

Organic matter affects fiddler crab distribution? Results from field and laboratorial trials

Fernando Rafael De Grande^a, Priscila Granado^a, Fábio Henrique Carretero Sanches^b,
Tânia Marcia Costa^{c,*}

^a Postgraduate Program in Biological Sciences (Zoology), Botucatu Biosciences Institute, São Paulo State University – UNESP, 18618-000, Botucatu, SP, Brazil

^b Center of Natural and Human Sciences, Federal University of ABC (CCNH/UFABC), 09210-170, Santo André, SP, Brazil

^c Biosciences Institute, São Paulo State University (UNESP), Coastal Campus, 11330-900, São Vicente, SP, Brazil

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ABSTRACT

Fiddler crabs are a key benthic macrofauna group in estuarine environments. Species distribution is determined by relatively distinct zones, based on biotic and abiotic factors. As sediment organic matter is thought to be one of the most important zoning factors of mangrove macrofauna, we tested the effects of organic matter content on the intra-specific distribution of the fiddler crabs *Leptuca thayeri* and *Leptuca uruguayensis*. Organic matter content and crab abundance and size were assessed in both species by field observations, while the choice of adult or juvenile *L. uruguayensis* for high -or low- organic matter was tested in the laboratory. Both species showed no relationship between organic matter and crab abundance or size. Furthermore, *L. uruguayensis* juveniles or adults did not show any preference for specific organic matter content. Therefore, fiddler crabs intra-specific distribution in mangrove forests is not dependent of the water-land gradient decrease of organic matter.

1. Introduction

How species distribution is affected by abiotic and biotic factors is a central concern in ecology, and studies on intertidal ecosystems, where organism zonation is markedly visible, have been important to increase the knowledge on this topic. Mangrove crabs, for example, may have their distribution boundaries influenced by competition for space (Cannicci et al., 2018), presence of vegetation (Nobbs, 2003), temperature (Nobbs and Blamires, 2015), and other factors (Ens et al., 1993; Daleo et al., 2003; Ribeiro et al., 2005; Checon and Costa, 2017). One of the most conspicuous benthic macrofaunal groups in tropical and subtropical estuarine environments, both in abundance and biomass, are fiddler crabs (Teal, 1962; Cammen et al., 1980; Macintosh et al., 2002; Koch et al., 2005). Several species naturally coexist in intertidal areas where they can share the same resources, including food and space (Crane, 1975; Checon and Costa, 2017). Their distribution may be regulated by macroscale factors, such as latitude (Crane, 1975; Sanford et al., 2006), and microscale factors, such as species zonation across the intertidal zone (Costa and Negreiros-Fransozo, 2001; Johnson, 2003; Nobbs, 2003; Ribeiro et al., 2005; Martins and Masunari, 2013).

Fiddler crabs are important to the intertidal trophic chain because

they alter the amount of resources available to other organisms (Kristensen, 2008). Their effect on the trophic chain can be direct, through consumption of resources when feeding, and indirect, via bioturbation of sediment when digging burrows (Botto and Iribarne, 2000; Kristensen, 2008; Michaels and Ziemann, 2013; Natalio et al., 2017). Furthermore, they can be predated by fish (Krumme et al., 2007), other crabs (Daleo et al., 2003), birds (Koga et al., 2001, 2015), and mammals (Rulison et al., 2012). They are therefore an important connector for the flow of energy and nutrients from the intertidal zone to aquatic and terrestrial environments (Teal, 1962).

Fiddler crab distribution may be governed by biotic factors like dispersion, larval settlement, predation and vegetation (Epifanio et al., 1988; Daleo et al., 2003; Nobbs, 2003; Thurman et al., 2013); and abiotic factors like temperature, tidal regime, salinity, sediment grain size and organic matter quantity (Teal, 1958; Icely and Jones, 1978; Genoni, 1985; Reinsel and Rittschof, 1995; Ribeiro et al., 2005; Sanford et al., 2006; Thurman et al., 2013; Mokhtari et al., 2015). The last two abiotic factors are particularly important, since fiddler crabs have specialized maxillipeds for mechanical separation of organic particles from sediment grains (Miller, 1961; Costa and Negreiros-Fransozo, 2001; Colpo and Negreiros-Fransozo, 2013). In this sense, sediment organic matter is considered the food source for fiddler crabs and it is

* Corresponding author. Biosciences Institute, São Paulo State University (UNESP), Coastal Campus, Praça Infante Dom Henrique, S/N, Parque Bitarú, 11330-900, São Vicente, SP, Brazil.

E-mail addresses: frdegrande@gmail.com (F.R. De Grande), tania.costa@unesp.br (T.M. Costa).

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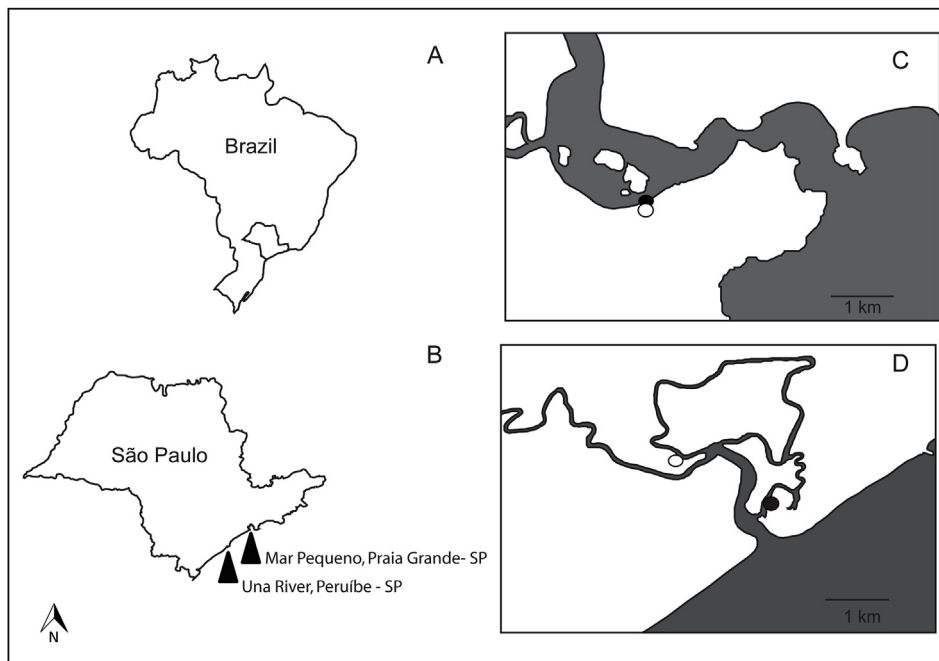


Fig. 1. The study areas. A: shows the São Paulo State at Atlantic coast of Brazil. B: shows the São Paulo coast, Mar Pequeno estuary in Praia Grande and Una River estuary in Peruíbe. C and D: represent, respectively, the Mar Pequeno and Peruíbe estuaries. The white circles in C and D represent the position of the populations studied for *Leptuca uruguayensis* and the black circles represent the populations of *L. thayeri*.

suggested as an important factor in determining their distribution (Crane, 1975; Icely and Jones, 1978; Reinsel and Rittschof, 1995). The sediment organic matter mainly consists of leaf litter and tree fragments and may be the carbon sources for some species of primary mangrove consumers (Guest et al., 2006; Kon et al., 2007).

In the intertidal zone, sediment organic matter shows a gradient of distribution that decreases from water to land (Huettel et al., 1996; Lallier-verges et al., 1998; Bouillon et al., 2003). This gradient of organic matter is proposed to be the cause of the zonation distribution pattern of mangrove fiddler crabs (see: Icely and Jones, 1978; Koch et al., 2005; Bezerra et al., 2006; Mokhtari et al., 2015). It is known that some species may co-occur in the same estuary in relatively well distinct patches (Crane, 1975; Bezerra et al., 2006; Costa e Negreiros-Fransozo, 2001; Booksmythe et al., 2010; Mokhtari et al., 2015; Checon and Costa, 2017). When the relationship between species abundance and sediment organic matter is analyzed across all intertidal zone from mangrove forests, some species seem to be more dependent on organic matter than others (Costa and Negreiros-Fransozo, 2001; Bezerra et al., 2006; Thurman et al., 2013). For example, while *Leptuca thayeri* show a positive relationship with organic matter in the infralittoral zone, *Leptuca uruguayensis* show a negative relationship in the supralittoral zone (see Costa and Negreiros-Fransozo, 2001). On the other hand, when analyzed in a monospecific patch, *L. uruguayensis* show a positive relationship between abundance and sediment organic matter (Ribeiro et al., 2005). In addition, sediment organic matter has a greater influence on abundance of *L. uruguayensis* adults than on juveniles, when analyzed in the same patch (Ribeiro et al., 2005). Since crab dependence on organic matter presents some uncertainties, the relationship analysis between organic matter and population structure characteristics (such as abundance or size) could be more straightforward when considered within a single patch. This approach should be more useful to the understanding of fiddler crab distribution at a microscale because the association between variables can be more accurate.

Although association tests point to a relationship between organic matter and distribution of crabs in the field, it is not possible to state that organic matter is necessarily a cause of this (Underwood, 1997; Zar, 2010). Other factors intrinsically linked to organic matter, such as sediment grain size, which also vary within the water to land gradient, could delimit fiddler crab distribution (Costa and Negreiros-Fransozo, 2001; Yang et al., 2008; Mokhtari et al., 2015). Therefore, controlling

other variables and carrying out laboratorial experiments is required to determine whether organic matter causes differential distribution of fiddler crabs.

In this work we aim to assess whether organic matter influences the intraspecific distribution of fiddler crabs. We evaluated the association between organic matter and abundance or body size of two fiddler crab species in the field: *L. thayeri* and *L. uruguayensis*. Both species were selected because they are key species in the estuaries of South America due to their abundance (Costa and Negreiros-Fransozo, 2003; Masunari, 2006), bioturbation potential (Natalio et al., 2017) and because previous studies showed that their distribution is associated with sediment organic matter (Costa and Negreiros-Fransozo, 2001; Ribeiro et al., 2005). Since the effect of organic matter on the abundance of juvenile and adult *L. uruguayensis* can be different (Ribeiro et al., 2005), we used this species as a model to test in the laboratory the hypothesis that fiddler crabs regardless of their size classes choose sediments with high amounts of organic matter to feed or inhabit. Choice tests were made in order to test whether organic matter causes variation of the intraspecific distribution of these fiddler crabs.

2. Methods

2.1. Study area

The field experiment was conducted in two different estuaries in the state of São Paulo, Brazil: Mar Pequeno, in Praia Grande, 23°59'S – 46°24'W and Una River, in Peruíbe, 24°26'S – 47°04'W (Fig. 1A and B). Both estuaries were associated with mangrove forests under semi-diurnal tide systems and subtropical climate without dry season (Alvares et al., 2014). In the Praia Grande estuary, *Leptuca thayeri* and *Leptuca uruguayensis* populations occur in nearby areas, but the first inhabits the infralittoral zone and the second, the supralittoral zone (Fig. 1C). Although distribution boundaries of both species overlap at some points, we studied each population separately. In the Peruíbe estuary, the *L. thayeri* population was located near the mouth of the river while *L. uruguayensis* was located at the head of the river (approximately 2.8 km away from each other; Fig. 1D). We studied two sites per species to assess whether organic matter is associated with fiddler crab abundance or size variation independently of their location. In all populations other fiddler crab species were present but those were

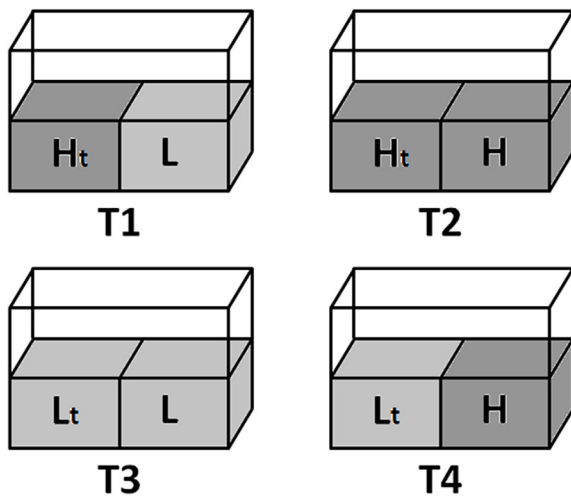


Fig. 2. Experimental design overview. Treatments (1–4) used in the experiments to determine *Leptuca uruguayensis* choice for sediment organic matter, in both adult and juvenile crabs. Dark gray color and *H* indicate high organic content, light gray and *L* represent low organic content, and *t* indicates the reference compartment in which the proportion of total number of crab scoop, pellets and burrows was estimated.

not considered in this study.

For the laboratory experiment, crabs and sediment were collected from the Mar Pequeno estuary in Praia Grande.

2.2. Field experiment

To assess the association between organic matter and abundance or body size in *L. thayeri* and *L. uruguayensis*, field observations were made. Since sediment organic content decreases in a water to land gradient (Huettel et al., 1996; Lallier-verges et al., 1998; Bouillon et al., 2003), we made fifteen transects perpendicular to the water line for each population during the warm season from September 2014 to February 2015, when fiddler crabs are most active. A 75 cm-side quadrat (experimental unit) was placed every 100 cm along each transect where we sampled crabs and sediment. The criterion used to start or end transects was the presence or absence of the interest-species. Therefore, transects presented different sizes depending on the sampled population (the shortest transect for *L. thayeri* was 14 and 6 m long, and the longest was 21 and 13 m long in Praia Grande and Peruíbe, respectively; the shortest transect for *L. uruguayensis* was 6 and 6 m long, and the longest was 12 and 14 m long in Praia Grande and Peruíbe, respectively). This assured the evaluation of organic sediment content effect only within population boundaries. In addition, transect sampling was useful to sample populations homogeneously following the downward gradient of organic matter from water towards land.

Within each quadrat 5 sediment samples of 5 mm depth were collected with a 3.2 mm diameter core. Sediment samples were pooled with the purpose of estimating mean organic content of each experimental unit (*L. thayeri*: Praia Grande, $n = 177$; Peruíbe, $n = 117$. *L. uruguayensis*: Praia Grande, $n = 93$; Peruíbe, $n = 136$). We only collected surface sediment because we assumed surface organic content reflected food accessed by crabs. Sediment samples were placed into labeled plastic bags and frozen. In the laboratory, samples were dried at 72 °C for 48 h, weighted about 10 g, incinerated at 550 °C for 5 h and reweighted (adapted from Luczak et al., 1997). Organic matter percentage was obtained by subtracting incinerated material weight from dry sample weight.

Each burrow within the quadrat was excavated and all crabs were collected, identified, and measured (maximum carapace width in mm). Abundance and mean size of each sex was quantified per species and quadrat (experimental unit). Crabs were released into their habitat after

measurements.

2.3. Laboratory experiment

To test fiddler crab choice for sediment with either high or low organic content we used two size classes of *L. uruguayensis* males. In the state of São Paulo, *L. uruguayensis* reach sexual maturity at about 7 mm of carapace width (Hirose et al., 2012). Thus, we evaluated two crab sizes based on mean \pm standard deviation of carapace width ($t = -18.15$, $df = 78$, $p < 0.0001$): adults (10.49 ± 1.17 mm) and juveniles (5.99 ± 1.06 mm). We only used males to standardize response variables (number of scoops, pellets and burrows) once we knew such activity differed between sexes due enlarged claw present only in males (for example: females scooping twice faster than males and, consequently, producing more pellets; see Weissburg, 1992 and Weiss and Weiss, 2004). Furthermore we do not have any hypothesis for differences between sexes because we assumed that males and females show the same pattern of distribution since we did not observe variation of sexual proportion across the population in our field experiment (see supplementary material). We selected this species and these size classes because the relationship between organic matter and abundance is greater in adults than juveniles (Ribeiro et al., 2005) and therefore it is rational to assume that age could affect sediment choice. In addition, *L. uruguayensis* demand little space and sediment due to their small size.

Fiddler crabs choice was evaluated in both adults and juveniles, but not between size classes. Preference of large and small *L. uruguayensis* for sediment with differing organic content was tested using an experimental design consisting of three treatments, one with high organic content sediment only, one with low organic content sediment only and one with both sediments, with high and low organic content. This experimental design (Fig. 2, number of replicates per treatment = 12) was based on the work of Olabarria et al. (2002) and Underwood et al. (2004). Our response variables were proportion of scoops, pellets and burrows from the fiddler crabs.

To obtain different organic contents, we used 100 L of superficial sediment (5 cm deep) from the *L. uruguayensis* territory. Sediment was homogenized and 10 samples were separated for organic matter quantification as described in item 2.2. Subsequently, sediment was sieved in a 0.05 mm mesh to remove organic fragments and 10 new samples were produced to obtain organic matter. With this procedure we removed $8.76 \pm 2.68\%$ (mean \pm standard deviation) of initial organic matter resulting in sediment with organic content of $4.36 \pm 0.56\%$ (mean \pm standard deviation). Ten samples of organic material retained in the sieve were analyzed under stereomicroscopy to identify their composition. Organic material was composed of 96.8% plant fragments (leaves: 55.59%; roots: 35.87%; wood: 5.34%). To obtain sediment with a low amount of organic matter we added 2 L of the material retained in the sieve (tree debris) into 50 L of sifted sediment; to obtain high organic matter, we added 20 L of retained material into 50 L of sifted sediment. Thus we obtained sediment with a mean \pm standard deviation of $4.50 \pm 1.13\%$ low concentration organic matter and $9.4 \pm 1.17\%$ high concentration. All experimental trials sediment were checked to organic matter quantification as described in item 2.2.

Sediment grain size characterization was performed according to Suguio (1973). Sediment was composed of: 0.51% very coarse sand, 3.67% coarse sand, 19.87% medium sand, 28.89% fine sand, 7.31% very fine sand and 39.72% mud.

To evaluate the preference of crabs based on different organic content, we built microcosms (glass containers: 40 \times 10 \times 20 cm) divided by a glass wall (10 cm high) into two compartments (20 \times 10 \times 20 cm) filled with a sediment column of 10 cm. Microcosm area was based on the maximum density of *L. uruguayensis* observed in the Praia Grande estuary (see results, section 3.1), so that each compartment was sufficient for enclosing the territory of an individual crab (around 13 cm²). Depth of the sediment column (10 cm) was

established in accordance with the maximum burrow depth for this species (Machado et al., 2013). We used one crab per microcosm to avoid intra-specific competition for territory as an interference factor. Microcosm walls were covered with opaque black plastic to avoid visual interference between animals. To avoid side bias as an interference factor, half of the animals were released on the left side and the other half were released on the right side for each treatment.

Crabs were kept on a light regime consisting of 12 h of light and 12 h of darkness, and at an average temperature of 28.99 °C (SD ± 0.54). Crabs remained in the microcosms for 120 h based on preliminary observations wherein we evaluated the time necessary for the majority of active animals to be on the sediment surface. After this period each crab was observed for 10 min and the number of scoops was recorded. At the end of the observation, the number of pellets and burrows per compartment were recorded.

We compared the proportion of scoops, pellets and burrows dug out of one compartment (indicated by a subscript *t* in each treatment, Fig. 2) relative to both compartments of each sediment type with and without choice (see Olabarria et al., 2002). Thus, preference of *L. uruguayensis* for sediment with high organic content could be indicated by a greater proportion of scoops or burrows dug into this type of sediment, compared to what would be expected by chance if no choice was expressed. The odds of crabs scooping sediment and building burrows in each microcosm compartment was estimated from treatments where there was no choice. Crab choice for sediments with high organic content was assumed when the following hypothesis was accepted:

$$H1: \frac{n_{Ht1}}{N_1} > \frac{n_{Ht2}}{N_2}, \frac{n_{Lt3}}{N_3} > \frac{n_{Lt4}}{N_4}$$

In this equation, n_{Hti} or n_{Lti} is the number of scoops, pellets or burrows observed in a single microcosm compartment (identified by a subscript *t*) referring to the amount of organic matter content in that treatment (High: *H* or Low: *L* organic content); *N* is the total number of scoops or burrows observed in both compartments; and *i* = 1, 2, 3 and 4 indicates the treatment. Choice treatments were 1 and 4, and the ones without choice were 2 and 3 (Fig. 2).

If crabs chose sediment with high organic content, the proportion of scoops, pellets or burrows dug in compartment H_t in treatment 1 must have been greater than that observed in H_t^2 and L_t^3 where there was no choice and the same proportion was expected. In treatment 4, crabs would tend to feed and build their burrows in the high organic matter compartment, decreasing use of L_t^4 . Therefore, it was hypothesized that the proportion of scoops and burrows in H_t^1 would be larger than in H_t^2 , H_t^3 and the last ones greater than in H_t^4 .

2.4. Statistical analyses

Our goal was to test whether variation of abundance and size of fiddler crabs is associated with variation of organic matter in their habitat. Since males and females of some species of fiddler crabs may occupy different patches of the intertidal zone (Christy, 1983; Croll and McClintock, 2000), we used a simple regression to test whether the sex ratio of *L. thayeri* or *L. uruguayensis* changes according to abundance of crabs per quadrat. Territorial competition (Christy, 1983; Croll and McClintock, 2000) or habitat selection between adults and juveniles (Ens et al., 1993) could also be a confounding effect in our analysis and thus we used a simple regression to test whether body size variation of both species were associated with variation of their respective abundance. We did not observe any relationship between variations of abundance and sex ratio or crab size per quadrat (see supplementary material). Thus, the relationship between total abundance and sediment organic matter variation was tested independently of sex and the relationship between crab size and organic matter was tested independently of their abundance.

A general linear model (GLM) was used to compare the relationship of crab size or abundance against organic matter between estuaries. The

Table 1

Sediment organic matter and population characteristics of *Leptuca thayeri* and *L. uruguayensis* from both Praia Grande and Peruíbe estuaries. Data show maximum, minimum and mean organic matter, fiddler crab abundance and carapace width.

	Abundance				Carapace width			
	df	MS	F	p	df	MS	F	p
<i>Leptuca thayeri</i>								
Site	1	0.941	19.623	< 0.001	1	465.52	24.367	< 0.001
Organic matter	1	1.229	25.628	< 0.001	1	8.46	0.443	0.506
Error	291	0.047			291	19.10		
<i>Leptuca uruguayensis</i>								
Site	1	0.775	6.5721	0.011	1	46.573	23.991	< 0.001
Organic matter	1	6.501	55.1151	< 0.001	1	20.833	10.732	0.0012
Error	226	0.117			226	1.941		

predictor was represented by the different estuary sites and the percentage of organic matter represented the continuous variable. Standardized residuals were normally distributed and the scatter-plot of predicted values against residuals had a shotgun pattern. Abundance data were log (*x* + 1) transformed to attend the premise of normality. Simple linear regressions were used to explore any relationship among response variables and organic content.

The laboratory experiment hypotheses on crab choice were evaluated using a one-way analysis of variance (ANOVA). The proportional number of scoops, pellets and burrows dug by adult or juvenile crabs were arcsine transformed with the purpose of attending the ANOVA's premise of normality and homogeneity. We considered 95% as the significance level in all analyses.

3. Results

3.1. Field experiment

For *Leptuca thayeri* populations, the quantity of sediment organic matter in the Praia Grande was higher than in the Peruíbe estuary (Table 1). Abundance of *L. thayeri* also differed between estuaries (Table 2), with more crabs in Praia Grande than Peruíbe (Table 1). Abundance of tested crabs considering the effect of organic matter gradient differed between Praia Grande and Peruíbe (Table 2). Abundance of *L. thayeri* showed a small relationship with organic matter variation in Praia Grande but not in Peruíbe (Fig. 3 A).

For *Leptuca uruguayensis*, higher values of organic matter and crab abundance were observed in Peruíbe (Tables 1 and 2). Nevertheless, results from the regression test showed a weak relationship between abundance of *L. uruguayensis* and organic matter in Praia Grande (Table 2 and Fig. 3B).

Leptuca thayeri carapace mean size differed between estuaries, where they were larger in Peruíbe than in Praia Grande (Tables 1 and 2). No relationship was observed between *L. thayeri* size and organic matter variation (Table 2, Fig. 3, B). On the other hand *L. uruguayensis* carapace was larger in Praia Grande than in Peruíbe (Tables 1 and 2). Size variation of *L. uruguayensis* considering organic matter effect differed between estuaries (Table 2). In Peruíbe a weak relationship between *L. uruguayensis* size and organic matter was observed, but not in Praia Grande (Fig. 3).

3.2. Laboratory experiment

Leptuca uruguayensis showed no preference for feeding areas based on sediment organic matter content (Fig. 4). The proportion of scoops

Table 2

Mean (abundance and carapace width) of *Leptuca thayeri* and *L. uruguayensis* comparing Praia Grande and Peruíbe estuaries (categorical variable) considering the effect of organic matter (continuous variable). Level of significance adopted: $p < 0.05$ (GLMs).

	Organic matter of sediment (%)			Abundance			Carapace width (mm)		
	min	max	mean	min	max	mean	min	max	mean
Praia Grande	0.06	22.63	9.01	1	17	4.23	3.3	22.8	9.88
Peruíbe	1.66	11.9	5.1	1	12	3.25	3.6	24.32	12.7
Praia Grande	0.01	9.55	1.82	1	28	7.39	0.92	10.72	6.46
Peruíbe	0.48	6.18	2.27	2	87	19	3.4	7.6	5.42

was essentially the same between treatments for large crabs (one-way ANOVA: $F_{3,36} = 1.72$, $MS = 0.6728$, $p = 0.1787$) and small crabs ($F_{3,36} = 0.70$, $MS = 0.3410$, $p < 0.5568$). Similarly, the number of surface pellets did not differ between treatment trials for adults ($F_{3,36} = 1.02$, $MS = 0.4177$, $p = 0.3931$) and juveniles ($F_{3,36} = 1.17$, $MS = 0.4728$, $p = 0.3334$). Moreover, *L. uruguayensis* did not show burrowing location preference. Proportion of burrows did not differ between treatments for either big (one-way ANOVA: $F_{3,36} = 1.02$, $MS = 0.3425$, $p = 0.3927$) or small crabs (one-way ANOVA: $F_{3,36} = 0.40$, $MS = 0.1004$, $p < 0.7475$).

4. Discussion

Herein, we demonstrated that abundance and size of *Leptuca thayeri* and *Leptuca uruguayensis* are not influenced by the amount of organic matter in the mangrove sediment. In addition, we showed that *L. uruguayensis* adults and juveniles do not choose where to feed or dig their burrows due to organic matter concentration. Thus, our results suggest that the water-land gradient decrease of organic matter does not affect the intra-specific distribution of fiddler crabs in mangrove forests.

Despite there being substantial literature suggesting or describing organic matter as the main responsible for the differential distribution

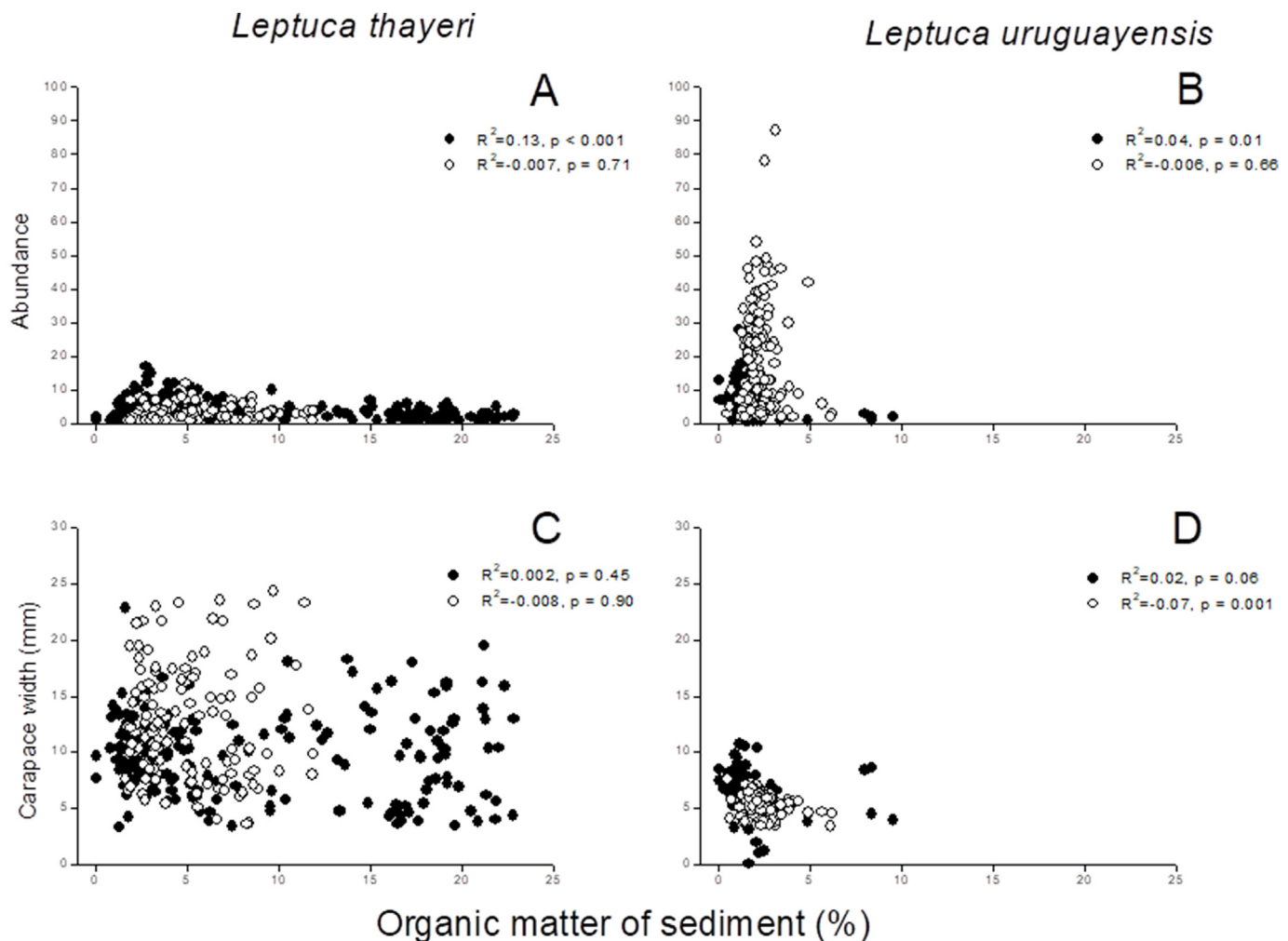


Fig. 3. Field experiment results. The relationship between fiddler crab abundance and carapace width to sediment organic matter variation. A and C show the data for *Leptuca thayeri* abundance and carapace width, respectively. B and D show the data for *L. uruguayensis* abundance and carapace width, respectively. The x-axis represents average organic matter per quadrat sampled along transects. The y-axis represents mean response variables (abundance or carapace width) per quadrat sampled. Black color represents the Praia Grande estuary and white color represents the Peruíbe estuary. R^2 and p from regression tests are shown at the top right of each graph.

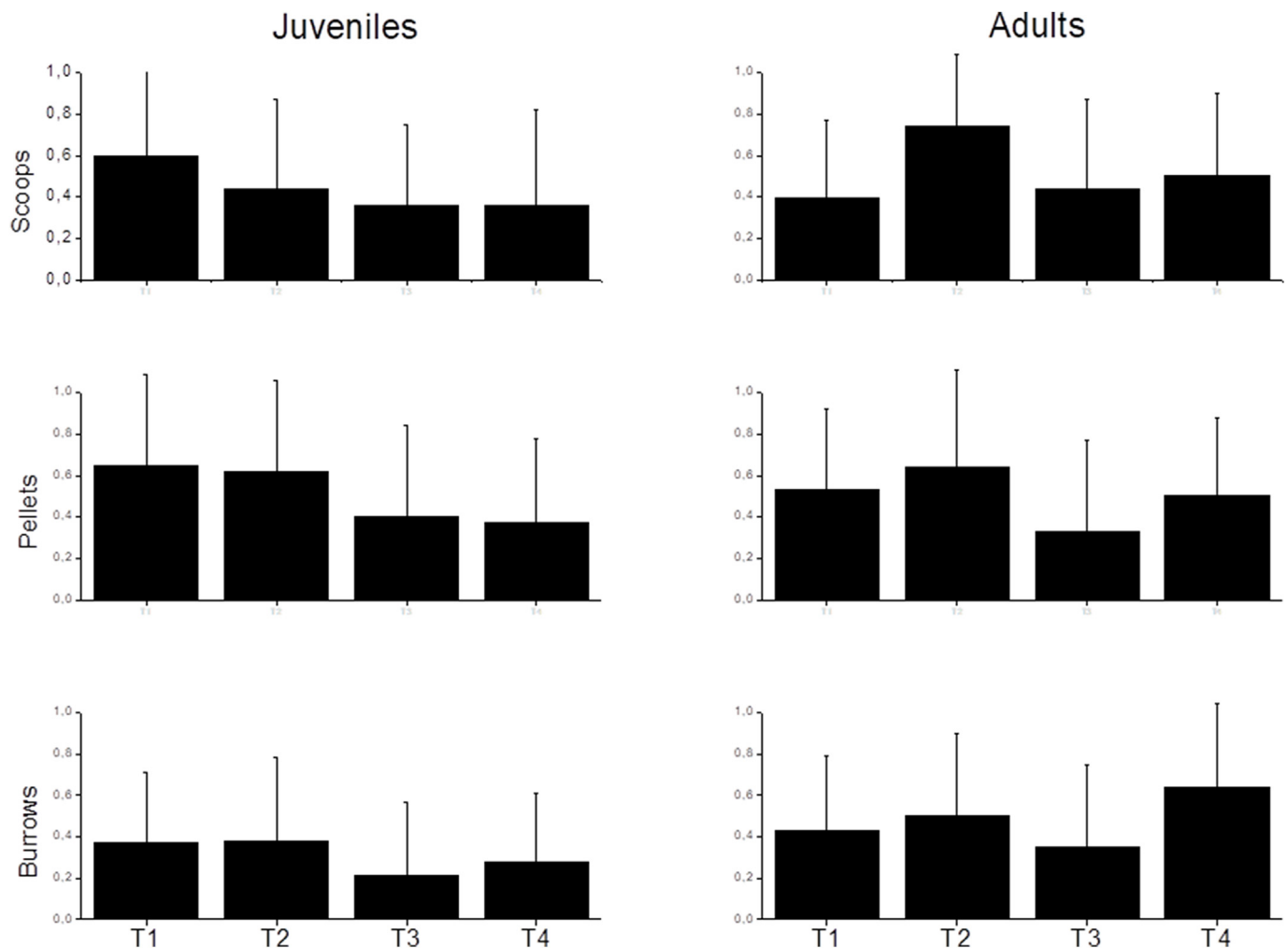


Fig. 4. Laboratory experiment results. Mean (+SD) crabs scoops (top row), pellets (central row) and burrows (bottom row) are indicated in the x-axis. Treatments are indicated in the y-axis. T1 indicates the proportion of response variables observed in the compartment with high organic matter in the multiple-choice treatments. T2 and T3 indicate the proportion of response variables observed in the compartment with, respectively, high and low organic matter in no-choice treatments. T4 indicates the proportions observed in the compartment with low organic matter in the multiple-choice treatment.

of fiddler crabs (Crane, 1975; Reinsel and Rittschof, 1995; Costa and Negreiros-Fransozo, 2001; Ribeiro et al., 2005; Bezerra et al., 2006; Thurman et al., 2013; Mokhtari et al., 2015), our study showed an opposite pattern to what has been previously described. In our field experiment, abundance and size of *L. thayeri* and *L. uruguayensis* showed a weak relation with organic matter. Furthermore, the intra-specific distribution of both species in the two studied locations was not dependent of organic matter concentration. In the same sense, in the laboratory, *L. uruguayensis* did not show preference behavior for sediment organic matter concentration, since we did not observe a greater proportion of digging or feeding behavior on sediment with high organic matter in the multiple-choice treatment. Disparity between the literature and our study indicates that quantity of organic matter may not be the main factor explaining fiddler crab distribution within a single patch. Others biotic or abiotic factors as intraspecific competition, predation, grain size or even organic matter quality could play a more important role in fiddler crab distribution, as proposed previously (Boto and Iribarne, 2000; Bouillon et al., 2002; Meziante et al., 2002; Kon et al., 2007; Checon and Costa, 2017).

In mangrove forests, the main source of sediment organic matter is leaf litter and other tree fragments (Bouillon et al., 2003; Kon et al., 2007), validating their use as the main source of organic matter in our laboratorial experiments. Tree debris can be the primary carbon source for some consumers in mangrove forests (Kon et al., 2007), as many

infaunal or epifaunal macroinvertebrates feed on tree fragments in the sediment (Guest et al., 2006; Kon et al., 2007). Nevertheless, the importance of tree fragment organic matter for primary consumers in mangrove forests has been overestimated (Bouillon et al., 2002, 2003; Kon et al., 2007; Lee et al., 2014). Tree debris presents high levels of low-digestible substances such as cellulose and tannins (Linton and Greenaway, 2007). Therefore, some selective consumers that inhabit the mangrove sediment may feed from other, easier to digest carbon sources, such as microphytobenthos or phytoplankton deposited on the sediment during high tides (Bouillon et al., 2002; Kon et al., 2007).

In the present study we did not evaluate whether *L. thayeri* or *L. uruguayensis* ingest the detritus of the trees. Nevertheless, the assumption that fiddler crabs ingest other sources of organic matter might be reinforced by the fact that fiddler crabs have, in the second maxilliped, specialized setae that they use to separate organic from nonorganic fractions of sediment. Setae morphology varies among fiddler crab species and these are used for food selection (Costa and Negreiros-Fransozo, 2001; Colpo and Negreiros-Fransozo, 2013). They are able to sort diatoms or bacteria from the sediment by a mechanism of water resuspension into the buccal chamber (Miller, 1961; France, 1998). Meziante et al. (2002) suggested that during sorting fiddler crabs may ingest mangrove debris but these are not digested. Moreover, Ribeiro et al. (2005) showed a positive relationship between abundance of *L. uruguayensis* and sediment organic matter in Argentina, studying a

population inhabiting a non-vegetated sandy bank. The main source of carbon in non-vegetated areas is the microphytobenthos (Miller et al., 1996; Kon et al., 2007; Ribeiro and Iribarne, 2011). In this sense, organic matter derived from tree debris would not be the main food source for fiddler crabs, a possible explanation why its quantity does not affect the intra-specific distribution of *L. thayeri* and *L. uruguayensis*. Other carbon sources could be more important in explaining the distribution of selective consumers and the identification of such sources is required at a species-specific level. Future studies on preference for a carbon source of certain quality could provide a better understanding of the distribution of fiddler crabs and whether their boundaries are limited by food or other biotic or abiotic factors.

5. Conclusion

Our work demonstrates that the quantity of organic matter does not explain fiddler crab intraspecific distribution in mangrove forests. Therefore, the variation of abundance or size within a single patch of fiddler crabs is not caused by the decrease of organic matter in a water-land gradient. More studies should evaluate if the quality of organic matter or other abiotic and biotic factors might be more important in this context.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.ecss.2018.07.005>.

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