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EDGE EFFECTS ON THE ABUNDANCE OF THE CRAB *Ucides cordatus* (DECAPODA: OCYPODIDAE) IN A NEOTROPICAL MANGROVE

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Abstract: Mangroves are among the most productive and biologically important ecosystems in the world and are currently undergoing extensive habitat loss and fragmentation. Such habitat loss and fragmentation result in the creation of edges, which can cause edge effects on the remaining habitat, resulting in changes in abiotic conditions, alterations in ecosystem functioning, and loss of biodiversity. The crab *Ucides cordatus* (Linnaeus, 1763), locally known as "caranguejo-uçá," is a species of great economic and ecological importance in these environments. This species is also considered an important indicator of environmental quality, being sensitive to various pollutants. Therefore, we evaluated how anthropogenic edges affect the *U. cordatus* population in a mangrove area and compared these patterns to those observed at natural edges. We found a positive effect of edge creation on crab abundance for the total number of burrows and the number of open burrows, but no effect on the number of closed burrows. Conversely, we detected a negative effect of natural edges on the quantity of closed burrows. Our findings suggest that anthropogenic edges may alter crab abundances, becoming the preferred habitat for young crabs. However, we emphasize that the interior of the mangrove is also crucial for species maintenance, especially for adult crabs and juveniles during molting.

Keywords: burrow; crabs; edge influence; fragmentation; mangrove habitat.

INTRODUCTION

Mangrove forests are among the most productive and biologically important ecosystems in the world (Giri *et al.* 2011). In addition to providing shelter, refuge, and food resources for local animals (Hutchings & Saenger 1987), mangroves also play a key role in human sustainability and livelihoods (Hayashi *et al.* 2018). However, between 2000 and 2012, the world lost between 1.97% and 4.73% of mangrove forest cover (Hamilton & Casey 2016), with population growth and urban development being identified as the primary drivers of mangrove habitat loss worldwide (Bennett *et al.* 2001, Valiente-Banuet *et al.* 2015).

The loss and fragmentation of mangrove habitat, among other effects, can lead to edge effects in the remaining habitat. Edge effects can be understood as the effect of processes (both abiotic and biotic) at the edge that result in a detectable difference in composition, structure, or function near the edge, as compared with the ecosystem on either side of the edge (Harper *et al.* 2005). Thus, anthropogenic (or created) edges may be responsible for changes in abiotic conditions, disruption of ecosystem functioning, and biodiversity loss (Murcia 1995, Harper *et al.* 2005), although such effects are not always detected (Caitano *et al.* 2018). The creation of forest edges can also lead to increased abundance of certain invertebrates, including termites and butterflies (Fowler *et al.* 1993, Souza & Brown 1994, Brown & Hutchings 1997), as well as favor invasive species and non-social insects (Caitano *et al.* 2020). In addition, recent studies have shown that edge effects in mangrove forests can alter the substrate's abiotic variables (pH and temperature) (Medellu *et al.* 2012), result in tree mortality (Zamprogno *et al.* 2016), and compromise the diversity of benthic macroinvertebrates (Amortegui-Torres *et al.* 2013, Arroyave-Rincón *et al.* 2014) which may compromise ecosystem processes (*e.g.*, organic matter processing) crucial for maintaining biodiversity in these environments.

Decapod crustaceans are important members of benthic communities in tropical and subtropical mangroves (Almeida *et al.* 2006, Arroyave-Rincón *et al.* 2014). Among these invertebrates, the crab *Ucides cordatus* (Linnaeus, 1763), locally known as "caranguejo-uçá", is a species of great economic and ecological importance in these environments (Wunderlich *et al.* 2008), acting in ecological processes such as leaf litter processing (Nordhaus *et al.* 2006) and carbon and organic matter cycling (Guest *et al.* 2006, Wunderlich *et al.* 2008). This species is also considered an important indicator of environmental quality, as it is sensitive to various pollutants (Santos 2002, Castilho-Westphal *et al.* 2008).

Considering the importance of this species, it is relevant to understand the effects of mangrove habitat modification, including the creation of edges, on the population of *U. cordatus*. To our knowledge, there is only one study of this kind for the Brachyura infraorder, which demonstrated a negative effect of mangrove conversion to pasture on the abundance and physiological condition (weight and size) of blue land crabs (*Cardisoma guanhumi* Latreille, 1825) (Arroyave-Rincón *et al.* 2014). Understanding how the *U. cordatus* population responds to edge effects in the mangrove habitat is thus crucial for a better assessment of the impacts to which this species is subjected in these increasingly anthropized environments, and for a better understanding of the impacts of habitat loss and fragmentation in mangroves.

We assessed how anthropogenic edges affect the population of *U. cordatus* in a mangrove area and compared these effects with patterns observed at natural edges in north-eastern Brazil. We expected to find a decrease in abundance at anthropogenic edges, indicating the negative impacts of human influence. We also expected not to find such a decrease at natural edges, considering that this is an environment for which this species is expected to be adapted.

MATERIALS AND METHODS

Study area

We performed this study in a mangrove remnant approximately 18 hectares in size within the Todos os Santos Bay, specifically in the Ilha de Maré island, in Salvador, Bahia, north-eastern Brazil (12° 45' 06" S, 38° 31' 07" W). The climate of the region is characterized as highly humid tropical (Nimer 1989), with an average precipitation exceeding 1,500 mm/year and a mean temperature in the coldest month surpassing 22°C. Part of the periphery of the remnant is under strong anthropogenic influence and there is weak evidence of human activity in the interior. We thus classified this remnant in the third category of anthropogenic impact based on the classification proposed by Delabie *et al.* (2006), which categorizes the level of human impact on mangroves into six classes considering parameters such as deforestation, land filling, and abandoned waste. The periphery of the remnant alternates between natural and anthropogenic edges. The natural edges (without evidence of human impact) sampled included an edge with a remnant of restinga (coastal scrub) (1 edge) and with a muddy sediment beach (1 edge), whereas the anthropogenic edges sampled included edges with football fields (3 edges) and dirt roads (2 edges).

Field procedures

We collected data during several days in August (second half of the month) and September (first half of the month) of 2020 during low tide. We established 50 transects perpendicular to natural (n = 22) and anthropogenic edges (n = 28) (Figure 1). To avoid multiple edge effects (Porensky *et al.* 2013), we positioned all initial transects at least 30 m from the beginning of all sampled edges, and all transects were spaced at least 30 m apart from each other. Along each transect, we indirectly estimated the population density of *U. cordatus* by counting the burrows found in 2x2 m sampling plots located at 0 m (immediate edge), 15 m, and 30 m from the edge towards the mangrove along each transect. For density estimation, we considered only the burrows with evidence of presence of *U. cordatus* according to Wunderlich *et al.* (2008): 1) open burrow with biogenic activity (accumulation of fluid mud, feces, and crab trails near the opening); and 2) closed burrow, including recently closed burrows with the opening occluded by a "lid" of moist sediment and old closed burrows (or "batumadas") without a visible opening, recognized by the elevation and rougher texture of the sediment, confirmed by excavation. We did not include open burrows without biogenic activity. We identified *U. cordatus* burrows by their oblique position of the opening, inclined at a 45° angle to the sediment surface (Wunderlich *et al.* 2008), distinguishing them from burrows excavated by other species of the *Ucides* genus.

Data analysis

To determine if there were statistical differences in the abundance of burrows (open burrows, closed burrows, and total number of burrows) of *U. cordatus* at different distances from the edges, we applied Generalized Linear Mixed Models (GLMMs) with a negative binomial distribution using transect as a random factor, with the 'glmer.nb' function from the 'lme4' package (Bates *et al.* 2015) in the R environment v. 4.3.2 (R Core Team, 2023). For all response variables, we tested five models with the following explanatory variables: 1) edge distance, edge type, and interaction; 2) edge distance and edge type; 3) edge distance; 4) edge type; and 5) null (intercept-only) model. We used distance as a categorical variable in all analyses. Next, we used model selection based on

Figure 1. Types of edges sampled in the studied mangrove remnant: a) natural edge between the mangrove and muddy sediment beach, b) anthropogenic edge dominated by *Avicennia schaueriana* Stapf & Leechm. ex Moldenke individuals, c) edge with a soccer field, and d) edge with dirt road.

the Akaike Information Criterion (AIC) (Akaike 1998) to choose the simplest model among those with a ΔAICc (*i.e.* the difference in AICc – a version of AIC corrected for small sample size – between each model and of the best model) of up to 2.0. To calculate the ΔAICc values, we used the 'AICctab' function from the 'bbmle' package (Bolker and Core Team 2022), also in the R environment. Finally, when the null model was not selected, we applied the 'emmeans' function (Lenth R 2023) to determine which distances and edge types differed from one another.

RESULTS

In the 150 plots, we found a total of 684 burrows: 483 open burrows and 201 closed burrows (Supplementary Material). The number of burrows per plot ranged from 0 to 15 (Table 1). Plots sampled at anthropogenic (created) edge transects included 68.7% (470 burrows) of all the burrows, with 328 open burrows and 142 closed burrows. Plots in natural edge transects accounted for 31.3% (214 burrows) of the total burrows, with 155 open burrows and 59 closed burrows.

Table 1. Comparison of mean densities (burrows/m²) ± SD, minimum and maximum (in parentheses), and total number (N) of burrows of *Ucides cordatus* (Linnaeus, 1763) at different distances (m) from natural and anthropogenic (created) edges.

Distance (m)	Natural Edges	Anthropogenic Edges
0	3.7 ± 3.4 (0-11), n=82	7.3 ± 3.4 (0-15), n=205
15	2.8 ± 2.0 (0-6), n=62	5.6 ± 3.5 (0-14), n=158
30	3.2 ± 2.2 (0-8), n=70	3.8 ± 2.8 (1-10), n=107

Table 2. Results of Generalized Linear Mixed Models (GLMMs) selection (transects were included as a random factor) for the relationship between burrow density (absolute, open burrow, and closed burrow of *U. cordatus* (Linnaeus, 1763) and environmental variables (distance from the edge and edge type) of the studied mangrove remnant, showing the ΔAIC values (dAICc) and degrees of freedom (Df) of competing models. The selected models are in bold and underlined.

Response variable	Predictor variables/model	dAICc	Df
Absolute density of burrows	Edge distance, Edge type + interaction	0.1	8
	<u>Edge distance, Edge type</u>	**<u>0.0</u>**	**<u>6</u>**
	Edge distance	18.2	5
	Edge type	5.5	4
	Null	23.5	3
Density of open burrows	Edge distance, Edge type + interaction	1.1	8
	<u>Edge distance, Edge type</u>	**<u>0.0</u>**	**<u>6</u>**
	Edge distance	9.3	5
	Edge type	21.8	4
	Null	30.2	3
Density of closed burrows	**<u>Edge distance, Edge type + interaction</u>**	**<u>0.0</u>**	**<u>8</u>**
	Edge distance, Edge type	2.4	6
	Edge distance	13.9	5
	Edge type	8.1	4
	Null	17.9	3

For the total burrow density and for the density of open burrows, the best model selected was the one with edge distance and edge type as explanatory variables, without interaction, whereas for the number of closed burrows the full model (edge distance, edge type, and interaction) was selected (Table 2); detailed pairwise comparisons are shown in the Supplementary Material. For total burrow density, there were more burrows at the anthropogenic edges than at natural edges for each distance from the edge ($p < 0.0001$; Figure 2a, b). In addition, there were more burrows at the immediate edge than at 30 m from into the mangrove ($p = 0.019$; Figure 2a, b). The density of open burrows was also greater at the anthropogenic than natural edges, for all distances from the edge ($p = 0.0066$), and at the immediate edge than at 15 and 30 m into the mangroves ($p < 0.008$) (Figure 2c, d). Finally, the density of closed burrows differed between anthropogenic and natural edges only for the distance of 0 m ($p = 0.0066$), being greater at the anthropogenic edge (Figure 2e, f). The number of closed burrows did not differ between the distances from the anthropogenic edges ($p > 0.66$) (Figure 2e) but was lower at the immediate natural edge (distance of 0 m) than at 15 or 30 m into the mangrove ($p < 0.05$) (Figure 2 f).

DISCUSSION

Our study presents new information on the effects of anthropogenic edges in mangrove habitats on the population of *U. cordatus*, as well as a comparison of these effects with patterns observed at natural edges in north-eastern Brazil. Surprisingly, the abundance of *U. cordatus*, indirectly estimated by burrow density, was higher near anthropogenic edges, both for the total number of burrows and the number of open burrows. We suggest that such responses might indicate the preference of young crabs for this type of environment (high zones of mangroves) that presents environmental (greater availability of essential nutrients for individual growth) and ecological conditions (lower intraspecific competition during the juvenile stage) crucial for the maturation of individuals (Genoni 1991, Hattori 2006). On the other hand, the quantity of closed burrows was significantly higher within the mangrove remnant than at the natural edges. We suggest that this response is related to the crabs' preference for molting, due to more stable environmental conditions (humidity, air and water temperature, and soil) inside the mangrove habitat compared to the edges (Nobbs & Blamires 2015). Thus, although altered edges may favor crab abundance, we emphasize that the interior of the mangrove is also important for the species' persistence. Below, we will discuss possible explanations and interpretations for our results.

The estimated average density value in this study (4.56 ± 2.26 burrows/m^2) is higher than values found in other regions, where it has been observed to range from 3.7 ± 1.5 to 3.9 ± 1.5 (Hattori 2006, Goes *et al.* 2010). The abundance *U. cordatus* was higher at edges than in the mangrove interior (considered here as distances of 15-30 m from the edge), both in terms of the total number of burrows and of open burrows. Thus, our results agree with some studies that showed edge effects on aquatic invertebrates in mangroves (Amortegui-Torres *et al.* 2013, Arroyave-Rincón *et al.* 2014), but differ, for example, from the findings of Caitano *et al.* (2018), who found no edge effects on the ant community in mangrove fragments in southern Brazil, for either natural or anthropogenic edge. The anthropogenic edges also showed higher abundance of *U. cordatus* (*i.e.*, absolute density, number of open burrows and, to a smaller degree, number of closed burrows) when compared to natural edges.

The anthropogenic edges sampled in this study are oriented towards the mainland and are dominated by individuals of *Avicennia schaueriana* Stapf & Leechm. ex Moldenke (pers. obs.). According to Christofoletti (2005), *U. cordatus* shows a higher preference for leaves of *A. schaueriana*, which are more nutritious compared to those of other plant species commonly found in mangrove forests (*Rhizophora mangle* L. and *Laguncularia racemosa* (L.) C.F.Gaertn.). Furthermore, studies have shown that the population structure of *U. cordatus* in upper areas of mangroves, areas near terrestrial edges and under less influence of flooding, consists of smaller individuals than those typically found in lower mangrove zones (Alves & Nishida 2004, Hattori 2006, Schmidt *et al.* 2009, Goes *et al.* 2010). According to Hattori (2006), young *U. cordatus* individuals occur at higher densities

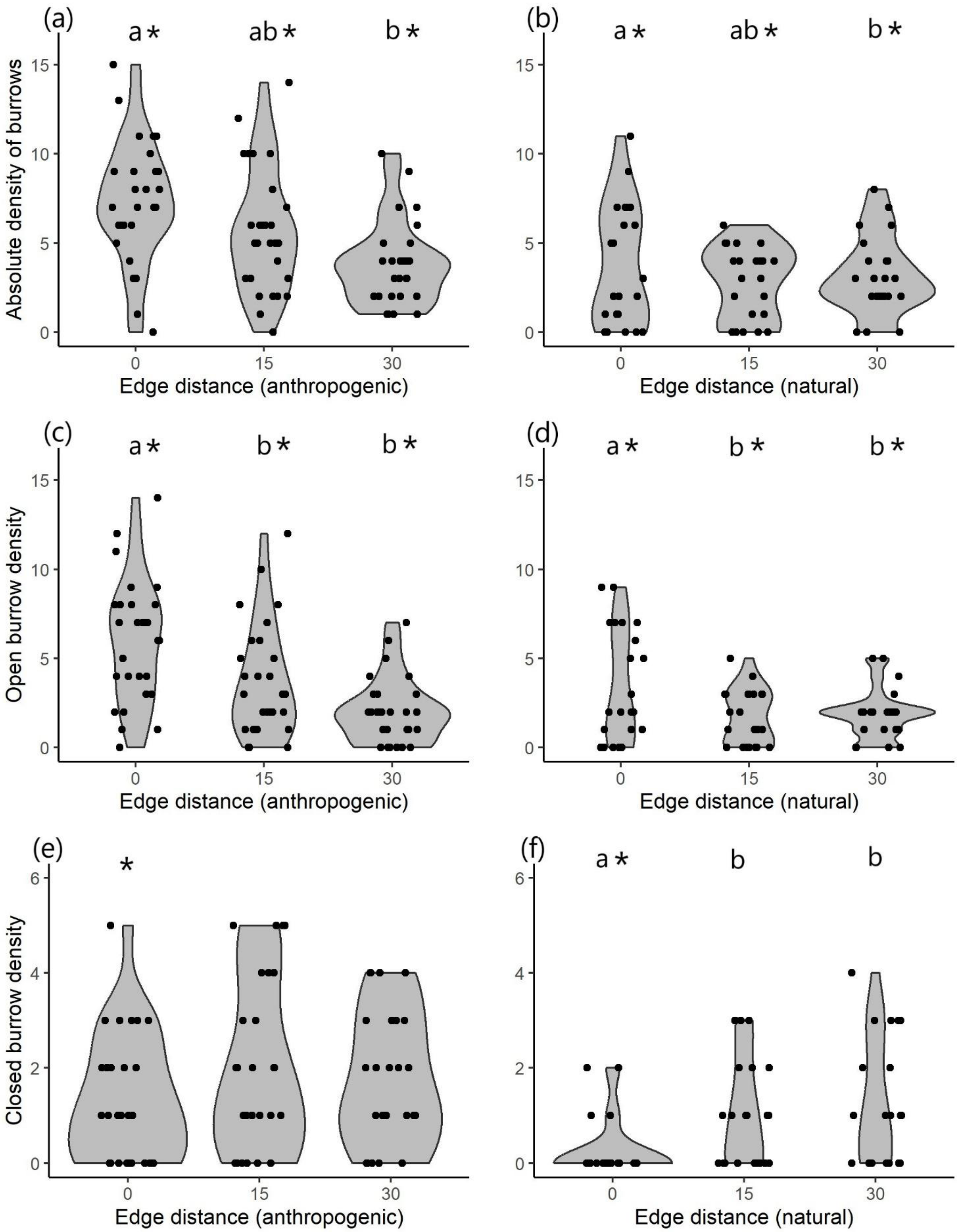

Figure 2. Absolute burrow density (a, b), open burrow density (c, d), and closed burrow density (d, e) of *Ucides cordatus* (Linnaeus, 1763) at different distances (m) from anthropogenic edges (a, c, e) and natural edges (b, d, f) of the studied mangrove remnant. Different letters indicate statistical differences between distances (p <0.05), and asterisks indicate statistical difference in the pairing of equal distances between edge classes. In the bean plots, each point corresponds to a sampled plot.

in high mangrove regions due to environmental conditions, especially higher temperatures (air, soil, and water) and greater soil concentrations of Calcium and Magnesium, factors that positively influence the growth of these individuals. Genoni (1991) emphasized that some crab species in the Uca genus, when juveniles, exhibit less competition for food resources, allowing for closer proximity in burrow excavation. Thus, we believe that the observed positive edge effect on the abundance of *U. cordatus* at anthropogenic edges was a reflection of the synergistic action of factors including favorable environmental conditions for the growth of young individuals, greater availability of food resources, and a higher potential for aggregation of juvenile burrows as a result of lower intraspecific competition during this life stage. However, the changes in the feeding habits of *U. cordatus* during juvenile development are unknown. Such changes in feeding habits could stimulate migratory processes of these crabs among different types of mangrove forests (Hattori 2006).

In opposition to the increased density of open burrows at the edges, closed burrows were less common at the mangrove's natural edges than further into the mangrove. According to Alves & Nishida (2002), *U. cordatus* closes the entrance of its burrow during the molting process, which lasts for about 28 to 29 days. Furthermore, Nobbs & Blamires (2015) identified the importance of substrate characteristics (sediment mounds, soil moisture, soil penetrability, surface temperature), canopy density, and site elevation on the spatial abundance of some Ocypodidae species, highlighting the significant effect of improved shading on temperature and humidity levels in the intertidal zone of tropical mangroves, where environmental conditions are harsh during low tides (McGuinness 1994). Such conditions can affect the distribution (Macnae 1969) and thermoregulatory behavior (Smith & Miller 1973) of Uca spp. crabs and other tropical mangrove invertebrates (Macnae 1969, Madeleine Nobbs 2003). Therefore, assuming that *U. cordatus* is more vulnerable to the effects of severe environmental changes during molting, the more unstable environmental conditions at the mangrove edge compared to its interior emerge as the primary driving factor for the reduction in the quantity of closed burrows with proximity to the natural mangrove edge .

We thus conclude that edge effects in mangroves may have important implications for the population of *U. cordatus*, at both natural and anthropogenic edges. Edges appear to result in an increase in the abundance of crab burrows compared to the interior of the mangrove. This may be related to the preference of young crabs for this environment. While altered edges seem to favor crab abundance, we emphasize that the interior of the mangrove is also crucial for species maintenance, especially for adult crabs and juveniles during molting. Therefore, we recommend assessing the distribution of young and adult crabs between the edge and interior of the mangrove. It is important to note that the sampled anthropogenic and natural edges had relatively low anthropic impacts or edge contrast. Considering that edge contrast, that is, the difference between the natural area and the adjacent anthropic area, is one of the main factors modulating edge effects (Harper *et al.* 2005), it is possible that the effect in areas with higher contrast would be different, potentially leading to a reduction in *U. cordatus* abundance. Thus, we call for studies in areas with higher contrast, such as urban areas and areas with polluting activities.

We acknowledge that the abundance of crabs estimated in this study may be biased considering that adult and juvenile crabs can coexist in the same burrow (Schmidt & Diele 2009). Therefore the number of crabs per m² may be higher than the number of burrows. It is important to note that our distance gradient from the edges towards the interior of the mangrove reaches 30 meters; though, it is possible that the extent of the edge effect reaches greater distances towards the interior of the mangrove. However, the short length of our transects in fact highlights the importance of edge effects in this environment: as we were able to show variation along such a short gradient, it is likely that the observed edge effects would be even stronger if we had longer transects. Future studies may assess edge effects on *U. cordatus* over longer gradients. Finally, we must acknowledge that we sampled a single mangrove fragment, which necessarily limits how much we can generalize our results. Nevertheless, we believe that our results show that the studied species may indeed be affected by edges, warranting further studies. We also suggest collecting data on environmental variables that may be important for the growth and maintenance of the species (*e.g.*, air, water, and soil temperatures, Calcium and Magnesium soil concentrations, and substrate characteristics) at different distances from the edge, in order to explain the mechanisms of edge effects.

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SUPPLEMENTARY MATERIAL

Supplementary Material 1. Results of the *emmeans* test comparing the different distances and edge types for the number of closed burrows, open burrows, and all burrows per plot, for the different distances from natural and created mangrove edges.

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