a negative binomial error distribution with a  
315 log link since it is appropriate to deal with overdispersion data (Zuur et al., 2013). We  
316 analysed the count data as a subset of different GLM candidate models and compared  
317 them using the Akaike information criterion adjusted for small sample size (AICc) (See  
318 Table 1 for details). Then, we selected the models with the lowest  $\Delta\text{AICc}$  values and  
319 higher Akaike weights, which could provide the best-estimated-predictive accuracies to  
320 support our results (Burnham and Anderson, 1998). The statistical significance of the

321 factors was assessed by comparing the model with and without the factor included using  
322 likelihood-ratio tests (LRT). Where relevant, post-hocs for all comparisons at different  
323 levels between factors were performed using an *lsmeans* package (Lenth, 2016) with  
324 Tukey's tests for multiple comparisons. We considered 95% as the significance level in  
325 all analyses.

### 326 **3. Results**

#### 327 **3.1 Territorial distribution**

328 In the field, the resident species *L. uruguayensis* showed a mean density of  
329  $11.87 \pm 12.53$  ind./m<sup>2</sup> and mean CW (carapace width) of  $6.29 \pm 2.76$ . The population of  
330 *L. uruguayensis* was composed of 49.14% females of which 11.8% were ovigerous.  
331 *Leptuca cumulanta* showed a density of  $2.93 \pm 2.67$  ind./m<sup>2</sup> and mean CW of  $7.23 \pm$   
332  $3.03$ . The *L. cumulanta* population was composed of 43.83% females of which 12.5%  
333 were ovigerous.

334 The higher densities of *L. cumulanta* were observed in the lower intertidal level  
335 (Fig. 3: T1–T3), while higher densities of *L. uruguayensis* were found in the upper  
336 intertidal level (Fig. 3: T3–T5). However, the distribution of the range-extending  
337 species *L. cumulanta* overlapped the entire distribution of the resident species *L.*  
338 *uruguayensis* (Fig. 3: T2–T5). Thus, both species occur in the same level of the  
339 intertidal zone, composing a mixed assemblage of fiddler crabs. We observed the range-  
340 extending and resident species living in neighbouring burrows.

#### 341 **3.2 Habitat selection**

342 Males of *L. uruguayensis* did not show any pattern of microhabitat choice  
343 regarding the presence of a conspecific or heterospecific stimulus (Fig. 4). Neither of  
344 our hypotheses was corroborated and no significant differences were observed for initial  
345 (GLM:  $X^2_8 = 1.7314$ ,  $P = 0.98$ ) and final selection (GLM:  $X^2_8 = 1.3698$ ,  $P = 0.99$ ) of  
346 microhabitats according to each treatment type.

### 347 3.3 Agonistic interaction

348 We retained the first three models based on  $\Delta\text{AICc}$  and weights comparisons in  
349 the final set (Table 1), regarding the relative strength of support of these models in  
350 agonistic interactions between the fiddler crabs fights. The most parsimonious model  
351 only included the fighting group as a fixed factor (AICc: 230.0, weights: 0.240; Table  
352 1). There was a significant effect on the amount of touch/push behaviour depending on  
353 the fighting group type (GLM: fight group effect:  $X_2^2 = 7.0006$ ,  $P < 0.05$ ). Males  
354 employed more touching/pushing movements in conspecific fights of *L. uruguayensis*  
355 than compared with conspecific fights between *L. cumulanta* males ( $Z = -2.586$ ,  $P <$   
356  $0.05$ , Tukey post-hoc, Fig. 5). There was no difference in touch/push movements  
357 employed between *L. uruguayensis* x *L. uruguayensis* treatment and *L. uruguayensis* x  
358 *L. cumulanta* treatment ( $Z = -1.479$ ,  $P = 0.30$ , Fig. 5), as well as for fights between *L.*  
359 *cumulanta* x *L. cumulanta* and *L. uruguayensis* x *L. cumulanta* ( $Z = -1.146$ ,  $P = 0.48$ ,  
360 Fig. 5). The second predictive model (AICc: 230.6, weights: 0.181) contained the  
361 fighting group as a fixed effect and the CSD as a covariate, but only the fighting group  
362 (GLM: fight group effect:  $X_2^2 = 7.1935$ ,  $P < 0.05$ ) had effect on males agonistic  
363 behaviour, with no effect of CSD (GLM: CSD effect:  $X_1^2 = 1.8220$ ,  $P = 0.17$ ). The third  
364 model (AICc: 231.3, weights: 0.125) contained the DRB as covariate, however, there  
365 was no evidence of its effect on touch/pushing behaviour between the resident males  
366 (GLM: DRB effect:  $X_1^2 = 2.9475$ ,  $P = 0.08$ ).

### 367 4. Discussion

368 We tested whether the recent extension of *L. cumulanta* into the territory of *L.*  
369 *uruguayensis* could have ecological and behavioural effects on the native species. We  
370 found that *L. cumulanta* overlaps the entire distribution of *L. uruguayensis* in the  
371 intertidal zone, composing a mixed assembly of fiddler crabs. However, *L.*



372 *uruguayensis* males were unresponsive in habitat choice and agonistic behaviour to the  
373 presence of *L. cumulanta*. Other biotic and abiotic factors such as temperature,  
374 predation, quality of food resources, and mean grain size of sediment may play an  
375 important role in fiddler crab distribution (Botto and Iribarne, 2000; Bouillon et al.,  
376 2002; Meziane et al., 2002; Sanford et al., 2006; Kon et al., 2007; Checon and Costa,  
377 2017). These factors could be more determinant in the distribution of *L. uruguayensis*  
378 than the presence of their congener *L. cumulanta*. Thus, our initial hypotheses were  
379 refuted. Low interference between recent heterospecific neighbours sharing the same  
380 habitat revealed no negative effects on habitat selection or agonistic interactions  
381 between these fiddler crab species under this scenario—an early stage of species  
382 overlap.

383         Herein we showed that the density of  $11.87 \pm 12.53$  ind./m<sup>2</sup> of resident species  
384 *L. uruguayensis* is similar to that described in previous studies conducted in the same  
385 area of the present study (see Checon and Costa, 2017; De Grande et al., 2018). On the  
386 other hand, the range-extending species *L. cumulanta* increased more than 20 times in  
387 less than one decade, from 0.14 ind./m<sup>2</sup> in 2010 (Checon and Costa, 2017) to 2.93  
388 ind./m<sup>2</sup> in 2017 (present work). We found 12.5% of ovigerous females in the *L.*  
389 *cumulanta* population, which suggests it is well established and shows the potential to  
390 increase in population density in the Santos/São Vicente estuary in the next few years.  
391 Considering that the increase of the average global temperature can favour the  
392 expansion of fiddler crabs into higher latitudes zones (Sandford et al., 2006; Johnson,  
393 2014; Rosenberg, 2018), we suggest that *L. cumulanta* could reach southern latitudes.  
394 Further studies should continue to monitor the expansion of this and other fiddler crab  
395 species over spatial and temporal scales as well as their potential ecological impact in  
396 newly established areas.

397           Considering territorial distribution, our field results showed that *L. uruguayensis*  
398 overlapped territories and lived in habitats at the same level of the intertidal zone as *L.*  
399 *cumulanta*, which corroborated the results from the laboratory experiment about habitat  
400 selection. The presence of *L. cumulanta* as a stimulus did not influence the microhabitat  
401 choice of *L. uruguayensis*, which chose where to dig their burrows regardless of the  
402 presence of conspecific or heterospecific stimuli. Habitat avoidance is expected when  
403 heterospecifics represent a strong competitor able to monopolise resources and,  
404 consequently, dislodge inferior competitors to marginal areas and less desirable habitats  
405 (Larson, 1980; Hudina et al., 2014). Since *L. uruguayensis* do not avoid habitats  
406 occupied by *L. cumulanta*, the latter might not cause negative impacts on *L.*  
407 *uruguayensis* behaviour.

408           In the habitat choice experiment, heterospecific and conspecific males were used  
409 as stimuli but were contained so they were unable to dig a burrow during the  
410 experiment. The burrow is a valuable resource to resident males, which demands time  
411 and energy to dig or to repair after every tide. Floater males are more motivated to take  
412 a burrow from resident males, staying longer in fights as compared to neighbouring  
413 males (Jennions and Backwell, 1996; Cannicci et al., 1999; Fogo et al., 2019). Once in  
414 the terrarium microhabitat where burrows were not available to focal males, they could  
415 be indifferent to *L. uruguayensis* in choosing a side with a heterospecific or conspecific  
416 presence, since neither side represented a great investment in terms of resource values.  
417 Furthermore, our study was conducted in a scenario in which *L. cumulanta* showed a  
418 low density, and their effects on *L. uruguayensis* may be dependent on density. In this  
419 sense, future studies considering a scenario of higher densities of *L. cumulanta* will be  
420 necessary to better understand the ecological interaction between species.

421 Males of *L. uruguayensis* did not increase touch/push behavior when its  
422 neighbour was an *L. cumulanta*. This result suggests that *L. uruguayensis* males do not  
423 adjust their aggressiveness or have no behavioral implication due to the presence of *L.*  
424 *cumulanta*, an expansive, larger and less aggressive species. In other fiddler crab  
425 species, maintaining a known neighbour might be less costly than renegotiating  
426 territorial boundaries with a new neighbour, irrespectively of species (Sanches et al.,  
427 2018). Interactions between fiddler crabs may be due to the level of threat that an  
428 individual represents rather than the species itself (heterospecific), which could explain  
429 the non-influence of aggressiveness of *L. cumulanta* on *L. uruguayensis* in our study.  
430 The fact that fiddler crabs accept neighbours of other species suggests that they are able  
431 to live in mixed assemblages and share the same physical niche (Clark and Backwell,  
432 2017). The threat posed by an intruder is higher than between known neighbours  
433 (Booksmythe et al., 2010a), and the fight between a resident x floater conspecific lasts  
434 longer and is more intense than a resident x floater heterospecific (Fogo et al., 2019).  
435 Thus, the expansion of latitudinal distribution of some species of fiddler crabs (see  
436 Nabout et al., 2009; Johnson, 2014; Rosenberg, 2018) and the consequent overlapping  
437 habitats—similar species may be able to occupy the same space—were evidenced  
438 herein for *L. cumulanta* and *L. uruguayensis*. On the other hand, Sanches et al. (2018)  
439 showed that living in mixed populations could be costly for *Austruca mjoebergi* because  
440 males do not recognise the females of their own species, causing an impact in the social  
441 and mating systems of this species. The less aggressive behaviour observed here for *L.*  
442 *cumulanta* could indicate a limitation of expansion into areas occupied by *L.*  
443 *uruguayensis*, a species that uses higher levels of aggressive behaviour. Therefore, the  
444 conclusions of this study are restricted to two fiddler crab species in the context bias  
445 mentioned above, where we analysed only one behavioural parameter. Agonistic

446 interactions can vary among fiddler crab species, so studies focusing territory range  
447 expansion and their effects in resident congeners of other species under different  
448 densities are also very relevant.

449         The impacts of climate change affect the distribution of various organisms, and  
450 poleward expansions of species can alter the functional structure of newly colonised  
451 communities due to interspecific competitive interactions (Kortsch et al., 2015). In the  
452 Barents Sea, the poleward expansion of the cod *Gadus morhua* due to temperature  
453 increase is associated with a decline of harp seals *Pagophilus groenlandicus* due to the  
454 competition for prey between species (Bogstad et al., 2015). The potential competition  
455 from the poleward extension of tropical reef corals *Acropora hyacinthus* and *A.*  
456 *muricata* in Japan might cause the decline of five endemic coral species and change the  
457 composition of the fish community (Yamano et al., 2011). An integrated assessment of  
458 how species composition and habitats respond to competitive processes caused by  
459 territorial shifts is needed, although there are a few studies on this topic (Dukes and  
460 Mooney, 1999; Musolin, 2007; Walther et al., 2009). In some cases, the newly settled  
461 species become essential for habitat functioning and local ecosystem services  
462 (Pessarrodona et al., 2018). The poleward extension of the temperate kelps into marine  
463 forest communities in the north-east Atlantic, for instance, increased the biomass  
464 production, the flux of detritus and support higher densities of native invertebrate  
465 grazers (Pessarrodona et al., 2018).

466         In summary, we demonstrated that *L. cumulanta* and *L. uruguayensis* are able to  
467 share habitat and live in mixed assemblages in the context of our study, thus presenting  
468 an early stage of overlapping species. The fact they share the same habitat and live in a  
469 mixed assemblage may not be disadvantageous for both species in a perspective of  
470 latitudinal expansion of species related to climate change. Other studies should be

471 performed to explore possible effects on resident species such as their reproductive  
472 period or if sexual maturity is altered by the presence of *L. cumulanta*, the availability  
473 of their food resources and in the context of increased density of populations of newly  
474 established species. Alternatively, further evaluation of potential competitive  
475 interactions between *L. uruguayensis* and *L. cumulanta* during early ontogenetic phases,  
476 such as in settlement and juvenile stages, could improve our understanding of habitat  
477 sharing by fiddler crabs.

#### 478 **5. Acknowledgments**

479 We would like to thank Dr. Hélio H. Checon and Msc. Ivan R. A. Laurino for  
480 their valuable comments on this manuscript, Msc Marcelo Wendeborn Miranda de  
481 Oliveira for his help in field data collection and the structural support from Coastal  
482 Campus of São Vicente, of São Paulo State University (UNESP). This work was  
483 developed during a course in estuarine systems offered by the PPG in Biological  
484 Sciences under the coordination of Prof. Dr. Tânia M. Costa, Dr. Fábio H.C. Sanches,  
485 and Dr. Caio A. Miyai. This research had permission from the System of Authorisation  
486 and Information on Biodiversity (Sisbio), Brazilian Ministry of the Environment  
487 (number: 62200-1). All applicable institutional and/or national guidelines for the care  
488 and use of animals were followed. This work was financially supported by grant  
489 #2015/50300-6, São Paulo Research Foundation (FAPESP) (Costa, T.M.).

#### 490 **6. Bibliographic references:**

491 Bogstad, B., Gjørseter, H., Haug, T., Lindstrøm, U., 2015. A review of the battle  
492 for food in the Barents Sea: cod vs. marine mammals. *Front. Ecol. Evol.* 3, 29.  
493 <https://doi.org/10.3389/fevo.2015.00029>

- 494 Booksmythe, I., Jennions, M.D., Backwell, P.R., 2010a. Investigating the ‘dear  
495 enemy’ phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*. Anim.  
496 Behav. 79, 419-423. <https://doi.org/10.1016/j.anbehav.2009.11.020>
- 497 Booksmythe, I., Jennions, M.D., Backwell, P.R. 2010b. Interspecific assistance:  
498 fiddler crabs help heterospecific neighbours in territory defence. Biol. letters. 6, 748-750.
- 499 Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs  
500 (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and  
501 transport in estuarine environments. Estuar. Coast. Shelf. Sci. 51, 141-151.  
502 <https://doi.org/10.1006/ecss.2000.0642>
- 503 Bouillon, S., Koedam, N., Raman, A., Dehairs, F., 2002. Primary producers  
504 sustaining macro-invertebrate communities in intertidal mangrove  
505 forests. Oecologia. 130, 441-448. <https://doi.org/10.1007/s004420100814>
- 506 Brown, B.J., Mitchell, R.J., Graham, S.A., 2002. Competition for pollination  
507 between an invasive species (purple loosestrife) and a native congener. Ecology. 83,  
508 2328-2336. <https://doi.org/10.2307/3072063>
- 509 Burnham, K.P., Anderson, D.R., 1998. Practical use of the information-theoretic  
510 approach, in: Burnham, K.P., Anderson, D.R. (Eds.), Model Selection and Inference.  
511 Springer, New York, 75-117. [https://doi.org/10.1007/978-1-4757-2917-7\\_3](https://doi.org/10.1007/978-1-4757-2917-7_3)
- 512 Cannicci, S., Fratini, S., Vannini, M., 1999. Short-range Homing in Fiddler Crabs  
513 (Ocypodidae, Genus *Uca*): A Homing Mechanism not Based on Local Visual Landmarks.  
514 Ethology. 105, 867-880. <https://doi.org/10.1046/j.1439-0310.1999.00453.x>
- 515 Checon, H.H., Costa, T.M., 2017. Fiddler crab (Crustacea: Ocypodidae)  
516 distribution and the relationship between habitat occupancy and mouth appendages. Mar.  
517 Bio. Res. 13, 618-629. <https://doi.org/10.1080/17451000.2016.1273530>

- 518           Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid  
519 range shifts of species associated with high levels of climate warming. *Science*. 333,  
520 1024-1026. <https://doi.org/10.1126/science.1206432>
- 521           Clark, H.L., Backwell, P.R.Y., 2017. Territorial battles between fiddler crab  
522 species. *R. Soc. Open Sci.* 4, 160621. <https://doi.org/10.1098/rsos.160621>
- 523           Cordeiro, C.A.M.M., Costa, T.M., 2010. Evaluation of solid residues removed  
524 from a mangrove swamp in the São Vicente Estuary, SP, Brazil. *Mar. Pollut Bull.* 60,  
525 1762-1767. <https://doi.org/10.1016/j.marpolbul.2010.06.010>
- 526           Crane, J., 1975. *Fiddler Crabs of the World*. Princeton University Press, New  
527 Jersey
- 528           De Grande, F.R., Granado, P., Sanches, F.H.C., Costa, T.M., 2018. Organic matter  
529 affects fiddler crab distribution? Results from field and laboratorial trials. *Estuar. Coast.*  
530 *Shelf. Sci.* 212, 138-145. <https://doi.org/10.1016/j.ecss.2018.07.005>
- 531           Di Virgilio, A., Ribeiro, P.D., 2013. Spatial and temporal patterns in the feeding  
532 behavior of a fiddler crab. *Mar. Bio.* 160, 1001-1013. [https://doi.org/10.1007/s00227-](https://doi.org/10.1007/s00227-012-2153-9)  
533 [012-2153-9](https://doi.org/10.1007/s00227-012-2153-9)
- 534           Duckworth, R.A., Badyaev, A.V., 2007. Coupling of dispersal and aggression  
535 facilitates the rapid range expansion of a passerine bird. *Proc. Natl. Acad. Sci. U.S.A.*  
536 104, 15017-15022. <https://doi.org/10.1073/pnas.0706174104>
- 537           Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of  
538 biological invaders? *Trends. Ecol. Evol.* 14, 135-139. [https://doi.org/10.1016/s0169-](https://doi.org/10.1016/s0169-5347(98)01554-7)  
539 [5347\(98\)01554-7](https://doi.org/10.1016/s0169-5347(98)01554-7)
- 540           Eaton, J.G., Scheller, R.M., 1996. Effects of climate warming on fish thermal  
541 habitat in streams of the United States. *Limnol. Oceanogr.* 41, 1109-1115.  
542 <https://doi.org/10.4319/lo.1996.41.5.1109>

- 543           Ernakovich, J.G., Hopping, K.A., Berdanier, A.B., Simpson, R.T., Kachergis,  
544 E.J., Steltzer, H., Wallenstein, M.D., 2014. Predicted responses of arctic and alpine  
545 ecosystems to altered seasonality under climate change. *Glob. Change. Biol.* 20, 3256-  
546 3269. <https://doi.org/10.1111/gcb.12568>
- 547           Fogo, B.R., Sanches, F.H., Costa, T.M., 2019. Testing the dear enemy relationship  
548 in fiddler crabs: Is there a difference between fighting conspecific and heterospecific  
549 opponents? *Behav. Processes.* 192, 90-96. <https://doi.org/10.1016/j.beproc.2019.02.001>
- 550           Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species  
551 richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393-403.  
552 <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- 553           Hirose, G.L., Fransozo, V., Tropea, C., López-Greco, L.S., Negreiros-Fransozo,  
554 M.L., 2013. Comparison of body size, relative growth and size at onset sexual maturity  
555 of *Uca uruguayensis* (Crustacea: Decapoda: Ocypodidae) from different latitudes in the  
556 south-western Atlantic. *J. Mar. Biol. Assoc. U.K.* 93, 781-788.  
557 <https://doi.org/10.1017/s0025315412001038>
- 558           Hudina, S., Hock, K., Žganec, K., 2014. The role of aggression in range expansion  
559 and biological invasions. *Curr. Zool.* 60, 401-409.  
560 <https://doi.org/10.1093/czoolo/60.3.401>
- 561           Jaroensutasinee, M., Tantichodok, P., 2002. Effects of size and residency on  
562 fighting outcomes in the fiddler crab, *Uca vocans hesperiae* (Decapoda, Brachyura,  
563 Ocypodidae). *Crustaceana.* 75, 1107-1117.  
564 <https://doi.org/10.1163/156854002763270509>
- 565           Jennions, M.D., Backwell, P.R., 1996. Residency and size affect fight duration  
566 and outcome in the fiddler crab *Uca annulipes*. *Biol. J. Linn. Soc.* 57, 293-306.  
567 <https://doi.org/10.1111/j.1095-8312.1996.tb01851.x>



- 568 Johnson, D.S., 2014. Fiddler on the roof: a northern range extension for the marsh  
569 fiddler crab *Uca pugnax*. J. Crustac. Biol. 34, 671–673.  
570 <https://doi.org/10.1163/1937240x-00002268>
- 571 Jones, C.G., Lawton, J.H., Shachak, M., Jones, C.G., Lawton, J.H., Shachak, M.,  
572 1994. Organisms as ecosystem engineers. Oikos. 69, 373–386.  
573 <https://doi.org/10.2307/3545850>
- 574 Kon, K., Kurokura, H., Hayashizaki, K., 2007. Role of microhabitats in food webs  
575 of benthic communities in a mangrove forest. Mar. Ecol. Prog. Ser. 340, 55-62.  
576 <https://doi.org/10.3354/meps340055>
- 577 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V., Aschan, M., 2015.  
578 Climate change alters the structure of arctic marine food webs due to poleward shifts of  
579 boreal generalists. Proc. R. Soc. B. 282, 20151546.  
580 <https://doi.org/10.1098/rspb.2015.1546>
- 581 Larson, R.J., 1980. Competition, habitat selection, and the bathymetric  
582 segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50, 221-239.  
583 <https://doi.org/10.2307/1942480>
- 584 Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat.  
585 Soft. 69, 1-33. <https://doi.org/10.18637/jss.v069.i01>
- 586 Machado, G.B.O., Gusmão-Junior, J.B., Costa, T.M., 2013. Burrow morphology  
587 of *Uca uruguayensis* and *Uca leptodactylus* (Decapoda: Ocypodidae) from a subtropical  
588 mangrove forest in the western Atlantic. Integr. Zool. 8, 307-314.  
589 <https://doi.org/10.1111/j.1749-4877.2012.00297.x>
- 590 Mandrak, N.E., 1989. Potential invasion of the Great Lakes by fish species  
591 associated with climatic warming. J. Great. Lakes. Res. 15, 306-316.  
592 [https://doi.org/10.1016/s0380-1330\(89\)71484-2](https://doi.org/10.1016/s0380-1330(89)71484-2)

- 593 Maximov, A.A., 2011. Large-scale invasion of *Marenzelleria* spp. (Polychaeta;  
594 Spionidae) in the eastern Gulf of Finland, Baltic Sea. Russ. J. Biol. Invasions. 2, 11-19.  
595 <https://doi.org/10.1134/s2075111711010036>
- 596 McCraith, B.J., Gardner, L.R., Wethey, D.S., Moore, W.S., 2003. The effect of  
597 fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic  
598 gradient in a southeastern salt marsh. J. Mar. Res. 61, 359-390.  
599 <https://doi.org/10.1357/002224003322201232>
- 600 Meziane, T., Sanabe, M.C., Tsuchiya, M., 2002. Role of fiddler crabs of a  
601 subtropical intertidal flat on the fate of sedimentary fatty acids. J. Exp. Mar. Biol.  
602 Ecol. 270, 191-201. [https://doi.org/10.1016/s0022-0981\(02\)00019-9](https://doi.org/10.1016/s0022-0981(02)00019-9)
- 603 Morrell, L.J., Backwell, P.R., Metcalfe, N.B., 2005. Fighting in fiddler crabs *Uca*  
604 *mjoebergi*: what determines duration?. Anim. Behav. 70, 653-662.  
605 <https://doi.org/10.1016/j.anbehav.2004.11.014>
- 606 Munguia, P., Backwell, P.R., Darnell, M.Z., 2017. Thermal constraints on  
607 microhabitat selection and mating opportunities. Anim. Behav. 123, 259-265.  
608 <https://doi.org/10.1016/j.anbehav.2016.11.004>
- 609 Musolin, D.L., 2007. Insects in a warmer world: ecological, physiological and  
610 life-history responses of true bugs (Heteroptera) to climate change. Global Change Biol.  
611 13, 1565-1585 <https://doi.org/10.1111/j.1365-2486.2007.01395.x>
- 612 Nabout, J.C., Júnior, M., Bini, L.M., Diniz Filho, J.A.F., 2009. Distribuição  
613 geográfica potencial de espécies americanas do caranguejo “violinista” (*Uca* spp.)  
614 (Crustacea, Decapoda) com base em modelagem de nicho ecológico. Iheringia. 99, 92-98  
615 <https://doi.org/10.1590/s0073-47212009000100013>
- 616 Natálio, L.F., Pardo, J.C., Machado, G.B., Fortuna, M.D., Gallo, D.G., Costa,  
617 T.M., 2017. Potential effect of fiddler crabs on organic matter distribution: A combined

- 618 laboratory and field experimental approach. *Estuar. Coast. Shelf. Sci.* 184, 158-165.  
619 <https://doi.org/10.1016/j.ecss.2016.11.007>
- 620 Olabarria, C., Underwood, A., Chapman, M., 2002. Appropriate experimental  
621 design to evaluate preferences for microhabitat: an example of preferences by species of  
622 microgastropods. *Oecologia*. 132, 159-166. <https://doi.org/10.1007/s00442-002-0940-6>
- 623 Orians, G.H., 2000. Behavior and community structure. *Etologia*. 8, 43-51.
- 624 Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change  
625 impacts across natural systems. *Nature*. 421, 37-42. <https://doi.org/10.1038/nature01286>
- 626 Pessarrodona, A., Moore, P.J., Sayer, M.D., Smale, D.A., 2018. Carbon  
627 assimilation and transfer through kelp forests in the NE Atlantic is diminished under a  
628 warmer ocean climate. *Global Change Biol.* 24, 4386-4398.  
629 <https://doi.org/10.1111/gcb.14303>
- 630 Poff, N.L., Brinson, M.M., Day, J.W., 2002. Aquatic ecosystems & Global  
631 climate change: Potential impacts on Inland Freshwater and Coastal Wetland  
632 Ecosystems in the United States. *Pew Center on Global Climate Change*. 44, 1-36.
- 633 Pralon, B.G.N., Negreiros-Fransozo, M.L., 2008. Relative growth and  
634 morphological sexual maturity of *Uca cumulanta* (Crustacea: Decapoda: Ocypodidae)  
635 from a tropical Brazilian mangrove population. *J. Mar. Biol. Assoc. U.K.* 88, 569-574.  
636 <https://doi.org/10.1017/s0025315408000453>
- 637 R Core Team, 2018. R: A language and environment for statistical computing. R  
638 Foundation for Statistical Computing, Vienna, Austria.
- 639 Rahel, F.J., Olden, J.D., 2008. Assessing the effects of climate change on aquatic  
640 invasive species. *Conserv. Biol.* 22, 521-533. [https://doi.org/10.1111/j.1523-  
641 1739.2008.00950.x](https://doi.org/10.1111/j.1523-1739.2008.00950.x)

- 642 Reinsel, K.A., 2004. Impact of fiddler crab foraging and tidal inundation on an  
643 intertidal sandflat: season-dependent effects in one tidal cycle. *J. Exp. Mar. Biol. Ecol.*  
644 313, 1-17. <https://doi.org/10.1016/j.jembe.2004.06.003>
- 645 Rombouts, I., Beaugrand, G., Ibañez, F., Gasparini, S., Chiba, S., Legendre, L.,  
646 2009. Global latitudinal variations in marine copepod diversity and environmental  
647 factors. *Proc. R. Soc. B.* 276, 3053-3062. <https://doi.org/10.1098/rspb.2009.0742>
- 648 Rosenberg, M.S., 2018. New record and range extension of the fiddler crab *Uca*  
649 *princeps* (Smith, 1870) (Brachyura, Ocypodidae) from California, USA. *J. Crustac. Biol.*  
650 38, 823-824. <https://doi.org/10.1093/jcbiol/ruy071>
- 651 Sanches, F.H.C., Costa, T.M., Barreto, R.E., Backwell, P.R.Y., 2018. The cost of  
652 living in mixed species populations: A fiddler crab example. *J. Exp. Mar. Biol. Ecol.* 500,  
653 30-33. <https://doi.org/10.1016/j.jembe.2017.12.010>
- 654 Sanford, E., Holzman, S.B., Haney, R.A., Rand, D.M., Bertness, M.D., 2006.  
655 Larval tolerance, gene flow, and the northern geographic range limit of fiddler  
656 crabs. *Ecology.* 87, 2882-2894. [https://doi.org/10.1890/0012-9658\(2006\)87\[2882:lgtfat\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[2882:lgtfat]2.0.co;2)
- 657
- 658 Scheffel, W.A., Heck, K.L., Johnson, M.W., 2018. Tropicalization of the northern  
659 Gulf of Mexico: impacts of salt marsh transition to black mangrove dominance on faunal  
660 communities. *Estuaries Coasts.* 41, 1193-1205. <https://doi.org/10.1007/s12237-017-0334-y>
- 661
- 662 Sharma, S., Jackson, D.A., Minns, C.K., Shuter, B.J., 2007. Will northern fish  
663 populations be in hot water because of climate change? *Global Change Biol.* 13, 2052-  
664 2064. <https://doi.org/10.1111/j.1365-2486.2007.01426.x>
- 665
- 666 Shih, H.T., Ng, P.K., Davie, P.J., Schubart, C.D., Türkay, M., Naderloo, R., Jones,  
D., Liu, M.Y., 2016. Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea:

667 Brachyura), based on phylogenetic relationships, with a reorganization of subfamily  
668 rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its  
669 subgenera. Ruffles Bull. Zoology. 64, 139-175.

670 Skálová, H., Jarošík, V., Dvořáčková, Š., Pyšek, P., 2013. Effect of intra-and  
671 interspecific competition on the performance of native and invasive species of *Impatiens*  
672 under varying levels of shade and moisture. PLoS ONE. 8, e62842.  
673 <https://doi.org/10.1371/journal.pone.0062842>

674 Smith, N.F., Wilcox, C., Lessmann, J.M., 2009. Fiddler crab burrowing affects  
675 growth and production of the white mangrove (*Laguncularia racemosa*) in a restored  
676 Florida coastal marsh. Mar. Bio. 156, 2255-2266. [https://doi.org/10.1007/s00227-009-](https://doi.org/10.1007/s00227-009-1253-7)  
677 [1253-7](https://doi.org/10.1007/s00227-009-1253-7)

678 Somero, G.N., 2010. The physiology of climate change: how potentials for  
679 acclimatization and genetic adaptation will determine 'winners' and 'losers'. J. Exp. Biol.  
680 213, 912-920. <https://doi.org/10.1242/jeb.037473>

681 Spivak, E. D., Gavio, M. A., Navarro, C. E., 1991. Life history and structure of  
682 the world's southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in  
683 Mar Chiquita Lagoon (Argentina). Bull. Mar. Sci. 48, 679-688.

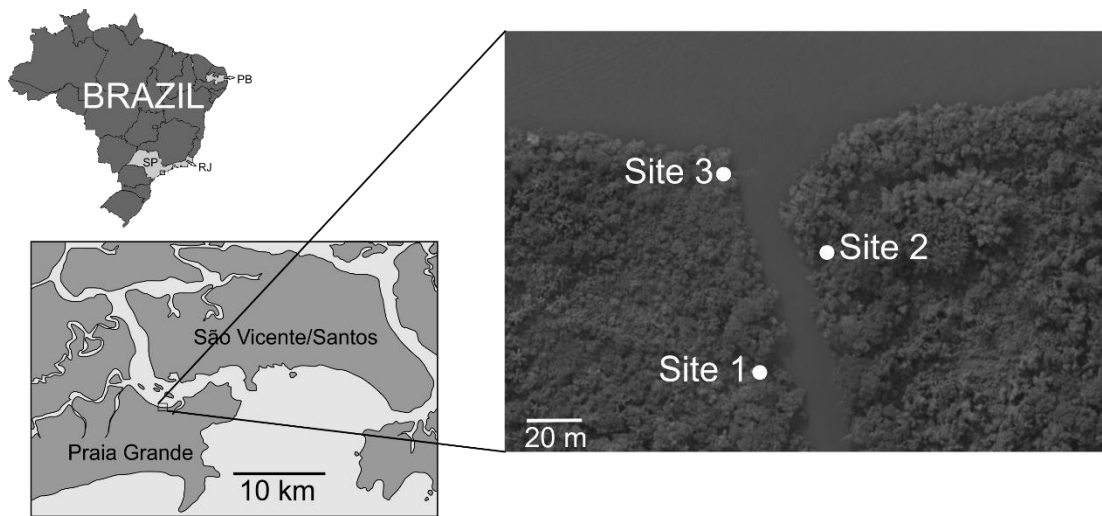
684 Suguio, K., 1973. Introdução à sedimentologia, first ed. São Paulo University  
685 Press, São Paulo.

686 Thurman, C.L., Faria, S.C., McNamara, J.C., 2013. The distribution of fiddler  
687 crabs (*Uca*) along the coast of Brazil: implications for biogeography of the western  
688 Atlantic Ocean. Mar. Biodiversity Rec. 6, 1-21.  
689 <https://doi.org/10.1017/s1755267212000942>

690 Truchet, D.M., Buzzi, N.S., Carcedo, M.C., Marcovecchio, J.E., 2019. First record  
691 of the fiddler crab *Leptuca* (= *Uca*) *uruguayensis* in the Bahía Blanca Estuary (Buenos

- 692 Aires, Argentina) with comments on its biology in South America. Reg. Stud. Mar.  
693 Sci. 27, 100539. <https://doi.org/10.1016/j.rsma.2019.100539>
- 694 Underwood, A.J., Chapman, M.G., Crowe, T.P., 2004. Identifying and  
695 understanding ecological preferences for habitat or prey. J. Exp. Mar. Biol. Ecol. 300,  
696 161-187. <https://doi.org/10.1016/j.jembe.2003.12.006>
- 697 Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4nd ed.  
698 Springer-Verlag, New York. <https://doi.org/10.1007/978-0-387-21706-2>
- 699 Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel,  
700 M., Bacher, S., Zoltán, B.D., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík,  
701 V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Netwig, W., Ott, J., Panov, V.E.,  
702 Reineking, B., Robinet, C., Semchenko, V., Solarz, W., Thuiller, W., Vilà, M.,  
703 Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and  
704 opportunities. Trends Ecol. Evol. 24, 686-693.  
705 <https://doi.org/10.1016/j.tree.2009.06.008>
- 706 Wu, L., Cai, W., Zhang, L., Nakamura, H., Timmermann, A., Joyce, T.,  
707 Mcphaden, M.J., Alexander, M., Qiu, B., Visback, M., Chang, P., Chiesi, B., 2012.  
708 Enhanced warming over the global subtropical western boundary currents. Nat Clim  
709 Change. 2, 161-166 <https://doi.org/10.1038/nclimate1353>
- 710 Yamano, H., Sugihara, K., Nomura, K., 2011. Rapid poleward range expansion of  
711 tropical reef corals in response to rising sea surface temperatures. Geophys. Res. Lett. 38,  
712 L04601. <https://doi.org/10.1029/2010gl046474>
- 713 Zuur, A.F., Hilbe, J., Ieno, E.N., 2013. A beginner's guide to GLM and GLMM with R:  
714 A frequentist and Bayesian perspective for ecologists. Newburgh, U.K.: Highland  
715 Statistics.
- 716

717

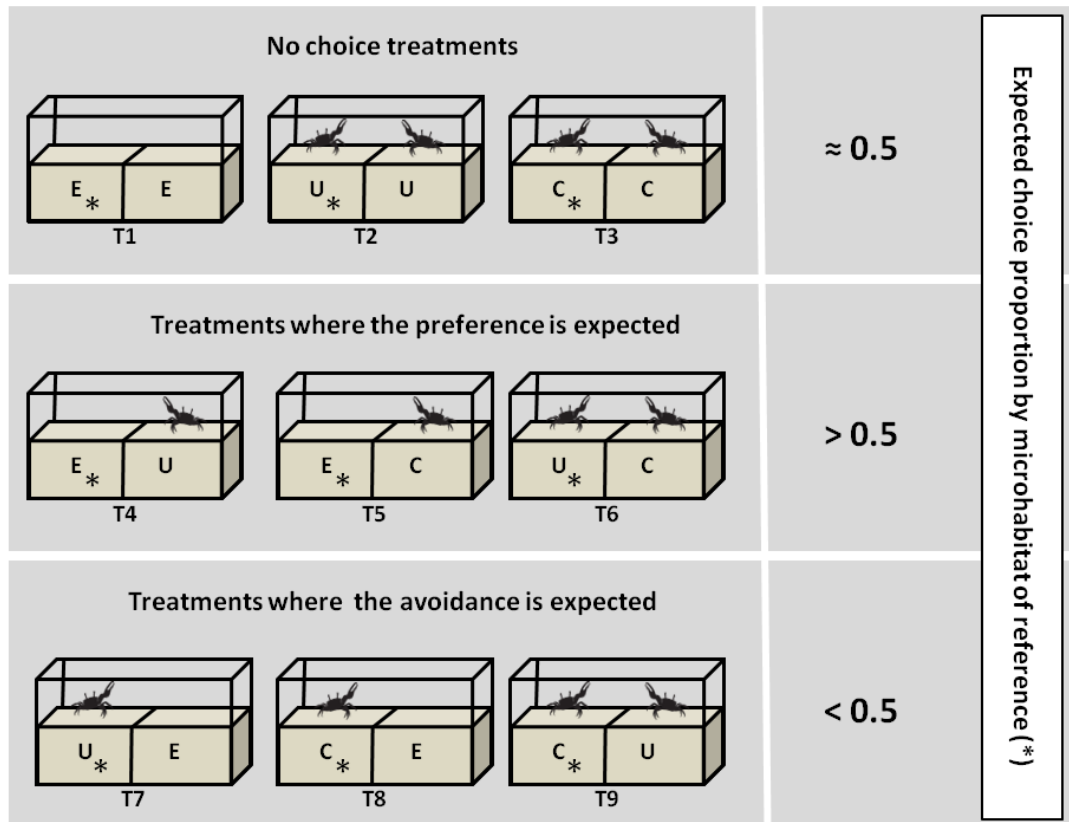


718

719 **Figure 1.** The experimental area in Praia Grande, São Paulo-SP where *Leptuca*  
 720 *uruguayensis* and *Leptuca cumulanta* are currently found (Checon and Costa 2017;  
 721 present study). Points indicate the sites used to describe territorial distribution of species  
 722 (site 1), the site where the species were collected for the experiment in the laboratory  
 723 (site 2), and the site used to evaluate the agonistic interactions (site 3). The arrows  
 724 indicate previous reports of the distribution limit of *Leptuca cumulanta* off the Brazilian  
 725 Coast: first in the Paraíba (PB) coast (Crane, 1975) and then in Rio de Janeiro (RJ)  
 726 coastal waters (Thurman et al., 2013).

727

728



729

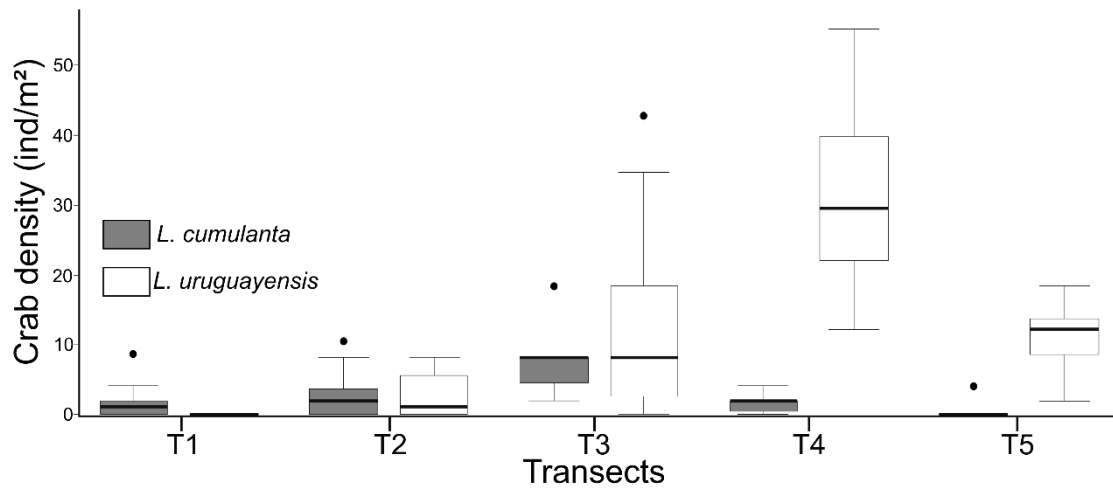
730 **Figure 2.** Experimental design. Nine treatments (T1–T9) used to evaluate the habitat  
 731 choice of *Leptuca uruguayensis* with different visual stimuli: empty microhabitat (E),  
 732 microhabitat occupied by *Leptuca uruguayensis* (U), or microhabitat occupied by range-  
 733 extending species *Leptuca cumulanta* (C). No choice treatments (T1, T2 and T3) were  
 734 composed of the same visual stimulus. Choice for a reference side is expected (T4, T5  
 735 and T6) when it is empty or when the reference side contains a *L. uruguayensis* and the  
 736 other side contain a *L. cumulanta*. Avoidance for a reference side is expected (T7, T8  
 737 and T9) when the opposite side is empty or when the reference side contains a *L.*  
 738 *cumulanta* and the other side contain a *L. uruguayensis*. The expected choice proportion  
 739 by microhabitat of reference (indicated by an asterisk) was expressed as the number of  
 740 choices for one side of terrarium out of the total number of choices made by individuals  
 741 from a group of four.

742



743

744

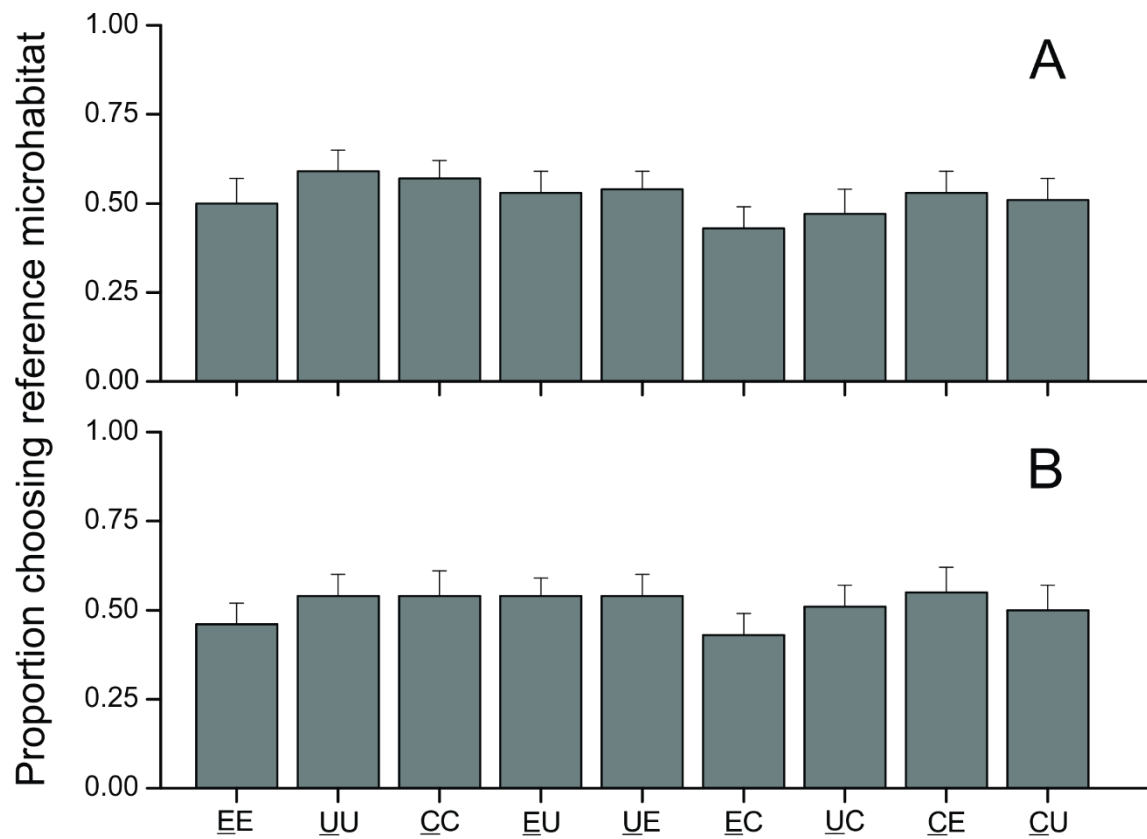


745

746 **Figure 3.** Distribution of *Leptuca uruguayensis* and *Leptuca cumulanta* along the  
 747 intertidal zone. Mean density  $\pm$  standard deviation of both species along five transects  
 748 (T1–T5) from lower (T1) to upper (T5) levels of the intertidal zone. Black circles  
 749 indicate outliers.

750

751



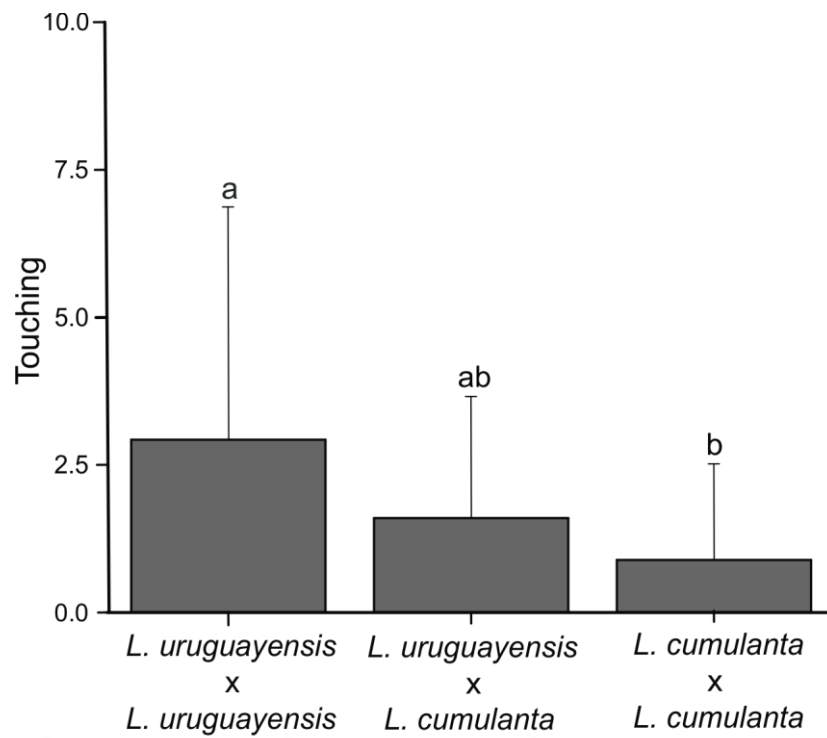
752

753 **Figure 4.** The proportion ( $\pm$  SD) of *Leptuca uruguayensis* choosing the reference  
 754 microhabitat (indicated by the underlined letter) when offered two microhabitat choices.  
 755 Microhabitats offered include: empty (E), with the presence of *Leptuca cumulanta* (C),  
 756 and with the presence of *Leptuca uruguayensis* (U). Panel (A) shows initial  
 757 microhabitat selection, while panel (B) shows final microhabitat selection.

758

759

760



761

762 **Figure 5.** Mean  $\pm$  standard deviation of agonistic interactions (touching/pushing)763 observed among *Leptuca uruguayensis* and *Leptuca cumulanta*. Different letters above

764 the mean of each behaviour indicate a significant difference between treatments (Tukey

765 test,  $P < 0.05$ ).

766

767

768

769

770

771

772

773

774

775

776

777

778 **Table 1** – Models were compared using Akaike information criterion ( $\Delta AIC_c$ ) and ranked

779 according to the difference between the most parsimonious model and the following with

780 the lowest value and higher Akaike weights ( $w_i$ ).

<b>Model</b>		<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b><i>df</i></b>	<b><i>w<sub>i</sub></i></b>
Model 1	touch/push ~ fight group	230.0	0.0	4	0.240
Model 2	touch/push ~ fight group + CSD*	230.6	0.6	5	0.181
Model 3	touch/push ~ DRB**	231.3	1.3	3	0.125
Model 4	touch/push ~ CSD	231.5	1.5	3	0.114
Model 5	touch/push ~ fight group + CSD + DRB	231.6	1.6	6	0.107
Model 6	touch/push ~ fight group + DRB	231.9	1.8	5	0.095
Model 7	touch/push ~ intercept	232.0	1.9	2	0.091
Model 8	touch/push ~ fight group + CSD + fight group x CSD	234.2	4.2	7	0.029
Model 9	touch/push ~ fight group + DRB + fight group x DRB	235.7	5.7	7	0.013
Model 10	touch/push ~ fight group + CSD + DRB + fight group x CSD + fight group x DRB	240.2	10.2	10	0.001

781 \*CSD – Claw size difference

782 \*\*DRB – Distance between the resident burrows

783