Intraspecific facilitation of the recruitment of a burrowing mangrove crab 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 to the benthic juvenile, but the environmental drivers involved are not well understood. We postulate that recruitment is facilitated by conspecific crabs. We investigated in the field whether the number of recruits is higher near conspecific burrows than in areas without conspecific bioturbation. Recruit sampling was conducted monthly between April 2008 to May 2009 along an environmental gradient. First U. cordatus recruits of the year appeared between March and July. Intraspecific facilitation was indicated by significantly higher recruit numbers in bioturbated compared to non-bioturbated substrates. Recruits were most abundant in zones characterized by 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 avoidance of less inundated zones helps to escape more stressful drier environmental conditions. The observed habitat-specific recruitment pattern needs to be considered when designing field assessments of the population structure of U. cordatus, which should include sampling recruits, and when 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, 2003; Bruno et al., 2003). Intra and interspecific facilitation can be important in stressful environments and, in the marine environment, 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; Westerbon et al., 2019). In contrast, few studies emphasized the importance of ecological facilitation in soft-bottom intertidal communities. Some examples are the intra and interspecific facilitation of sandflat colonization by bivalves, polychaetes and crustacea (Gallagher et al., 1983; Thrush et al., 1992; Méndez-Casariiego et al., 2009; Donadi et al., 2014) and the facilitation of ghost shrimp recruitment by conspecific adults (Tamaki and Ingle, 1993). These studies show that in soft-bottom communities, bioturbation is important for the occurrence of facilitation. In fact, many facilitation examples are linked to habitat modifications in which one 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; Jones et al., 1997).

Some of the most important engineers in mangrove ecosystems are burrowing crabs (Kristensen, 2008; Diele et al., 2010b; Cannicci et al., 2021; Fusi et al., 2022). They dig and maintain burrows that are used as refuge from predators, shelter against extreme environmental conditions and, in several cases, serve 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 III 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 invertebrate on this continent (Schmidt and Diele 2023). Burrow density and size vary along the physical gradient of the mangroves and smaller ones have been mostly observed in less flooded areas (Diele et al., 2005; Schmidt et al., 2009; Schmidt et al., 2013; Wunderlich and Pinheiro, 2013). A typical burrow of U. cordatus has an elliptical opening, with the largest diameter corresponding to the total height of the crab and the smaller diameter corresponding to the length of the carapace (Schmidt et al., 2008a; 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, and then it curves and descends steeply (Figure 2) reaching the water table, sometimes until a total depth of up to 2 m (De Geraldes 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. The digging, maintaining, closing and opening of a burrow leads to sediment accumulation around the entrance and therefore to an elevated microtopography (Schmidt and Diele 2023).

U. cordatus spends most of its time inside its burrows and when outside, the crabs 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 the estuary 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 where settlement takes place (Diele, 2000; Smith and Diele, 2008a). Laboratory experiments showed that U. cordatus settlement is triggered by conspecific odours (Diele and Simith, 2007; Smith and Diele, 2008b; Smith et al., 2013; Smith et al., 2017). Accordingly, recruits (mostly with CW < 1 cm) were (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 to be tested as recruit numbers in bioturbated substrates have not yet been compared to those in non-bioturbated substrates.

Knowledge about the specific microhabitat and possible conspecific facilitation of recruitment is important for optimizing procedures for the introduction of laboratory cultivated megalopae and juveniles into the wild for stock enhancement purposes (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 et al., 2010a; 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). In the present study we sampled recruits of U. cordatus inside substrates with and without bioturbation caused by conspecifics along the environmental gradient of a mangrove forest, including its transition to the hinterland. The objectives of the study were 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 of *U. cordatus* recruitment.

**METHODS**

**STUDY AREA**

Field work was conducted near Caravelas, NE-Brazil, in a mangrove forest located between a tidal creek and the hinterland, characterized by a sandbank with Restinga vegetation (517°42' W039°18'). The study site is characterized by the following four zones from creek to hinterland: (i) forest dominated by taller *Rhizophora mangle* near the creek, (ii) forest with smaller *R. mangle*, (iii) 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 1A).

**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 towards the hinterland (Figure 1A). At each vegetation zone (Figure 1C), 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 m²) and litter fall was measured with four 1 x 1 m traps installed one meter above substrate and emptied after one week (see Nordhaus et al., 2006) (Figure 1C).

In order to characterize the inundation gradient, seven 500 m lines with 5 m in between were marked parallel to the hinterland (Figure 1B). From February to December 2006, once a month, eight random points were marked at each line with the aid of a GPS odometer and, at each point, BH was measured (see above). In addition, inundation was measured directly in May 2008, three days before (waxing) and four days after (waning) 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 1B). At each point, inundation time was measured over a 12 h tidal period during daytime. At the same points, inundation height was measured during slack high tide.

To characterize the gradient of physico-chemical parameters, the study area was divided into six contiguous 5 x 500 m subareas (Figure 1B). Within each subarea, luminosity (with a luxmeter), sediment consistency, air temperature, sediment temperature, pore water salinity and pH (with a pH meter) were measured at 24 random points, during low tide, between 12:00h and 15:00h. Sampling was performed at neap tide (first quarter) and syzygy (full moon) of May 2011. Due to logistical reasons, pH was measured only at the neap tide.

**ABIOTIC DATA COLLECTION NEAR THE RECRUITS**

From April 2008 to May 2009 at neap tide days, between 5 and 15 cm away from the found recruits (Figure 1A), the following parameters were measured: air temperature, sediment temperature in 3 cm depth, pore water salinity (by digging a hole until water percolated through the sediment and accumulated, allowing the collection and measurement with a refractometer), sediment consistency (using a Humboldt H-4200 soil penetrometer, pocket type, with 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; Blankensteyn et al., 1997; Rützler and Feller, 1999; Cunha et al., 1999; Cunha and Costa 2002).

**Sampling of recruits**

In this paper we define the term recruit as a “settler that reached a size large enough to allow its visual detection in the field (Keough and Downes, 1982; Bertness et al., 1992). Due to the cryptic habitat of the 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 visible own burrow, are named “free-living”. All crabs that live in their own burrows large enough to be detected visually are 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 inside eight randomly selected plots (30 x 1 m) placed perpendicularly to a 500 m long section of hinterland (Figure 1A). 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 2). Approximately 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 2): burrow entrance (including crab tracks in front of it), roof of horizontal burrow duct, floor of horizontal burrow duct, plug (sediment used to close the entrance – not always present) and smooth surface (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 2). Recruits were carefully separated from the sediment by hand and their carapace width (CW) measured with a caliper rule to the nearest mm. They were released at the same place after capture. Due to their small size, they could not be sexed in the field.

**Measurement of the burrows of owner crabs**

Inside the eight plots (Figure 1A) all burrows openings of hosting owners were measured. In July 2008 and January 2009, burrows of non-hosting owners were also measured. The diameter of the burrow openings was measured applying the method described in Schmidt et al. (2008a). Burrow diameter (BD) was transformed to carapace length (CL) using the equation “BD = 0.244952 + 1.04026*CL” obtained through linear regression (R² = 75.2, N = 341). Values of CL were then transformed to carapace width (CW) using the equation “CW = -0.0376206 + 1.30283*CL” also obtained through linear regression (R² = 98.4, N = 341). The two regressions were based upon data collected in the same study area between February 2006 and July 2008 (Schmidt et al., unpublished results).

**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. Mean CW of recruits found in bioturbated and non-bioturbated rings, as well as mean CW of hosting and non-hosting owners were compared with Student “t” Test. Mean CW and abundance of recruits along time, as well as means of abiotic parameters along the profile were compared with Repeated Measures ANOVA followed by a Bonferroni post-hoc test. The sphericity assumption was tested with Mauchly’s
Test and the Huynh-Feldt correction was performed when necessary. Means of litter fall and standing stock were analyzed by ANOVA considering vegetation zone as a factor, followed by a Tukey HSD Test. Data were square root or log transformed when necessary to reach homoscedasticity, tested with Cochran’s “C” Test. Even after transformations, heterogeneous variances occurred between salinity samples obtained during neap tide. In these samples we observed that two subsets of data presented homogeneous variances: one comprising the three landward subareas and another comprising the three subareas closer to the creek. For each of these subsets of samples a separate analysis was performed. 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 together with the standard errors. Frequencies and ratios were compared with Chi-Square Analysis. Data obtained near the rings where 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 by their standard deviations. This procedure allowed the investigation of the relationships between these multivariate data through a Principal Components Analysis – PCA.

RESULTS

VEGETATION STRUCTURE, ZONATION AND ABIOTIC GRADIENTS

Tree height increased from the hinterland to the tidal creek, as well as litter standing stock and litter fall (Figures 3A, 3B and 3C; Table I). Mean height of the Bostrychietum band (BH) did not vary temporally, but spatially, increasing from hinterland to creek (Figure 3D; Table I). Inundation time and height also increased from hinterland to creek (Figures 3E and 3F; Table I). In contrast, means of the following parameters decreased from hinterland to creek at both neap and spring tides: sediment consistency (Figure 3G), luminosity (Figure 3H), air temperature (Figure 3I) and sediment temperature (Figure 3J; Table I). Pore water salinity did not fluctuate along the profile during spring tide (Figure 3K). At the landward subareas salinity was lower next to the hinterland, while the means in the subareas near the creek did not differ (Figure 3L; Table I). At neap tide, pH was significantly lower at the two subareas closest to the hinterland (Figure 3L; Table I).

NUMBER OF RECRUITS IN BIOTURBATED AND NON-BIOTURBATED RINGS

A total of 474 U. cordatus recruits were found, 96% inside bioturbated rings (co-inhabitants) versus 4% inside non-bioturbated rings (free-living) ($\chi^2 = 390.08$, SL = 0.05, DF = 1). This proportion did not vary significantly between the six subareas ($\chi^2 = 8.75$, SL = 0.05, DF = 5). From the 455 co-inhabitants, 43% were found in the sediment of the roofs of the burrow ducts, 29% in plugs, 27% in the owner’s sediment tracks at the entrance and 1% in the floor of the ducts (Figure 2). Of the 19 recruits observed in the non-bioturbated rings, 79% occurred in the sediment of mounds, 16% were found in sediment of smooth surfaces and 5% was found under a wooden stick (Figure 2). A total of 408 hosting owners’ burrows were found, 89.7% with one co-inhabitant, 9.3% with two, 0.7% with three and 0.2% with four co-inhabitants. The entrance and floor of all hosting burrows had fresh tracks of U. cordatus 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 where recruits had been found were: BH = 21.2 ± 0.46 cm, sediment consistency = 0.13 ± 0.004 Kg/cm², air temperature = 26.8 ± 0.11 °C, sediment temperature = 25.5 ± 0.12 °C and salinity = 31.1 ± 0.27. Pooling together data from these variables and data of the abundance of recruits, the 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, presents highest weights for air
and sediment temperatures (0.62 and 0.64 respectively), which are negatively correlated to abundance of
recruits and BH, and positively correlated to sediment consistency (Figure 4A). Component 2, explaining 23.4%
of the variance, presents highest weights for sediment consistency (-0.64) and BH (0.65), variables that have an
inverse correlation with each other (Figure 4A). Component 3 explains 18.10% of the variance and presents
highest weights for abundance of recruits (0.62) and salinity (-0.77), which are inversely correlated (Figure 4B).

The relationship between the abundance of recruits and the BH measured close to the rings was best
explained by a third degree model (Correlation coefficient = 0.78, R² = 0.61, n = 51). Recruitment was highest in
zones with 18.5 cm BH (Figure 5A). The relationship between the abundance of hosting owners and BH
measured close to the rings was best explained by a fourth degree model (Correlation coefficient = 0.78, R² =
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 m 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).

SIZE OF RECRUITS ALONG THE ENVIRONMENTAL GRADIENT

The smallest and largest co-inhabiting recruit measured 0.15 cm and 2.20 cm CW, respectively. Mean recruit
size was 0.82 ± 0.02 cm (Figure 6). The smallest and largest free-living recruit had a CW of 0.25 cm and 1.90 cm,
respectively, and mean size was 0.97 ± 0.11 cm (Figure 6). There was no significant size difference between CW
of co-inhabitants and free-living recruits. Also, there was no significant correlation between recruit size and BH.

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 ±
0.06 cm (Figure 6). In July 2008 and January 2009, when the opening size of all crab burrows (hosting and non-
hosting ones) was measured, 8% of the total burrows had co-inhabiting recruits. Mean CW of hosting and non-
hosting owners was 3.9 ± 0.06 and 3.8 ± 0.16 in July and 4.4 ± 0.06 and 5.2 ± 0.17 in January. In July and January
mean size of hosting and non-hosting crabs did not differ statistically from each other. CW of both hosting and
non-hosting owners increased from hinterland to creek. The relationship between their CW and BH was best
explained when applying the quadratic regression (R² = 0.60), although the coefficient of determination was low
(R² = 0.35, n = 1034) (Figure 5C).

ABUNDANCE AND SIZE OF RECRUITS ALONG TIME

While the abundance of recruits did not differ significantly between months, their size did (Repeated
Measures ANOVA: df = 13; F = 5; P < 0.0001). Mean CW was smallest in July 2008 (Figure 7d). The smallest
recruits with a CW of up to 0.2 cm were only found between April and July 2008 (Figures 7A, 7B, 7C and 7D). Such
small crabs were absent in subsequent months and re-appeared between March and May 2009 (Figures 7L, 7M
and 7N). Mean CW was largest in January 2009 (1.05 ± 0.07), when the frequency of recruits in the upper size
classes was highest (Figure 7J).

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. In the following we first discuss the temporal and spatial pattern of recruitment in *U. cordatus* in more detail and finish with demonstrating the relevance of the study for the management of *U. cordatus*.

### TEMPORAL PATTERN OF RECRUITMENT

Throughout the entire year, only few adult crab burrows with young recruits were found, likely reflecting the difficulty to find such small-sized cryptic specimens. The occurrence of recruits in the smallest size class with up to 2 mm carapace width between March and July reflects the multiple larval releases that occur each year between February and May in the study region (Schmidt et al., 2012). The zoea larvae, which are released into estuarine waters at spring tides, develop offshore and take about one month to develop to megalopaee and to re-invade the estuarine environment to settle (Diele, 2000). First instar crabs with an initial CW ranging between 1.37 to 1.55 mm had reached a size of approx. 2 mm after 1 month in the laboratory and 7.83 to 11.53 mm after 6 months (Diele and Koch, 2010a), which closely agrees with our field findings: for example, the last recruits in the smallest size class were found in July 2008, all of them with a CW of 2 mm. These two- or third instar stages had probably metamorphosed to crab one month earlier and had been released yet another month earlier, in May. Recruits grew throughout the year as indicated by the increase in frequency in 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 more *U. cordatus* recruits will be encountered inside conspecific burrows compared to non-bioturbated substrates, likely due to intraspecific facilitation. Facilitation may simply be a side effect of the digging of a burrow, by changing mangrove topography. Indeed, heterogeneity and complexity of the substratum by itself have been positively related to settlement success in several species and habitats (e.g. Barry and Dayton, 1993; Pech et al., 2006). However, without neglecting the physical effects of bioturbation, other factors may further contribute to the findings. Laboratory experiments showed that chemical cues emitted by conspecific *U. cordatus* specimens, induce the settlement and enhance survivorship 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. Such habitat-specific recruitment may be considered an example of commensalistic (+,0) facilitation (see review of Stachowicz, 2001), as it does not cause any harm to the hosting owner and provides at least 3 advantages for the co-inhabiting recruit. Firstly, it can be assumed that food is more abundant inside crab burrows than outside. Crab burrows increase the passive deposition and settlement of meiofaunal organisms (DePatra and Levin, 1989; Botto and Irriarne, 1997) which are eaten by juvenile *U. cordatus* (Diele and Koch, 2010b). Larger recruits can also feed on shredded plant matter resulting from sloppy feeding of burrow owners (Diele and Koch, 2010b), but may not yet be able to collect leaves themselves and shred them. A second advantage is that conspecific burrows provide a refuge from predators (Bliss, 1979; Warren, 1990; Luppi et al., 2002), particularly when closed by plugs (and plugging can often be observed in *U. cordatus*). In addition, 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 in particular are less tolerant to environmental extremes than adults (Wolcott and Wolcott, 1988) and their comparably larger body surface area make them more susceptible to desiccation (Diele, 2000). Similar findings from other species, e.g. *Neosarmatium meinertii* (Emmerson, 2001), *Neohelice...
**RECRUITMENT IN RELATION TO ENVIRONMENTAL GRADIENTS**

At our study site, both recruits and small hosting owners were most common in subarea 4, which we therefore name "recruitment zone". We argue that the lower limit of the recruitment zone is set by biotic processes while the upper limit is set 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.

The 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 by recruits. Abundance of recruits at these zones is likely also limited by desiccation, as suggested by the results of the PCA demonstrating an inverse correlation of this parameter with air and sediment temperatures (Figure 4A). High temperatures further lead to an increase in salinity, which, in extreme cases, can negatively affect crab abundance, as reflected by the PCA (Figure 4B). However, it’s important to consider that data used in the PCA were only collected during neap tides, and the other set of data used for the determination of 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. The high temperature at the upper landward limit can be explained 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 the food supply of the crabs.

Below the lower seaward limit of the recruitment zone, fish species such as Bairdiella ranchus, 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 does not seem to be important either, since recruits inhabit burrows of conspecific adults (Schmidt and Diele, 2009) and tolerate high density of recruits when meiofauna is abundant (Ventura et al., 2011). However, once crabs start to dig their own burrows and begin to feed on litter, intraspecific competition should increase. Competition for resources as food and space triggers the movement of U. cordatus crabs from areas with high burrow density to areas with lower burrow density (Piou et al., 2007). We therefore assume that, as crabs grow, their action radius increases and so does intraspecific competition, which forces them to move from the recruitment zone to the more inundated zone. Once in the most flooded zone, the environmental conditions for acquiring energy for growth probably outweigh the risk of predation.
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 and thus provides abundant fresh leaf litter as food, muddy substrate which is less compact and thus easier to burrow in, a dense canopy creating shadow and thus lower temperatures, a more stable salinity due to lower evaporation and terrestrial drainage and a less acid pH due to a higher pore water renewal through the nearby creek.

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

The proximate cause of higher recruit numbers in the intermediate zone is still unclear. On the one hand it may simply mirror the higher number of conspecific burrows and thus increased microhabitat availability in this zone, compared to the adjacent zones. On the other hand it may also be due to otherwise more favorable environmental conditions in the intermediate zone, as discussed above, or a combination of both factors. Furthermore it is still 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 asymmetric post-settlement survival of the recruits resulting in the observed spatial pattern of recruitment.

**IMPLICATION FOR MANAGEMENT**

There is growing interest to enhance *U. cordatus* stocks through the release of 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). Our study indicates that a suitable site for the introduction of megalopae and recruits of *U. cordatus* would be inside conspecific burrows located in intermediate inundation areas. 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 CONTRIBUTION**

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


Aquicultura e Biologia Aquática.


Figure 1. Sampling design. Each marker represents a measurement or a set of measurements. (a) Plots for sampling *U. cordatus* crabs and parameters in the places where recruits were found (used at PCA); and transects for drawing the zonation profile of the area. (b) Transects for measuring Bostrychietum band height, inundation height and inundation time; and subareas between transects for measuring of abiotic parameters. (c) Mangrove zones where litter standing stock and litter fall was measured.
Figure 2. Sampling of *U. cordatus* recruits. Continuous thick lines: metal rings placed on the sediment surface, either around a conspecific burrow ("bioturbated ring") or on sediment not bioturbated by *U. cordatus* ("non-bioturbated rings"). Dashed thick 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, until curving down and descending steeply. Letters indicate places where recruits were found. Bioturbated rings: (a) entrance area of burrow, (b) roof of horizontal duct, (c) floor of horizontal duct (see cross-section) and (d) smooth sediment surface. Non-bioturbated rings: (e) smooth sediment surface, (f) sediment mound (g) sediment under wooden sticks.

277x91mm (400 x 400 DPI)
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) Bostrychium 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.
Table 1. Results of the Analysis of Variance and post hoc tests of the parameters studied to characterize vegetation structure, zonation and abiotic gradients.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Analysis of Variance</th>
<th>Post hoc test</th>
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<tr>
<td></td>
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<td>Tree height</td>
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<td>at waxing</td>
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246x207mm (300 x 300 DPI)
Figure 4. Principal component analysis of abundance of U. cordatus recruits (R), Bostrychietumband 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.

198x203mm (300 x 300 DPI)
Figure 5. Polynomial regressions of the dependent variables (a) abundance of *U. cordatus* recruits (cohabitants 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 where the respective crab had been sampled.

106x206mm (400 x 400 DPI)
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.

114x67mm (400 x 400 DPI)
Figure 7. Monthly size frequency distributions of *U. cordatus* recruits, (co-inhabitants and free-living) between April 2008 and May 2009 (means and standard errors). Measurements were missed in April-08 (two) and in October-08 (three).

151x173mm (400 x 400 DPI)

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