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Contrasting activity patterns at high and low tide in two Brazilian fiddler crabs (Decapoda: Brachyura: Ocypodidae)

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ABSTRACT

Fiddler crabs are known as ecosystem engineers as well as important connectors of energy flow between the intertidal zone and the adjacent marine and terrestrial environments, being predated by both marine and terrestrial species. Studies on their activity patterns are critical to understand their overall role in the function of estuarine ecosystems. Recent studies have found that fiddler crabs, which are active at low tide, are the main food item of fishes hunting at high tide in the intertidal zone, suggesting that some species could also be active at high tide. We assessed the activity patterns of two fiddler crabs, *Leptuca leptodactyla* (Rathbun, 1898) and *L. thayeri* (Rathbun, 1900) using pitfall traps deployed at different diurnal and tidal conditions at two southeast Brazilian estuaries. Our data shows that *L. leptodactyla* was mostly active at low tide during both day and night, whereas *L. thayeri* was active at low and high tide, a behavior uncommonly reported for fiddler crabs. Our results also confirm that some fiddler crabs can have a previously unreported importance as food for aquatic predators.

Key Words: fish predation, *Leptuca leptodactyla*, *Leptuca thayeri*, underwater activity

INTRODUCTION

Fiddler crabs are a crucial component of the estuarine communities. They are considered "ecosystem engineers" (Kristensen, 2008) since their feeding and burrowing activity can change the biogeochemical characteristics of the sediment, which ultimately affects the availability of resources for other organisms (Botto & Iribarne, 2000; Kristensen, 2008; Michaels & Zieman, 2013; Natalio *et al.*, 2017). Furthermore, fiddler crabs are important connectors of nutrient and energy flow between the intertidal zone and both the aquatic and terrestrial environments (Teal, 1962). These intertidal crabs feed on debris, bacteria, microalgae, and nematodes, and they are preyed by marine animals, including swimming crabs and fishes, as well as by terrestrial species such as birds and mammals (Dye & Lasiak, 1987; France, 1998; Hsieh *et al.*, 2002; Daleo *et al.*, 2003; Reinsel, 2004; Krumme *et al.*, 2007; Rulison *et al.*, 2012; Koga *et al.*, 2015)

Studies on the activity of fiddler crabs are critical to understand when and how much they impact the sediment and how they affect the overall functioning of ecosystems. Their activity varies strongly with the tides as in most intertidal invertebrates. Several studies have indicated that fiddler crabs feed, burrow, mate, and undertake other surface activities at low tide only, and remain inside their burrows at high tide (Barnwell, 1966; Crane, 1975; Ens *et al.*, 1993; Reinsel, 2004; Sanford *et al.*, 2006; Zeil & Hemmi, 2006; Dugaw *et al.*, 2009; Kim & Christy, 2015). Indeed, some species actively close the entrance of their burrows with sediment at the end of low tide periods waiting for the next flooding tide (de la Iglesia *et al.*, 1994; Ribeiro & Iribarne, 2011; Fusi *et al.*, 2015). Laboratory experiments have shown that fiddler crabs are active at both diurnal and nocturnal low tides, indicating that their activity rhythm is modulated by an internal biological clock in phase with tidal cycles (Brown *et al.*, 1954; Bennett *et al.*, 1957; Fingerman, 1960; Barnwell, 1966; Powers & Cole, 1976).

Reports of underwater activity of fiddler crabs at high tide are rare (but see Teal, 1958). Stomach-contents analyses of estuarine fishes such as the pufferfish (*Colomesus psittacus* Bloch & Schneider, 1801) and killifish (*Fundulus grandis* Baird & Girard, 1853) showed nevertheless that fiddler crabs are consumed by these predatory fishes (Rozas & LaSalle, 1990; Krumme *et al.*, 2007), which access the intertidal belt colonized by fiddler crabs at high tide only. The fiddler crab *Leptuca thayeri* was also observed feeding while submerged by a high tide on mud flats along the mangrove forests in São Paulo State, Brazil (Una River, 24°18′S, 47°00′W; Portinho mangrove, 23°59′S, 46°24′W; Itapanhaú River, 23°50′S, 46°09′W; personal observation).

On the basis of this preliminary line of evidence, we studied the activity patterns of the fiddler crabs *Leptuca leptodactyla* (Rathbun, 1898) and *Leptuca thayeri* (Rathbun, 1900), mainly focusing on their activity patterns at high tide. We conducted field surveys and transects to compare the surface activity of these species across tidal phases and diurnal and nocturnal hours.

MATERIAL AND METHODS

Study area and model species

The study was undertaken at two sites on the subtropical coast of São Paulo state, southern Brazil: the mouth of the Una River, Peruíbe (24°18′S, 47°00′W), and the bank of the Itapanhaú River, Bertioga (23°50′S, 46°09′W). The region has relatively constant high humidity and equally distributed rainfall through the year (Rolim *et al.*, 2007; Alvares *et al.*, 2014). Moreover, this coast is characterized by differences of about 1.5 hours in day/night periods between the seasons. The tides are semi-diurnal, and the average amplitude of spring tides at both study sites is 1.4 ± 0.1 m. The study was conducted from June 2010 to November 2011 only at spring tides because the area colonized by the two species is not submerged at high neap tide.

Leptuca leptodactyla and *L. thayeri* are key species in the subtropical Brazilian estuaries due to their abundance and distribution. Populations of *L. leptodactyla* are typically found in sandy, non-vegetated areas (Masunari, 2006; Colpo & Negreiros-Fransozo, 2011; Checon & Costa, 2017), whereas those of *L. thayeri* are usually found in muddy substrates under mangrove trees (Costa & Negreiros-Fransozo, 2001; Gusmão-Junior *et al.*, 2012). We studied the population of *L. leptodactyla* inhabiting a sandbank of about 330 m^2 at the mouth of the river. *Leptuca thayeri* colonized a mangrove stand of approximately 300 m^2 on the river bank.

Sampling

We used pitfall traps to quantify the activity of crabs at low and high tide, and during day and night periods. Such traps are an effective way to estimate the activity of crabs in the field (Williams *et al.*, 1985; Varnell & Havens, 1995; Ashton, 2002; Luppi *et al.*, 2013). Each trap consisted of a cylindrical PVC section 20 cm long and 10 cm in diameter open at the top and closed with a 1 mm mesh screen at the bottom, which allowed water to drain out but prevented crabs from escaping. Preliminary laboratory tests evaluated whether individuals of the two species studied could escape from the top of the traps when submerged or exposed to air. Underwater tests (high and low tide simulations) involved 10 crabs in each test, a total of 20 crabs, 10 males and 10 females of each species. We placed 10 traps in 66 × 33 × 34 cm tanks, each containing a crab. To simulate the high tide condition, the tanks were filled with estuarine water (35 cm depth) under constant aeration; a 3 mm layer of water simulated low tide. The crabs were kept 24 hrs (12 hours light, 12 hrs dark) in each test. No crabs escaped from the traps during the test period, showing that the traps were effective at both low and high tides.

We randomly deployed 20 pitfall traps along a transect line at each study area, and carefully leveled the upper end of the traps with the substrate surface in order to minimize avoidance by crabs. All the traps were established along the same tidal elevation, between high and low tide, in order to standardize the time of submersion and exposure of traps to approximately 6 hrs to prevent over- or underestimation of one of the tidal phases.

The traps installed in each area were removed and replaced with empty ones when the water reached the traps at flooding tides and when the water left the traps at ebbing tides. The removal and replacement procedure did not take more than 30 min, ensuring that traps checked at the end of one period did not capture active crabs from next activity period. The traps were inspected after removal, the captured crabs were identified, and their carapace width (CW) measured. We performed this procedure over a day (24 hrs), allowing estimates of activity for each species for the four possible combinations of daily (day *versus* night) and tidal (high *versus* low) periods. After sampling, the crabs were released in their respective areas away from traps zone to prevent their recapture. The sampling procedure was performed on five different dates at each area.

We used a three-way mixed-model ANOVA to test for the effects of the daily cycle (fixed, orthogonal factor with two levels: diurnal and nocturnal), the tidal cycle (fixed, orthogonal factor with two levels: high and low tide), and the date (random, orthogonal factor with five levels) on the number of crabs caught in the traps. A two-way ANOVA design was used to test for differences in average size or sex of the crabs caught at different daily cycle (fixed, orthogonal factor with two levels: diurnal and nocturnal) and tidal phases (fixed, orthogonal factor with two levels: high and low tide). The Levene test was applied to check for heteroscedasticity and the data were log transformed when the ANOVA assumptions were not met. Post-hoc Student-Newman-Keuls tests were applied for multiple comparisons when needed. The Chi-square test was used to evaluate the sex ratio. The analyses were performed using Statistica 7.0 software (www.statsoft.com).

RESULTS

The deployed pitfall traps captured 298 individuals of *L. leptodactyla* over the five sampling dates. The average CW of the population was 6.4 ± 1.6 mm, with the smallest and largest specimens measuring 3 mm and 10.3 mm, respectively. Individuals crabs of both sexes were found in all size classes (Fig. 1A).

During daytime, a higher number of *L. leptodactyla* individuals were captured during low tide than during high tide on every sampling date (Table 1, Fig. 2A). The same pattern was observed during the night, except on sampling dates 1 and 5, when the number of trapped specimen was low and not significantly different between low and high tides (Table 1, Fig. 2B).

Over the five sampling dates, the traps captured 234 individuals of *L. thayeri*, with an average CW of 10.2 ± 4.9 mm. The CW of the smallest and largest *L. thayeri* was 3.5 mm and 20.7 mm, respectively. Within that range, we found crabs of both sexes in all size classes, but with a slight predominance of juveniles (Fig. 1B).

There was no significant difference in the numbers of trapped *L. thayeri* between low tide and high tide on all the sampling dates during daytime (three-way ANOVA; Table 1, Fig. 3A). At night, specimens of *L. thayeri* were trapped in significantly higher numbers during low than at high tide on dates 1 and 2, whereas on the sampling date 3 there were more crabs in the traps at the end of the high tide and there was no significant difference between the tidal phases on dates 4 and 5 (three-way ANOVA; Table 1, Fig. 3B).

There was no differences in the average size of crabs trapped at high in contrast to low tide ($F_1 = 0.30$, $P = 0.59$ and $F_1 = 0.30$,

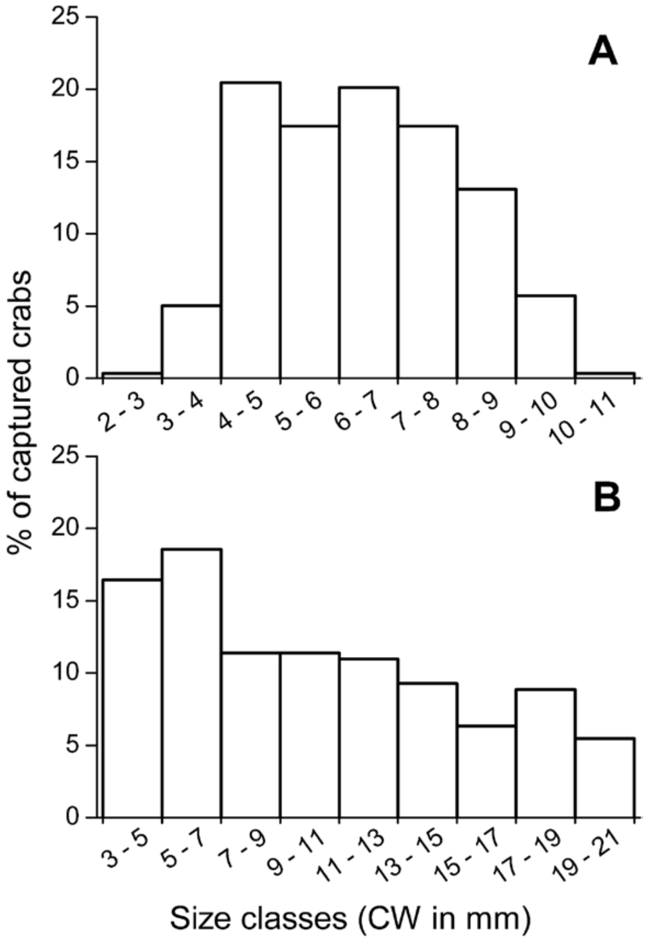

Figure 1. Size class distribution of the fiddler crabs *Leptuca leptodactyla* (**A**) and *L. thayeri* (**B**) captured in pitfall traps in southern Brazil. CW, carapace width.

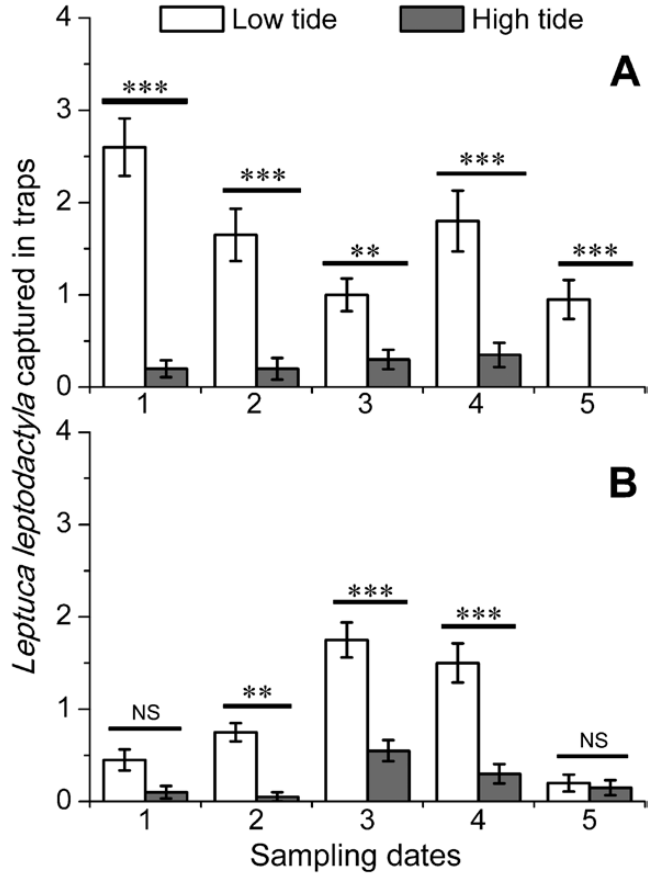

Figure 2. Mean number (±1 SE) of individuals of *Leptuca leptodactyla* captured by pitfall traps at each sampling time (tidal and daily cycles: diurnal (**A**), nocturnal (**B**). NS, non-significant; ** $P < 0.01$; ***$P < 0.001$.

Table 1. Results of a mixed-model three-way ANOVA testing the effects of the daily cycles (fixed; diurnal and nocturnal) and the tidal cycles (fixed; low and high) on the activity of *Leptuca leptodactyla* and *L. thayeri* across different sampling dates (random; dates 1 to 5).

		L. leptodactyla			*L. thayeri*		
	df	MS	F	*P*	MS	F	*P*
Daily cycle – Day	1	0.28	11.7	< 0.001	0.14	0.05	0.829
Tidal cycle - Tide	1	5.48	227.4	< 0.001	0.56	0.62	0.477
Date	4	0.29	12.2	< 0.001	1.13	6.67	< 0.001
Day × Tide	1	0.38	15.8	< 0.001	0.21	0.32	0.602
Day × Date	4	0.28	11.7	< 0.001	2.65	15.6	< 0.001
Tide × Date	4	0.08	11.7	0.007	0.91	5.38	< 0.001
Day × Tide × Date	4	0.15	6.4	< 0.001	0.65	3.86	0.004
Residual	380	0.24			0.17		

$P = 0.60$, for *L. leptodactyla* and *L. thayeri*, respectively (two-way ANOVA, Fig. 4) and during the day in contrast to night time ($F_1 = 0.30$, $P = 0.52$ and $F_1 = 0.30$, $P = 0.72$), for *L. leptodactyla* and *L. thayeri*, respectively (two-way ANOVA, Fig. 4). We also found no differences in the sex ratio for both species at high in contrast to low tide ($F_1 = 0.00009$, $P = 0.99$ and $F_1 = 0.03$, $P = 0.84$, for *L. leptodactyla* and *L. thayeri*, respectively (two-way ANOVA, Fig. 5) and day in contrast to night tine ($F_1 = 0.31$, $P = 0.58$ and $F_1 = 0.03$, $P = 0.84$, for *L. leptodactyla* and *L. thayeri*, respectively (two-way ANOVA, Fig. 5). For *L. leptodactyla*, 43% of crabs trapped were male ($\chi^2 = 14.6$, $P = 0.0002$), whereas 55% of *L. thayeri* were male ($\chi^2 = 3.3$, $P = 0.08$). We did not find ovigerous *L. thayeri* females throughout the study. Three (2.85%) of the *L. leptodactyla* females were ovigerous at diurnal low tide, one (6.25%) at diurnal high tide, and five (8.6%) at nocturnal low tide, and none at nocturnal high tide.

DISCUSSION

We report clear evidence that at least one of the studied species of fiddler crabs was active at both low and high tides. Our data show that, while individuals of *L. leptodactyla* were mainly trapped at low tide, as expected from the results available in the literature for a number of fiddler crabs species, *L. thayeri* were equally trapped during high tide and low tide. Our traps were deployed to capture crabs as they actively walk over the sediment performing their activities (feeding, searching for new territories and burrows, mating, and agonistic meeting), thus the number of crabs trapped is in strong relationship with their overall surface activity. *Leptuca leptodactyla* and *L. thayeri* are particularly known to forage near their own burrows, and their activities usually involve movements over short distances (Crane, 1975; Salmon, 1987). The crabs captured by our traps were inhabitants of the burrows situated near the traps, freely and actively walking on the surface during both high and low tides.

Individuals of *L. leptodactyla* were caught in traps during both diurnal and nocturnal low tides. This species closes with sediment the entrance of its burrows just before the flooding tide (Matthews, 1930). This behavior was also described for other species such

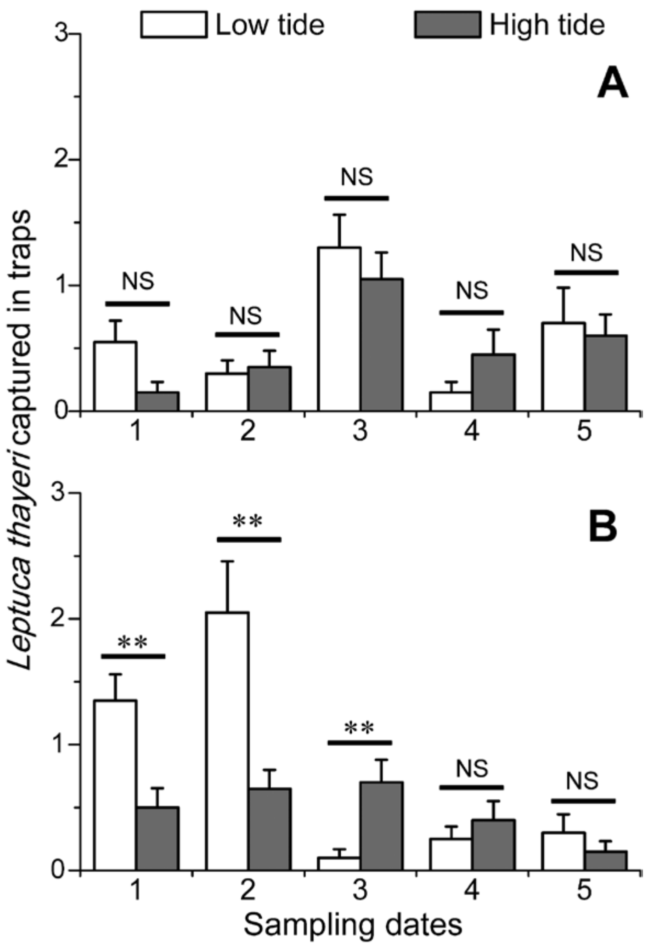

Figure 3. Mean number (±1 SE) of individuals of *Leptuca thayeri* captured by pitfall traps at each sampling time (tidal and daily cycles: diurnal (**A**), nocturnal (**B**). NS, non-significant; ** $P < 0.01$.

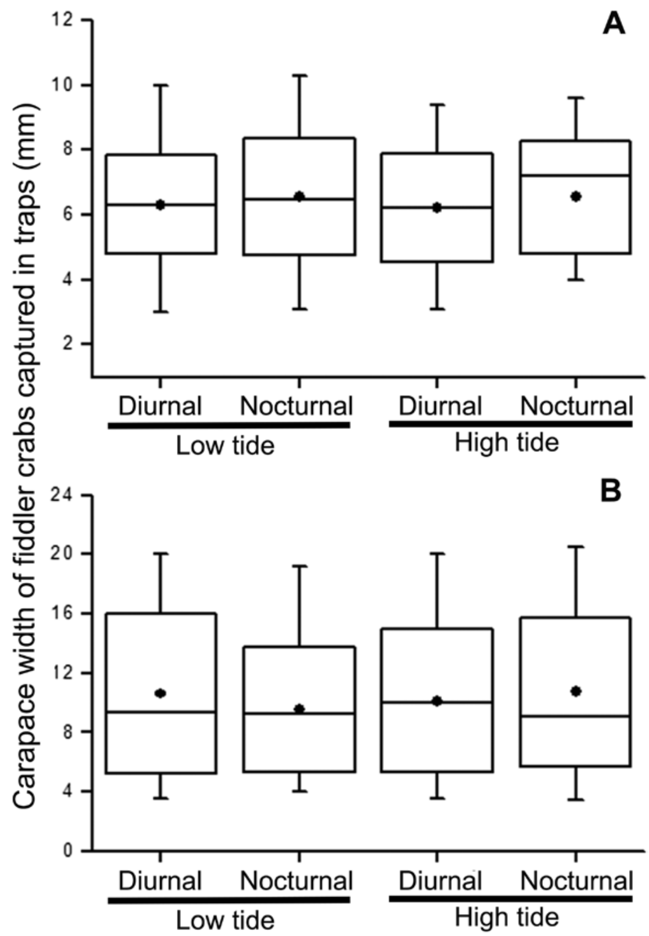

Figure 4. Size (carapace width in mm) of individuals of *Leptuca leptodactyla* (**A**) and *L. thayeri* (**B**) trapped in pitfall traps at different diurnal and tidal phases. Dots and horizontal lines within the boxes indicate mean and median values, respectively. Boxes are the standard deviations and the whiskers are minimum and maximum values.

as *L. uruguayensis* Nobili 1901 (de la Iglesia, 1994) and *L. pugilator* Bosc, 1801 (Teal, 1958). Crabs keep air chambers when they close their burrows, and an adaptive behavior to breath air at high tide (de la Iglesia, 1994). Morphological analysis of the branchiostegal chamber of the fiddler crab *Gelasimus vocans* Linnaeus 1758 suggests that this species has a branchiostegal lung more tailored to aerial breathing than aquatic (Paoli *et al.*, 2015). These behavioral and anatomical adaptations suggest that some species of fiddler crabs are highly adapted to terrestrial life.

We nevertheless showed that individuals of *L. thayeri* were active on the sediment surface at both high and low tide. Unlike *L. leptodactyla*, individuals of *L. thayeri* were never reported to plug their burrows at flooding tides, and they did not show this behavior at the study site. There is evidence that other fiddler crabs can be active at high tide and therefore subject to predation by fishes. For example, *Minuca longisignalis* Salmon & Atsaides 1968 was one of the main food items recorded in the stomach of the killifish *Fundulus grandis* (Rozas & LaSalle, 1990). Teal (1958) showed that *Minuca pugnax* Smith 1870, *Leptuca pugilator* and *M. minax* LeConte, 1855 were active at high tide and fed underwater, suggesting that some fiddler crabs may be more aquatic than previously thought.

The size structure of the samples collected in the traps reflect the population structure in the study areas of the two species studied. The maximum size of the captured individuals of *L. leptodactyla* and *L. thayeri* (10.3 mm CW and 20,7 mm CW, respectively) was lower than in other studies for the same species (see Masunari & Swech-Ayoub, 2003; Bedê *et al.*, 2008 and Machado *et al.*, 2013 for *L. leptodactyla*; Costa & Negreiros-Fransozo, 2003 and Negreiros-Fransozo *et al.*, 2003 for *L. thayeri*). Although smaller, the trapped samples of *L. leptodactyla* and *L. thayeri* included both juveniles and adults (see Cardoso & Negreiros-Fransozo, 2004 and Negreiros-Fransozo *et al.*, 2003 for size at the sexual maturity of both species), which shows that the traps were able to capture all size classes and ages. Moreover, no differences in average size were found between crabs trapped at high *versus* low tide for both species, showing that high tide activity of *L. thayeri* is not dependent on size- or age.

The sex ratio of *L. thayeri* was 1:1 as previously shown (Costa & Negreiros-Fransozo, 2003; Bezerra & Matthews-Cascon, 2007). For *L. leptodactyla* more females were trapped (57 %) than the expected 1:1 ratio (see Bezerra & Matthews-Cascon, 2007). The difference in sex ratios could be explained by the mating strategies of the two species. Females of *L. leptodactyla* leave their burrows and wander long distances searching for mates, whereas both sexes of *L. thayeri* wander on the sediment surface in search for mates. (Salmon, 1987; Rodrigues *et al.*, 2016). Because female fiddler crabs release their larvae mainly during nocturnal spring tide (Christy, 1982; Morgan & Christy, 1995; Christy & Wada, 2015), we expected to capture more females during this sampling period. Females were nevertheless trapped in the same proportion than males in both diurnal and nocturnal high tides. Ovigerous females of *L. thayeri* and a few ovigerous females of *L. leptodactyla* were trapped throughout the study. Females of *Austruca lactea* De Haan, 1835 remain in their burrows during larval release (Yamaguchi, 2001). Such behavior in the two

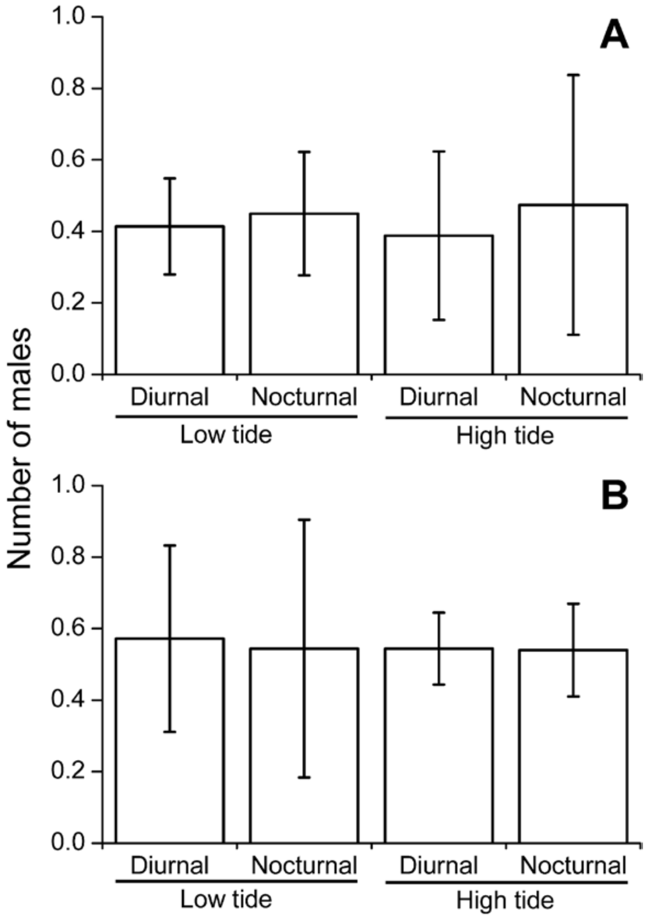

Figure 5. Sex ratios of individuals of *Leptuca leptodactyla* (**A**) and *L. thayeri* (**B**) trapped in pitfall traps at different diurnal and tidal phases.

species studied would explain why they were not more females than males trapped during the nocturnal spring tide.

We showed that two fiddler crab species have contrasting activity patterns. *Leptuca leptodactyla* showed to be mostly active at low tide, irrespective of nocturnal and diurnal conditions, whereas *L. thayeri* was active at low and high tide, a behavior uncommonly reported for fiddler crabs. Future studies should assess whether these contrasting patterns are related to differences in morphological as well as physiological adaptations. The activity pattern of other fiddler crabs could also be investigated considering the differences between their habitats. Species that live in mangroves, where tree roots could protect them from large predatory fishes, could be more active than those living on sandy and open banks where they are exposed to predators. Our results confirm that some species of fiddler crabs constitute a food source for particular estuarine fishes and could have a previously unreported importance in the food web of such aquatic species.

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