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STATUS OF THE POPULATION STRUCTURE OF THE MANGROVE CRAB *UCIDES CORDATUS* (DECAPODA: OCYPODIDAE) ON THE PIRAQUÊ-AÇU RIVER ESTUARY, ESPÍRITO SANTO, BRAZIL

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ABSTRACT

The land crab *Ucides cordatus* is a keystone species of neotropical mangrove forests and an important resource of the artisanal fisheries. The spatial and temporal distribution of *U. cordatus* in the mangrove area of the Piraquê-açu river estuary was determined following a longitudinal estuarine salinity gradient (lower, middle, upper estuary) and along the vertical intertidal gradient. The numbers of open and closed burrows were counted monthly on fixed transects, the inhabiting crabs were caught, sexed and the carapace width measured, during 1 year. The mean crab density was 2.5 ind.m^{-2}. The highest crab density (3.9 ind.m^{-2}), linked to high numbers of juvenile crabs, was found on the upper estuary and correlated with lower salinities. High intertidal levels had higher crab densities than lower intertidal levels, except in the upper estuary. Males were smaller than females; the mean carapace width of the population was 4.89 cm, below the minimum legal harvesting size (6 cm). The predominance of females over males at some sites (especially close to villages) brought out the advanced level of overfishing of this *U. cordatus* population and highlights the urgent need of management actions.

RESUMO

O caranguejo *Ucides cordatus* é uma espécie chave nos manguezais da região neotropical e um importante recurso pesqueiro para populações tradicionais. A distribuição espacial e temporal de *U. cordatus* no manguezal do Rio Piraquê-açu foi estudada ao longo de um gradiente de salinidade, no estuário inferior, médio e superior na faixa entre-marés. Mensalmente durante um ano. O número de tocas abertas e fechadas ao longo de transectos fixos, foi contado mensalmente, ao longo de um ano, e os caranguejos capturados foram sexados e medidos quanto à largura da carapaça, sendo posteriormente liberados. A densidade média de caranguejos foi de 2,5 ind.m^{-2}. A maior densidade (3,9 ind.m^{-2}), juntamente com o maior número de jovens, foi encontrada na parte superior do estuário, correlacionada com baixas salinidades. Nos níveis mais altos de maré a densidade de caranguejos sempre foi alta, exceto na região superior do estuário. Os machos foram menores do que as fêmeas; o tamanho médio da carapaça da população total foi de 4,89 cm, abaixo do tamanho legal permitido para captura (6 cm). A predominância de fêmeas sobre machos em alguns pontos, principalmente próximos às vilas, revela o avançado nível de sobreexplotação da população de *U. cordatus*, evidenciando a necessidade urgente de ações fiscalizadoras.

Descriptors**:** Mangrove crab, Estuarine salinity gradient, Brazilian mangrove forests, Intertidal distribution.
Descritores**:** Caranguejo de mangue, Gradiente estuarino de salinidade, Manguezais brasileiros, Distribuição no entremarés.

INTRODUCTION

The semi-terrestrial crab *Ucides cordatus cordatus* (Linnaeus, 1763) is one of the most abundant species of Brazilian mangrove crabs, representing up to 76% of the benthic biomass in these mangrove ecosystems (KOCH and WOLFF, 2002). Endemic from Florida (USA) to the South Brazilian coast, this species exhibits territorial behaviour, living in individual burrows up to 2 meters deep (COSTA, 1979; KOCH and WOLFF, 2002). *U. cordatus* play a very important ecological role in mangrove areas, because its burrow activity is essential for soil drainage and aeration, and nutrient exchange between water and sediments (COSTA, 1979; MICHELI, 1993; NORDHAUS *et al.*, 2006). The litter consumption by this crab accelerates nutrient cycling and represents an important input in mangrove productivity, through nutrient retention (MACINTOSH, 1988; LEE, 1998; KOCH and WOLFF, 2002; NORDHAUS *et al.*, 2006). Many authors have considered *U. cordatus* a keystone species for Brazilian mangrove forests due to its important ecological role in the mangrove ecosystems (SCHORIES *et al.*, 2003; DIELE *et al.*, 2005).

Besides its ecological importance, *U. cordatus* represents a valuable fishery resource, exploited by local fishermen, both for their subsistence and also as a cash income source (CASTRO, 1986; HATTORI and PINHEIRO, 2003; SCHORIES *et al.*, 2003; ALVES *et al.*, 2005). Nowadays, the strong human pressure on natural populations due to uncontrolled catches, habitat destruction or diseases (BOEGER *et al.*, 2005) can cause a decrease in the stock size, the consequences of which have been but little studied. Estimates of the population density of *U. cordatus* in Brazilian mangrove forests differ significantly between studies: ALCÂNTARA-FILHO (1978) found 4.75 ind.m^{-2} on the northeastern coast (Ceará river) while BRANCO (1993) registered 1.1 ind.m^{-2} in South Brazil, but differences in crab densities may be related to primary productivity, patterns of larval recruitment, level of crab exploitation, or even to their catchability, as the methods used by each researcher may vary greatly. In spite of the importance of *U. cordatus* to the ecosystem as well as to artisanal fishery, there are few studies focusing on the population ecology of this species in Southeastern Brazil (GÓES, 2003).

The aim of this study was to determine the spatial and temporal distribution of *U. cordatus* in a tropical estuary, along a salinity gradient (lower, middle and upper estuary zone) and along the intertidal level of air exposure (low, medium and high intertidal level) on the Piraquê-açu river estuary, in Southeastern Brazil.

MATERIAL AND METHODS

Study Area

The study was undertaken along the Piraquê-açu river estuary (19º 54’ S; 40º 10’ W), in the municipality of Aracruz, Espírito Santo State, Southeastern Brazil (Fig. 1). This estuary is part of a complex estuarine system that is linked to the Piraquê-mirim river. It presents a luxuriant mangrove forest (1,234 ha), dominated by the red mangrove *Rhizophora mangle* bordering the channel (forming an almost monospecific fringe, that delimits the aquatic and intertidal domains, representing 60% of the floristic composition, with densities of 11.72 ind/m^2, *Laguncularia racemosa* with 32.7% of arboreal species (6.44 ind/m^2), dominating the upper estuary, and the black mangrove *Avicennia schaueriana* only on the lower and middle estuary, with 7.3% of mangrove trees (1.44 ind/m^2). The total average height of the trees was 6.63 m (± 2.9 m) and the average DAP was 8.88 cm (±7.8 cm) (DEPIZZOL et al, unpublished ms.). The mean tidal range is 0.8 m but semidiurnal spring tides can exceed 2 m. Mean annual rainfall is 1,309 mm (ANA, 2006), with a rainy season between October and March. Estuarine stratification is weak, due to low volumes of freshwater input (MAGRIS and LOUREIRO-FERNANDES, 2005).

From Setember/2004 to August/2005, three sites were randomly established along the Piraquê-açu river estuary, following a salinity gradient (lower, middle and upper estuary). Site 1 (T1) was located near the river mouth (lower estuary, with 306 m of intertidal flooded extension, with the 3 species of mangrove tree, *A. schaueriana* being the tallest one, up to 7.7 m high, though numerically less frequent), Site 2 (T2), located in the middle zone (159 m in extent, in the vicinity of a small fishing village, *R. mangle* being the tallest tree, 7.6 m in height, and numerically dominant, just as in T1). Site 3 (T3) was in the upper estuarine zone (with 115 m of intertidal flooded extension, dominated by *L. racemosa* of 6.6 m high, with some *R. mangle* of 12.1 m high) (DEPIZZOL et al, unpublished ms.) (Fig. 1). At each site, one fixed transect perpendicular to the river, ranging from the lower to upper intertidal level was marked out by a rope. On each transect, three plots of 10 m^2 each (1 m x 10 m, subdivided into subplots of 1 m^2) were delimited within the intertidal zone: the first plot was close to the channel (F1), the second at the mean intertidal level (F2) and the third on the higher intertidal level (F3), locally called “apicum” (Fig. 1).

Environmental Parameters

Monthly, during the low spring tides, the air temperature (in the shade), the surface sediment and crab burrow water temperatures were determined with a thermometer. Water samples from open and sealed crab burrows were collected for laboratory analysis of salinity and pH, with a refractometer and peagameter. A sample of the sediment (100 g) from each plot and site was analyzed for particle size composition and organic matter contents, after being dried at 60ºC and sieved through granulometric meshes (500, 250, 125 and 62.5 µm) and weighed. The organic matter content of each sample was determined by burning 5g of the sediment in an oven (550ºC for 2 h). The organic matter content was determined as the difference in weight before and after incineration.

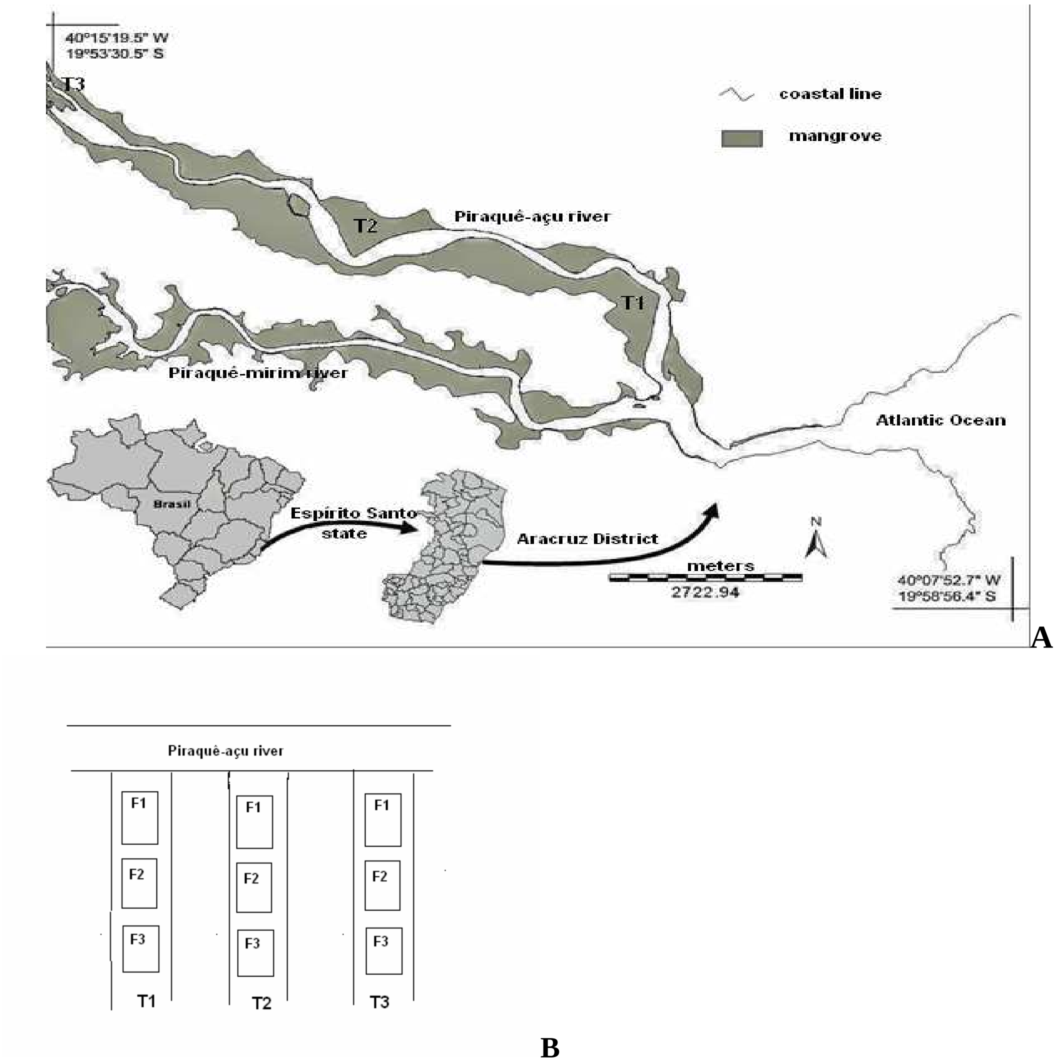

Fig. 1. A: Location of sampling sites on the Piraquê-açu river estuary (Aracruz), Espírito Santo, Brazil. T1, T2 and T3 indicate the study sites, in the lower, middle and upper estuary, respectively. B: Diagram showing the 3 estuarine sites with the distribution of mangrove intertidal levels sampled.

Crabs and Burrow Samplings

Monthly samplings were taken at each intertidal level and site during diurnal low tides. Empty burrows were not registered. All crabs caught had their carapace width measured with a vernier caliper and sex determined according to the abdominal morphology (PINHEIRO *et al.*, 2005). The crabs were released after measurement. Specimens > 4.5 cm of carapace width were considered adults (SAMPAIO, 2002). All the *Ucides cordatus* and their burrows (open or sealed) were counted. To determine the crab density (ind./m^2), each burrow (open or sealed) was considered as being inhabited by a single crab (COSTA, 1979; ALVES *et al*. 2005). The presence of ovigerous females was also registered, so that the reproduction period of *U. cordatus* in our study area could be determined.

Statistical Analysis

We used three-way analyses of variance (ANOVA) to test whether environmental parameters (salinity, pH, temperatures of air, sediment and burrow water), the number of crab burrows, juveniles, adults and ovigerous females differed among estuarine sites and intertidal levels over the year. The Tukey test was used for post-hoc comparisons (Zar, 1996). Student t-test was used to compare the numbers of juveniles and adults at the three estuarine sites and intertidal levels. The χ^2 test was used to test whether the male:female proportion differed from 50:50. Pearson´s correlations were used to test for linear relationships among environmental parameters and the number of juveniles and adults and the total number of crab burrows.

RESULTS

Environmental Parameters

Minimum and maximum temperatures were recorded in July (air: 22.7ºC, sediment: 22.6ºC, burrow water: 22.4ºC) and March, respectively (air: 27.7ºC, sediment: 28.3ºC, burrow water: 27ºC). In any given month the temperatures were similar among sites. The upper intertidal levels always had the highest air and sediment temperatures (Table 1). Burrow water temperatures exhibited smaller annual variations than did the air temperature (Table 1 and 2).

The lowest burrow water salinities were verified in February at the lower estuarine site T1: 16‰ (± 4), in March at T2: 3‰ (± 1) and from February to July at the upper estuarine T3, when salinity was 0‰. The highest values occurred in September at T1: 41 (± 8) and T3: 18 (± 1), and in October at T2: 29 (± 1). These salinities varied significantly over the months ($p < 0.01$; Table 2). The salinities of channel water and burrow water also varied significantly ($p < 0.001$) among the three sites; the highest values being registered at T1, decreasing towards the upper estuary (T3) (Table 1 and 2), revealing that the three areas are clearly different and exhibit a salinity gradient. When considering the intertidal zone, higher salinity and range occurred at the upper intertidal level of T1 ($p < 0.05$) (Table 1 and 2). The highest temperatures reflect the highest potential for evaporation.

Crab burrow waters tended to be acid, mainly in September, with the lowest value (5.7 ± 0.66) at T3 (Table 1), the highest pH occurring in March (7.5 ± 0.43). The channel water pH was significantly different among transects ($p < 0.05$) (Table 2). The burrow water pH was significantly different ($p < 0.001$) over the months and transects, but there were no differences among intertidal levels (Table 2).

The sediment was predominantly sandy mud in all samples, with at least 56% of sand, except at the medium intertidal level of T2, with 18% of sand, with no differences in sand percentage detected ($p > 0.05$). The organic matter in the sediment varied from 7.8 to 24.5%, with no spatial differences (Table 1 and 2).

Table 1. Range (minimum-maximum) of environmental parameters of air, water and sediment of the mangrove sites of the Piraquê-açu river estuary, Espírito Santo, Brazil. Samples from September/2004 to August/2005.

Estuarine sites	**Lower (T1)**			**Middle (T2)**			**Upper (T3)**		
	Intertidal levels								
	Low (F1)	Medium (F2)	High (F3)	Low (F1)	Medium (F2)	High (F3)	Low (F1)	Medium (F2)	High (F3)
Temperature (ºC) Air	21.2 – 27	21.7 - 28.3	22.3 - 31.3	20.8 - 28	21.5 - 27.7	21.8 - 29.7	20.3 - 30.3	20 - 31.2	20.7 - 32.7
Sediment	22.1 - 27.8	23 - 29.3	22.8 - 29.6	21.4 - 28.2	21.8 - 28.3	23.8 - 30.3	21.7 - 29.4	22.2 - 28.5	22.8 - 29.8
Burrow water	21.8 - 26.9	22.3 - 27.7	22.8 - 28.3	21.6 - 27.1	21.2 - 27.8	23.5 - 28.9	22.2 - 28.6	22.3 - 28.3	22.3 - 28.5
Salinity channel	0 - 34.3			0 - 26.3			0 - 7		
Burrow	17.8 - 37.1	10.6 - 37.4	19.8 – 49.9	3 - 28.3	2.6 - 28.1	1.7 - 30.7	0 -19.5	0 - 17.3	0 - 17.8
pH channel	5.9 - 7.9			6.8 - 7.6			5.7 - 7.9		
Burrow	6.2 – 8	5.9 - 7.8	5.9 - 7.9	5.7 - 7.8	6.4 - 7.8	6.4 - 7.8	3.9 - 7.9	4.8 - 7.9	5.3 - 7.9
OrganicMatter of sediment (%)	20.9	24.5	12.8	17.6	18.2	14.7	15.6	15.7	7.8
Sand (%)	67	72	66	57	18	69	56	81	82
Silt/clay (%)	33	28	34	43	82	31	44	19	18

Table 2. Results of 3-way ANOVA and Tukey´s test for the environmental parameters from the sites (T1, T2 and T3) and intertidal levels (F1, F2 and F3) of Piraquê-açu river estuary, Espírito Santo, Brazil.
NS = not significant

Variable	Source of Variability		*F*	*P* (<0.05)	interaction	Tukey's Test
Air	Site		0.335	NS	Site* level NS	
Temperature		T1	3.842	<0.05		F1=F2; F2=F3
					Site* Month	
	Level	T2	0.487	NS	NS	
		T3	0.081	NS	Level*	
						Jun Jul Aug Sep Oct Nov Feb Apr May Dec Jan Mar
	Month		6.110	<0.001	Month NS	
Sediment	Site		0.625	NS	Site* level NS	
		T1	1.837	NS		
Temperature	Level	T2	4.161	<0.05	Site*	F1=F2; F2=F3
		T3	0.762	NS	Month NS	
						Jul Jun Sep May Aug Oct Nov Dec Feb Apr Jan Mar
					Level*	
	Month		14.074	<0.001	Month NS	
					Site* level	
Water	Site		1.404	NS	NS	
temperature						
of		T1	0.813	NS		
	Level	T2	2.159	NS	Site*	
Crab burrow		T3	0.488	NS	Month NS	
						Jul Jun Sep May Aug Nov Oct Feb Apr Dec Jan Mar
					Level*	
	Month		21.020	<0.001	Month NS	
Water salinity of river	Site		14.456	<0.001	Site*month	T1≠T2≠T3
Channel	Month			NS	NS	
Water salinity	Site		89.375	<0.001	Site* level NS	T1≠T2≠T3
		T1	4.325	<0.05		F1=F2; F1=F3
of crab burrow	Level	T2	0.009	NS	Site*	
		T3	0.029	NS	Month NS	
						Jun Feb Mar Apr Jan May Jul Aug Dec Nov Sep Oct
					Level*	
	Month		2.733	<0.01	Month NS	
Water pH of	Site		4.403	<0.05	Site*month	T1=T2; T1=T3
River channel	Month		1.329	NS	NS	
water pH of	Site		14.366	<0.001	Site* level	T1=T2
		T1	0.895	NS	NS	
Crab burrow	Level	T2	0.104	NS	Site*	
		T3	0.636	NS	Month NS	
						Sep Oct Nov Dec Jan Jul Aug Feb Apr Jun May Mar
					Level*	
	Month		5.608	<0.001	Month NS	
% of sand	Site		1.695	NS		
% of silt-clay	Site		1.695	NS		
% of organic matter of sediment	Site		1.540	NS		

Burrow Density

A total of 7,996 crab burrows were counted. Open burrows predominated from September to April, when the crabs were also more frequent; sealed burrows dominated from May to August, when crabs c hange their carapace and are soft (Fig. 2). The majority of burrows were registered in the upper estuarine area T3: 52.3%, while the lower areas T1 and T2 had 24.7% and 23%, respectively. Assuming that each burrow (open or sealed) was inhabited by a single crab, the mean crab density in the mangrove forest of the Piraquê-açu river estuary was 2.5 (± 1.2) ind.m^{-2}. T3 had a significantly higher density of crabs than T1 and T2 (p < 0.001) (Table 3). The high intertidal levels of T1 and T2 had higher numbers of crabs (p < 0.001), while at T3 the crabs were equally abundant throughout the intertidal zone. The number of burrows was negatively correlated with burrow water salinity (ρ = -0.275; p < 0.01) and with pH (ρ = -0.389; p < 0.001) but a positive correlation was found with air temperature (ρ = 0.232; p < 0.05).

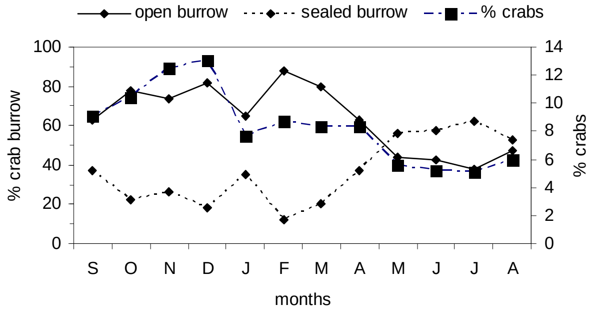

Fig. 2. Relative abundance of opened and sealed crab burrows and the total number of captured mangrove crabs *Ucides cordatus* on the Piraquê-açu river estuary, Espírito Santo, Brazil, from Setember/2004 to August/2005.

Table 3. Results of 3-way ANOVA and Tukey's test for total number of crab burrows, total number of crab juveniles and adults and ovigerous females at the sites (T1,T2 and T3), intertidal levels (F1, F2 and F3) and by month in the Piraquê-açu river estuary, Espírito Santo, Brazil. NS = not significant

Variable	Source of variability		*F*	*p*<0.05	Interaction	Tukey's test
Number of	Sites		36.835	<0.001	Site*level NS	T1=T2
Burrows		T1	28.587	<0.001		F1≠F2≠F3
	Level	T2	31.861	<0.001	Level*months NS	F1≠F2≠F3
		T3	3.013	ns		
	Months		0.528	ns	Months* sites NS	
Total of	Sites		7.504	<0.01	Site*level NS	T1=T3
Juvenile		T1	30.662	<0.001	Level*months NS	F1=F2
Crabs	level	T2	5.620	<0.01	Months* sites NS	F1=F2; F1=F3
		T3	9.869	<0.001		F2=F3
	Months		0.484	NS		
	Sites		8.405	<0.001	Site*level NS	T1=T2; T2=T3
Total of adult		T1	16.743	<0.001	Level*months NS	F1≠F2≠F3
Crabs	Level	T2	7.421	<0.01	Months* sites NS	F2=F3
		T3	0.236	NS		
	Months		1.602	NS		
Total of	Sites		1.047	NS	Site*level NS	
Ovigerous		T1	3.415	<0.05	Level*months NS	F1=F2; F2=F3
Females	Level	T2	2.341	NS	Months* sites NS	
		T3	2.615	NS		
					Sep Oct Nov Dec Jan May Jun Jul Aug Mar Feb Apr	
	Months		2.888	<0.01		

Population Structure

A total of 1,524 crabs were caught, representing 19.1% of the total number of burrows sampled. Crabs from sealed burrows were not removed because they were soft shelled. From September to April (spring to autumn) catches were significantly higher than from May to August (ANOVA: $F_{(11;\ 96)}= 1.899$; $p < 0.05$) (Fig. 2). Considering all the crabs, the mean carapace width was 4.89 cm (± 1.43). The most abundant size class was 4.0–4.5 cm (larger juvenile crabs). Only 25.2% of the crabs had >6 cm of carapace width, the legal minimum size for harvesting (Fig. 3). Juvenile crabs were found to be more abundant in T3 and T1 (49.6% and 39.0% respectively), and significantly fewer in T2 (11.4%) ($p < 0.01$) (Table 3; Fig. 4). Significantly more adult crabs occurred in T1 (47.7%) and T2 (33.6%) (t-Student: $p < 0.05$ and $p < 0.001$) than in T3 (18.7%; t-Student: $p < 0.05$), with carapace width of 6.0-6.5 cm and 5.5-6.0 cm, respectively, more frequent. At T3, juvenile crabs dominated, more frequently with 4.0-4.5 cm of carapace width (Fig. 4). Adult crabs were significantly more abundant at the lower intertidal levels of T1 and T2 ($p < 0.01$), but on T3 adult crabs were found to be evenly distributed ($p > 0.05$), whereas juveniles were concentrated on the low intertidal levels ($p < 0.001$) (Table 3; Fig. 4).

The number of juvenile crabs was positively correlated only with air temperature ($\rho = 0.222$; $p < 0.05$), demonstrating that they occur under less dense canopy coverage, at high intertidal levels. Adult crabs were positively correlated with salinity ($\rho = 0.302$; $p < 0.01$) and organic matter content of sediment ($\rho = 0.791$; $p < 0.05$), corroborating their higher abundance near the estuary mouth and at low intertidal levels.

Male crabs with carapace width of from 4.0 to 5.0 cm were more frequent, though ranging from 0.6 cm to 8.47 cm. Female crabs ranged from 1.0 to 7.83 cm, being more common between 4.0 and 4.5 cm (Fig. 3). Only 24% and 28% of male and female, respectively, were bigger than 6.0 cm, the legal harvest size. Males were significantly smaller than females, with a mean carapace width of 4.77 cm (±1.47) vs. 4.98 cm (±1.39) for females (t-Student= -2.884; $p < 0.01$). When considering all the sites, at T2 this pattern was repeated (t-Student= -3.009; $p < 0.01$) but at T3 males were larger than females (t-Student=3.599; $p < 0.01$); at T1 there was no difference.

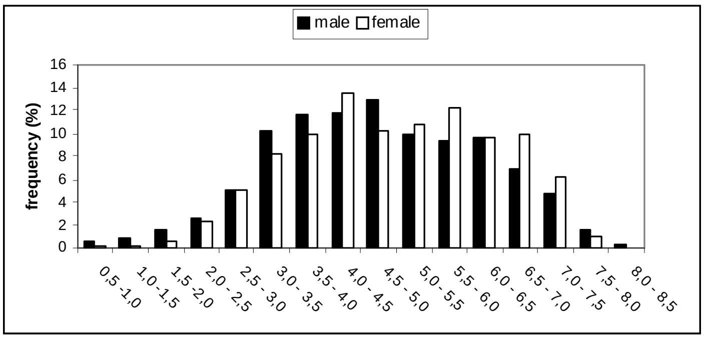

Fig. 3. Size-frequency distribution of male and female mangrove crab *Ucides cordatus* on the Piraquê-açu river estuary, Espírito Santo, Brazil.

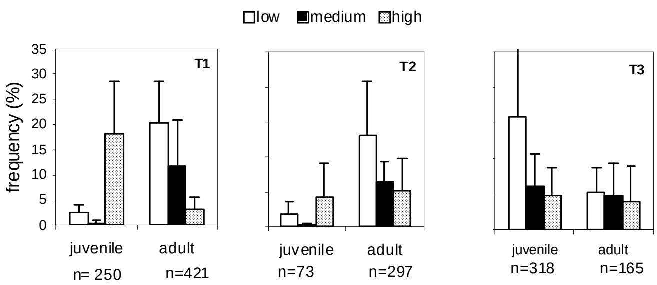

Fig. 4. Relative abundance of juvenile and adult *Ucides cordatus* crabs along the intertidal level (low, medium and high intertidal) at three sites (T1=lower estuary, T2: middle and T3: upper estuary) on the Piraquê-açu river estuary, Espírito Santo, Brazil. Juvenile crabs are < 4.5cm carapace length.

Table 4. Number of male and female crabs *Ucides cordatus*, sex-ratio and χ^2 test for crabs caught in the Piraquê-açu river estuary, Espírito Santo, Brazil. * p<0.05; ** p<0.01; *** p<0.001; NS = not significant.

Transect/Level of intertidal	Males	Females	% of males	Sex-ratio	χ^2	
T1	297	374	44.26	1:1.2	8.836	**
Low	121	154	44.00	1:1.3	3.96	*
Medium	50	92	35.21	1:1.8	12.42	**
High	126	128	49.61	1:1	0.016	NS
T2	134	236	36.22	1:1.8	28.119	***
Low	58	120	32.58	1:1.8	21.59	***
Medium	19	60	24.05	1:3.2	21.28	***
High	57	56	50.44	1:1	0.009	NS
T3	262	221	54.24	1:0.8	3.480	NS
Low	141	110	56.18	1:0.8	3.83	NS
Medium	62	67	48.06	1:1.1	0.19	NS
High	59	44	57.28	1:0.8	2.18	NS
Total	693	831	45.47	1:1.2	12.496	***

Throughout the sites, the proportion of ovigerous females was of 11, 51, 29, 45 and 8% between January and May, respectively. However, ovigerous females were more abundant at the low intertidal levels, mainly at T1 ($p < 0.05$; Table 3). The smallest ovigerous female had 3.13 cm of carapace width.

Sexual Proportion

The overall relationship between males and females was 1.0:1.2 ($p < 0.001$). Considering the three sites, females predominated over males at T1 and T2 ($p < 0.01$ and 0.001, respectively), at T3 males and females were found in equal numbers ($p > 0.05$) (Table 4). At the lower and medium intertidal levels of T1 and T2, females were significantly more abundant than males ($p < 0.01$ and $p < 0.001$, respectively). At high intertidal levels and throughout T3, males and females were equally abundant, with no significant difference ($p > 0.05$) (Table 4).

Females were significantly more abundant in the 4.0-4.5 cm, 5.5-6.0 cm and 6.5 to 7.5 cm size classes ($p < 0.05$) (Fig. 3); in the other size classes, males and females occurred in the same proportion. Females predominated over males almost throughout the year, except in December, but this difference was significant only in April ($p < 0.05$) (Fig. 5).

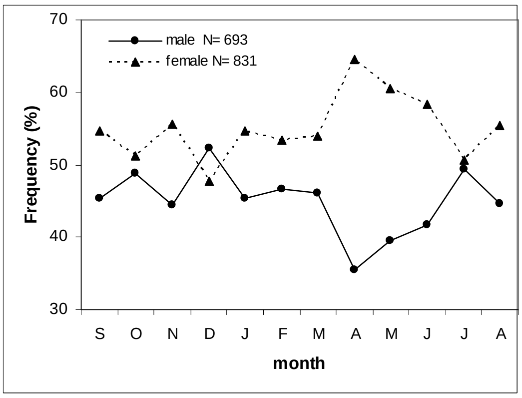

Fig. 5. Frequency of male and female *Ucides cordatus* crabs captured from Setember/2004 to August/2005 on the Piraquê-açu river estuary, Espírito Santo, Brazil.

Discussion

Environmental Parameters

The three sites were similar in relation to environmental parameters such as air, sediment and burrow water temperatures. The higher temperatures registered at upper intertidal levels were due to the less dense canopy cover (mainly of *Avicennia schaueriana*, that, due to the salinity of the high intertidal levels, grow less than *Rhizophora mangle*). However, salinity varied greatly among the sites, exhibiting a salinity gradient that decreased towards the upper estuary (due to its greater distance from the sea), also observed on the Piraquê-mirim river, a tributary of the Piraquê-açu river (Gilberto Barroso, pers. communication). Seasonal differences in salinity were also observed and related to the rainy season. Higher salinity fluctuation was verified at T1 and T2, mainly at upper intertidal levels, where the mangrove covering is less dense and higher evaporation rates occur, coupled with a higher tidal range. The intertidal range of T3 was narrow (nearly 1/3 that of T1) and as it flooded at every high tide it prevented any salt concentration. During the wet season, salinities drop almost to freshwater levels, which makes this site more osmotically demanding on *Ucides cordatus*, whose optimal salinity is from 25 to 30 (OLIVEIRA, 1946). However, DIELE and SIMITH (2006) have pointed out that both juveniles and adults can survive long exposures (> 3 weeks) to freshwater.

Burrow Density

Open burrows were more frequent than sealed ones, revealing the activity of *U. cordatus*, which sealed their burrows only during crab moulting, as a protection against predation (COSTA, 1979; ALVES, 2004). Sealed burrows were more frequent from May to August, coinciding with dry and lower temperature months. According to ATKINSON and TAYLOR (1988) and SPIVAK (1997), many crabs remained inactive in their burrows during the colder months. ALCÂNTARA-FILHO (1978) and NASCIMENTO *et al.* (1982) suggested that moulting occurred mainly during the dry season. On the Piraquê-açu river estuary, both dry and cold seasons occurred from May to August, corroborating their findings, in spite of the mild tropical winter.

The mean crab density found on the Piraquê-açu river estuary is lower than that registered by ALCÂNTARA-FILHO (1978), COSTA (1979), NASCIMENTO *et al.* (1982), CASTRO (1986) and GÓES (2003), in other tropical Brazilian mangrove forests, but it is higher than that of a subtropical Brazilian mangrove forest (BRANCO, 1993) or than the mangrove area studied by SCHORIES *et al.* (2003) and DIELE *et al.* (2005) in Pará, North Brazil and that studied by ALVES and NISHIDA (2004) in Paraíba, in North-eastern Brazil. These differences can be related to intrinsic factors of a particular mangrove forest (primary productivity, patterns of larval recruitment, among others), or even to the exploitation of crabs or sampling techniques. In general, recent papers have registered smaller crab densities than the older studies, probably revealing that the crab population has been overfished, mainly due to unsustainable practices such as lassos and meshes.

Low crab densities were observed at the low intertidal levels of T1 and T2 and are probably related to capture pressure, because these areas are easily harvested (compared to the upper intertidal ones) due to the proximity of small villages and easy accessibility to boats. In other Brazilian mangrove forests, overfishing is also decreasing crab densities (ALVES, 2004; ALVES and NISHIDA, 2004). Juvenile crabs had been found far more frequently at the upper intertidal levels of T1 and T2 and also at T3 on the upper estuary. BLANKENSTEYN *et al.* (1997) and GÓES (2003) also verified higher crab densities at upper intertidal levels, contrary to the findings of COSTA (1979), NASCIMENTO *et al.* (1982), BRANCO (1993), who observed a landward reduction in crab densities. This might be due to differences in vegetation structure, as this upper intertidal zone (called “apicum”) can be quite different, in terms of species composition and soil type.

The negative correlation of crab burrows and the environmental parameters such as salinity and pH corroborates the tendency for more juveniles to inhabit both the upper estuary and the intertidal levels, contrasting with the findings of GÓES (2003), who reported a positive correlation between salinity and pH with crab density, probably because he analyzed the intertidal levels, whereas in our study, both intertidal and the estuarine gradient were sampled. The ability to survive long term exposures to freshwater (>3 weeks) (DIELE and SIMITH, 2006) enables *U. cordatus* to colonize these areas with extreme salinity values. There was also a positive correlation between air temperature and the number of crab burrows, with increased numbers of juveniles at upper intertidal levels, where the black mangrove *Avicennia schaueriana* dominated, and the canopy coverage was less dense. These upper estuarine and intertidal levels are not, in fact, the most suitable places for crabs, because *Rhizophora mangle* leaves, from the low intertidal level, are preferred by them (NORDHAUS *et al.,* 2006). Instead, juvenile crabs are displaced to these marginal habitats, probably because adults outcompete over the juveniles in the search for preferred burrowing sites. DIELE *et al*. (2005) confirmed the preference of adults of *U. cordatus* for shadier inner forest areas, less vulnerable to predation and under *R. mangle* stands.

Population Structure

The difference between the total number of crab burrows (7,996) and the total number of crabs (1,524) can be attributed to the difficulties encountered in capturing crabs, which frequently burrow down between dense mangrove roots. SCHORIES *et al.*

(2003) collected 10% of the total burrowing crabs sampled; IVO *et al.* (2000) also had difficulty in catching crabs, differently from NORDHAUS *et al.*, (2006) who showed an average capture efficiency of 73%. During cold months, the present authors collected fewer crabs probably due to their greater inactivity, when they stayed longer and deeper in their burrows (ATKINSON and TAYLOR, 1988; WILSON, 1989; SPIVAK *et al.*, 1994; ALVES 2004; CÉSAR *et al.*; 2005).

The mean carapace width of the crabs registered on the Piraquê-açu river estuary was below the legal minimum market size of 6.0 cm (IBAMA, 2003), probably due to overfishing, in spite of capture prohibitions during the reproductive season (a process known locally as "andada").

The dominance of juveniles on the upper estuary could be related to the presence of predators such as fish and paddle crabs on the lower and middle estuary (WILSON, 1989; ALVES and NISHIDA, 2002; DANKWA and GORDON, 2002 and KRUMME, 2004), while the upper estuary crabs are less vulnerable to predation. Upper estuarine areas are inundated only during spring tides and remain under water for a shorter time, thus reducing predation risk (GÓES, 2003; PAULA *et al.*, 2003 and KRUMME, 2004). These juveniles can walk down the estuary as they grow older, and enjoy a greater competitive advantage for more suitable locations near riverine areas, with preferred food (leaves of *R. mangle*), soft sediment which facilitates burrowing (NORDHAUS *et al.*, 2006) and proximity to water for spawning. *U. cordatus* prefers *R. mangle* to *Avicennia germinans* leaves, because they are more easily masticate and digested mechanically (NORDHAUS and WOLFF, 2007).

So T3 could be considered a nursery area for this semi-terrestrial crab while T1 and T2 are reproductive areas. Considering the intertidal level, COSTA (1979), ALVES and NISHIDA (2002) and GÓES (2003) also found more juveniles on the upper intertidal level, and they attributed this to intraspecific competition, because adult crabs prefer a denser canopy covering. On the Piraquê-açu river estuary, a denser canopy covering occurs on the low intertidal level, under *R. mangle* stands, with a higher density by area than is associated with the other two mangrove species.

Male and female crabs of medium carapace width dominated the population, with only 24% and 28% of the males and females, respectively, being larger than 6.0 cm, the minimum harvest size. This differs from the findings of ALCÂNTARA-FILHO (1978), CASTRO (1986) and DIELE *et al.* (2005), who found crabs of around 6 cm of carapace width as the most frequent size class for males and 5.5 for females. According to HARTNOLL and BRYANT (1990), long-living species such as *U. cordatus*, which can live at least 10 years (PINHEIRO; *et al.*, 2005), would be expected to form groups of larger sizes, but the present authors verified the opposite, with smaller crabs being the most frequent. DIELE *et al.* (2005) pointed out that males grow faster than females, due to reproductive investment, so the normal pattern is for males to be larger than females, contrary to the size frequency observed on the Piraquê-açu estuary. Our findings revealed that few individuals of *U. cordatus* can be harvested, suggesting that fishing pressure is beyond the population´s replacement capacity.

Ovigerous females were found from January to May, revealing that this is the reproductive season in this mangrove forest, and this differs from the findings of ALCÂNTARA-FILHO (1978), CASTRO (1986), DIELE *et al.* (2005), SAMPAIO (2002) and PINEIRO *et al.* (2005), relating to other Brazilian mangrove forests. But all the studies agree that spring and summer are the reproductive season. These females were more frequent at low intertidal levels, favoring spawning. The smallest ovigerous female found (3.13 cm of carapace width) was below that reported by other authors such as SAMPAIO (2002) but is close to the findings of DIELE *et al.* (2005) and PINHEIRO *et al.* (2005).

Sex Ratio

Female crabs dominated over male crabs; female dominance was more evident near small villages (as occurred at T2). Males are preferred due to their larger body and claw sizes than those of the females, which render more meat (ALVES and NISHIDA, 2004; DIELE *et al.*, 2005). Females also dominated over males in other mangrove areas (ALCÂNTARA-FILHO, 1978; GÓES, 2003) whereas males were more common in others (NASCIMENTO *et al.*, 1982; CASTRO, 1986; BRANCO, 1993; ALVES and NISHIDA, 2004; DIELE *et al.*, 2005). Among the juveniles, the sex ratio was more even, probably because they are not harvested.

The female crab dominance, the reduced mean size and the size distribution skewed towards females suggest that the population of *U. cordatus* in the mangrove forest of the Piraquê-açu river estuary has been subject to overfishing. *U. cordatus* has been considered a threatened species (ALVES and NISHIDA, 2004). Further, the lethargic crab disease has become widespread in Brazilian mangrove areas (BOEGER *et al.*, 2005). All these facts constitute a menacing scenario which threatens the population´s survival. Thus more effective management and conservation measures such as a local interruption of crab collection are necessary to allow the stock to recover. This action is necessary to protect this fisheries resource both for the traditional population as well as for the regional culture and economy and the health of the mangrove ecosystem. Meanwhile, more detailed studies on the role of other factors (e.g. the biotic parameters such as predation and intraspecific competition) are needed better to characterize the dynamics of crab populations.

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