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Population biology of *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae) from two tropical mangroves sites in northeast coast of Brazil

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Abstract. The aim of the present study was to characterize and compare the population biology of *Ucides cordatus* in two mangrove sites with different level of anthropogenic impact (Ariquindá and Mamucabas) at state of Pernambuco, northeast Brazil. Crabs were handily collected (April 2008 to March 2009) by a capture per unit effort by one person, during low tide period. Altogether, we obtained 609 specimens (334 males and 275 females, including 25 ovigerous females) in Ariquindá, and 769 specimens (421 males and 348 females, including 35 ovigerous females) in Mamucabas. Males were significantly larger and heavier than females in both mangroves. The size and weight of each sex were similar in the two populations. The overall sex ratio favoured males (1.21 males: 1 female) in both populations. Ovigerous females occurred only in summer and autumn (February through April), indicating seasonal reproduction of *U. cordatus* for both populations. Juveniles were more intense in autumn and winter at both sites, which are related to greater reproductive activity during the warmer months of the year. Although these mangrove sites differ in the level of human impact (Mamucabas is more impacted), both populations of *U. cordatus* showed similar population biology.

Key words: size, sex-ratio, reproduction, semiterrestrial crab, Brazilian mangroves

Resumo. Biologia populacional de *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae) em duas áreas de manguezais tropicais da costa nordestina do Brasil. O objetivo do presente estudo foi caracterizar e comparar a biologia populacional de *Ucides cordatus* em duas áreas de manguezais com diferentes níveis de impacto antropogênico (Ariquindá e Mamucabas) do Estado de Pernambuco, nordeste do Brasil. Os caranguejos foram coletados manualmente (Abril/2008 a Março/2009) por meio de esforço de captura de uma pessoa, durante a maré baixa. Um total de 609 caranguejos foi coletado em Ariquindá, sendo 334 machos e 275 fêmeas (33 fêmeas ovígeras). Em Mamucabas, 769 caranguejos foram amostrados, sendo 421 machos e 348 fêmeas (35 fêmeas ovígeras). Os machos são significativamente maiores e mais pesados do que as fêmeas em ambos os manguezais. O peso médio de machos e fêmeas não diferiram entre as duas populações analisadas. A proporção sexual total favoreceu os machos em ambas as populações (1,21: 1). As fêmeas ovígeras ocorreram apenas no verão e outono (fevereiro a abril), caracterizando uma reprodução sazonal para *U. cordatus* em ambas as populações analisadas. Os juvenis ocorreram com maior intensidade no outono e no inverno em Ariquindá e Mamucabas em decorrência da atividade reprodutiva ocorrida no verão e no outono. Apesar das áreas de manguezais diferirem em relação à ação antrópica (Mamucabas mais impactado), ambas as populações de *U. cordatus* apresentaram uma dinâmica populacional semelhante.

Palavras chave: tamanho corpóreo, proporção sexual, reprodução, caranguejo semiterrestre, manguezais brasileiros

Introduction

Mangroves are true renewers of the marine aquatic fauna, serving as a barrier against the force of fresh and salt waters, being in this manner a natural nursery for many species of marine organisms, which spawn in this environment. Fish, birds, crustaceans, mollusks, and other invertebrates find food available in the mangrove, a refuge from predators, and areas for reproduction and growth. Crabs, together with mollusks, are the most abundant macrofaunal animals in mangroves, in terms of both biomass (Jones 1984) and species diversity (Aveline 1980).

The population structure of mangrove crabs has been analyzed mainly with respect to the distribution of individuals by size classes, comparing the body size of males and females, age distribution, proportion of males and females, recruitment, and the reproductive period (Díaz & Conde 1989, Castiglioni *et al*. 2006, Nicolau & Oshiro 2007, Silva *et al*. 2007, Bezerra & Matthews-Cascon 2007, Hirose & Negreiros-Fransozo 2008, Gregati & Negreiros-Fransozo 2009, Costa & Soares-Gomes 2009). This information about populations adds to the knowledge of the ecological stability of species in a given habitat, and leads to greater understanding of their biology, especially those species with commercial value.

The mangrove crab *Ucides cordatus* (Linnaeus, 1763) is one of the most common species of crustaceans in Brazilian mangrove ecosystems, mainly in the North and Northeast regions of the country (IBAMA 1994). It is the largest ocypodoid that is endemic to the Atlantic coast of the Americas, with its distribution extending from Florida, Gulf of Mexico, Central America, Antilles, and northern South America including the Guyana, to Brazil (Melo 1996). In the state of Pernambuco (northeast Brazil), this species is found from the municipality of Goiana (North Coast) by the municipality of São José da Coroa Grande (South Coast), with emphasis on the production of the municipalities of Cabo de Santo Agostinho, Sirinhaém, Rio Formoso and Tamandaré (Botelho *et al.* 1999). This crab species also plays an important ecological role in the mangrove ecosystem, in processing litter as part of the energy flow in the sediment, and in bioturbation to aid in the cycling of carbon and organic matter (Wolff *et al.* 2000, Amouroux & Tavares 2005, Nordhaus *et al.* 2006, Guest *et al.* 2006). This species is widely exploited as a fishery resource because of the large size of adults, and is therefore economically important, providing income to communities along estuaries of Brazil (IBAMA 1994, GEO BRAZIL 2002, Glaser & Diele 2004, Passos e Di Beneditto 2005, Jankowsly *et al.* 2006). The crab is sold at good process in major cities and is in high demand by tourist (Nascimento 1993), mainly in northern and northeastern Brazil where it is fished intensively, and the state of Pernbambuco production was estimated at 100 t (IBAMA/CEPENE 1997). Its socioeconomic importance is more relevant in the northeast of the Brazilian coast, where the species is caught in large volumes, being one of the main food items of regional cuisine and, above all, much appreciate by tourists (Botelho *et al.* 1999). The Ordinance n° 34/03 of July 24, 2003 regulates the exploitation of species in the states of Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia, prohibiting each year during the period from 1 December to 31 May, the capture, keeping in captivity, transport, processing, manufacturing and marketing of females of this species (IBAMA 2003). The continuing decline in population stocks and reducing the size of some crab species, such as *Cardisoma guanhumi* (Latreille, 1825) and *U. cordatus* was mentioned by Amaral & Jablonski (2005). Such reduction according to these researchers can be attributed to overfishing, selective capture and degradation of mangroves areas where these species live. In this sense, the studies on population dynamics and reproductive period have great biological importance, mainly for the commercially exploited species and by promoting the development of closed laws contributing to maintenance of conscious stocks (Dalabona & Silva 2005).

Research on the population biology of *U. cordatus* has intensified in recent years (Andrade *et al.* 2007, Wunderlich *et al.* 2008, Araújo & Calado 2009). Nevertheless, little and older information is available on its population biology in mangroves in the state of Pernambuco in northeastern Brazil (Botelho *et al.* 1999, Monteiro & Coelho-Filho 2004). Recently, the relative growth and morphological and physiological sexual maturity were analyzed for populations of this work by Castiglioni & Coelho (2011) and Castiglioni *et al.* (2011). Therefore, we characterized and compared the population dynamics of *U. cordatus* in two mangrove areas with different level of anthropogenic impact (Ariquindá and Mamucabas) at state of Pernambuco, northeast Brazil. The populations were analysed with regard to the following aspects: the size-class frequency distribution of carapace width (CW), mean carapace width and weight of males and females, sex ratio, reproductive period, and recruitment, during a one-year period.

Material and Methods

The specimens of *U. cordatus* were collected in the mangroves of the Ariquindá River (8°46'43.69" S and 35°06'25.87" W) and the Mamucabas River (8°41'28.48" S and 35°06'09.32" W), both in the municipality of Tamandaré, state of Pernambuco. According to Ivo *et al.* (2000), the municipality of Tamandaré, along with Cabo de Santo Agostinho, Sirinhaém and Rio Formoso are responsible for producing enough *Ucides cordatus* in the state of Pernambuco. According to the Köppen classification, the regional climate is type As' (warm and humid), with mean temperatures ranging between 25 and 30 ºC, and annual precipitation about 2000 mm. The seasons are well defined, with a dry season from September through December, and a rainy season from January through August (Duarte 1993, Moura & Passavante 1995).

The Ariquindá River is contained within the Guadalupe APA (Environmental Preservation Area). The river is 7 km long, and together with its tributary the União River, forms an important component of the Formoso River basin (CPRH 1999). It's considered one of the last non-polluted rivers of state of Pernambuco. The mangrove area of the Ariquindá River selected to collect the crabs is located near the confluence of the Ariquindá and Formoso rivers, on Carneiros Beach. The mangrove is composed predominantly of *Rhizophora mangle*, followed by *Laguncularia racemosa* and in lower frequency by *Avicennia* spp. The substrate of these areas is sand-mud.

The Mamucabas River is contained almost entirely within the municipality of Tamandaré. The Mamucabas arises west of the Saltinho Biological Reserve, near Engenho Barro Branco. Where the river enters the reserve, it is impounded to form the reservoir that supplies the city of Tamandaré. From its headwaters to the Coastal Plain, which extends to the outskirts of Tamandaré, the Mamucabas flows northwest-southeast, and then turns southward and continues until it joins the Ilhetas River, and together these flow into the Pontal which bears this name (CPRH 2001). By entering in the reserve, it suffers the first environmental impact, being dammed to form the reservoir that supplies the municipality of Tamandaré. It meets the Ilhetas River and together they disembogue in a spit (CPRH 2001). Besides the damming, it's considered an impacted river due to the great deposition of solid waste and deforestation, as well as the housing occupation in the surrounding areas (Santos *et al.* 2001). The area where the specimens of *U. cordatus* were collected is located near the mouth of these rivers. There the mangrove is composed predominantly of *Laguncularia racemosa*, followed by *Rhizophora mangle* and in lower abundance by *Avicennia* spp. The sampling areas have a sand-mud substrate.

The crabs were collected monthly from April 2008 to March 2009, by a professional crabber who used his arm or a hook in the burrow, in three different areas (25 m^2) of each mangrove. These areas were located along the river and 20 m distant from each other. Sampling was carried out during low tide around the full or new moon; because the forest is flooded only during spring high tides, the crabs can be caught more easily in the softened sediment at these times.

The crabs were placed in plastic bags and transported to the laboratory, where each individual was washed, sexed, and measured (with a precision calliper to the nearest 0.01 mm) for carapace width (CW). The ovigerous condition of females was also noted. We also recorded the total wet weight (PE) with a precision balance (0.01 g), after blotting the crabs with paper towels.

Test of normality (Kolmogorov-Smirnov) and homoscedasticity (Levene) were carried our prior to the all analysis, as pre-requisites for the statistical test uses (Zar 1996).

Previously to the crabs sampling, the number of open and closed burrows of *U. cordatus* in each area were recorded. Subsequently, the density of open and closed burrows, and the total burrows per m^2 in each mangrove were calculated (Skov *et al.* 2002, Wunderlich *et al.* 2008). We also estimated the density of crabs per m^2 monthly by calculating the density of crabs per m^2 for each mangrove area. The densities of open, closed, total burrows, and crabs were compared between the Ariquindá and Mamucabas mangrove areas by *t* test (α= 0.05) (Zar 1996). According to Costa (1979) and Wunderlich *et al.* (2008), each burrow is inhabited by only one specimen of *U. cordatus.*

The frequency distribution of size classes for males and females was analyzed monthly during a 1-year period, in order to follow temporal variations in population frequency distribution, and to analyze the seasonality of some processes, such as reproduction and recruitment of the species. For these analyses, the crabs were grouped by demographic category (males and females) and were arranged in 15 size classes based on carapace width (CW), each class of 5.0 mm. The number of classes was obtained by the Sturges formula (Conde *et al.* 1986). The frequency distribution of the male and female crabs sampled during the one-year period was tested for normality using the Shapiro-Wilk test (α= 0.05) (Zar 1996).

The mean size of the carapace width and weight for each sex and mangrove was compared by

t test (α= 0.05) (Zar 1996).

The sex ratio was determined for the total number of crabs and for each season, and carapace-width size class in both populations. We used the test of goodness of fit (chi-square) to verify if the sex ratio found for *U. cordatus* followed the expected 1:1 proportion (α= 0.05) (Zar 1996).

To determine the reproductive period of *U. cordatus*, the frequency of ovigerous females in relation to adult females was calculated for each season in Ariquindá and Mamucabas mangroves areas. These proportions were then compared using the multinomial proportions test (MANAP) (α= 0.05) (Curi & Moraes 1981).

To estimate recruitment, crabs with carapace width less than the values determined for the sexual maturity of males and females by means of the allometric technique (morphological sexual maturity) and gonad development (physiological sexual maturity) (Castiglioni & Coelho 2011) at the two localities were considered juveniles. In Ariquindá, males with CW smaller than 38.5 mm and females with CW smaller than 37.8 mm were considered to be juveniles. In Mamucabas, these sizes were 37.3 and 35.4 mm for males and females respectively (Castiglioni & Coelho 2011). The proportion of juveniles was compared among seasons using the multinomial proportions test (MANAP, α= 0.05, Curi & Moraes 1981).

Results

A total of 609 crabs were collected from the Ariquindá River mangrove, including 344 males (54.9%) and 275 females (45.1%, of which 25 were ovigerous). In the Mamucabas mangrove, 769 crabs were collected, comprising 421 males (54.8%) and 348 females (45.2%, of which 35 were ovigerous). Table I show the number of crabs of each sex collected in each month over the period of one year in the Ariquindá and Mamucabas mangroves, wherein it is noted that male and female *U. cordatus* were sampled in all months of the year in both mangroves.

Table I. Number of specimens of *Ucides cordatus* (males, females, and ovigerous females) sampled in each month during the course of one year in the Ariquindá (AR) and Mamucabas (MA) river mangroves, state of Pernambuco, Brazil.

Months	Males		Females		Ov. females		Total		M:F		χ^2	
	AR	MA	AR	MA	AR	MA	AR	MA	AR	MA	AR	MA
Apr/08	20	29	26	38	10	7	56	74	0.55:1	0.64:1	4.57 *	3.45 ns
May/08	36	37	34	85			70	122	1.05:1	0.43:1	0.06 ns	18.9 *
Jun/08	34	40	26	35			60	75	1.30:1	1.14:1	1.07 ns	0.33 ns
Jul/08	13	42	32	25			45	67	0.40:1	1.68:1	8.02 *	4.31 *
Aug/08	23	24	27	21			50	45	0.85:1	1.14:1	0.32 ns	0.20 ns
Sep/08	14	25	30	27			44	52	0.46:1	0.92:1	5.82 *	0.07 ns
Oct/08	16	49	13	20			29	69	1.23:1	2.45:1	0.31 ns	12.18 *
Nov/08	45	29	9	25			54	54	5.00:1	1.16:1	24.0 *	0.30 ns
Dec/08	43	51	9	6			52	57	4.78:1	8.50:1	22.2 *	35.53 *
Jan/09	37	45	11	1		1	48	47	3.36:1	22.5:1	14.1 *	39.34 *
Feb/09	26	24	10	18	8	12	44	54	1.44:1	0.80:1	1.45 ns	0.67 ns
Mar/09	27	26	15	12	15	15	57	53	0.90:1	0.96:1	016 ns	0.02 ns
Total	334	421	242	313	33	35	639	769	1.21:1	1.21:1	5.72 *	6.93 *

Note: *= significant at 5%, NS= no significant at 5%.

Normality was rejected for the overall frequency distributions obtained for both sites (Ariquindá: males W= 0.9674 and females W= 0.9675; Mamucabas: males W= 0.9772 and females W= 0.9669; $p<0.05$), using pooled data. The size-class frequency distribution of carapace width of males and females was unimodal for both populations (Figures 1a and 1b). However, the monthly size-frequency distributions of *U. cordatus*, as shown in Figure 2 for Ariquindá and Figure 3 for Mamucabas, evidenced polymodality for the populations from both sites. At Ariquindá, two age groups (juveniles and adults) were perceptible in the size-frequency distributions from June to September 2008. At Mamucabas, two age groups could be perceived from April to September 2008, when juveniles became more abundant in both populations.

The estimated densities of open and closed burrows were 0.93 ± 0.18 and 0.34 ± 0.09 burrows.m^{-2} respectively in Ariquindá, and 0.97 ± 0.23 and 0.41 ± 0.16 burrows.m^{-2} respectively in

Mamucabas. The total density of burrows was 1.28 ± 0.19 burrows.m^{-2} in Ariquindá and 1.37 ± 0.24 burrows.m^{-2} in Mamucabas, which did not differ significantly between the mangroves (t= -1.07, p>0.05). The density of crabs was 0.68 ± 0.13 indiv.m^{-2} in Ariquindá and 0.85 ± 0.28 indiv.m^{-2} in Mamucabas, and was significantly higher in Mamucabas (t= -1.99; p<0.05).

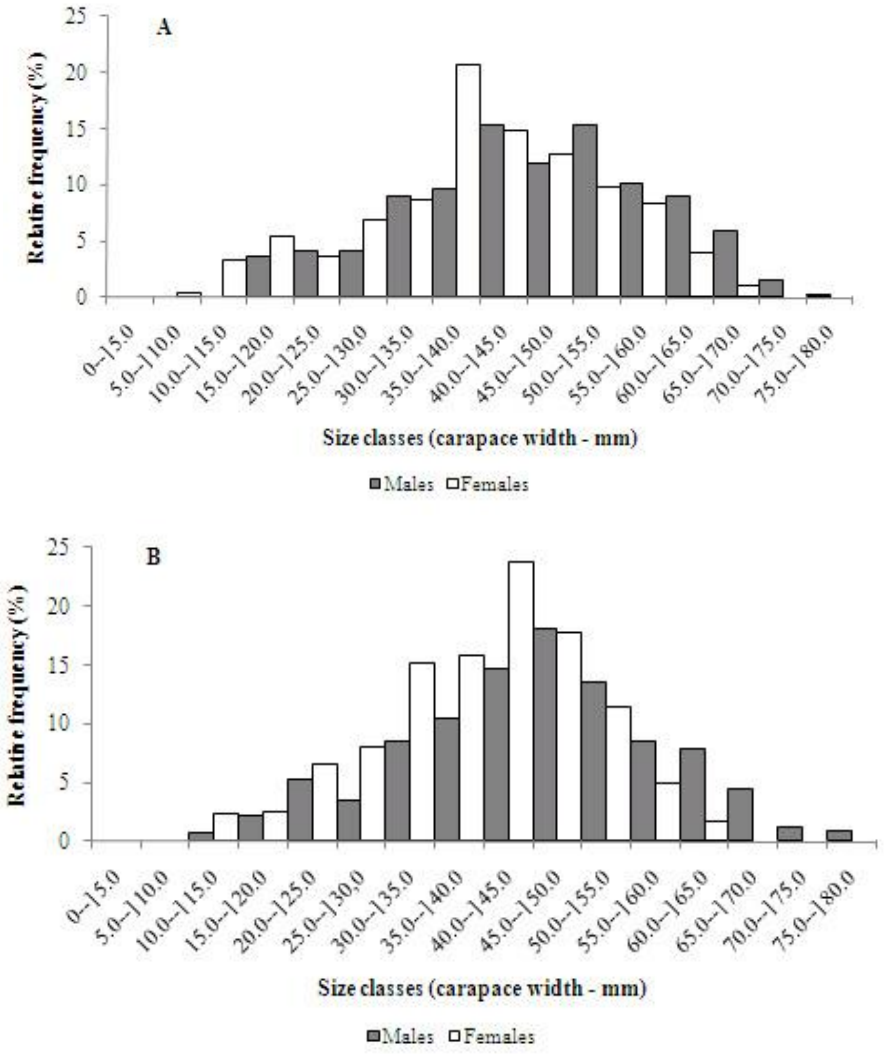
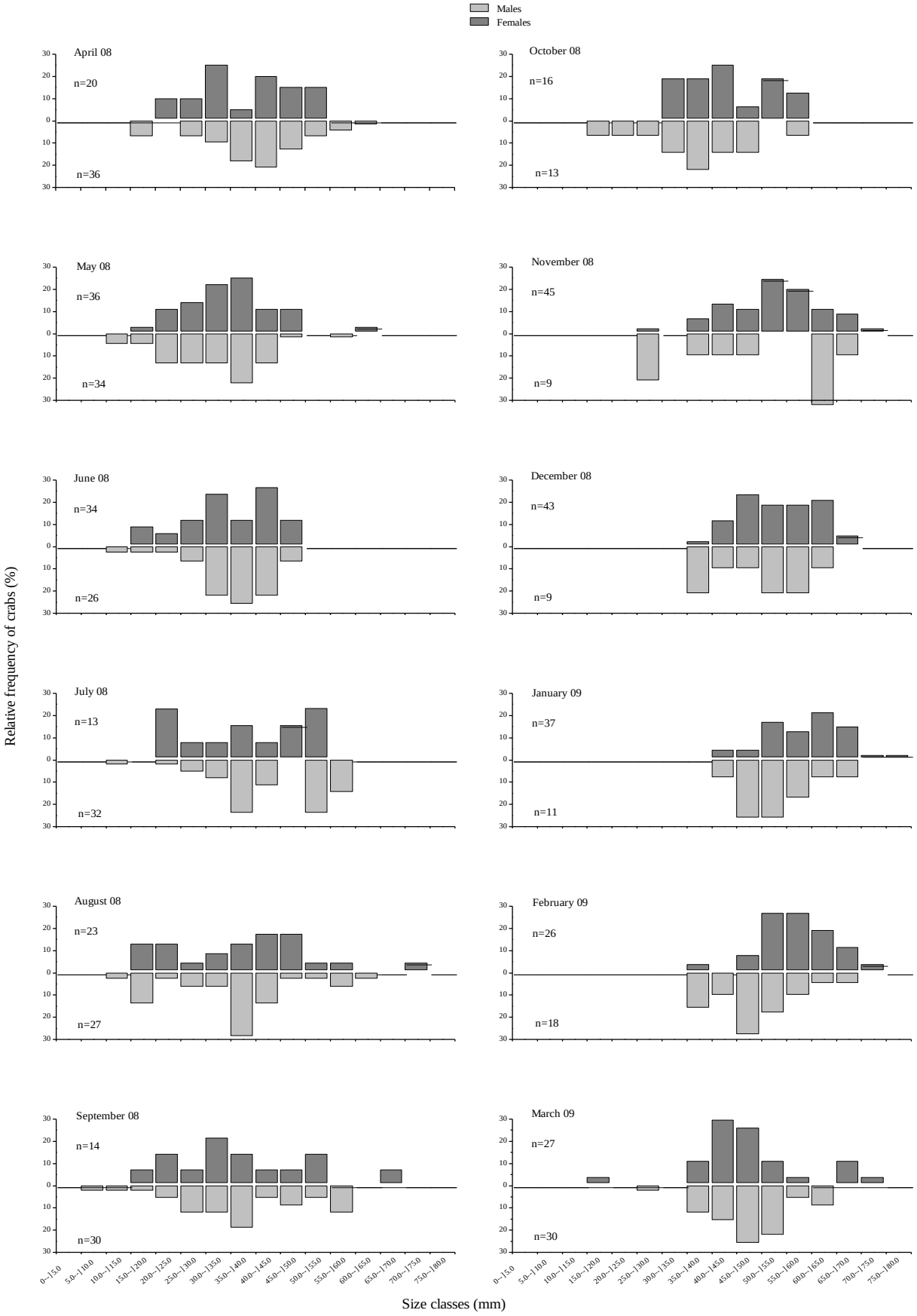


Figure 1. Total size-frequency distribution of carapace width (CW) of males and females of *Ucides cordatus* sampled at Ariquindá (A) and Mamucabas (B) mangroves, state of Pernambuco, Brazil.

The carapace width (CW) of male crabs ranged from 15.08 to 79.1 mm (mean ± SD: 46.69 ± 13.58 mm), and that of females from 9.32 to 67.89 mm (39.94 ± 12.52 mm) in Ariquindá. At Mamucabas, the carapace width of males ranged from 12.98 to 79.5 mm (45.68 ± 12.93 mm), and that of females from 10.59 to 61.78 mm (40.20 ± 10.35 mm). With respect to wet weight, male crabs from Ariquindá showed a range of 1.5 to 185.09 g (55.72 ± 39.90 g), and for females the range was 0.80 to 130.79 g (35.99 ± 25.98 g). At Mamucabas, the mean weight of males was 51.91 ± 36.76 g, ranging from 1.0 to 188.17 g; the females showed a mean weight of 34.26 ± 21.46 g, ranging from 1.0 to 105.8 g. Males were significantly larger and heavier than females in both populations (carapace width – Ariquindá t= 6.65 and Mamucabas t= 6.65; weight – Ariquindá t= 6.86 and Mamucabas t= 7.47; p<0.05). However, the mean size of males and females did not differ between the two populations (p>0.05) (males: t= 1.05 and females: t= -0.27). The mean weight of males and females was also similar in the Ariquindá and Mamucabas populations (p>0.05) (males: t= 0.86 and females: t= 1.33).



Figurre 2. Monthly size-frequency distributions of *Ucides cordatus* from Ariquindá River mangrove, state of Pernambuco, Brazil.

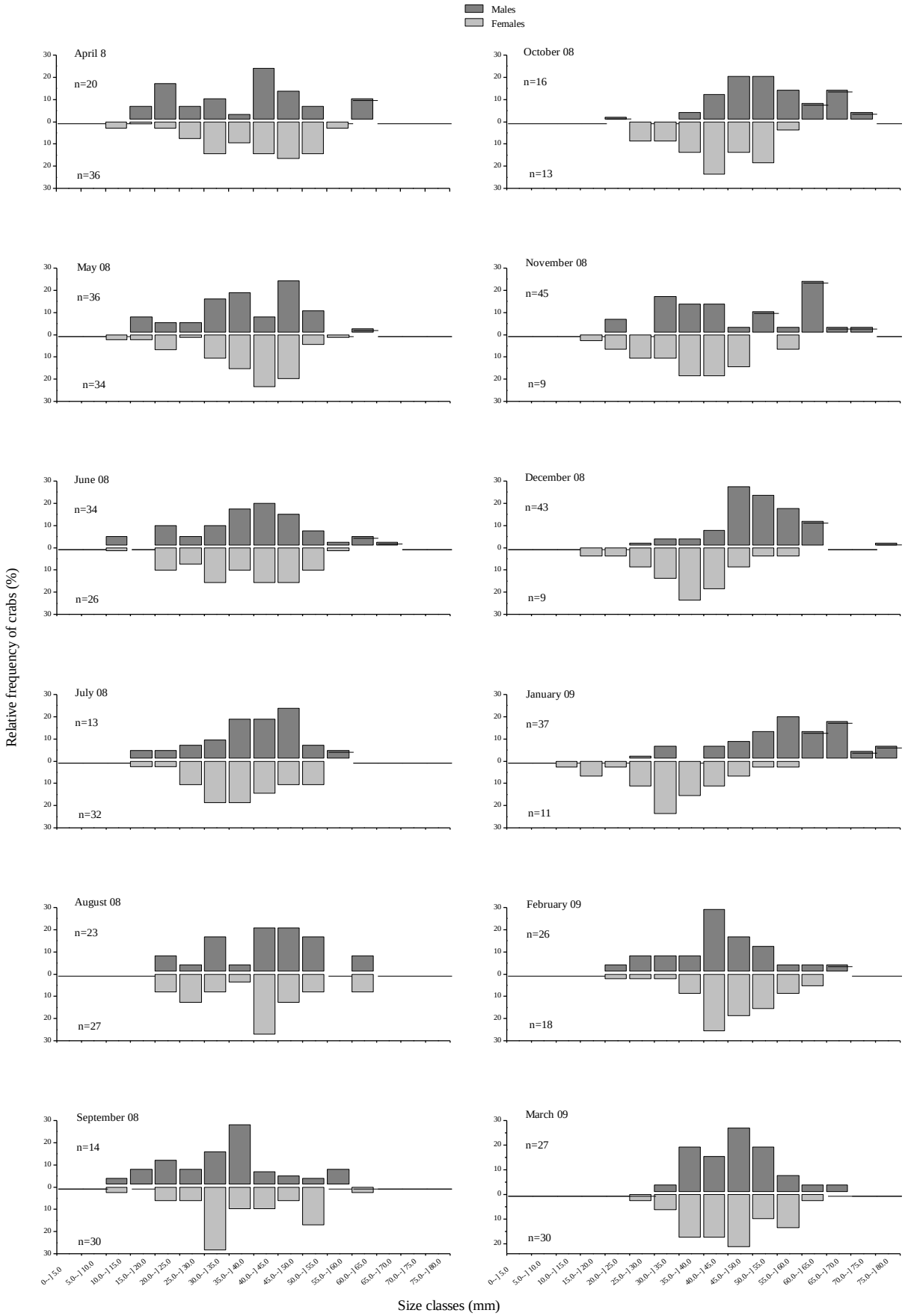


Figure 3. Monthly size-frequency distributions of *Ucides cordatus* from Mamucabas River mangrove, state of Pernambuco, Brazil.

The overall sex ratio was 1.21:1 (males: females) and differed significantly from the expected 1:1 proportion; males were more abundant than females in both populations ($p<0.05$; Ariquindá $\chi^2= 5.72$; Mamucabas $\chi^2= 6.93$). The analysis of monthly sex ratios showed that males were more frequent than females in November 2008 ($\chi^2= 24.0$), December 2008 ($\chi^2 = 22.23$), and January 2009 ($\chi^2= 14.08$), and females were more abundant in April ($\chi^2= 4.57$), July ($\chi^2= 8.02$), and September 2008 ($\chi^2= 5.82$) ($p<0.05$) (Table I) in Ariquindá. In the Mamucabas River mangrove, males of *U. cordatus* were more frequent than females in July 2008 ($\chi^2= 4.31$), October 2008 ($\chi^2= 12.19$), December 2008 ($\chi^2= 35.53$), and January 2009 ($\chi^2= 39.34$), and females were found in greater abundance than males only in May 2008 ($\chi^2= 18.89$) ($p<0.05$) (Table II).

With respect to seasonal changes in sex ratio, males were more abundant than females in spring and summer in both Ariquindá (spring $\chi^2= 39.47$ and summer $\chi^2= 12.09$) (Figure 4a) and in Mamucabas (spring $\chi^2= 33.80$ and summer $\chi^2= 8.42$) (Figure 4b) ($p<0.05$). The females were significantly more frequent in winter in Ariquindá ($\chi^2= 10.94$) (Figure 4a) and autumn in Mamucabas ($\chi^2= 12.85$) (Figure 4b) ($p<0.05$). Males predominated in the upper size classes in both populations ($p<0.05$) (Figure 5). In the smaller size classes (<45.0 mm), the sex ratio showed no differences ($p>0.05$), or females were more frequent than males ($p>0.05$) (classes: 10.0–| 15.0 mm $\chi^2= 9.0$ and 35.0–| 40.0 mm $\chi^2= 7.02$) (Figure 5a). However, in the smaller size classes (<55.0 mm) the sex ratio was equal and did not deviate from the expected ratio of 1:1 in the Mamucabas population ($p>0.05$) (Figure 5b).

Ovigerous females occurred only in summer and autumn (February through April) (Table I), indicating a seasonal reproduction for *U. cordatus*, but with greater intensity in summer ($p<0.05$) for both populations (Figure 6).

Juveniles occurred year-around, with the highest frequency in the autumn and winter for both populations, probably to reproductive activity in the summer and autumn (Figure 7). The juveniles that were found in spring and summer were probably recruited in the breeding season of the previous year.

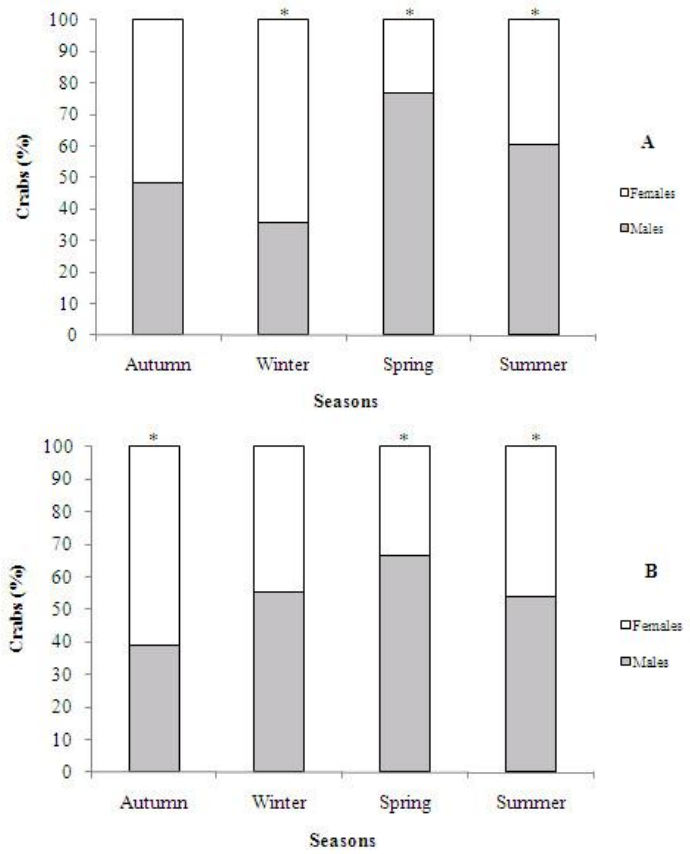


Figure 4. Sex ratio by season of *Ucides cordatus* sampled in the Ariquindá (A) and Mamucabas (B) mangroves, state of Pernambuco, Brazil. * above a column indicates a significant difference in the proportion of males and females ($p<0.05$).

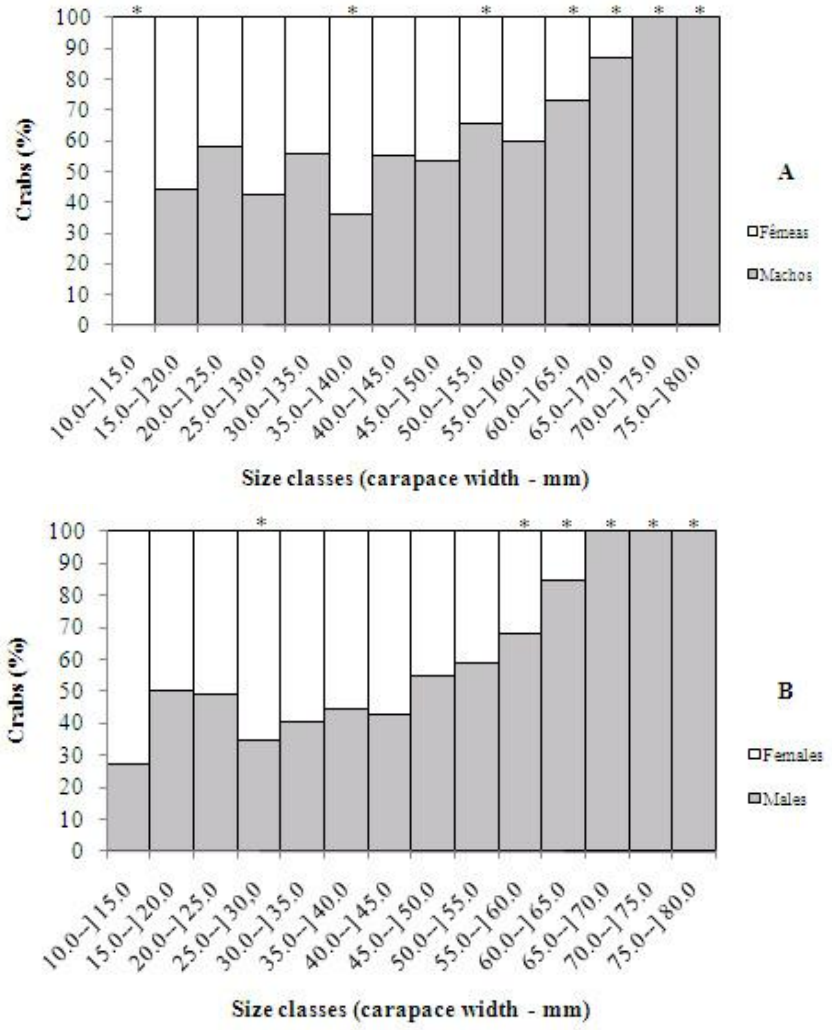


Figure 5. Sex ratio by size class of carapace width of *Ucides cordatus* sampled in the Ariquindá (A) and Mamucabas (B) mangroves, state of Pernambuco, Brazil. * above a column indicates a significant difference in the proportion of males and females ($p<0.05$).

Discussion

The size-class frequency distribution of a population is a dynamic characteristic that can vary throughout the year, as a result of rapid reproduction and recruitment of larvae and juveniles, and also because of the death of individuals (Thurman 1985, Díaz & Conde 1989). The unimodal size-class frequency distribution of the carapace width for males and females of *U. cordatus* in the Ariquindá and Mamucabas mangroves may indicate that these populations are stable, with continuous recruitment and constant mortality rates over the life cycle (Díaz & Conde 1989, Hartnoll & Bryant 1990). Polymodal populations are composed of various age groups, probably resulting from migration, differential mortality, slow rates of growth in mature or immature stages, or pulses of recruitment (Díaz & Conde 1989, Yamaguchi 2001). Unimodality was also observed by Alves & Nishida (2004) for a population of *U. cordatus* from a mangrove area in the state of Paraíba; by Monteiro & Coelho-Filho (2004) for a population in Itamaracá, Pernambuco; and by Diele *et al.* (2005) for a population in the state of Pará.

The mean density of *U. cordatus* in the Tamandaré mangroves was similar to the density estimated by Ivo *et al.* (2000) in the estuaries of the Rio Formoso and Ilhetas (0.73 indiv.m^{-2}), both also located in the municipality of Tamandaré. The mean density of *U. cordatus* on the mangrove coast of Pernambuco was lower compared to mangroves in other regions of Brazil (1.1 indiv.m^{-2} in Itacorubi, state of Santa Catarina, found by Branco, 1993; 1.45 ± 0.5 indiv.m^{-2} in Caeté Estuary, Pará, by Diele *et al.* 2005; and 2.05 ± 1.00 indiv.m^{-2} in Babitonga Bay, state of Santa Catarina, according to Wunderlich *et al.* 2008). This comparatively low density of crabs in the Ariquindá and Mamucabas mangroves probably results from more intense exploitation of *U. cordatus* for consumption by coastal residents and

tourists visiting the region. Furthermore, the crab density was higher in Mamucabas mangrove, despite this area being impacted when compared to longer Ariquindá.

The populations of *U. cordatus* from Ariquindá and Mamucabas were similar in body size and weight. Males were significantly larger and heavier than the females; and the populations were very uniform, with no difference in size and weight. Botelho *et al.* (1999), studying two different populations of *U. cordatus*, also from Tamandaré, and Araújo & Calado (2009) in Manguaba (state of Alagoas) did not observe sexual dimorphism. On the other hand, several studies on *U. cordatus* in other mangrove areas in Brazil did find sexual dimorphism, with the males being larger than the females (Alcantara-Filho 1978, Vasconcelos *et al.* 1999, Alves & Nishida 2004, Monteiro & Coelho-Filho 2004, Dalabona & Loyola-Silva 2005, Wunderlich *et al.* 2008). According to Costa & Soares-Gomes (2009), males use the largest part of their energy for body growth and growth of the chelipeds, which makes them more attractive to females and more likely to succeed in intraspecific competitions with other males, thus increasing their chances of mating. The crab's size difference between sexes appears to be related to a rapid growth rate or a longer growth period in males. Females direct a large part of their energy reserves to gonad development and support of the egg mass during the incubation period, when the females interrupt their somatic growth (Warner 1967, Díaz & Conde 1989, Hartnoll, 2006).

Dominance of male crabs, as observed in the two mangrove areas, was also reported for other *U. cordatus* populations on the Brazilian coast (Monteiro & Coelho-Filho 2004, Alves & Nishida 2004, Diele *et al.* 2005). Biological features such as differential growth and mortality rates, spatial and temporal distribution, differential gamete production, different maximum sizes, and longevity all influence the sex ratio (Wenner 1972, Johnson 2003). Deviations in sex ratio may also result from reproductive migration and behavioral differences between males and females, especially during the growth and reproductive cycles, when both males and females burrow deeply and are difficult to catch (Margalef 1977, Costa 1979).

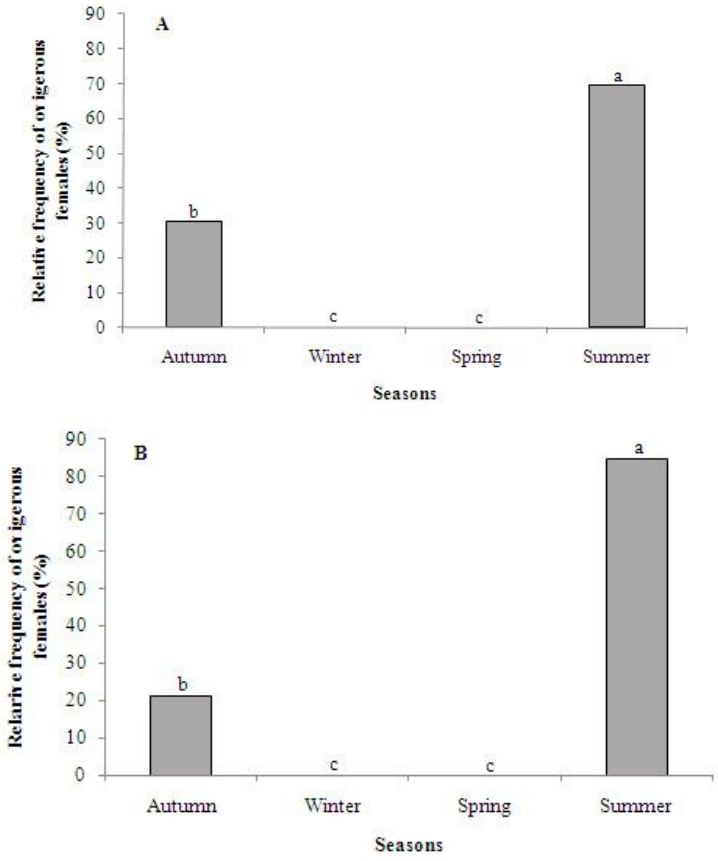


Figure 6. Relative frequency (%) of ovigerous females of *Ucides cordatus* during the sampling period in the Ariquindá (A) and Mamucabas (B) mangroves, state of Pernambuco, Brazil. Bars with at least one letter in common do not differ significantly ($p>0.05$).

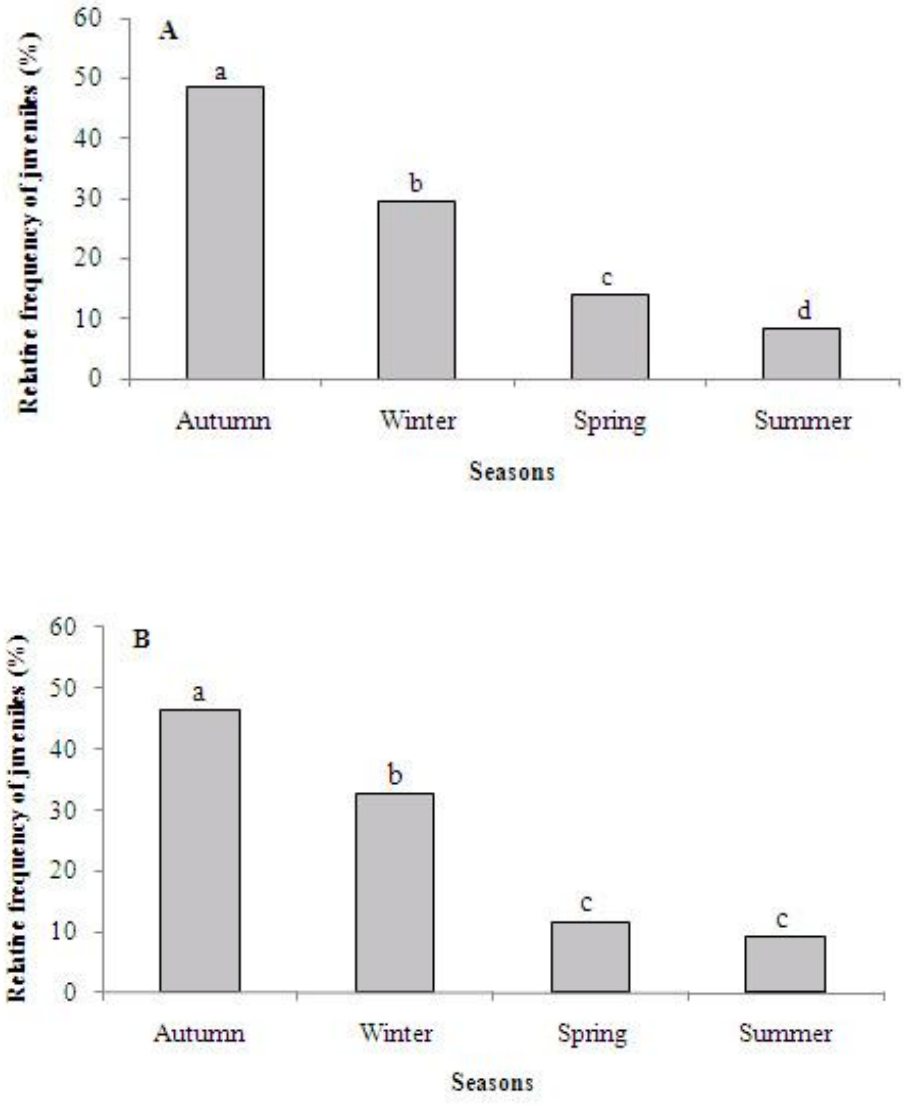


Figure 7. Relative frequency (%) of juveniles of *Ucides cordatus* over the sampling period in the Ariquindá (A) and Mamucaas (B) mangroves. Bars with at least one letter in common do not differ significantly ($p>0.05$).

In the analysis of seasonal sex ratio, males of *U. cordatus* were more abundant than females in summer and spring; inversely, females were more frequent in autumn (Mamucabas) and winter (Ariquindá). Females of *U. cordatus* remain in their burrows during the breeding season (spring and summer), which probably explains their lower catch rate during these seasons. This may be related to the large energy investment in reproduction, because while females are incubating eggs, somatic growth, which is antagonistic to reproductive events, ceases and consequently delays their growth (Adiyodi & Adiyodi 1970). The predominance of males in the largest size classes also shows that in brachyuran crustaceans, growth and reproduction are antagonistic processes competing for the same energy resources. Probably more energy is allocated to reproduction in females, and more energy is needed for the production of oocytes than for spermatocytes (Hartnoll 1985, 2006). Moreover, when the females reach sexual maturity, they direct their energy reserves toward the production and release of eggs, thereby reducing or suspending their growth during the incubation period (Alunno-Bruscia & Sainte-Marie 1998, Hartnoll 1985, 2006). A predominance of males in the upper size classes was also observed for a population of *U. cordatus* from Caeté in Pará, northern Brazil (Diele *et al.* 2005).

Reproductive intensity in brachyuran can be measured by assessing the relative frequency of ovigerous females in the population throughout the

year. The beginning and the duration of the reproductive period are dependent on the occurrence of favorable environmental conditions (Sastry 1983). The presence of ovigerous females at certain times of year may be related to temperature, day length, availability of food for larvae, rainfall, and photoperiod (Thorson 1950, Sastry 1983, Meusy & Payen 1988, Zimmerman & Felder 1991). The ovigerous females of *U. cordatus* occurred in the warmer months, which probably minimizes the duration of the embryonic/larval stages and predation on the planktonic stages (Morgan 1996, Morgan & Christy 1996). As reported by Mota-Alves (1975), a population of *U. cordatus* from a mangrove in Ceará reproduces between January and May, which suggests a seasonal recruitment in summer and autumn. In other mangrove areas of Brazil, the reproduction of *U. cordatus* is also seasonal, occurring during the warmer or rainy months of the year (Botelho *et al.* 1999, Ivo *et al.* 1999, Diele 2000, Monteiro & Coelho-Filho 2004, Dalabona & Loyola-Silva 2005, Wunderlich *et al.* 2008, Araújo & Calado 2009).

This crab population received recruits throughout the year, but more intensely during certain months, indicating a seasonal recruitment. Many brachyurans in temperate regions follow a seasonal reproductive cycle, mainly during spring and summer, when the environmental conditions are more favorable for survival (Sastry 1983, Ramirez-Llodra 2002, Litulo 2006). This results in a higher incidence of juveniles in the population during the colder months of the year, as observed for *U. cordatus* in this study, and also for other mangrove crab species (Costa & Negreiros-Fransozo 2003, Castiglioni *et al.* 2006, Litulo 2006, Hirose & Negreiros-Fransozo 2008, Mokhtari *et al.* 2008).

The mangroves studied here differ in the degree of human pressure: the mangrove of Mamucabas is more impacted than Ariquindá, not only by overfishing during the summer in parts the study area, as mentioned by Botelho *et al*. (1999), but also by environmental impacts from other activities, for instance, discarding waste (personal observation). The results obtained here suggest despite of difference in the level of pressure from human activities between the analyzed areas, both populations of *U. cordatus* seem to be stable, showing very similar population biology, mainly with respect to the larger size and weight of males, reproductive period, and seasonal recruitment. These aspects are also similar to other populations from northeastern Brazil (Alcântara-Filho 1978, Botelho *et al*, 1999, Monteiro & Coelho-Filho 2004, Araújo & Calado 2009).

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