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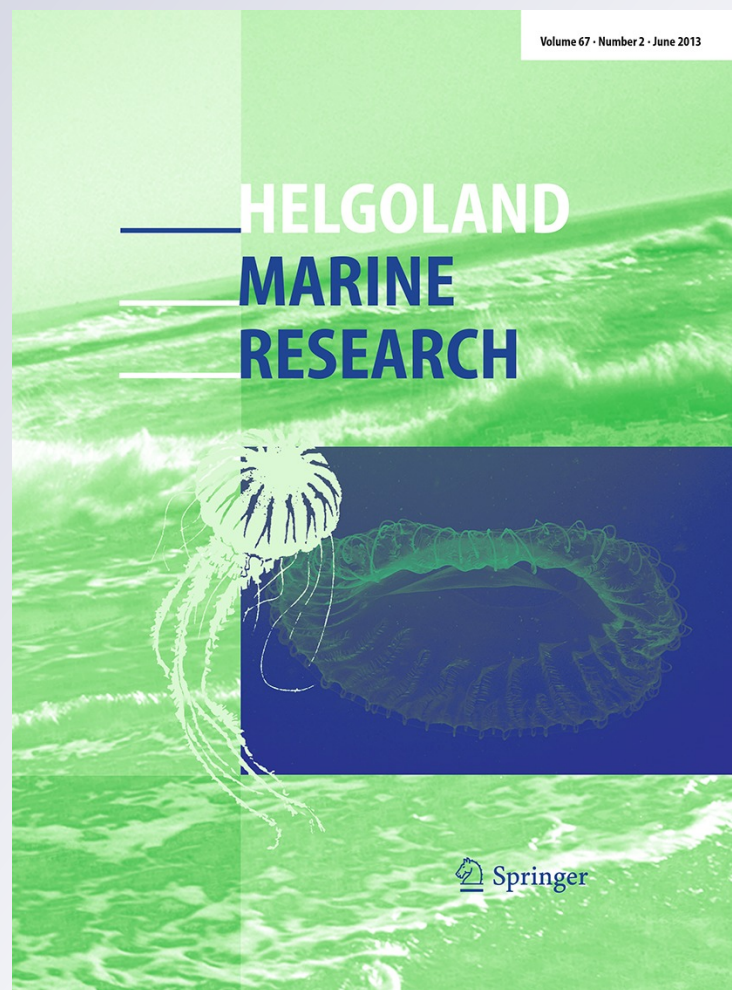
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Mangrove habitat partitioning by *Ucides cordatus* (Ucididae): effects of the degree of tidal flooding and tree-species composition during its life cycle

A. C. Wunderlich · M. A. A. Pinheiro

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Abstract Environmental factors strongly affect mangrove crabs, and some factors modulate population structure and habitat partitioning during the crabs' life cycle. However, the effect of these environmental factors on habitat selection by mangrove crabs is still unknown. We evaluated habitat selection by the mangrove crab *Ucides cordatus* in mangrove forests with different degrees of predominance of *Rhizophora mangle*, *Laguncularia racemosa* or *Avicennia schaueriana*, two tidal flooding levels (less- and more-flooded), and two biological periods (breeding and non-breeding seasons). Sampling was conducted in four mangrove forests with different influences of these biotic and abiotic parameters. We used the data for sex ratio to explain environmental partitioning by this species. Females predominated in *R. mangle* mangroves, independently of the biological period (breeding or non-breeding seasons), and males predominated only in the less-flooded *L. racemosa* mangroves. The flooding level affected the sex ratio of *U. cordatus*, with a predominance of males in less-flooded mangroves, independently of the biological period; and a gender balance in the more-flooded mangroves only during the breeding season. Outside the breeding season, the largest specimens were recorded in the

R. mangle mangroves, but in the breeding season, the largest crabs were recorded in the *L. racemosa* mangroves with a higher level of flooding. These results suggest that tree-species composition and tidal flooding level can have a significant effect on the habitat partitioning of sexes and sizes of the mangrove crab *U. cordatus* both during and outside the breeding season.

Keywords Flood · Habitat selection · Neotropical mangroves · Sex ratio · Tidal effects · *Ucides cordatus*

Introduction

Environmental effects on the population structure and sex ratio in mangrove crabs have been little studied (deRivera 2003), particularly in species of the genera *Uca* (Frith and Brunenmeister 1980; deRivera 2003; Mokhtari et al. 2008) and *Ucides* (Monteiro and Filho 2004; Diele et al. 2005; Piou et al. 2009). However, the influences of certain abiotic and biotic parameters on the population biology of these brachyurans are comparatively well known, especially the effects of temperature (Kelemec 1979), salinity (Frusher et al. 1994), tides (Reinsel 2004; Turra et al. 2005), species composition of mangrove trees (Icely and Jones 1978), and sediment granulometry (Mouton and Felder 1996; Morrissey et al. 1999; Ribeiro et al. 2005).

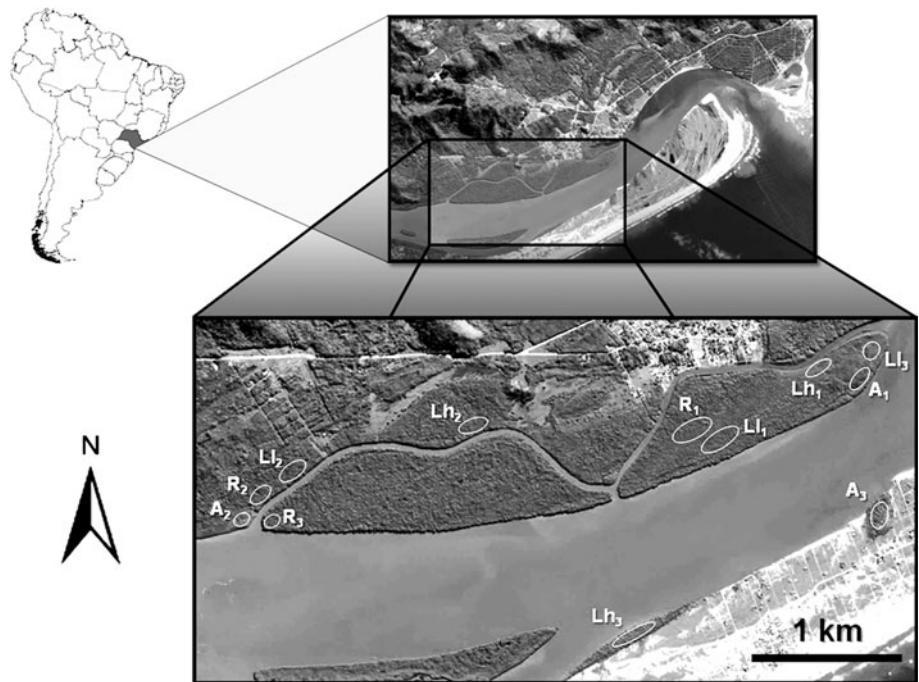
According to Icely and Jones (1978), Piou et al. (2009), and Sandrini-Neto and Lana (2011), the spatial distribution and population structure of mangrove crabs can change as a function of one or more parameters, especially the species composition of the mangroves (Schories et al. 2003; Koch et al. 2005; Nordhaus and Wolff 2007), degree of flooding (Whitehouse et al. 2001; Reinsel 2004), and texture and organic matter content of the sediment (Frusher et al. 1994),

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Fig. 1 Location of each mangrove forest, with a predominance of *Laguncularia racemosa* (Lh_{1-3} high mangroves; Ll_{1-3} low mangroves), *Avicennia schaueriana* (A_{1-3}), or *Rhizophora mangle* (R_{1-3}), at Iguape Municipality, State of São Paulo, southeast Brazil (Source Ikonos IV® Satellite image provided by EngesSat®)



leading to habitat partitioning (Caravello and Cameron 1987) and a possible change in the sex ratio. The sex ratio may also be influenced by different exploitation rates (Campbell 1992; Diele et al. 2005), growth and mortality levels (Wenner 1972; Emmerson 1994; Johnson 2003), predation (Iribarne and Martinez 1999; Jaroensutasinee and Jaroensutasinee 2004), or salinity (Jury et al. 1994).

Studies of the sex ratio of *Ucides cordatus* (Linnaeus 1763) (Brachyura, Ucridae) have reported either a gender imbalance (Alcântara-Filho 1978; Castro 1986; Ivo et al. 1999; Alves and Nishida 2004; Diele et al. 2005; Wunderlich et al. 2008; Góes et al. 2010) or an equal proportion between the sexes (Ivo et al. 2000; Alves et al. 2005; Araújo and Calado 2008), although they have not clarified the possible causes. For this reason, in this study, we proposed two competing hypotheses to explain this phenomenon: (1) males and females occupy similar mangrove forests, independently of the predominant tree species, flooding level, or biological period; or (2) the two sexes occupy mangroves differently with respect to these characteristics. To evaluate these hypotheses, we compared the sex ratio of *U. cordatus* among three mangrove forests (with a predominance of *Laguncularia racemosa* Gaertn., *Rhizophora mangle* L., or *Avicennia schaueriana* Stapf & Leechman), two tidal flooding levels (lower, in high mangroves; and higher, in low mangroves), and between two biological periods of this species (breeding and non-breeding seasons).

This treatment was proposed based on differences previously found for population density of *U. cordatus* (structure; see Hattori 2006) and trophic ecology (availability of

leaf litter; see Christofolletti 2005), in the same Neotropical mangrove areas studied here.

Methods

Study area

The study was carried out in mangroves of the Cananéia-Iguape-Peruíbe Environmental Protection Area (APA/CIP), between 24°21'S–46°59'W and 25°18'S–48°06'W, on the south coast of the state of São Paulo, Brazil. The mangroves are located in Iguape Municipality, next to Barra de Icapara (24°41'S and 47°28'W), between Comprida Island and the continent; this extensive mangrove-bay complex is known as the “Mar de Dentro” (Fig. 1). The APA/CIP is about 75 km long (Mendonça 2007), comprising 2 mouths—‘Icapara’ (North) and ‘Cananéia’ (South). Miyao et al. (1986) recorded salinities from 18 to 30, and Cunha-Lignon et al. (2009) characterized this area as: (1) mean annual rainfall 2,300 mm (with most precipitation between January and March); (2) mean annual temperature 23.8 °C (lowest in July and highest in February, with 19.8–27.8 °C); (3) micro-tidal regime with semi-diurnal and diurnal inequalities.

Sampling methods

During June 2007 through November 2008, crabs were collected in 12 mangrove forests ($\pm 3,600$ m² each), which were characterized by a predominance of different tree

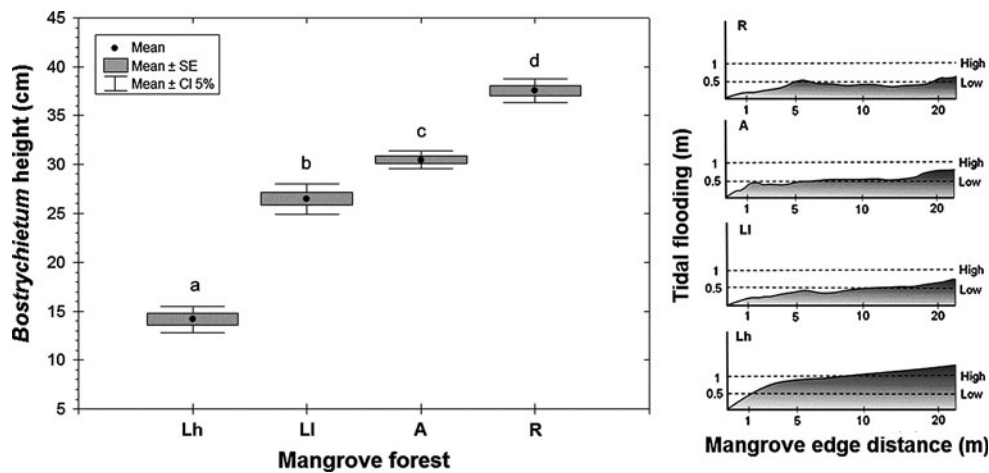


Fig. 2 Box and whisker plots of *Bostrychietum* height (left) to characterize the flooding level and its topographic profile with tidal flooding levels (right), in each mangrove forest according to the predominance of *Laguncularia racemosa* (Lh high mangrove; LI low mangrove), *Avicennia schaueriana* (A), or *Rhizophora mangle* (R), at

Iguape Municipality, State of São Paulo, southeast Brazil, where SE standard error, CI 5 % confidence interval at 5 % = $1.96 \times SE$; means indicated with a different letter were statistically heterogeneous ($P < 0.01$)

species (>80 %), comprising six mangrove forests of *Laguncularia racemosa* (L), and three each of *Avicennia schaueriana* (A) and *Rhizophora mangle* (R) (Fig. 1). To analyze the effect of tidal flooding level on the sex ratio, we used six areas of *L. racemosa* (three replicates for each flooding level), which were categorized as: (1) *high mangroves* (Lh), with lower level or rare frequency of flooding during some spring tides; and (2) *low mangroves* (LI), with higher levels or frequency of flooding during neap and spring tides (see Fig. 2). The height of the *Bostrychietum* on the mangrove stems and roots was used to characterize the flooding level of each area (Fig. 2). The *Bostrychietum* is a group algae, mainly members of Rhodophyceae—*Bostrychia* Mont., *Caloglossa* (Harv.) G. Martens and *Catenella* Grev., according to Pedroche et al. (1995)—that occur as epiphytes on basal stems of mangrove trees (Post 1936; Feller and Sitnik 1996), and is a useful indicator of flooding level in these ecosystems (Alves 2011).

Crabs were caught by “braceamento”, a manual method where the fisherman inserts his arm into the burrow and catches the crab by its dorsal carapace (Nordi et al. 2009). This method is permitted by the Brazilian law that protects this species (Brasil 2011). We used the same crab-catcher in all the mangrove areas to avoid a bias in the data. In each mangrove forest ($\pm 10,800 \text{ m}^2$), a minimum of 200 specimens of *U. cordatus* were randomly collected per biological period, sexed by inspection of the abdomen shape and number of pleopods (Pinheiro and Fiscarelli 2001), measured (CW, carapace width) with a precision vernier caliper (0.05 mm), and released in the same place where they were caught.

Data analysis

The influence of the mangrove tree-species composition on the *U. cordatus* population sex ratio was evaluated by excluding the effect of flooding level and comparing data among mangrove forests with similar levels and frequencies of flooding. To evaluate the effect on the biological period of this species, we compared the data obtained for the same mangrove forests in two biological periods (June–July 2007 and October–November 2008), which correspond to the non-breeding (April–September) and breeding (October–March) seasons for this species (see Pinheiro and Fiscarelli 2009).

The sex ratio as a function of size (CW) was evaluated according to Wenner (1972), by analyzing the distribution of the specimens in size classes (5 mm), establishing the proportion of males in each class (minimum of 10 specimens/class), and verifying the classification by the trend of the empirical points. The difference in sex ratio was evaluated by χ^2 test (Wilson and Hardy 2002; Zar 2010), with a comparison between mangrove forests of the same tree species (using replicates), forests with different tree composition (Lh, LI, A, or R predominance), biological period (non-breeding and breeding seasons), and level of flooding (high and low mangroves). The data for size (carapace width) for each sex in different mangrove forests were submitted to ANOVA and their means compared by Tukey’s test (5 %) (Sokal and Rohlf 1995).

The normality of data was assessed by Kolmogorov–Smirnov test (Zar 2010). All statistical analyses and graphs were performed in R software (R Development Core Team 2009).

Table 1 Sex ratio (male/female) of *Ucides cordatus* in each mangrove forest with different predominant tree species (L, *Laguncularia racemosa*; A, *Avicennia schaueriana*; and R, *Rhizophora**mangle*), flooding level (Lh less-flooded; Ll more-flooded), and biological period (NB non-breeding season; B breeding season), in Iguape Municipality, State of São Paulo, southeast Brazil

Biological periods/mangrove forests	Males		Females		Sex ratio (M:F)	χ^2
	<i>N</i>	%	<i>N</i>	%		
<i>Non-breeding (NB)</i>						
Lh	191	77.6	55	22.4	1:0.29	75.18***
Ll	132	58.7	93	41.3	1:0.70	6.76*
A	92	40.5	135	59.5	1:1.47	8.14*
R	95	42.2	130	57.7	1:1.37	5.44*
<i>Breeding (B)</i>						
Lh	206	66.9	102	33.1	1:0.49	35.11***
Ll	152	48.3	163	51.7	1:1.07	0.38 ^{ns}
A	140	55.8	111	44.2	1:0.80	3.35 ^{ns}
R	98	39.7	149	60.3	1:1.52	10.53*
<i>Total (NB + B)</i>						
Lh	397	71.7	157	28.3	1:0.39	193.97***
Ll	284	52.6	256	47.4	1:0.90	1.45 ^{ns}
A	232	48.5	246	51.5	1:1.06	0.41 ^{ns}
R	193	40.9	279	59.1	1:1.44	15.66***
Total	1.106	54.1	938	45.9	1:0.85	13.81**

χ^2 test of goodness of fit testing the null hypothesis of equal proportions between sexes for each area; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ^{ns} $P > 0.05$

Results

We collected a total of 2,044 crabs (1,106 males and 938 females) in the 12 mangrove areas. The overall sex ratio was 1:0.85 (males/females), which differed statistically from the 1:1 expected for most crustaceans ($\chi^2 = 13.81$; $P = 0.002$) (Table 1). The mangroves differed in the topography (based on the Bostrychietum height), with four distinct flooding levels ($F = 313.82$; $P < 0.001$) following the hierarchical sequence Lh < Ll < A < R (Fig. 2).

The overall sex ratio of *U. cordatus* changed with the biological period ($\chi^2 = 14.69$; $P < 0.001$). During the non-breeding season (NB), one sex predominated ($P < 0.05$), with the proportions differing among the forests with different dominating mangrove species; that is, males in *L. racemosa* areas and females in *A. schaueriana* and *R. mangle* forests (Table 1). This changed in the breeding season (B), when the sex ratio was similar in the intermediate-flooded areas Ll ($P = 0.22$) and A ($P = 0.52$), although the previous pattern was maintained in Lh and R, with males and females dominating, respectively. This same pattern was confirmed when the data were grouped (see Table 1).

The mean size of the specimens (CW) also differed between the mangrove types during the non-breeding season ($F = 44.3$; $P < 0.0001$) (Table 2; Fig. 3), with the largest specimens associated with *Rhizophora* and

Avicennia mangroves (more-flooded areas), compared to the less-flooded *L. racemosa* mangroves (Lh and Ll). Size differences were also recorded in the breeding season ($F = 65.5$; $P < 0.0001$), when the largest specimens occurred in the more-flooded *L. racemosa* areas (Ll), and the smallest ones were associated with Lh (females) or Lh and R mangrove areas (males). During the breeding season, the mean size decreased in both sexes only in the *Rhizophora* mangroves, and increased in more-flooded areas of *Laguncularia* (Ll) (Fig. 3).

Hence, the sex ratio of *U. cordatus* differed according to flooding level (Fig. 4), with a lower frequency of mature females (CW > 43 mm) in less-flooded mangroves (Lh), and males over 45 mm predominating. An inverse pattern occurred in the more-flooded mangroves (Ll), where females predominated in nearly all size classes, except for CW > 65 mm, in which males predominated.

In most of the mangrove forests (Lh, A, and R), the sex ratio as a function of size showed a similar trend between biological periods, despite the differences related to flooding level (Fig. 5). These areas contrasted with the more-flooded *Laguncularia* forest (Ll), where a high proportion of females occurred during the breeding season. In the Lh forest, males (CW > 45 mm) dominated in both biological periods.

The population structure of each sex changed somewhat as a function of the biological period (Fig. 6). There was an

Table 2 Biometry of *Ucides cordatus* in each mangrove forest with different predominant tree species (L, *Laguncularia racemosa*; A, *Avicennia schaueriana*; and R, *Rhizophora mangle*), flooding level (Lh less-flooded; Ll more-flooded), and biological period (NB non-breeding season; B breeding season), in Iguape Municipality, State of São Paulo, southeast Brazil

Site	Sex	n	Carapace width (mm)			
			Min	Max	Mean $\pm$ SE*	CV (%)
<i>Non-breeding (NB)</i>						
Lh	M	191	37.5	74.0	52.4 $\pm$ 0.6 b	16.4
	F	55	24.7	70.0	45.9 $\pm$ 1.1 a	17.7
Ll	M	132	30.1	84.5	51.6 $\pm$ 0.8 b	17.6
	F	93	30.2	72.1	47.1 $\pm$ 0.8 a	16.8
A	M	92	30.8	81.1	58.3 $\pm$ 1.0 cd	17.0
	F	135	38.8	71.7	55.7 $\pm$ 0.6 c	13.5
R	M	95	31.3	83.2	63.1 $\pm$ 1.0 de	15.2
	F	130	41.7	72.9	58.4 $\pm$ 0.5 c	10.4
<i>Breeding (B)</i>						
Lh	M	206	20.3	77.9	55.2 $\pm$ 0.7 b	18.7
	F	102	30.1	65.6	46.7 $\pm$ 0.7 a	15.6
Ll	M	152	44.6	84.3	68.3 $\pm$ 0.6 e	10.1
	F	163	38.9	77.4	59.6 $\pm$ 0.5 d	11.2
A	M	140	32.5	81.4	58.8 $\pm$ 0.8 cd	16.8
	F	110	31.9	78.2	55.2 $\pm$ 0.8 bc	15.2
R	M	97	32.0	81.0	55.5 $\pm$ 1.1 bc	20.0
	F	149	35.2	73.0	54.1 $\pm$ 0.6 b	13.5

SE standard error, CV coefficient of variation

* Means followed by a same letter are not significantly different ($P > 0.05$)

increase in abundance of mature females (CW > 40 mm) in Lh and Ll forests during the breeding season, while most females were immature (CW < 45 mm) during non-breeding season. In mangrove forests A and R, the abundance of females remained in equilibrium (independent of the biological period), with most females being mature individuals (CW > 45 mm). The abundance of large males (CW > 65 mm) increased slightly in the breeding season.

Discussion

We rejected the hypothesis of an equal ratio between the sexes in different mangrove forests and confirmed the alternative hypothesis, where the sexes and ages showed differences in occupation of these mangroves, with juvenile males mainly found in less-flooded *L. racemosa* forests and adult females in more-flooded ones (*L. racemosa* low, *A. schaueriana*, and *R. mangle*). Our results suggest that habitat selection of *U. cordatus* is strongly affected by the interplay between the type of mangrove forests and the tidal flooding level. We found that females occurred mainly in mangrove forests with the highest flooding level. According to a previous study of the same areas (Christofoletti 2005),

these mangroves are characterized by greater availability of litter, richness in nutrients (N and P), and a low concentration of polyphenols. In general, female crustaceans require more high-energy food items during gonadal maturation (Sastry 1983), with a significant feeding reduction when they are ovigerous (as confirmed for *U. cordatus* by Christofoletti 2005), due to their cryptic behavior. Besides, when the sex ratio is male-biased, the movement of males increases, to avoid male–male competition for females (Hazlett et al. 2005), causing changes in the sex ratio in some places. Juveniles of *U. cordatus* were recorded in higher densities in less-flooded *L. racemosa* forests (Hattori 2006), avoiding sites with adult males, because of intense competition for burrows and territories (Nordhaus et al. 2009). However, Diele and Simith (2007) suggested that *U. cordatus* megalopae settle in areas populated by conspecific crabs and/or muddy habitats, and generally cohabit in their burrows. This suggests that intraspecific competition occurs only after the pubertal molt, when morphological and hormonal changes lead to different reproductive behaviors and searching for preferred habitats, explaining the differential population structure observed in this study. Piou et al. (2009) mentioned differences in the spatial patterns according to developmental stage (juvenile and adult)

Fig. 3 Box and whisker plots of carapace width (CW, in mm) of *Ucides cordatus* in each mangrove forest, with a predominance of *Laguncularia racemosa* (Lh high mangroves; Ll low mangroves), *Avicennia schaueriana* (A), or *R. mangle* (R) by sex and biological period (breeding and non-breeding seasons), where SE standard error, CI 5 % confidence interval at 5 % = $1.96 * SE$; means indicated with a different letter were statistically heterogeneous ($P < 0.01$)

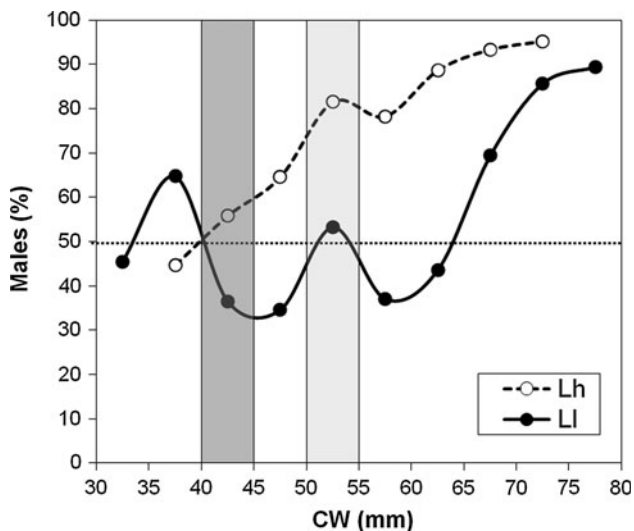
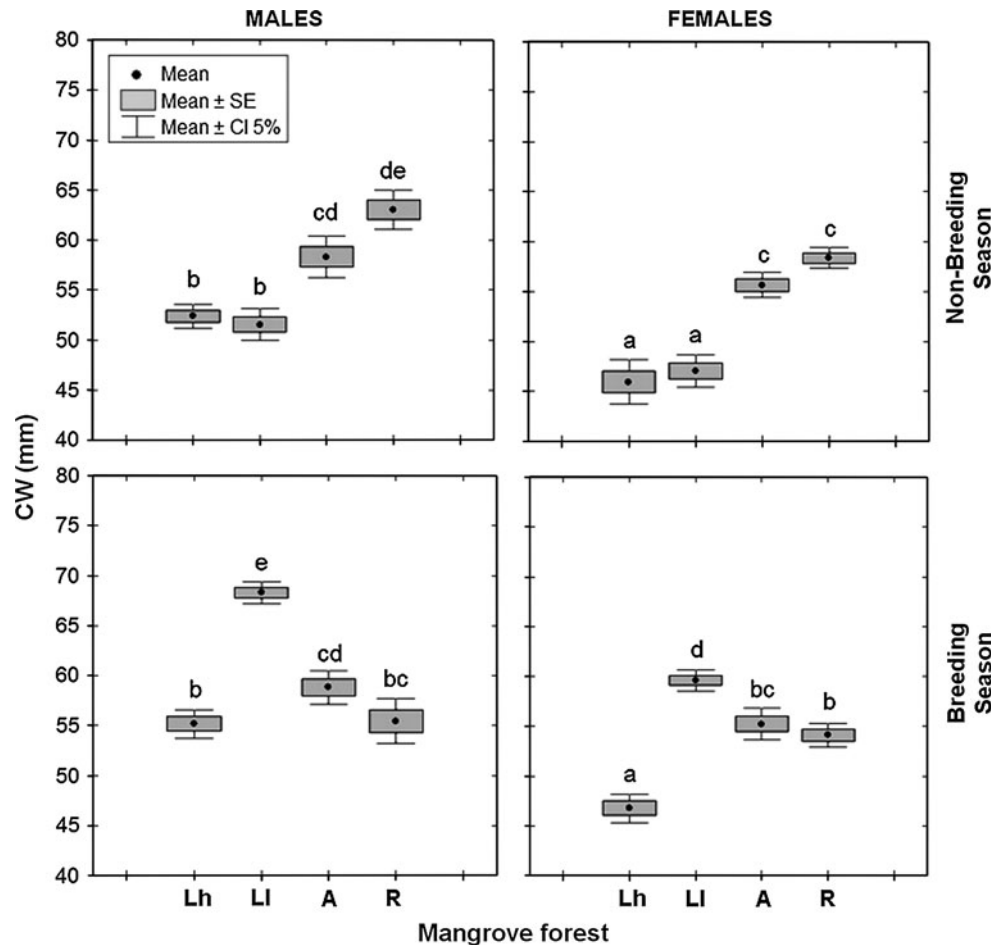


Fig. 4 Percentage of *Ucides cordatus* males by size classes (CW carapace width in millimeters) in two mangrove forests of the same tree-species composition (*Laguncularia racemosa*), but different flooding levels (Lh high mangrove, with less-flooded level; and Ll low mangrove, with more-flooded level). Bars indicate size intervals, where size at onset of maturity occurs for females (dark gray) and males (light gray), according to Pinheiro and Fiscarelli (2001)

of *U. cordatus*, attributed to exclusion of juvenile crabs due to the presence of adults. These authors explained this differential pattern in Neotropical mangroves by the influence of spatial distribution and preferred habitats on a regional scale; however, Sandrini-Neto and Lana (2011) established that a complex mosaic of patches exists on the small scale, as examined in this study.

Reviewing data obtained by Hattori (2006) in the same mangrove forests confirmed a greater abundance of juveniles in less-flooded *L. racemosa* forests, a balanced sex ratio in *A. schaueriana* and more-flooded *L. racemosa* forests, and a greater abundance of females in the *R. mangle* and *A. schaueriana* (Pinheiro et al. 2005; Hattori 2006), possibly because their leaves have higher nutritional value (N and P) and lower polyphenol concentration compared to *L. racemosa* leaves (Christofolletti 2005). Leaves of

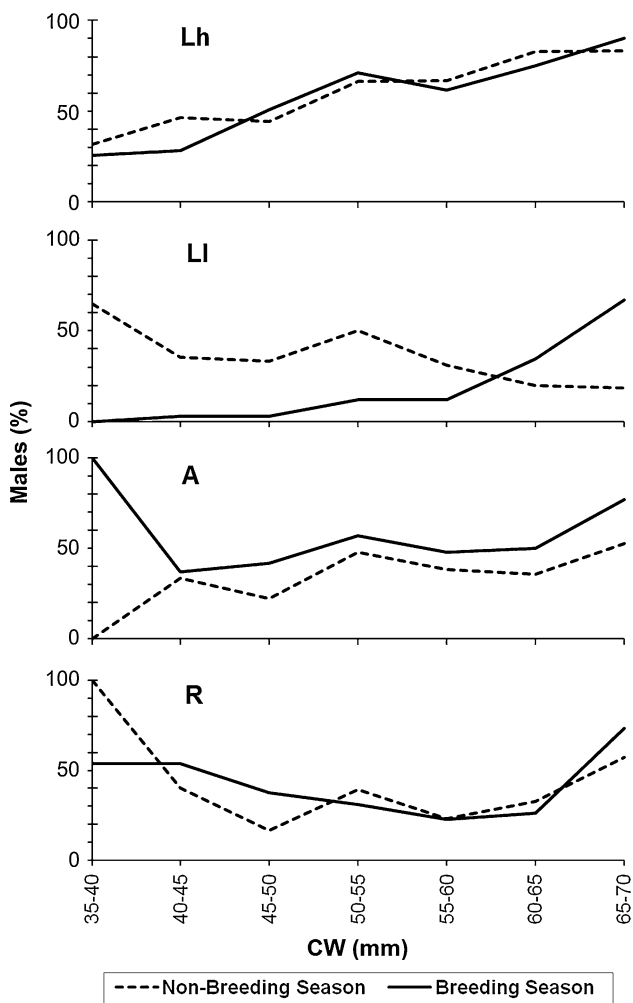


Fig. 5 Comparison of the percentage of *Ucides cordatus* males by size classes (CW carapace width in millimeters) in each mangrove forest (Lh *Laguncularia racemosa* high mangrove; Ll *Laguncularia racemosa* low mangrove; A, *Avicennia schaueriana*; R, *Rhizophora mangle*) as a function of the biological period (breeding and non-breeding season)

L. racemosa in the study areas had a total polyphenol concentration approximately 10 times higher than those of *R. mangle* and *A. schaueriana* (Christofoletti 2005), which would have a negative influence on the growth/fattening of this crab, as observed for other crabs (Conde et al. 1995; Erickson et al. 2004) and arthropods (Reese et al. 1982; Fleck and Layne 1990; Hai and Yakupitiyage 2005). These phenolic compounds (polyphenols and tannin) can disrupt digestion and form complexes that resist digestion by this species (Rhoades and Cates 1976; Lacerda et al. 1986). Linton and Greenaway (2007) mentioned that leaves with high tannin content are not easily digested by crabs, confirming their anti-herbivory property (Godoy et al. 1997; Kandil et al. 2004); this explains the preference of some sesamid crabs for mangrove leaves with lower concentrations of this alkaloid (Micheli 1993; Guerrero-Ocampo

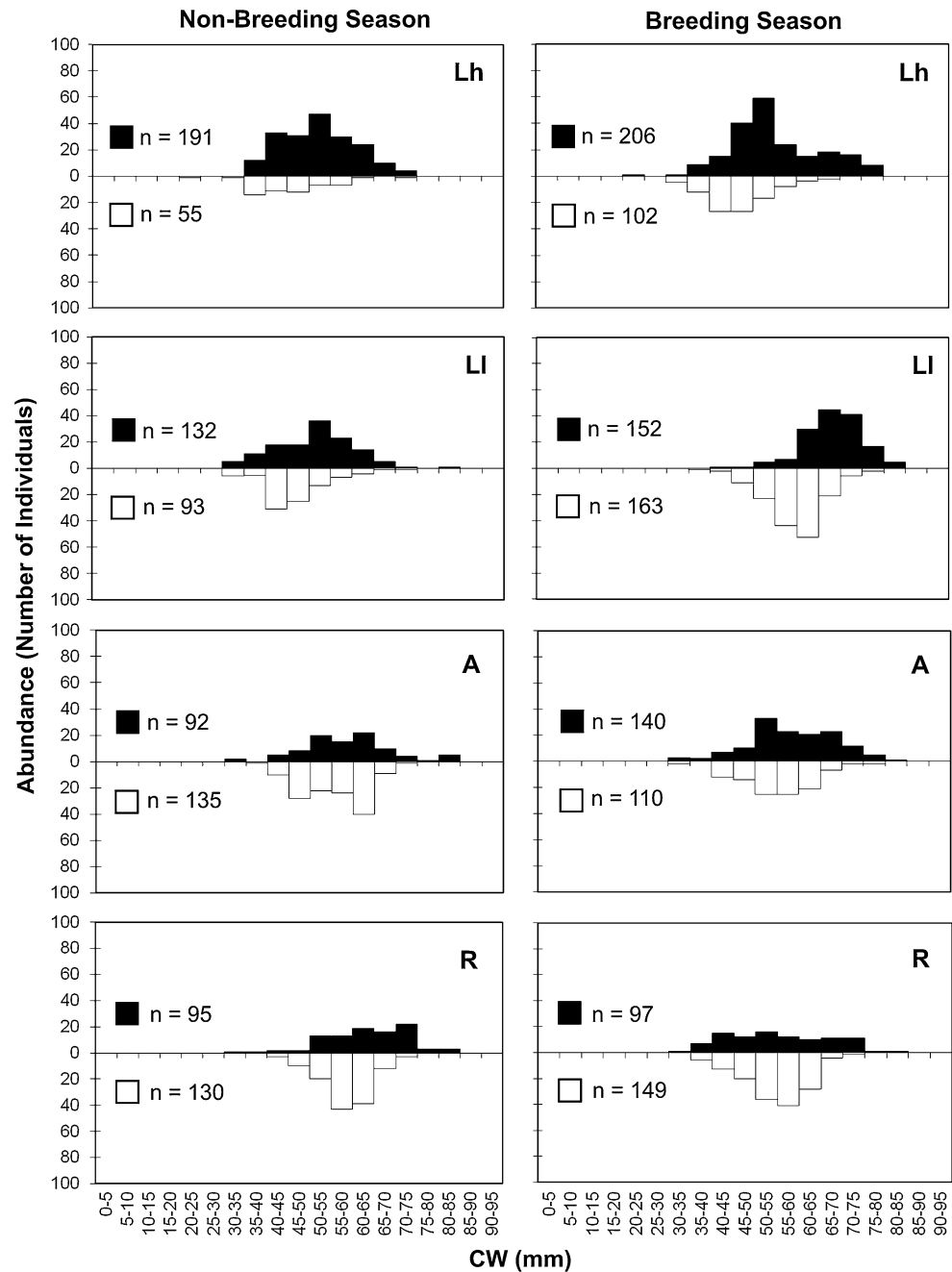
2002). Data obtained by Nordhaus and Wolff (2007) suggest that the capacity of *U. cordatus* to digest leaves is not hampered by tannins, but also indicate that this species prefers *R. mangle* over *Avicennia germinans* leaves, due to a higher nitrogen content and lower C/N ratio and tannin content. High tannin concentration may also decrease the availability of total leaf N content (Lacerda et al. 1986). Nordhaus et al. (2006) assumed that crabs fed more on propagules of *R. mangle*, which have a higher nutritive value than leaf litter; however, this was not confirmed by Christofoletti (2005), who reported a higher prevalence of leaves than propagules in stomach contents of *U. cordatus*.

In any event, the nutritional preference for leaves of certain tree species can markedly influence reproduction, particularly in females, as previously mentioned. On the other hand, the topographic heterogeneity of the mangrove, in particular the flooding level, leads to different local abundance patterns in crustacean populations (Rossi and Chapman 2003; Koch et al. 2005), as well as in the zonation patterns of the mangroves (Alongi and Sasekumar 1992). Different patterns of distribution in the size of mature specimens (CW > 60 mm) and density of *U. cordatus* were mentioned by Hattori (2006) and Schmidt (2006), as a function of tidal flooding in mangroves, reflecting the composition/vegetation structure and availability of leaves for feeding. However, based on a certain critical flooding level (not established in our study), the density would decline as a function of the longer exposure time during low tides, which limits foraging of *U. cordatus*. Also, less-flooded mangrove forests tend to have a more-saline soil, which causes physiological stress on the crabs, slowing their growth and fattening rates (Sastry 1983; Christofoletti 2005; Schmidt 2006).

Diele et al. (2005) and others studying the sex ratio of *U. cordatus* found a predominance of males, particularly in areas where crab-catchers visit less often or those are less accessible. The mangrove areas in this study also are used by crab-catchers, but with no preference for specific mangrove forests (*L. racemosa*, *A. schaueriana*, and *R. mangle*), and therefore undergo similar exploitation pressure. Furthermore, in these mangrove forests, the crab-catchers do not prefer one gender only, as in north and northeast Brazil (Alves et al. 2005; Diele et al. 2005) where only males are sought because of their larger size.

The present study also showed that the sex ratio can vary as a function of tidal flooding level, which limits the diversity and nutritional value of the food in less-flooded *L. racemosa* forests, which do not receive leaves from adjacent forests. Although leaves of *L. racemosa* contain high concentrations of polyphenols (Lacerda et al. 1986; Christofoletti 2005), in more-flooded *L. racemosa* forests, these compounds significantly decrease with oxidation on soil (Godoy et al. 1997). Moreover, in more-flooded

Fig. 6 Abundance of *Ucides cordatus* (males, black bars; females, white bars) by size classes (CW carapace width in millimeters), in mangrove forests with a predominance of *Laguncularia racemosa* (Lh high mangrove; Ll low mangrove), *Avicennia schaueriana* (A), or *Rhizophora mangle* (R), during breeding and non-breeding seasons



mangrove forests, the microbial decomposition process is more efficient, increasing the C:N rates and reducing the astringency of the leaves (Alongi 1997; Christofolletti 2005). Hence, in less-flooded *L. racemosa* forests, the crabs are smaller and grow more slowly.

In *U. cordatus*, the predominance of females in more-flooded mangrove forests may result from the need for water during embryonic and larval development; for instance, Santos et al. (2009) observed that 70 % of the females' burrows have their openings oriented toward the mangrove edge. This facilitates the access of ovigerous females to water, to release the larvae for dispersal by the

tides (Diele 2000), explaining the migratory behavior previously reported for this species by Góes et al. (2000), and the greater abundance of females in more-flooded mangrove forests. According to Diele et al. (2005), this abundance of females is common at mangrove edges, favors the export of larvae, and improves their survival in the more-stable conditions outside the estuary (Diele and Simith 2006).

Our results provide insight into mangrove habitat partitioning by *U. cordatus*, revealing a significant relationship to environmental factors (tree-species composition and tidal flooding level) and biological period (breeding or

non-breeding season). This contribution improves understanding of ecological processes in this species, particularly for the National Management Plan for sustainable harvesting of *U. cordatus*, proposed by the Brazilian Ministry of the Environment (Brasil 2011).

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