PRIMARY RESEARCH PAPER

Propagule predation in a Neotropical mangrove: the role of the Grapsid crab *Goniopsis cruentata*

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Abstract In Neotropical mangroves the crabs *Ucides cordatus* and *Goniopsis cruentata* have been considered the most significant propagule consumers, but their relative importance has not been investigated. The aim of this study was to compare the magnitude of predation by these crabs on three mangrove species propagules: *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*. We found that *G. cruentata* is a more important predator than *U. cordatus* in both natural and restored areas. We also tested the hypothesis that *Ucides* and *Goniopsis* have antagonistic effects on propagules predation using a cage experiment where the presence/absence of these species was manipulated in a 2 × 2 factorial design. The effects of *Goniopsis* were stronger in the absence of *Ucides* due to negative interactions between these predator species. Moreover, we found that *Goniopsis* preference for *A. schaueriana* and *L. racemosa* can favor the dominance of *R. mangle* in Neotropical mangroves. This study suggests that propagule predation by *Goniopsis* should be controlled in mangrove restoration programs at abandoned shrimp farms and destroyed areas, if dominance by *R. mangle* is undesirable relative to mixed species communities.

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Introduction

Mangroves are extremely productive and highly dynamic biological communities (Thom, 1967; Cintrón & Schaeffer-Novelli, 1983; Ferreira, 1998). They are subjected to great variation in edaphic (substrate composition, particle size, and topography) and hydrological (tidal flooding and salt levels) conditions. Changes in these conditions were viewed traditionally as establishing spatial gradients of mangroves in the littoral habitat (Davis, 1940; Chapman, 1944; Dansereau, 1947; Coelho, 1965; Warner, 1969; Lugo, 1980). However, frequent deviations of these patterns are observed (Snedaker, 1989; Ferreira, 1998; Bernini & Rezende, 2004; Clarke, 2004; Ferreira et al., 2007). Indeed, mangroves are constantly responding and adjusting to dynamic estuarine environment, where landforms are continuously being built, modified and eroded by abiotic (Thom, 1967; Cintrón & Schaeffer-Novelli, 1983; Woodroffe, 1983; Clarke & Allaway, 1993; Krauss et al., 2008) and also biotic forces (Warren & Underwood, 1986; Lee, 1999; Minchinton, 2001; Cannicci et al., 2008). Factors such as plant–soil

interactions (McKee, 1993, 1995b; Lovelock et al., 2005), competition for light (Smith III, 1987a; Sousa & Mitchell, 1999; Clarke, 2004), differential seed dispersal (Rabinowitz, 1978; Sousa et al., 2007) and predation (Smith III, 1987a, b; Smith III et al., 1989; Sousa & Mitchell, 1999; Lindquist et al., 2009) are recognized as important forces controlling the distribution of mangrove tree species.

Seed predation can exert a strong influence on tree recruitment and forest dynamics (Lindquist et al., 2009) determining patterns of tree diversity and distribution (Wang & Smith, 2002) or altering competitive relationships among species (Hulme, 1996). Effects are more significant when seed and seedling loss to predators is high (Smith III et al., 1989; Asquith et al., 1997; Ferreira et al., 2007). Several studies have investigated the impact of herbivores on vegetation structure and ecosystem function in mangrove forests (Cannicci et al., 2008 for a review). Crabs of the families Ocypodidae and Grapsidae are among the most abundant and ecologically significant animals found in mangroves, playing a key role in food webs and energetic flux (Macintosh, 1988; Koch & Wolff, 2002; Cannicci et al., 2008; Kristensen, 2008). In particular, the Neotropical Ocypodid *Ucides cordatus* (Linnaeus, 1763) is mentioned as an important propagule consumer in Caribbean (McKee, 1995a, Sousa & Mitchell, 1999) and Brazilian mangroves (Branco, 1993; Paludo & Klonowsky, 1999; Koch & Wolff, 2002; Schories et al., 2003; Nordhaus et al., 2006). However, the active predator Grapsid *Goniopsis cruentata* (Latreille, 1803) (Warner, 1969) is another common consumer (Smith III et al., 1989; McKee, 1995a; Sousa & Mitchell, 1999; Ferreira et al., 2007) that has frequently been overlooked. It can heavily prey upon restored mangrove stands, decreasing survival rates of planted mangrove propagules (Ferreira et al., 2007).

Several factors may influence the magnitude of propagule predation by crabs including seed species (Smith III, 1987b; McKee, 1995a; McGuiness, 1997a, b; Sousa & Mitchell, 1999; Souza & Sampaio, 2011), stranding position (Dahdouh-Guebas et al., 1998; Clarke & Kerrigan, 2002; Bosire et al., 2005), shore level (Smith III, 1987a; Sousa & Mitchell, 1999; Krauss & Allen, 2003), and interference among predators. Interference among crab predators have been addressed in other ecosystems by Jensen et al. (2002), DeGraaf & Tyrrell (2004), Quijón &

Snelgrove (2005), Griffen (2006), Griffen & Byers (2006a, b), and Griffen & Williamson (2008). However, to our knowledge, no previous studies have investigated how multiple crab predators interact to influence the magnitude of propagule consumption in both natural and restored mangrove stands.

Therefore, the aim of this study was to compare the magnitude of predation by the Grapsid *G. cruentata* and the Ocypodid *U. cordatus* on propagules of three mangrove tree species: *Avicennia schaueriana* Stapf. & Leech., *Laguncularia racemosa* Gaertn. and *Rhizophora mangle* L. We tested the hypothesis that predation by *G. cruentata* is more important than predation by *U. cordatus* and that these consumers have antagonistic effects on propagule predation. We investigate these ecological aspects in natural and restored areas with the aim of improving mangrove management and restoration in the Neotropics.

Materials and methods

Studied area

The studies were conducted in a mangrove area in Jaguaribe River (35°14′06″W/5°45′42″S), an affluent of the Potengi River estuary in the city of Natal, Rio Grande do Norte State, Northeastern Brazil (Fig. 1). The climate is warm and humid with average air temperatures between 20 and 31°C and annual average precipitation around 1,800 mm. Tides are semidiurnal and spring tides rarely reach more than 1.2 m above mean sea level. The littoral areas of Potengi estuary, including Jaguaribe River, are covered by mangrove trees of the species *R. mangle* (largely the most abundant), *L. racemosa* and *A. schaueriana* (Ferreira & Sankarankutty, 2002). Extensive mangrove areas have been cleared for shrimp breeding ponds in the past years, but the activity is falling today, leaving many abandoned and degraded areas in need for restoration programs.

Two mid-littoral areas were selected for this study (Fig. 1B): (1) an area reforested in 2005 and 2006 with *R. mangle*, called "restored area" (3.17–4.71 trees m^{-2}, average height = 1.5 m); and (2) a contiguous area with *R. mangle* forest (0.4–1.1 tree m^{-2}, average height = 5–8 m), called "mangrove area". These sites (0.5 h each) are separated by a small creek, having freshwater influence in upper littoral zone and
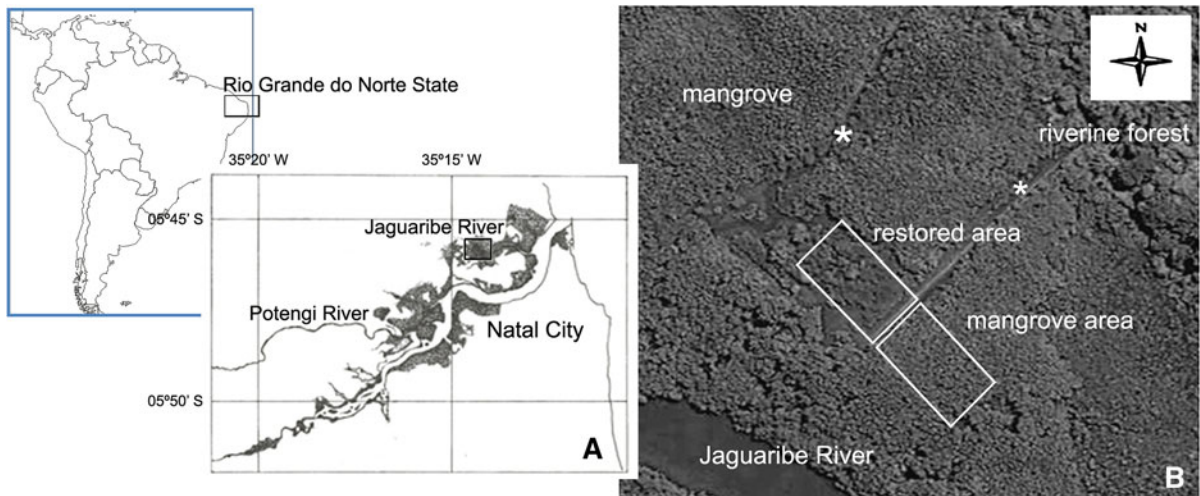
Fig. 1 Study area in Rio Grande do Norte State, Brazil. **A** Potengi River estuary: *shaded areas* represent mangroves. The study site in Jaguaribe River is located in the *black box*. **B** Mangrove and restored study sites; *asterisk* freshwater creeks

coverage by semidiurnal tide. Young trees of restored area form a patchy environment allowing light penetration on bare soil.

The sediment of both areas is wet and muddy, characterized as silty-sand (Shepard, 1954). Interstitial salinity was also similar in two areas, a pattern also showed by soil 'penetrability' (Botto & Iribarne, 2000) and percentages of Silt + Clay (Table 1). Only the organic matter content was markedly higher in mangrove area. Sediment grain size composition and organic matter content were determined at the laboratory of EMPARN (Rio Grande do Norte's Agriculture Company).

Previous work looking at the carcinofauna of the study area showed that Grapsids and Ocypodids are the most abundant and rich crab groups (Ferreira & Sankarankutty, 2002). Density of Ocypodids *Uca* spp. and *U. cordatus* were estimated by counting burrows in a square of 50 × 50 cm inside five replicated plots defined for experiments in each area, and transformed to express in burrows m^{-2}. This is equivalent to individuals m^{-2}, as burrow number is a good estimator of crab population (Branco, 1993; Skov & Hartnoll, 2001; Smith et al., 2009; Carmona-Suárez & Guerra-Castro, 2012). The restored area was more exposed to the sun and presented more *Uca cumulanta* burrows (Crane, 1975; Ferreira, 1998) than mangrove area, while the density of *G. cruentata* and *U. cordatus* showed an opposite trend (Table 1). Grapsid crab burrows were not counted because they are frequently small and constructed under roots, wood debris or litter. Because *G. cruentata* is a highly mobile and non-burrowing crab (Warner, 1969), its density was estimated by counting individuals in plots with ≥10 m distance during daytime before approaching the plots for counting the *Uca* burrows. *G. cruentata* is a medium-size crab (<50 mm carapace width), while *U. cordatus* can reach 90 mm carapace width. *Uca* and other Grapsid species present are small crabs (<25 mm carapace width).

Table 1 Sediment parameters and crab density (average individuals m^{-2}) measured in two studied areas

	Penetrability (cm)[a]	Salinity	% Clay + Silt	% OM	*Uca* species	*Uca* burrows	*Goniopsis cruentata*	*Ucides cordatus* burrows
Restored	18.1 ± 3.3	17.2 ± 2.6	33.6 ± 7.0	3.2 ± 1.5	*U. cumulanta*	≅300	0.3 ± 0.3	0
Mangrove	16.2 ± 3.4	16.2 ± 3.6	34.8 ± 5.4	6.7 ± 2.0	*U. thayeri*	≅100	2.2 ± 0.3	4.0 ± 1.0

Values ± SD. *OM* organic matter

[a] Measured in each plot using a graduated steel rod of 45 cm length, 1.3 cm diameter and 370 g weight, released from a height of 1.2 m (modified from Morrisey et al., 2002)

First experiment

The experiment was conducted at the beginning of the rainy season, when the propagules mature and drop from parent trees (February–March). Propagules of *R. mangle*, *L. racemosa*, and *A. schaueriana* (hereafter referred by genus) were collected at Jaguaribe River coasts, and only those not attacked by fungus or damaged by herbivores were selected. Twenty propagules of each mangrove species were placed in five replicated plots of 2 m × 2 m in both restored and mangrove areas (total propagules per plot = 60). Among the 20 propagules of each species per plot, 10 were placed partially buried and 10 laid over the sediment. The *Rhizophora* propagules are elongated (22–30 cm), and were implanted by burying 5–8 cm of their hypocotyl (or proximal portion) in mud. The small *Laguncularia* propagules (2–2.5 cm long) were similarly implanted, by burying 50% of its major axis in mud. The *Avicennia* propagules (around 3–3.5 cm long) are scarce in Potengi River, so were all collected from ocean coast with their radicle and two pairs of cotyledons partially expanded; the implanted ones had the radicle partially buried leaving the cotyledons out of mud.

Three categories of propagule consumers were defined: (1) the Grapsid crab *G. cruentata*, (2) the Ocypodid *U. cordatus* (both hereafter referred by genus); (3) a guild constituted by soil invertebrates of macro- and micro-fauna (Alongi & Christoffersen, 1992), which includes small (<25 mm c.w.) omnivorous Grapsid crabs of several species (*Pachygrapsus gracilis*, *Sesarma curacaoense*, *Sesarma rectum*, *Aratus pisonii*, *Armases angustipes* and juveniles of *Goniopsis*). This guild also includes Gastropod snails and other primary consumers like Nematodes, Polychaetes, small Crustaceans, and Turbellarians, among several others (Fauchald & Jumars, 1979; Alongi & Christoffersen, 1992; Camilleri, 1992; Yeates et al., 1993; Ruppert et al., 1996; Metcalfe & Glasby, 2008). The damage of crabs like *Goniopsis* and *Ucides* on propagules is recognizable by their magnitude, because in our study area they are the only seed predators that are able to remove large pieces or to carry the entire tethered propagule. *Ucides* carries rapidly their food to burrows (Ferreira, A.C., pers. obs.), while *Goniopsis* feed on the surface (McKee, 1995a). The effects of soil macro- and micro-fauna are associated with decomposer microorganisms, and were recognized through partial consumption of propagule tissues and burial in soil. Small Grapsids are unable to eat or completely extract the firmly tied propagules placed in the experiment allowing us to distinguish their damage from that of *Goniopsis* and *Ucides*. The resistant cuticle of *Rhizophora* propagules prevents rapid consumption by invertebrates and decomposers, oppositely to the other mangrove species that are smaller and lighter.

Propagules or cotyledons were tethered to 1-m-long nylon twines (Smith III, 1987b) and were tied to painted woody sticks fixed in the soil. A pair of propagules, one implanted and one laid, were tied by stick. The twine prevented the propagules to float away, and served as a "tracer" to recover it from predator crab burrows (Smith III, 1987b), allowing crab identification and predation effects to be assessed. Propagules were monitored and counted at low tides every 3 days during 2 weeks, and thereafter, in intervals of 5 days during 6 weeks. A propagule was considered consumed and nonviable when: (1) 50% of its mass had been consumed by predators, (2) it was entirely pulled down a crab burrow, or (3) their apical bud or cotyledons had been completely removed from propagule (Smith III, 1987b).

Second experiment

An exclusion experiment was performed in 2010 to discriminate the rates of propagule predation by *G. cruentata* and *U. cordatus* and to test for possible interference between the two crab species. The experiment had a 2 × 2 factorial design and manipulated by 2 weeks the presence/absence of the two crab species in four treatments: a control without crabs (C) and treatments with 3 *Ucides* (U), 3 *Goniopsis* (G) and with 3 *Ucides* and 3 *Goniopsis* (G + U). In this additive experimental design, both species composition and density are changing in the mixed crab treatment. The alternative would be to use a substitutive experimental design (total predator density constant) to address the effects of multiple crab predators. However, the appropriate design depends on the question of interest (Griffen, 2006) and the additive design is considered appropriate when the goal is to test simply whether interference among predators happens, as was the case in our study.

Crab densities were within the natural range of *Ucides* and *Goniopsis* densities in the mangrove area. Treatments were randomly allocated to four cages of

1 m^2 placed contiguously inside an experimental plot of 4 m^2 and were replicated 5 times in both the mangrove and restored area. The cages had 0.7 m height and the plastic mesh (1 cm—McGuiness, 1997a, b) walls were buried 20 cm in mud to prevent crab escape. The cage is expected to have low impact over sediment deposition rates (McGuiness, 1997a, b). Mesh walls surrounded trunks and roots, which were preserved inside the cages. The *Goniopsis* (35–45 mm c.w.) and *Ucides* (65–80 mm c.w.) specimens used were adults.

In each treatment, 5 propagules of *R. mangle* and 5 of *L. racemosa* (total of 40 per cage) were placed laid, as most in natural conditions. The propagules were tethered in twines with specific colors which were tied to roots or cage walls to serve as tracers. During 1 day prior to the beginning of the experiment crabs were allowed to excavate burrows and reduce capture stress. The cages were checked daily to assess escapes, and if escapes occurred, outlets were closed and new animals added. Litter fall over cages roof were introduced inside the cages to maintain natural litter input.

Statistical analyses

In the first experiment, a two-way Multivariate analysis of variance (MANOVA) was performed to test the effects of mangrove species and propagule position on predation during the experiment. Plots were considered as blocks. Mangrove species (*R. mangle*, *L. racemosa*, and *A. schaueriana*) and propagule position (implanted/laid) were the categorical variables, while the log-transformed numbers of propagules consumed at 11 different days were the dependent variables. We used time as a repeated factor and used MANOVA instead of repeated measures ANOVA to avoid the assumption of circularity (Gotelli & Ellison, 2004). In the second experiment, a two-way ANOVA was performed, using the presence/absence of *Goniopsis* and *Ucides* as categorical variables and the number of propagules consumed as the dependent variable. Statistica 7.1 (StatSoft Inc.) package was used to run the statistical analyses.

Results

Results of the first experiment show that most propagules (>97%) were quickly consumed at the

mangrove area mainly by *Goniopsis* (Table 2). At the restored area, however, *Goniopsis* density and predation rates were much lower than at mangrove, and most *Rhizophora* propagules were left unconsumed (Table 1). *Ucides* is not present in restored area so consumed 0 propagule during the experiment, but small invertebrates were important predators consuming 66% of all *Laguncularia* propagules available (Table 2), with small Grapsids accounting for 25% of all *Laguncularia* consumption.

The two-way MANOVA results revealed a significant interaction between propagule species and position on consumption by crabs at both mangrove and restored areas (Table 3). Propagules were more quickly consumed at the mangrove than at the restored area (Fig. 2), but this difference was not statistically tested because there is only one site of each kind. In both areas, *Rhizophora* propagules were less consumed than *Avicennia* and *Laguncularia*, but this was more evident at the restored area (Fig. 2A). Position also affected the consumption of *Rhizophora* propagules which were less consumed when implanted than when laid on the sediment mainly at the restored area (Fig. 2A).

The second experiment results show (Fig. 3) a significant effect of *G. cruentata* on *Rhizophora* propagules in mangrove area but this effect was only evident in the absence of *U. cordatus* (Fig. 3C). The two-way ANOVA results revealed a significant antagonistic interaction between *Ucides* and *Goniopsis* (Table 4). The ANOVA results also show a reduction of *Laguncularia* propagules by *Goniopsis* predation at the restored area (Fig. 3B; Table 4). *Ucides* showed restricted activity in restored open area treatments, remaining buried in mud to avoid temperature stress.

Discussion

The above results show that *G. cruentata* had a much more important role as propagule predator than *U. cordatus* in our study area. The relative role of these species has not been investigated before and may change in different places, but in both Caribbean and Panamanian coasts *G. cruentata* seems to be an important propagule predator (Smith III et al., 1989; McKee, 1995a; Sousa & Mitchell, 1999). This suggests that most previous works in the Neotropics have overlooked the importance of *Goniopsis* on the

Table 2 Percentage of propagules of three mangrove species consumed by *Goniopsis cruentata*, *Ucides cordatus* and small invertebrates in the first experiment in 2 weeks

Area	Restored			Mangrove		
Mangrove species	*R. m.*	*A. s.*	*L. r.*	*R. m.*	*A. s.*	*L. r.*
Consumer						
Goniopsis	11 (2.2 ± 2.1)	41 (8.2 ± 2.7)	19 (3.8 ± 1.8)	87 (17.4 ± 2.8)	97 (19.4 ± 0.9)	95 (19 ± 1)
Ucides	0	0	0	5 (1 ± 1.4)	1 (0.2 ± 0.4)	0
Small invertebrates	0	21 (4.2 ± 3.0)	66 (13.2 ± 0.8)	0	2 (0.4 ± 0.9)	5 (1 ± 1)
Totals	11	62	85	92	100	100

Values between parentheses represent the mean number of propagules (± SD) consumed per plot

R. m., *R. mangle*; *A. s.*, *A. schaueriana*; *L. r.*, *L. racemosa*

Table 3 MANOVA for propagules consumed in restored and mangrove areas in 50 days in the first experiment

Effect	Restored				Mangrove			
	Wilk's value	df	F	P	Wilk's value	df	F	P
Blocks	0.385	11	1.88	0.13	0.647	6	1.6	0.19
Species	0.017	22	7.86	**<0.01**	0.060	12	9.2	**<0.01**
Position	0.121	11	8.54	**<0.01**	0.178	6	13.8	**<0.01**
Species × position	0.048	22	4.20	**<0.01**	0.079	12	7.6	**<0.01**

Species: *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana*; Position: implanted/laid. Data of consumption were log-transformed. Significant values are in bold

mangrove food web. On the other hand, this study contradicts others emphasizing the role of *U. cordatus* (Schories et al., 2003; Glaser & Diele, 2004) as a propagule consumer in Brazilian mangroves (Branco, 1993; Wolff et al., 2000; Koch & Wolff, 2002; Nordhaus, 2003; Nordhaus et al., 2006). These contradictory results may be due to different population densities of the two species in different studies. However, results of our cage experiment with controlled densities of both species clearly demonstrate that *Goniopsis* is indeed more important than *Ucides* as a propagule consumer. Moreover, evidence from mangroves of Rio Grande do Norte State suggests that *Goniopsis* is a dominant species (McNaughton & Wolf, 1970) with an ample niche both in trophic (from detritus to small crabs) and spatial (burrows, substrate, and trees) dimensions (Burggren & McMahon, 1988; Ferreira & Sankarankutty, 2002).

Interestingly, we found a significant reduction on *Rhizophora* propagule consumption by *Goniopsis* in the presence of *Ucides*, suggesting some kind of interference of the latter species on *Goniopsis* foraging behavior at the mangrove area. Interactions among

predators sharing the same prey can lead to effects that cannot be predicted by summing the effect of each predator separately (Sih et al., 1998; Griffen, 2006). If the effects of *Goniopsis* and *Ucides* were additive, the consumption of *Rhizophora* propagules in the mixed crab treatment would be much higher than was observed. Therefore, the magnitude of this non-additive effect was both statistically and biologically significant contributing to enhance recruitment of *Rhizophora* seedlings in our study area. Interference between crab predators were studied in rocky shores (Griffen, 2006; Griffen & Williamson, 2008; Griffen & Byers, 2006a, b), but never in mangroves. Although the mechanisms of interference among *Ucides* and *Goniopsis* are not clear, it may occur when territorial *Ucides* leave their burrows to search for food and encounter the more active *Goniopsis* feeding on the surface. However, we observed interference of *Ucides* on *Goniopsis* feeding on *Rhizophora* but not on *Laguncularia* propagules probably because its handling time is lower than that of *Rhizophora*, exposing *Goniopsis* less to agonistic interactions with *Ucides*.
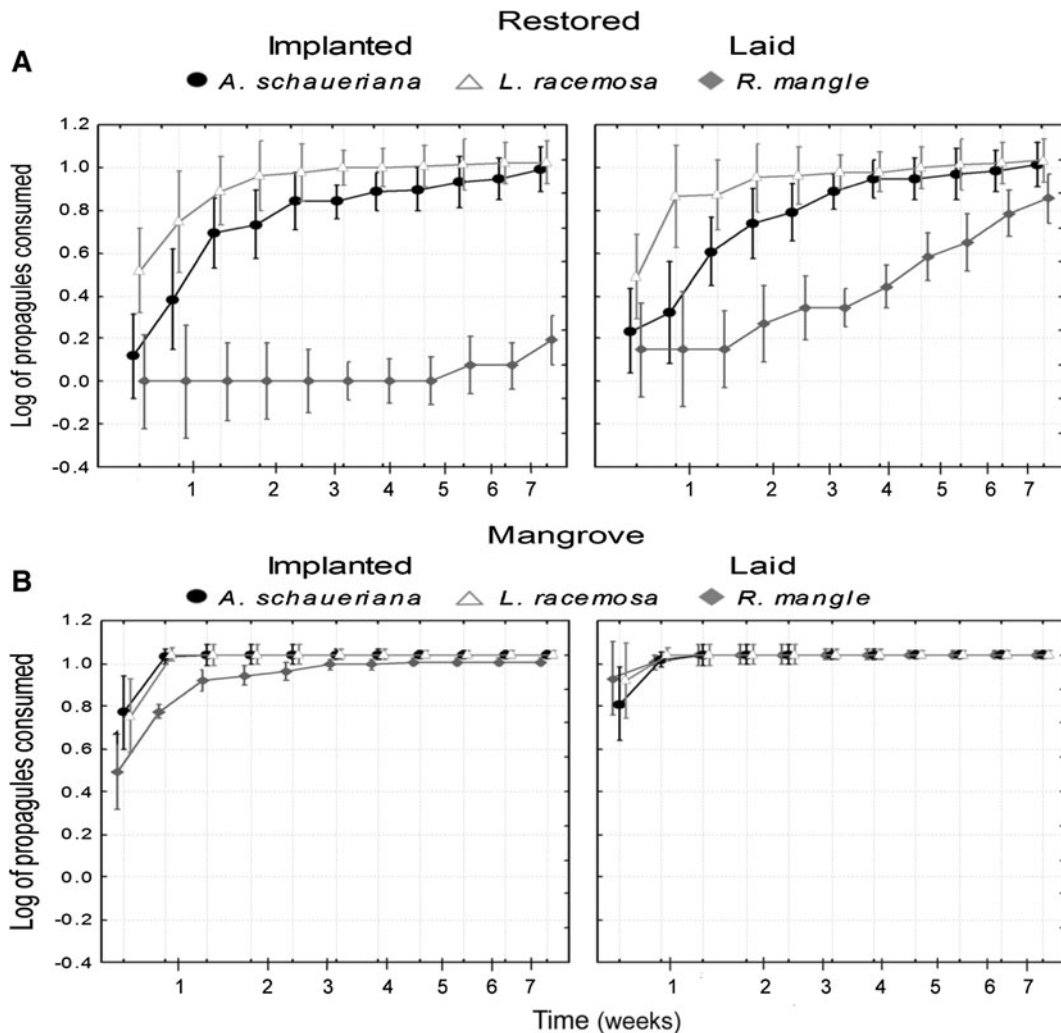
Fig. 2 Mean propagule consumption of *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle* in restored (**A**) and mangrove (**B**) areas during 50 days. Data were log transformed. *Bars* represent 0.95 confidence intervals. *Horizontal axes* represent time (weeks)

We found that the increased mortality of *Avicennia* and *Laguncularia* propagules is due to the preference of *Goniopsis* by these species. Preference by *Avicennia* sp. was also found in East Atlantic (McKee, 1995a; Sousa & Mitchell, 1999; Souza & Sampaio, 2011) and Australian mangroves (Smith III, 1987b; McGuiness, 1997a, b; Clarke & Kerrigan, 2002; Clarke, 2004), while *Laguncularia* propagules were preferred along the Pacific coast of Central America (Delgado et al., 2001). Preference for smaller propagules by crab predators is due to its easier manipulation and burial in burrows; *Avicennia* seems preferred also by their higher nutritive value or lower concentration of

inhibiting chemicals (Smith III, 1987b; McKee, 1995a; Sousa & Mitchell, 1999). The stranding position of *Avicennia* and *Laguncularia* propagules did not influence their rate of mortality, but *Rhizophora* suffer higher predation pressure when laid on the sediment than when vertically implanted. The vertical position for this large propagule may have influenced crab manipulation skills (Dahdouh-Guebas et al., 1998). These results have important implications for mangrove restoration programs as they suggest that the use of *Rhizophora* propagules would allow faster mangrove recovery (Ferreira et al., 2007) than *Avicennia* or *Laguncularia*. Additionally, *Rhizophora*
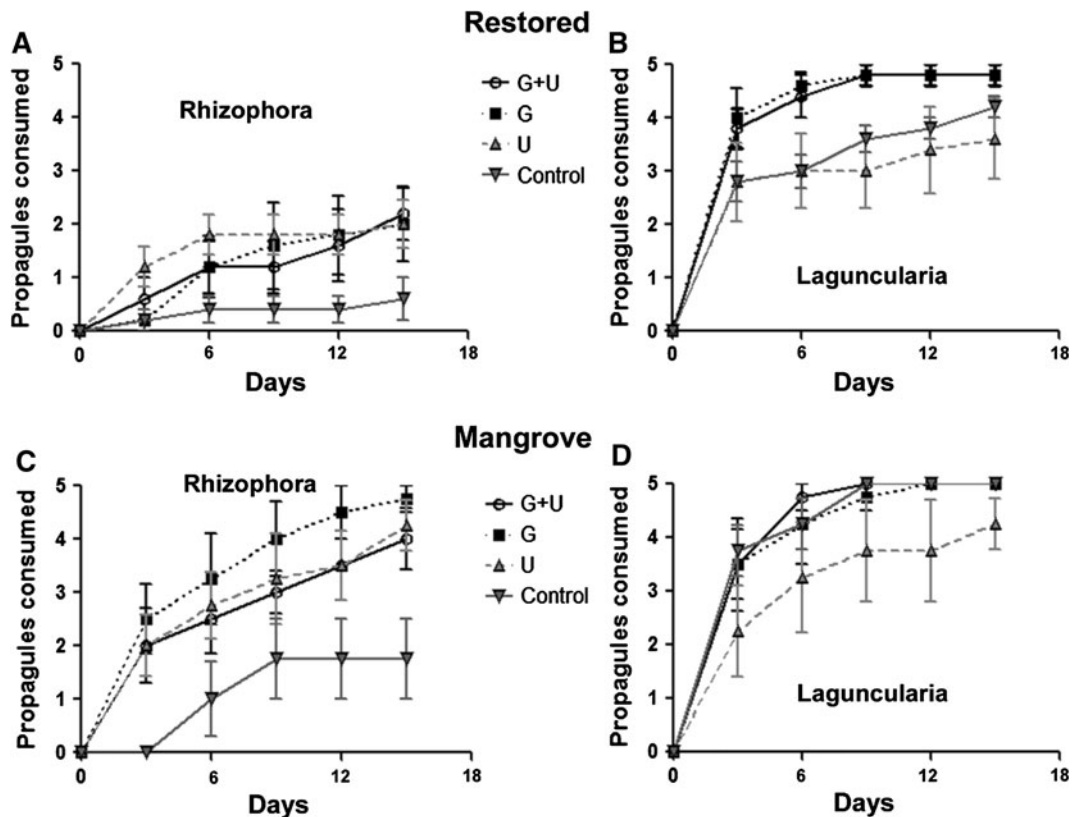
Fig. 3 Mean number of consumed propagules of *Rhizophora* mangle (**A**) and *Laguncularia racemosa* (**B**) in a restored area and *R. mangle* (**C**) and *L. racemosa* (**D**) in a mangrove area in 2 weeks. Propagule consumption was measured in four treatments: *Goniopsis* and *Ucides* (G + U), only *Goniopsis* (G), only *Ucides* (U) and a Control without these crabs. *Horizontal axes* represent time (days)

Table 4 Factorial Analysis of Variance (ANOVA) for predation by *Goniopsis cruentata* (G) and *Ucides cordatus* (U) on *Rhizophora mangle* and *Laguncularia racemosa* propagules in an enclosure experiment implemented in mangrove and restored areas

Effect	*Rhizophora* (mangrove)			*Rhizophora* (restored)			*Laguncularia* (mangrove)			*Laguncularia* (restored)		
	df	F	P	df	F	P	df	F	P	df	F	P
G. cruentata	1	**12.23**	**<0.01**	1	2.59	0.13	1	2.45	0.15	1	**7.71**	**0.01**
U. cordatus	1	4.95	0.05	1	2.59	0.13	1	2.45	0.15	1	0.85	0.37
Blocks	3	**4.68**	**0.03**	4	1.45	0.27	3	1.00	0.43	4	**3.47**	**0.04**
G × U	1	**17.09**	**<0.01**	1	1.45	0.25	1	2.45	0.15	1	0.85	0.37
Error	9	–	–	12	–	–	9	–	–	12	–	–

Significant values are in bold

propagules should be vertically implanted to reduce mortality by crab predation, and improve tree recruitment and recovery in restored areas (Dahdouh-Guebas et al., 1997, 1998; Bosire et al., 2005; Ferreira et al., 2007).

Differences in propagule predation between mangrove and restored areas seem to be strongly related to crab abundance. Higher crab densities exert predation pressure over seeds in coastal forests (Lindquist & Carroll, 2004; Lindquist et al., 2009). Propagule consumption was higher at the mangrove area where crabs are more abundant, showing that predation is more intense under closed canopies than in more open areas. This pattern was also found by Osborne & Smith

(1990), Clarke & Kerrigan (2002), and Clarke (2004), but is opposite to that found by Sousa & Mitchell (1999) and Souza & Sampaio (2011). Thermal and water stress limit crab populations in open areas (Warner, 1977), while food is more abundant in mangrove habitat (Ferreira, 1998). Small Grapsids (*Pachygrapsus gracilis* and *Goniopsis* juveniles) and Gastropods are more abundant under mangrove canopy (Ferreira & Sankarankutty, 2002; Maia & Tanaka, 2007), and could partially be responsible by a higher rate of burial/consumption of *Laguncularia* avoiding significant consumption by *Goniopsis* in treatments. Data suggest that rapid predation of propagules by high *Goniopsis* aggregation under canopy in the first experiment diminished propagule consumption by these small crabs. The lower rate of *Rhizophora* consumption by *Goniopsis* in restored area is also observed in the second experiment; probably territorial displays performed by *Uca cumulanta* in this open area could make it visually more conspicuous and nutritionally preferred item (Wolcott, 1988) than *Rhizophora* to *Goniopsis* (Ferreira, A.C., pers.obs.).

Several works have studied the effects of crabs on tree recruitment and community composition (Green et al., 1997; Sherman, 2002; Lindquist & Carroll, 2004; Lindquist et al., 2009), particularly in mangroves (Smith III, 1987a, b; McKee, 1995a; Osborne & Smith, 1990; Souza & Sampaio, 2011). Crab consumption of propagules is concentrated in the rainy season, when mangroves produce high amounts of tide-carrying propagules which strand in open and canopy areas. We observed that propagules of three mangrove species showed ability to grow in the same littoral areas along the Jaguaribe River, but need to survive from the predation by Grapsids and burial by fossorial crabs. In our study areas these biotic factors could limit the establishment and growth of propagules, especially *Avicennia* and *Laguncularia*. Therefore, the Grapsid crabs preference for these small propagules may explain in part the dominance of *Rhizophora* in our study area. Grapsid crabs have an important role in shaping mangrove community assemblage in the Indo-west Pacific (Smith III et al., 1989), and East Africa (Bosire et al., 2005; Dahdouh-Guebas et al., 1997, 1998). As expected, we found a similar ecological role (Smith III et al., 1991) of Grapsid crab *G. cruentata* in mangroves of Jaguaribe River. Dominance of *R. mangle*, due to higher tannins content (Alongi, 1987) and organic matter

accumulation on soils (Lacerda et al., 1995), may lead to changes in the chemical characteristics and availability of organic matter to soil biota, affecting the distribution and abundance of meiobenthos in estuary (Alongi, 1987). Moreover, this may lead to higher nutrient retention in the estuary and lower nutrient release to adjacent ecosystems (Lacerda et al., 1995). Hence, *G. cruentata* may exert a significant effect in mangrove community structure.

Conclusion

Previous works in Neotropical mangroves have emphasized *U. cordatus*, but overlooked the importance of the predator *G. cruentata* on mangrove food webs. This generalist Grapsid species has an important role determining through propagule predation which mangrove species can establish in mangrove areas, influencing mangrove community structure. *Ucides* can interfere in *Goniopsis* foraging on *R. mangle*. Moreover, predation by *Goniopsis* is able to eliminate most propagules of *L. racemosa* and *A. schaueriana*, mainly under native mangrove, where this crab species is more abundant. Our results have important implications for mangrove restoration, suggesting that propagule predation by *Goniopsis* should be controlled in restoration areas if dominance by *R. mangle* is undesirable relative to mixed species communities. On the other hand, if restoration attempts to restore *R. mangle*, it is most effective to insert propagules vertically into the soil to avoid undue predation from crabs on that species.

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