

# Intraspecific facilitation of the recruitment of a burrowing mangrove crab species along an environmental gradient

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## ABSTRACT

The exploited mangrove crab *Ucides cordatus*, an important ecosystem engineer in South American mangroves, has a biphasic lifecycle with pelagic larvae developing offshore. Megalopae return to the mangrove forest to settle, i.e., metamorphose into benthic juveniles but its environmental drivers remain poorly understood. We postulate that conspecific crabs facilitate recruitment. In the field, we investigated whether the number of recruits is higher near conspecific burrows than in areas without conspecific bioturbation. Recruit sampling was conducted monthly from April 2008 to May 2009 along an environmental gradient. First, *U. cordatus* recruits of that year emerged from March to July. Intraspecific facilitation was indicated by significantly higher recruit numbers in bioturbated than in non-bioturbated substrates. Recruits were most abundant in zones with intermediate conditions of inundation, leaf litter standing stock, sediment consistency, luminosity, temperature, salinity, and pH. Avoidance of more inundated zones likely reduces predation by fishes and of less inundated zones helps individuals escape more stressful, drier environmental conditions. The observed habitat-specific recruitment pattern must be considered when designing field assessments of the population structure of *U. cordatus* (which should include sampling recruits) and enhancing stocks by releasing laboratory-cultivated larvae and first juveniles into the wild.

**Keywords:** Bioturbation, Burrow, Land crab, Settlement, *Ucides*

## INTRODUCTION

A facilitative interaction between two organisms occurs when at least one is benefited and neither is impaired (Stachowicz, 2001; Bruno et al., 2003). Intra- and interspecific facilitation can be important in

stressful environments and, in marine environments, have mostly been studied in intertidal communities, particularly rocky coasts, due to the ease of manipulation and monitoring of sessile organisms (e.g., Bertness, 1989; Bertness et al., 1999; Leslie, 2005; Rius and McQuaid, 2009) (Westerbom et al., 2019). In contrast, few studies emphasized the importance of ecological facilitation in soft-bottom intertidal communities. Some examples include the intra- and interspecific facilitation of sandflat colonization by bivalves, polychaetes, and crustacea (Gallagher et al., 1983; Thrush et al.,

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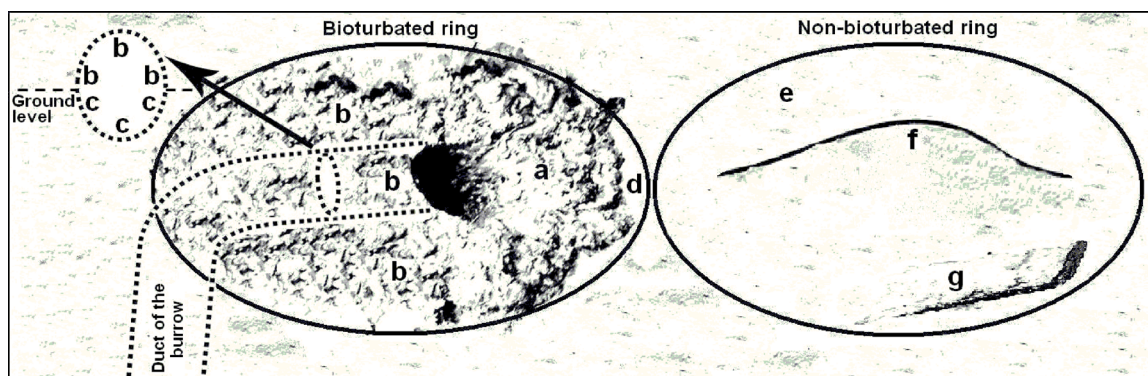


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1992; Méndez Casariego et al., 2009; Donadi et al., 2014) and the facilitation of ghost shrimp recruitment by conspecific adults (Tamaki and Ingole, 1993). These studies show that bioturbation is important for the occurrence of facilitation in soft-bottom communities. In fact, many facilitation examples are linked to habitat modifications in which an individual alters environmental conditions, making a stressful habitat more suitable for another (Stachowicz, 2001). Organisms that modify, maintain, or create habitats by physical actions and thereby control the availability of resources for other organisms are called “physical ecosystem engineers” (Jones et al., 1994, 1997).

Some of the most important engineers in mangrove ecosystems are burrowing crabs (Kristensen, 2008; Diele, Koch, et al., 2010; Cannicci et al., 2021; Fusi et al., 2022). They dig and maintain burrows, using them as refuge from predators, shelter against extreme environmental conditions, and, in several cases, as a place for food storage and mating (Bliss, 1979; Christy, 1982; Chan et al., 2006). Crab bioturbation aerates the substrate, which can benefit mangrove trees (Smith et al., 1991), and creates a micro-habitat for meiofauna (Dittmann, 1996). The magnitude of bioturbation caused by the burrowing crab *Ucides cordatus* is

remarkable in South American mangroves (e.g., Pülmanns et al., 2014; Aschenbroich et al., 2016; Pestana et al., 2017; Otero et al., 2020). With a carapace width (CW) of up to 9 cm, *U. cordatus* is also one of the largest mangrove invertebrates on this continent (Schmidt and Diele, 2023). Burrow density and size vary along the physical gradient of mangroves; smaller ones have been mostly observed in less flooded areas (Diele et al., 2005; Schmidt et al., 2009, 2013; Wunderlich and Pinheiro, 2013). A typical burrow of *U. cordatus* has an elliptical opening, with the larger diameter corresponding to the total height of the crab and the smaller diameter corresponding to the length of the carapace (Schmidt et al., 2008; Araújo and Calado, 2011). The duct of a typical *U. cordatus* burrow first runs horizontally below the surface (often indicated by a slightly domed substrate surface), curving and descending steeply (Figure 2), reaching the water table, sometimes up to a total depth of two meters (De Gerales and De Calventi, 1983; Santos et al., 2009; Araújo and Calado, 2011). Crabs often plug entrances with sediment collected from the surface outside their burrows. Digging, maintaining, closing, and opening burrows accumulate sediment around entrances and elevate the local microtopography (Schmidt and Diele, 2023).



**Figure 1.** Sampling of *U. cordatus* recruits. Continuous thick lines: metal rings placed on the sediment surface either around a conspecific burrow (“bioturbated ring”) or on not-bioturbated sediment by *U. cordatus* (“non-bioturbated rings”). Thick dashed line: burrow duct and cross-section of the duct. A typical burrow duct of *U. cordatus* first runs horizontally below the sediment (often indicated by a slightly domed surface), curving down and descending steeply. Letters indicate places where recruits were found. Bioturbated rings: (a) burrow entrance area, (b) horizontal duct roof, (c) horizontal duct floor (see cross-section), and (d) smooth sediment surface. Non-bioturbated rings: (e) smooth sediment surface, (f) sediment mound, and (g) sediment under wooden sticks.

*U. cordatus* spends most of its time inside its burrows. When outside, they stay immobile

at the entrances or collect litter, which is then consumed inside the burrows (Nordhaus et al.,

2009). Burrowless crabs are rarely encountered in the forest, except during the few mating days in the reproductive season (Schmidt et al., 2012). Females release larvae into estuaries at spring ebb tides. In macro- and mesotidal environments, these tides can transport the larvae offshore, where they develop. After a month, they return to the estuarine environment, in which settlement takes place (Diele, 2000; Simith and Diele, 2008). Laboratory experiments showed that *U. cordatus* settlement is triggered by conspecific odors (Diele and Simith, 2007; Simith and Diele, 2008; Simith et al., 2013, 2017). Accordingly, recruits (mostly with CW < 1 cm) have been (coincidentally) found inside burrows of larger conspecifics (Schmidt and Diele, 2009). These findings raised the hypothesis that burrows and their hosting owners facilitate recruitment. However, this assumption remains untested as recruit numbers in bioturbated substrates have not yet been compared to those in non-bioturbated substrates.

Knowledge about specific microhabitats and possible conspecific facilitation of recruitment is important to optimize procedures to introduce laboratory cultivated megalopae and juveniles into the wild for stock enhancement (e.g., Ventura et al., 2011). Such actions, if carried out thoughtfully, can contribute to the management of *U. cordatus*, an important fishing resource in Brazil (Glaser and Diele, 2004; Diele, Araújo, et al., 2010; Nascimento et al., 2017), which has already suffered stock losses due to mass mortalities caused by a fungal disease (Schmidt et al., 2008; Orélis-Ribeiro et al., 2011). This study sampled recruits of *U. cordatus* inside substrates with and without bioturbation caused by conspecific organisms along the environmental gradient of a mangrove forest, including its transition to the hinterland. This study aimed to (i) test the hypothesis that conspecific burrows and their hosting owners facilitate *U. cordatus* recruitment, (ii) determine whether recruitment varies spatially along the environmental gradient of the studied mangrove forest, and (iii) identify possible temporal patterns in *U. cordatus* recruitment.

## METHODS

### STUDY AREA

Field work was conducted near Caravelas, in the Brazilian Northeast, in a mangrove forest located between a tidal creek and the hinterland, characterized by a sandbank with restinga vegetation (S17°42' W039°18". The study site is characterized by the following four zones (from creek to hinterland): (i) a forest dominated by taller *Rhizophora mangle* near its creek, (ii) a forest with a smaller *R. mangle*, (iii) a forest with *Laguncularia racemosa*, and (iv) predominantly bare ground with sporadic *Acrostichum aureum* ferns in the transition from forest to hinterland. The study area comprised a 500-m section of mangrove forest (Figure 2A).

### VEGETATION STRUCTURE, ZONATION, AND ABIOTIC GRADIENTS

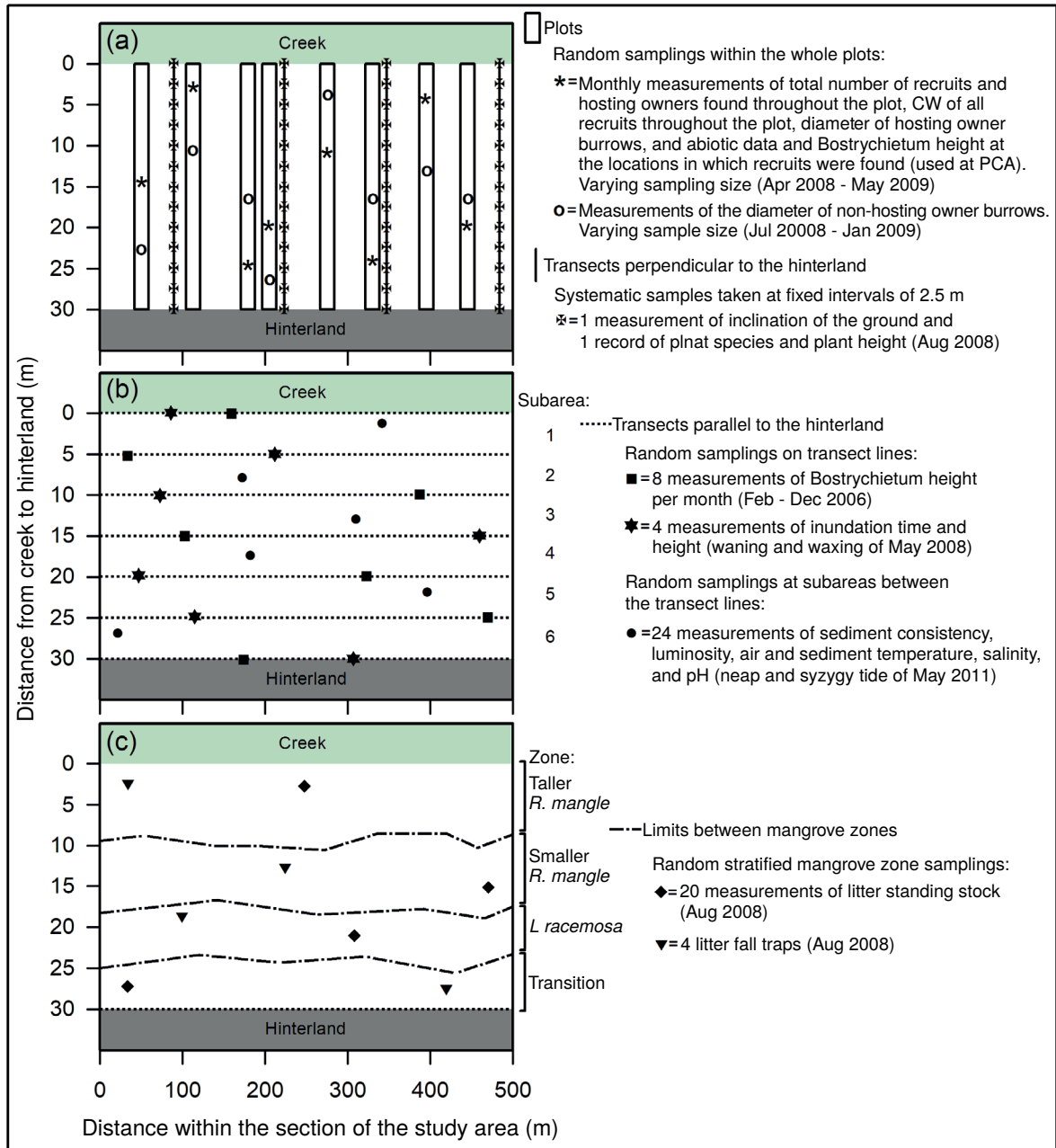
A profile of topography and vegetation was drawn by measuring angles (with a digital inclinometer) and recording the floral species and their estimated height. Measurements were performed every 2.5 m along four 30-m random transects running perpendicular from the tidal creek toward the hinterland (Figure 2A). At each vegetation zone (Figure 2C), a stratified random sampling of litter standing stock and litter fall was conducted in August 2008. Standing stock was measured by collecting litter from the substrate surface within a radius of 1 m around 20 *U. cordatus* burrows (3.14 m<sup>2</sup>) and litter fall was measured with four 1 x 1 m traps installed one meter above the substrate and emptied after one week (see Nordhaus et al., 2006) (Figure 2C).

To characterize the inundation gradient, seven 500-m lines with 5 m in between were marked parallel to the hinterland (Figure 2B). Once a month from February to December 2006, eight random points were marked at each line with the aid of a GPS odometer. BH was measured (see above) at each point. Inundation was measured directly in May 2008, three days before (waxing) and four days after (waning) the full moon, when tidal height was equivalent to the annual mean tidal height. During these periods, four random points on the substrate were marked at each line with the aid of an odometer (Figure 2B). At each point, inundation

time was measured during the day over a 12-h tidal period. At the same points, inundation height was measured during slack high tide.

To characterize the gradient of physicochemical parameters, the study area was divided into six contiguous 5 x 500 m subareas (Figure 2B). Within each subarea, luminosity (by a luxmeter),

sediment consistency, air temperature, sediment temperature, pore water salinity, and pH (with a pH meter) were measured at 24 random points during the low tide from 12 p.m. to 3 pm. Sampling was performed at neap tide (first quarter) and syzygy (full moon) of May 2011. The pH was measured only at neap tide due to logistical reasons.



**Figure 2.** Sampling design. Each marker represents a measurement or a set of measurements. (a) Plots for sampling *U. cordatus* crabs and parameters in the places in which recruits were found (used at PCA); and transects for drawing the zonation profile of the area. (b) Transects for measuring *Bostrychietum* band height and inundation height and time and subareas between transects for measuring abiotic parameters. (c) Mangrove zones in which litter standing stock and litter fall was measured.

## ABIOTIC DATA COLLECTION NEAR THE RECRUITS

At neap tide days from April 2008 to May 2009, the following parameters were measured from 5 to 15 cm away from the found recruits (Figure 2A): air temperature, sediment temperature at 3 cm depth, pore water salinity (by digging a hole until water percolated across the sediment and accumulated, enabling collection and measurement with a refractometer), sediment consistency (using a pocket Humboldt H-4200 soil penetrometer with an adapter foot), and the maximum height above ground of the *Bostrychietum* algal band growing on roots and stems of mangrove trees (hereafter referred as BH). BH is an indicator for mean high tide level (Oliveira, 1984; Cunha et al., 1999; Rützler and Feller, 1999; Rodrigues et al., 2000; Cunha and Costa, 2002).

## SAMPLING OF RECRUITS

In this study, a recruit was defined as a “settler that reached a size large enough to enable its visual detection in the field” (Keough and Downes, 1982; Bertness et al., 1992). Due to the cryptic habitat of small crabs, a manual search of the sediment was necessary to locate them (Schmidt and Diele, 2009). Recruits associated with burrows of larger conspecifics are called “co-inhabitants,” whereas those found outside conspecific burrows (but without a visible burrow of their own) are named “free-living.” All crabs that live in their own burrows and that are large enough to be detected visually were called “owners.” Owners hosting co-inhabitants are called “hosting owners” and those not hosting co-inhabitants are called “non-hosting owners.”

Sampling was performed once a month in eight randomly selected plots (30 x 1 m) placed perpendicularly to a 500-m long section of hinterland (Figure 2A). Sampling was conducted from April 2008 to May 2009 at neap tide days. In each plot, a wire ring with a diameter of 25 cm was placed over each visible *U. cordatus* burrow (“bioturbated ring”). As close as possible to each “bioturbated ring”, another ring was placed on the substrate surface which was not bioturbated by *U. cordatus* (“non-bioturbated ring”) (Figure 3). About 1 L of sediment was taken from the area inside each bioturbated and non-bioturbated ring. In non-bioturbated rings, this amount was equivalent to a 3-cm

surface layer of sediment, whereas, in bioturbated rings, it comprised not only surface sediment but also the sediment excavated by the crabs. The substrate from bioturbated rings was categorized as follows (Figure 3): burrow entrance (including crab tracks in front of it), roof of the horizontal burrow duct, floor of the horizontal burrow duct, plug (sediment used to close the entrance – often missing), and smooth surface (a non-bioturbated surface, sometimes present in rings around smaller burrows). The substrate from non-bioturbated rings was categorized as smooth surface, mound, and sediment under wooden twigs (Figure 3). Recruits were carefully separated from the sediment by hand and their carapace width (CW) was measured with a caliper rule to the nearest mm. They were released at the same place after capture. Field sexing was impossible due to their small size.

## MEASUREMENT OF THE BURROWS OF OWNER CRABS

Inside the eight plots (Figure 2A), all burrow openings of hosting owners were measured. The burrows of non-hosting owners were also measured in July 2008 and January 2009. The diameter of burrow openings was measured applying the method described in Schmidt et al. (2008). Burrow diameter (BD) was transformed to carapace length (CL) using the equation “ $BD = 0.244952 + 1.04026 \times CL$ ,” obtained by linear regression ( $R^2 = 75.2$ ,  $N = 341$ ). CL values were then transformed to carapace width (CW) using the equation “ $CW = -0.0376206 + 1.30283 \times CL$ ,” also obtained by linear regression ( $R^2 = 98.4$ ,  $N = 341$ ). Both regressions were based upon data collected in the same study area from February 2006 to July 2008 (Schmidt, 2012).

## STATISTICAL ANALYSIS

Polynomial regressions were performed for the dependent variables “abundance of recruits,” “abundance of hosting owners’ burrows,” “CW of recruits,” and “CW of hosting and non-hosting owners estimated by burrow openings” (in relation to BH). The mean CW of recruits found in bioturbated and non-bioturbated rings and the mean CW of hosting and non-hosting owners were compared using the Student’s *t*-test. Mean

CW, abundance of recruits over time, and abiotic parameters along the profile were compared with Repeated Measures ANOVA, followed by a Bonferroni post-hoc test. The sphericity assumption was tested with the Mauchly's test (the Huynh-Feldt correction was performed when necessary). Litter fall and standing stock means were analyzed by ANOVA considering vegetation zone as a factor, followed by a Tukey's HSD test. Data were square root or log transformed when necessary to reach homoscedasticity and tested with Cochran's "C" test. Even after transformations, salinity samples obtained during neap tide showed heterogeneous variances. In these samples, two subsets of data showed homogeneous variances: one comprising the three landward subareas and another comprising the three subareas closer to the creek. A separate analysis was performed for each of these subsets of samples. Some data remained non-normal even after transformation but parametric statistics was still applied due to the robustness of ANOVA (Underwood, 1997). All average values are given with standard errors. Frequencies and ratios were compared by Chi-Squared analysis. Data obtained near the rings in which recruits had been found (abundance of recruits, air temperature, sediment temperature, sediment consistency, pore water salinity, and BH) were standardized by subtracting their means

and dividing them by their standard deviations. This procedure enabled the investigation of the relationships between these multivariate data by Principal Components Analysis – PCA.

## RESULTS

### VEGETATION STRUCTURE, ZONATION, AND ABIOTIC GRADIENTS

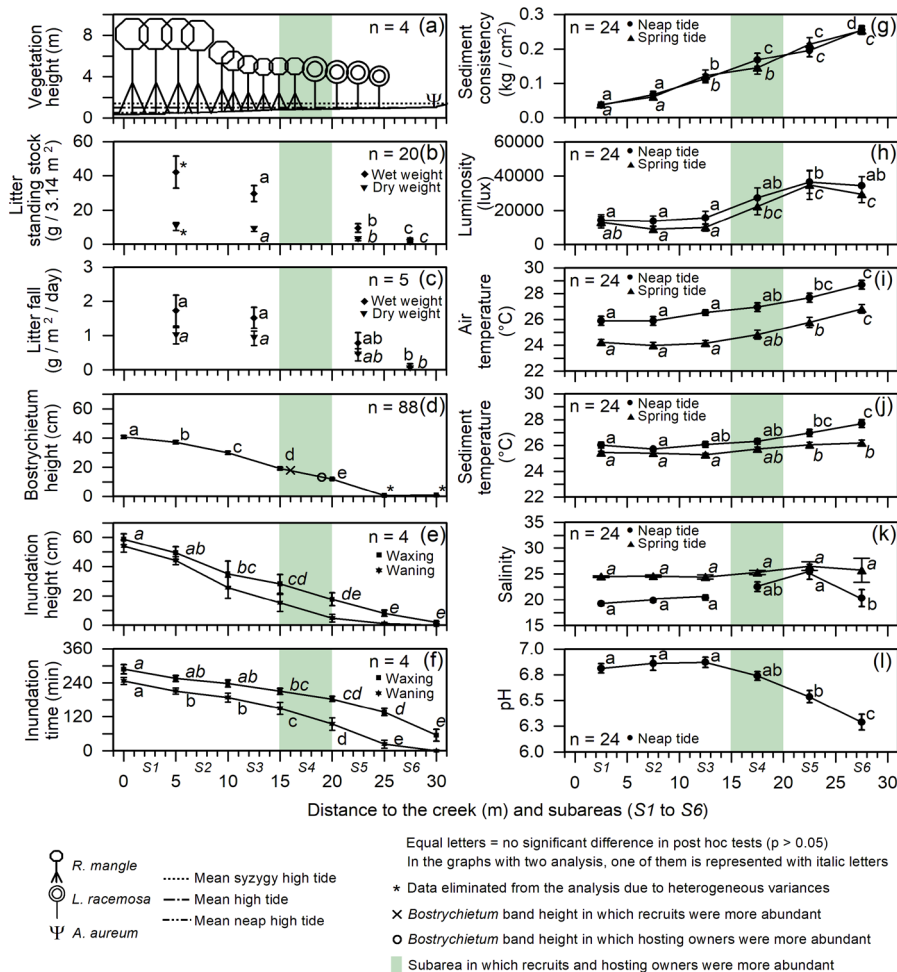
Tree height, litter standing stock, and litter fall increased from the hinterland to the tidal creek (Figures 3A, 3B and 3C; Table 1). The mean height of the *Bostrychietum* band (BH) varied spatially (rather than temporally), increasing from hinterland to the creek (Figure 3D; Table 1). Inundation time and height also increased from hinterland to creek (Figures 3E and 3F; Table 1). In contrast, the means of the following parameters decreased from hinterland to creek at both neap and spring tides: sediment consistency (Figure 3G), luminosity (Figure 3H), and air (Figure 3I) and sediment temperature (Figure 3J; Table 1). Pore water salinity remained stable along the profile during spring tide (Figure 3K). At the landward subareas, salinity was lower next to the hinterland, whereas the means in the subareas near the creek failed to differ (Figure 3K; Table 1). At neap tide, pH was significantly lower at the two subareas closest to the hinterland (Figure 3L; Table 1).

**Table 1.** Results of Analysis of Variance and the post hoc tests of the parameters characterizing vegetation structure, zonation, and abiotic gradients.

Parameter	Analysis of Variance			Post hoc test	
	df	F	P	P	
Tree height	2	35.26	< 0.0001	< 0.05	
Litter standing stock (dry weight)	2	36.06	< 0.0001	< 0.05	
Litter fall (wet weight)	3	5.69	< 0.01	< 0.05	
Litter fall (dry weight)	3	5.68	< 0.01	< 0.05	
Height of <i>Bostrychietum</i> band	3.3	323.6	< 0.0001	< 0.05	
Inundation time	at waning	6	148.4	< 0.0001	< 0.05
	at waxing	6	53.5	< 0.0001	< 0.05
Inundation height	at waning	6	49.7	< 0.0001	< 0.05
	at waxing	6	40.3	< 0.0001	< 0.05
Sediment consistency	at neap tide	4	72.4	< 0.0001	< 0.05
	at spring tide	4	53.9	< 0.0001	< 0.05

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Parameter	Analysis of Variance	Post hoc test			
		df	F	P	
Luminosity	at neap tide	4	72.4	< 0.0001	< 0.05
	at spring tide	3.5	12.7	< 0.0001	< 0.05
Air temperature	at neap tide	4	16.5	< 0.0001	< 0.05
	at spring tide	3	21.4	< 0.0001	< 0.05
Sediment temperature	at neap tide	5	11.9	< 0.0001	< 0.05
	at spring tide	4.6	7.2	< 0.0001	< 0.05
Pore water salinity	at neap tide (landward)	2	4.3	< 0.05	> 0.05
	at spring tide (by the creek)	2	2.7	> 0.05	< 0.05
Pore water pH	at neap tide	5	0.68	> 0.05	> 0.05
	at spring tide	5	15.5	< 0.0001	< 0.05



**Figure 3.** Biotic and abiotic gradients in the study area. (a) Ground profile, vegetation zonation, and inundation levels; (b, c) litter standing stock and litter fall in the zones of taller *R. mangle*, shorter *R. mangle*, *L. racemosa*, and at the transition to hinterland; (d) *Bostrychietum* band height measured every five meters along the profile; (e, f) inundation height and time measured every five meters along the profile at waxing and waning moon; (g, h, i, j, k, l) sediment consistency, luminosity, air temperature, sediment temperature, salinity, and pH, respectively, measured in the six subareas at neap and spring tides.

## NUMBER OF RECRUITS IN BIOTURBATED AND NON-BIOTURBATED RINGS

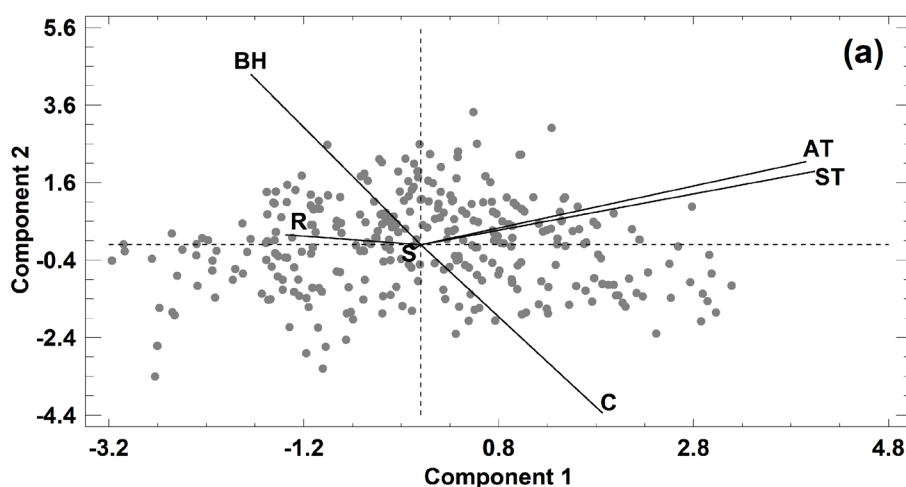
We found a total of 474 *U. cordatus* recruits, 96% of which inside bioturbated rings (co-inhabitants) versus 4% inside non-bioturbated rings (free-living) ( $\chi^2 = 390.08$ , SL = 0.05, DF = 1). This proportion failed to significantly vary between the six subareas ( $\chi^2 = 8.75$ , SL = 0.05, DF = 5). We found 43% of the 455 co-inhabitants in the sediment of the roofs of the burrow ducts, 29% in plugs, 27% in owner sediment tracks at the entrance of burrows, and 1% in the floor of ducts (Figure 2). We found 79% of the 19 recruits in the non-bioturbated rings in the sediment of mounds; 16%, in the sediment of smooth surfaces; and 5%, under a wooden stick (Figure 2). We found a total of 408 hosting owner burrows, 89.7% of which had one co-inhabitant; 9.3%, two; 0.7%, three; and 0.2%, four. The entrance and floor of all hosting burrows had fresh *U. cordatus* tracks, indicating that they were inhabited by the owner.

## ABUNDANCE OF RECRUITS AND HOSTING OWNERS ALONG THE ENVIRONMENTAL GRADIENT

The overall means of abiotic parameters near the rings in which we found recruits totaled: BH =  $21.2 \pm 0.46$  cm, sediment consistency =  $0.13 \pm 0.004$  Kg/cm<sup>2</sup>, air temperature =  $26.8 \pm 0.11$  °C, sediment temperature =  $25.5 \pm 0.12$  °C, and salinity =  $31.1 \pm 0.27$ . Pooling together data from these variables and from the abundance of recruits, PCA extracted three components

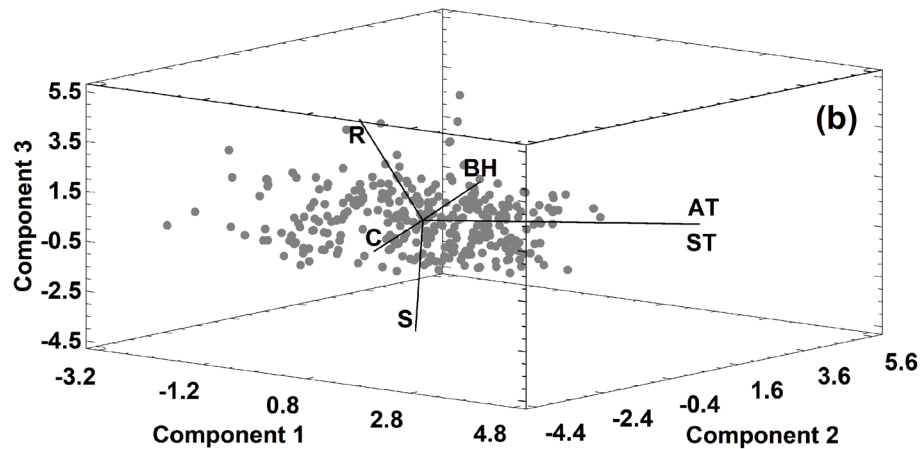
with eigenvalues greater than 1.0, accounting for 70.22% of the variability in the original data. Component 1 (explaining 28.7% of the variance) shows the highest weights for air and sediment temperatures (0.62 and 0.64 respectively) and a negative correlation to abundance of recruits and BH and a positive correlation to sediment consistency (Figure 4A). Component 2 (explaining 23.4% of the variance) showed highest weights for sediment consistency (-0.64) and BH (0.65), variables with an inverse correlation with each other (Figure 4A). Component 3 explained 18.10% of the variance and showed highest weights for abundance of recruits (0.62) and salinity (-0.77), inversely correlated variables (Figure 4B).

The relationship between abundance of recruits and the BH measured close to the rings was best explained by a third degree model (Correlation coefficient = 0.78,  $R^2 = 0.61$ ,  $n = 51$ ). Recruitment was highest in zones with 18.5-cm BH (Figure 5A). The relationship between abundance of hosting owners and the BH measured close to the rings was best explained by a fourth degree model (Correlation coefficient = 0.78,  $R^2 = 0.61$ ,  $n = 60$ ). Hosting owners were most abundant in zones with 13.5-cm BH (Figure 5B). According to the BH gradient graph (Figure 3D), maximum recruitment (BH = 18.5 cm) and abundance of hosting owners (BH = 13.5 cm) occurred at a distance of 16 and 19 m from the creek, respectively; both at subarea 4, the start of the less flooded zone dominated by small *L. racemosa* trees (Figure 3A).

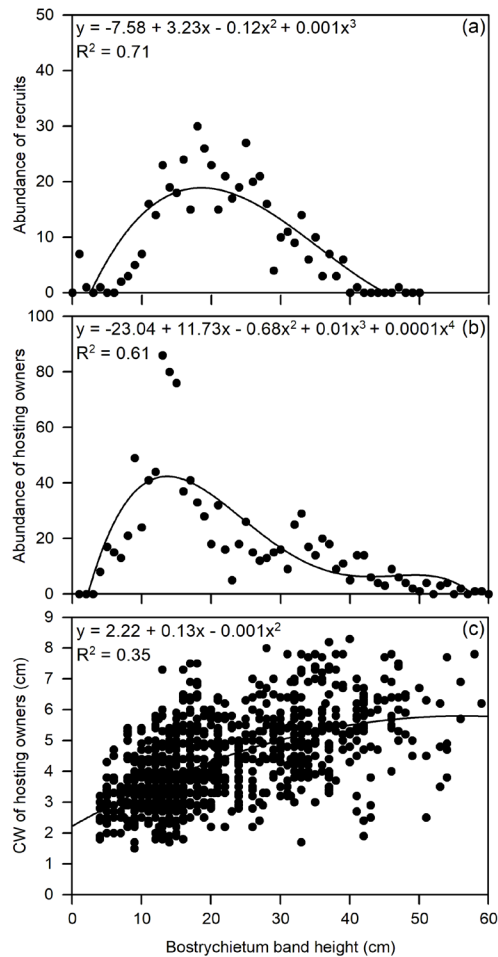


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**Figure 4.** Principal component analysis of the abundance of *U. cordatus* recruits (R), *Bostrychietum* band height (BH), consistency of the sediment (C), air temperature (AT), sediment temperature (ST), and pore water salinity (S). (a) Two-dimensional chart with components 1 and 2. (b) Three-dimensional chart with components 1, 2, and 3.

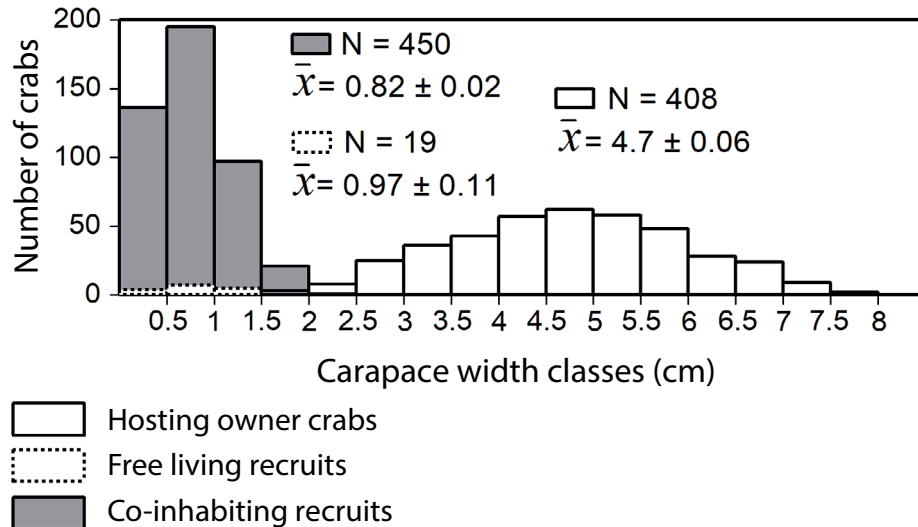


**Figure 5.** Polynomial regressions of the dependent variables (a) abundance of *U. cordatus* recruits (co-inhabitants and free-living), (b) abundance of hosting owners, and (c) carapace width of hosting owners in relation to the *Bostrychietum* band height measured at the place in which the respective crab had been sampled.

## SIZE OF RECRUITS ALONG THE ENVIRONMENTAL GRADIENT

The smallest and largest co-inhabiting recruit measured 0.15- and 2.20-cm CW, respectively. Mean recruit size was  $0.82 \pm 0.02$  cm (Figure 6).

The smallest and largest free-living recruit had a CW of 0.25 and 1.90 cm, respectively, and a mean size of  $0.97 \pm 0.11$  cm (Figure 6). We found neither a significant size difference between the CW of co-inhabitants and free-living recruits nor between recruit size and BH.



**Figure 6.** Size frequency distribution, means and standard errors of carapace width of *U. cordatus* hosting owner crabs, free-living recruits and co-inhabiting recruits found between April 2008 and May 2009. Measurements of 5 co-inhabitants were missed.

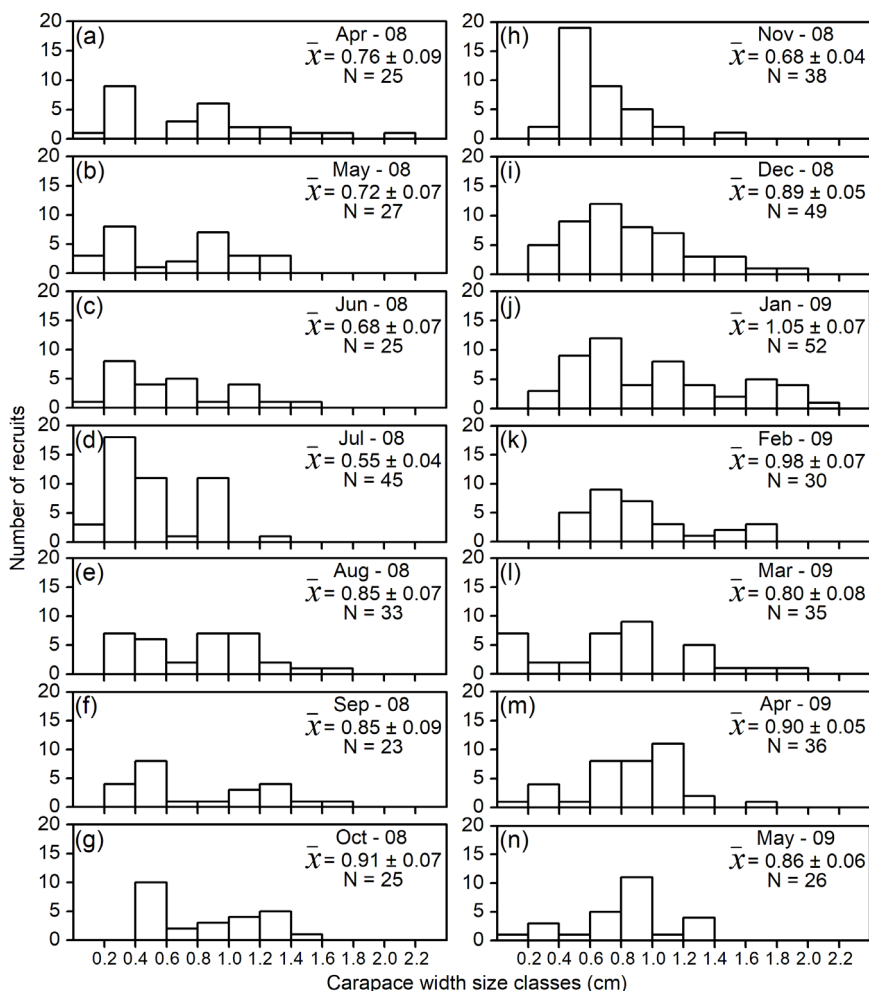
## SIZE OF HOSTING AND NON-HOSTING OWNERS ALONG THE ENVIRONMENTAL GRADIENT

The estimated CW of the hosting owners ranged between 1.7 to 8.9 cm, with an overall mean size of  $4.7 \pm 0.06$  cm (Figure 6). In July 2008 and January 2009, when we measured the opening size of all crab burrows (hosting and non-hosting ones), 8% of them had co-inhabiting recruits. Mean CW of hosting and non-hosting owners averaged  $3.9 \pm 0.06$  and  $3.8 \pm 0.16$  in July and  $4.4 \pm 0.06$  and  $5.2 \pm 0.17$  in January. In July and January, mean size of hosting and non-hosting crabs failed to differ statistically from each other. The CW of both hosting and non-hosting owners increased from hinterland to creek. The relationship between their CW and BH was best explained by the quadratic

regression ( $R = 0.60$ ), despite its low coefficient of determination ( $R^2 = 0.35$ ,  $n = 1034$ ) (Figure 5C).

## ABUNDANCE AND SIZE OF RECRUITS ALONG TIME

While the abundance of recruits failed to differ significantly between months, their size did (Repeated Measures ANOVA:  $df = 13$ ;  $F = 5$ ;  $P < 0.0001$ ). Mean CW was the smallest in July 2008 (Figure 7d). We found the smallest recruits (with a CW of up to 0.2 cm) from April to July 2008 (Figures 7A, 7B, 7C and 7D). Such small crabs were absent in subsequent months, re-appearing from March to May 2009 (Figures 7L, 7M and 7N). Mean CW was the largest in January 2009 ( $1.05 \pm 0.07$ ), when the frequency of recruits in upper-size classes was highest (Figure 7J).



**Figure 7.** Monthly size frequency distributions of *U. cordatus* recruits, (co-inhabitants and free-living) from April 2008 to May 2009 (means and standard errors). April and October 2008 have missing measurements (two and three, respectively).

## DISCUSSION

Recruits of *U. cordatus* occurred predominantly in conspecific burrows, irrespective of the tidal gradient, strongly suggesting intraspecific facilitation. Furthermore, the number of recruits and small owner crabs was highest in the zone with intermediate inundation, which may provide advantages such as avoiding high predation rates in more inundated seaward areas and extreme environmental conditions in less frequently inundated landward areas. Below, we first detail the temporal and spatial pattern of recruitment in *U. cordatus* and end this study by showing its relevance for the management of *U. cordatus*.

## TEMPORAL PATTERN OF RECRUITMENT

Throughout the entire year, we only found few adult crab burrows with young recruits, likely reflecting the difficulty of finding such small-sized cryptic specimens. The occurrence of recruits in the smallest size class with up to 2-mm carapace width from March to July reflects the multiple larval releases each year from February to May in the study region (Schmidt et al., 2012).

Zoea larvae, which are released into estuarine waters at spring tides, develop offshore and take about one month to develop to megalopae and reinvade the estuarine environment to settle (Diele, 2000). First, instar crabs with an initial CW

ranging from 1.37 to 1.55 mm had reached a size of about 2 mm after a month in the laboratory and 7.83 to 11.53 mm after six months (Diele and Koch, 2010a), which closely agrees with our field findings. For example, we found the last recruits in the smallest size class in July 2008, all of which had a CW of 2 mm. These two or three instar stages had probably metamorphosed into crabs a month earlier and had been released yet another month earlier, i.e., in May. Recruits grew throughout the year as indicated by the increase in frequency of upper-size classes, and a new cohort of recruits appeared in March 2009, as indicated by the distinct drop in mean recruit size. All recruits in the smallest size class found in March 2009 had a CW of 1.5 mm. This suggests that they were recently settled first instar crabs (see Diele and Koch, 2010a), originating from the larval release in February, the first larval release event in that year.

### RECRUITMENT IN RELATION TO CONSPECIFIC BIOTURBATION

We confirmed the hypothesis raised by Schmidt and Diele (2009) that conspecific burrows will have more *U. cordatus* recruits than non-bioturbated substrates, likely due to intraspecific facilitation. Facilitation may simply be a side effect of the digging of a burrow as it changes mangrove topography. Indeed, substratum heterogeneity and complexity have been positively related to settlement success in several species and habitats (e.g., Barry and Dayton, 1991; Pech et al., 2002). However, without neglecting the physical effects of bioturbation, other factors may further contribute to these findings. Laboratory experiments showed that chemical cues emitted by conspecific *U. cordatus* specimens induce the settlement and enhance the survival of *Ucides megalopae* (Diele and Simith, 2007; Simith and Diele, 2008; Ventura et al., 2011; Simith et al., 2013). The concentration of these cues is likely higher inside conspecific burrows than outside them. Such habitat-specific recruitment may be considered an example of commensalistic (+,0) facilitation (see the review in Stachowicz, 2001) as it avoids harming hosting owners and provides at least three advantages for co-inhabiting recruits. Firstly, we can assume that food is more abundant inside crab burrows than

outside them. Crab burrows increase the passive deposition and settlement of meiofaunal organisms (DePatra and Levin, 1989; Botto and Iribarne, 1997) which are eaten by juvenile *U. cordatus* (Diele and Koch, 2010b). Larger recruits can also feed on shredded plant matter resulting from the sloppy feeding of burrow owners (Diele and Koch, 2010b) but may still be unable to collect leaves themselves and shred them. A second advantage is that conspecific burrows provide refuge from predators (Bliss, 1979; Warren, 1990; Luppi et al., 2002), particularly when closed by plugs (as it often occurs with *U. cordatus*). Moreover, the presence of the hosting owner defending its burrow indirectly protects the co-inhabitants. Finally, burrows provide shelter against extreme conditions of temperature and humidity (Powers and Cole, 1976; Eshky et al., 1995; Chan et al., 2006). Juveniles are especially less tolerant to environmental extremes than adults (Wolcott and Wolcott, 1988) and their comparably larger body surface area makes them more susceptible to desiccation (Diele, 2000). Similar findings for other species, e.g., *Neosarmatium meinerti* (Emmerson, 2001), *Neohelice granulata* (Luppi et al., 2002; Méndez Casariego et al., 2009), and *Cardisoma carnifex* (Vannini et al., 2003) suggest that recruits co-inhabiting burrows of larger conspecifics may be common in semi-terrestrial crabs.

The size at which *U. cordatus* recruits begin to live independently varies, as indicated by the overlap in the size-frequency distribution of co-inhabitants and free-living crabs. The largest co-inhabitant had a CW of 2.2 cm, a size similar to that found by Schmidt and Diele (2009). Competition with owner crabs likely forces co-inhabitants to eventually leave the conspecific burrow. As the smallest hosting owners had a CW of 1.7 cm (see Schmidt and Diele, 2009) — thus smaller than the largest co-inhabitants —, crabs beginning an independent life may soon host recruits of subsequent cohorts. This assumption agrees with the results of studies that showed that the odor emitted by *U. cordatus* juveniles (from 0.15 cm CW) triggers megalopal settlement (as does that of adults; Simith et al., 2013, 2017). Most hosting owner burrows were co-inhabited by only one recruit, which was also observed by

Schmidt and Diele (2009). The higher occurrence of co-inhabitants in the roof, plug, and entrance of burrows (compared to their floor) and of free-living recruits in mounds than in smooth surfaces or under wooden sticks indicate that recruits prefer a higher microtopography. More elevated areas undergo shorter inundations and are therefore less exposed to predators.

## RECRUITMENT IN RELATION TO ENVIRONMENTAL GRADIENTS

At our study site, both recruits and small hosting owners occurred most often in subarea 4, which we therefore name “recruitment zone.” We argue that the lower limit of the recruitment zone is set by biotic processes, whereas the upper limit is defined by physical processes, similar to the pattern typical for most intertidal zones (Connell, 1972). The definition of the upper landward limit of the *U. cordatus* recruitment zone is certainly linked to the adverse conditions of the transition to the hinterland.

PCA results showed an inverse correlation between BH (inundation indicator) and sediment consistency (Figure 4A). The higher sediment consistency at the extremely shallow sandy zones hampers burrow excavation for recruits. Abundance of recruits at these zones is likely also limited by desiccation, as suggested by the PCA showing its inverse correlation with air and sediment temperatures (Figure 4A). High temperatures further increase salinity, which, in extreme cases, can negatively affect crab abundance, as per the PCA (Figure 4B). However, we should consider that we only collected the data used in PCA during neap tides and that the other set of data (used to determine abiotic gradients) showed different patterns between neap and spring tides (Figure 3). While spring tides provide more stable conditions for the landward zones, neap tides leave these zones more susceptible to the influence of occasional rain. Fresh water drainage may reduce salinity and pH (Figures 3k and 3l), imposing physiological limitations for recruits, regardless of the effects of evaporation resulting from high temperature. We can explain the high temperature at the upper landward limit by the high luminosity resulting from the low vegetation cover. Only few trees grow in the rarely

inundated upper zone, which also restricts litter fall and thus food supply.

Below the lower seaward limit of the recruitment zone, fish species such as *Bairdiella ronchus*, *Genidens genidens*, *Centropomus parallelus*, and *Cetengraulis edentulus* have more time to prey upon *U. cordatus* megalopae and recruits (Costa et al., 2009; Lima and Barletta, 2016). Interspecific competition with the abundant fiddler crabs in this zone seems unlikely since they are also abundant in the recruitment zone of *U. cordatus*. Intraspecific competition also seems to be unimportant since recruits inhabit the burrows of conspecific adults (Schmidt and Diele, 2009) and tolerate a high density of recruits when meiofauna is abundant (Ventura et al., 2011). However, intraspecific competition should increase once crabs start to dig their own burrows and to feed on litter. Competition for resources such as food and space triggers the movement of *U. cordatus* crabs from areas with high burrow densities to areas with lower burrow densities (Piou et al., 2007). We therefore suppose that, as crabs grow, their action radius and intraspecific competition increases, forcing them to move from the recruitment zone to a more inundated zone. Once in a more flooded zone, the environmental conditions for acquiring energy for growth probably outweigh the risk of predation. In fact, we found that larger crabs preferentially inhabit the more inundated zone (see also Diele et al., 2005; Piou et al., 2007; Schmidt et al., 2009). This zone is characterized by tall *R. mangle* (which provides abundant fresh leaf litter as food), a less compact muddy substrate (thus easier to burrow into), a dense canopy creating shadow (thus lowering temperatures), a more stable salinity due to lower evaporation and terrestrial drainage, and a less acidic pH due to higher pore water renewal by the nearby creek.

## PROXIMATE CAUSE OF HIGHER RECRUIT NUMBERS IN THE “RECRUITMENT ZONE”

The proximate cause of higher recruit numbers in the intermediate zone remains unclear. On the one hand, it may simply mirror the higher number of conspecific burrows (and thus the increased microhabitat availability in this zone), compared to the adjacent zones. On the other hand,

it may also stem from otherwise more favorable environmental conditions in the intermediate zone (as discussed above) or from a combination of both factors. Furthermore, it remains unknown whether the identified recruitment zone is the result of active larval choice or whether larvae settle homogeneously across the entire tidal gradient, followed by the asymmetric post-settlement survival of the recruits, resulting in the observed spatial pattern of recruitment.

### IMPLICATION FOR MANAGEMENT

The enhancement of *U. cordatus* stocks by releasing laboratory-cultivated megalopae and juveniles in coastal zones impacted by pollution or fungal infections — which have caused massive crab mortalities (Cottens et al., 2008; Ventura et al., 2011) — have received growing interest. Our study indicates that conspecific burrows in intermediate inundation areas can configure a suitable site for the introduction of *U. cordatus* megalopae and recruits. However, prior to any initiative, it should be ascertained whether natural recruitment is at all a limiting factor for the recovery of a specific stock and whether the potential benefits of the stock enhancement can outweigh the potential risk of introducing pathogens associated with laboratory cultivations. Hence, natural recruit densities should first be determined (which will be facilitated in the future given that the habitat of the young recruits is now known).

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### AUTHOR CONTRIBUTIONS

A.J.S.; K.D.: Conceptualization; Investigation; Discussion of results; Writing – original draft; Writing – review & editing.

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