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Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary, North Brazil: Indications for overfishing?

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Abstract – To evaluate the population structure of *Ucides cordatus* in the Caeté estuary, crabs were sampled bimonthly over 13 months in three *Rhizophora mangle* forest stands that differed in their accessibility and fishing history. Additionally, sex- and size composition of the commercial catch and catch per unit of effort (CPUE – the number of crabs captured per fisherman per day) were monitored between 1997 and 2003. Average and maximum crab sizes (carapace width, *CW*) from all three sampling sites combined were 6.1 cm and 8.8 cm in males, respectively, and 5.5 and 7.3 cm in females. Crabs were largest at the site that had been reportedly less exploited in the past. The overall sex ratio was skewed towards males (53−62%). Egg carrying females were only encountered during the rainy season. Mean crab abundance and biomass was 1.7 specimens m^{-2} and 142 g m^{-2} fresh mass. Only large males were commercially harvested (98% ≥ 6.5 cm *CW*). Their biomass was 53 g m^{-2} and the Caeté estuary yields an annual production of 1200 t of these large specimens. This is approximately the quantity that is currently being harvested. CPUE was similar in 1997 and 1998, then decreased by 15% until 2000 and stabilized for the rest of the study period. Mean capture size (cm *CW*) ranged between 7.2 ± 0.5 and 7.5 ± 0.2 and was above the size of 50% (and even 100%) male maturity and the legal minimum capture size. There is no evidence that the Caeté crab population is overfished, despite over 30 years of de facto open access exploitation. Apparently, the selectivity of fishermen and consumers for large male crabs as well as the local artisanal capture techniques are key factors in preventing an overfishing of the Caeté crab population until today. Our results suggest that the economic and social sustainability of this fishery will be affected well before the biological one, which should be considered in the recently proposed coastal co-management plan for the region.

Key words: Mangrove crab / *Ucides cordatus* / Biomass / Sex ratio / Artisanal fisheries / CPUE / Management / Brazil

Résumé – Structure de la population, composition des captures et CPUE du crabe de mangrove *Ucides cordatus* (Ocypodidae) capturé artisalement dans l'estuaire du Caeté, nord Brésil : signes de surexploitation ? Pour évaluer la structure de la population de *Ucides cordatus* dans l'estuaire du Caeté, ces crabes ont été échantillonnés tous les deux mois, sur une période de 13 mois, au niveau de trois sites de la mangrove à *Rhizophora mangle* qui diffèrent par leur accessibilité et leur historique de pêche. De plus, la composition (sexe et taille) des captures commerciales et celle par unité d'effort (CPUE – nombre de crabes capturés par pêcheur et par jour) ont été suivies entre 1997 et 2003. La taille moyenne et la taille maximale des crabes (largeur de la carapace, *CW*) de l'ensemble des 3 sites échantillonnés étaient de 6,1 et 8,8 cm pour les mâles, respectivement, et 5,5 et 7,3 cm pour les femelles. Les crabes étaient plus grands dans le site qui avait été moins exploité par le passé. Le sexe-ratio global est à la faveur des mâles (53−62%). Les femelles portant des œufs ont été rencontrées uniquement durant la saison des pluies. L'abondance moyenne et la biomasse des crabes étaient de 1,7 spécimens m^{-2} et 142 g m^{-2} (poids frais). Seuls, les grands mâles sont récoltés et commercialisés (98 % ≥ 6,5 cm *CW*). Leur biomasse était de 53 g m^{-2} et les rendements de l'estuaire du Caeté, en production annuelle, sont de 1200 t pour ces grands spécimens. Ceci correspond approximativement à la quantité qui est récoltée. Les CPUE sont similaires en 1997 et 1998, puis diminuent de 15 % jusqu'en 2000 et se stabilisent pour le reste de la période d'étude ; la taille moyenne de capture s'étend entre 7,2 ± 0,5 et 7,5 ± 0,2 cm, et était de 50 % (et même 100 %) au-dessus de la taille de maturité sexuelle des mâles et la taille légale minimum de capture. Il n'y a pas de preuve que la population de crabes du Caeté soit surexploitée, en dépit de plus de 30 ans d'exploitation en libre accès. Apparemment, la sélectivité, effectuée par les pêcheurs et les consommateurs, pour les grands mâles, ainsi que les techniques artisanales de capture, sont des facteurs-clés pour empêcher la surexploitation de ces crabes jusqu'à présent. Nos résultats suggèrent que l'équilibre économique et social de cette pêche sera affecté bien avant l'équilibre biologique, ce qui devrait être pris en considération, dans le récent plan de co-gestion côtière de cette région.

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1 Introduction

The natural resources of coastal ecosystems are increasingly utilized by the growing human population, especially in less-developed tropical and sub-tropical countries (Clark 1994; De Boer and Longamane 1996; Cicin-Sain and Knecht 1998; Krause et al. 2001). While many studies have focussed on the exploitation of fishes, shrimps and marine crabs (Ehrhardt et al. 1990; Jennings and Polunin 1996; Uphoff Jr. 1998) few have dealt with the exploitation of semi-terrestrial crabs living in the inter- and supratidal zone. Several of the larger species, such as *Ucides cordatus*, *Cardisoma* spp. and *Gecarcinus* spp., are important sources of food and income in tropical coastal communities but overexploitation and habitat destruction are threatening their populations (Feliciano 1962; Taissoun 1974; Foale 1999). Despite their socio-economic importance, the population status and ecology of semi-terrestrial crabs is generally not well known, which often hampers the development of effective management strategies. Their large size suggests a high vulnerability to exploitation as it is generally correlated with slow growth, high age at maturity, low reproductive output and low natural mortality (Pauly 1998; Jennings et al. 1998; Jennings et al. 1999).

This study focuses on an exploited population of the mangrove crab *U. cordatus* in the Caeté estuary, North Brazil. The species is an important fisheries resource throughout the coastal region of Brazil where mangrove stands can be found (Ogawa et al. 1973; Castro 1986; Nordi 1994; Glaser and Diele 2004). The crabs are slow growing and have a maximum life span of at least ten years (Ostrensky et al. 1995; Diele 2000; Pinheiro et al. 2005). Males grow larger than females, their maximum size (carapace width, *CW*) is generally 7.1 to 9.6 cm, while females reach 6.1−9.0 cm *CW*. The crabs construct up to 1.6 m deep burrows and feed mostly upon leaf litter (e.g. Nordhaus 2004). Besides the predation by humans, adult crabs are preyed upon by crab racoons and capucin monkeys.

In the Caeté estuary *U. cordatus* has been harvested for over three decades for commercial purpose and over half of the 2500 rural households of the research area depend on the species for at least part of their financial income (Glaser 2003). The area is part of a proposed coastal co-management area (Glaser and da Silva 2004). Currently, the capture of females is prohibited during the reproductive season from December to May in northern and north-eastern Brazil, while male capture is banned only during the few days of mass-mating events. However, crabs are harvested throughout the entire year as most fishermen do not know the legislation and law-enforcement is non-existent. Legal minimum market size is 6.0 cm *CW* (IBAMA N° 034/03-N, 24.06.03). The fishery is artisanal, fishermen catch crabs by introducing an arm or a hook into the burrows. Crabs are harvested in the entire Caeté mangrove forest today, although fishermen prefer stands of red mangrove (*Rhizophora mangle*) over black mangrove (*Avicennia germinans*), due to higher densities of large crabs and ease of capture. Annual landings are approximately 1150 tons (Araujó, pers. communication). The animals are sold either alive or their meat is extracted and sold on the local or regional market.

Declines of *U. cordatus* have been reported from many coastal regions of Brazil and were related to habitat destruction, diseases and overfishing (Maneschy 1993; Boeger et al. 2005). In the Caeté estuary, the mangrove forest habitat of *U. cordatus* is still comparably intact, however there is growing concern that the fishery and the population might collapse due to increasing fishing pressure. The number of crab collectors has grown by 20% between 1996 and 1998 due to demographic growth and draughts that caused people to move from the interior to the coast (Glaser 2003). Therefore, the overall objective of our study is to contribute to the development of a comprehensive management plan for the *U. cordatus* fishery in the Caeté estuary. Specifically, we determined (a) the population size structure, abundance, biomass and sex ratio of *U. cordatus* and (b) the sex and size composition and CPUE of the commercial crab catch. The study forms part of a resource evaluation program for this species that includes biological studies as well as fisheries and socio-economic aspects.

2 Material and methods

2.1 Study area

The Caeté estuary is located near the city of Bragança about 200 km east of Belém in North Brazil (Fig. 1) and is part of the second largest continuous mangrove area of the world (Kjerfve and de Lacerda 1993). The Caeté peninsula has an extension of about 250 km^2 with approx. 140 km^2 of mangrove cover. *Rhizophora mangle* is the dominant tree species, followed by *Avicennia germinans* and much less frequent *Laguncularia racemosa* (Mehlig 2001; Menezes et al. 2003). Tidal range is up to 5 m, but most of the mangrove forest is located above the mean high tide level and only flooded fortnightly at spring tide days. Mean annual rainfall is approximately 2500 mm with most precipitation occurring between January and June (INMET 1992). Salinity values range correspondingly between <10 psu during the rainy season to 39 psu at the end of the dry season. Average water (27−30 °C) and air temperatures (24−28 °C) vary little over the year (INMET 1992; MADAM-unpublished data).

2.2 Field sampling

In order to determine population structure, abundance, biomass and sex ratio of *U. cordatus,* three sampling sites were chosen in *R. mangle* forest stands in the northern part of the peninsula near the tidal channel Furo Grande, an important crab harvesting area (Fig. 1). While the sites were similar in forest structure and inundation frequency, they differed in their accessibility from the Furo Grande bridge, the central starting point of crab fishermen in the area: site A is reachable by foot, site B after canoeing 1.5 km and site C after 5 km. While today all sites are regularly harvested, up to the late eighties, when yields close to the road were still high, remote locations such as C were visited only infrequently (Domingos Pinho de Araújo, pers. comm.). Thus, we decided to sample sites with different exploitation histories that may have caused differences in the population structure of *U. cordatus*. Crabs were captured bimonthly from August 1997 to August 1998. At each site 6 to 8 replicate plots (25 m^2 each, 50 m between plots) were sampled along a transect that ran perpendicular

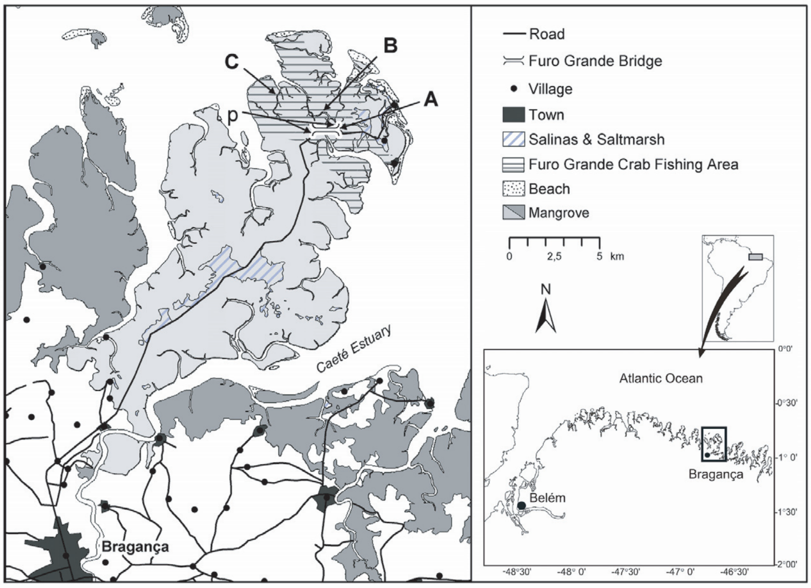

Fig. 1. Location of the Caeté estuary and the mangrove peninsula (light grey) near Bragança, North Brazil, including the Furo Grande crab fishing area. A, B, C: study sites in *Rhizophora mangle* dominated forest stands; *p*: "peripheral study sites" at the embankment of the road and in a forest gap. Access to the Caeté mangroves and their natural resources is facilitated by the road that connects Bragança with the northern beaches and villages of the peninsula.

to a tidal creek. On successive sampling occasions the transect was moved 100 m aside to the previous one to avoid effects of previous sampling on crab distribution and abundance. Sampling was always carried out during ebb tide around full and new moon, when crabs can be caught easier due to the softer sediment, as the forest is flooded only during spring high tides. In each plot a professional crab collector probed every *U. cordatus* burrow and caught the crab with his arm or a hook, yielding an average capture efficiency of 73%. In areas with very dense mangrove roots capture was impossible, because burrows were twisted around or partially blocked by roots. Crabs were sexed, females were checked for egg masses, the carapace width (*CW*) was measured with a calliper to the nearest mm, and wet-weight was determined to the nearest 0.1 g. After measuring the crabs were released. Crab abundance and biomass was calculated by correcting the catch with the capture efficiency (e.g. if the capture efficiency in a plot was 80% and 100 crabs with a total weight of 12 kg were caught, the corrected abundance and biomass would be $n = 125$ and 15 kg, respectively). The implicit assumption is that crabs from unfishable burrows did not differ significantly in sex ratio and size distribution from crabs that could be captured. Field observations with binoculars did not show any preference of females or males (recognizable by the size of chelipeds and setae on walking legs) for "unfishable areas". Furthermore, the comparison of the size of 142 burrows entrances (indicating the approximate size of their inhabitants) prior to crab capture showed no significant difference between "fishable" and "unfishable" burrows (t-test: $p > 0.05$; unfishable burrows: 5.19 cm, $n = 65$; fishable burrows: 5.21 cm, $n = 141$).

Juvenile crabs were rarely captured in the *R. mangle* forest habitat, but were abundant near the embankment of the road and in larger forest gaps. Therefore, these peripheral habitats were sampled in May 1998 to gather additional information on the smallest size classes. Due to higher densities of the juveniles a smaller plot size (6.25 m^2) was used. Five replicate plots were sampled per site (embankment and gap). Only size and sex of the crabs was determined.

The commercial catch from the Furo Grande area was monitored by contracted local fishermen at the bridge that serves as the central landing point for this fishing area (Fig. 1). Sex and size of the landed crabs was determined weekly between February 1998 and December 2003. Crabs were measured and sexed from at least three randomly chosen harvesting localities. CPUE, the number of crabs captured per fisherman per day was calculated from daily monitored fishery landings. Average daily working hours (only available from 1999 onwards) showed little variation over the years (±5%). One "man-day" is thus the effort unit utilized here.

2.3 Environmental parameters

Canopy and root coverage (in % of total area) was estimated visually for each plot as the canopy provides food for the crabs and the mangrove roots give shelter (stilt roots of *R. mangle*) or may hamper burrow construction (dense root mats of *A. germinans*). To determine silt/clay content in the sediment three samples were taken per plot using an open ended plastic syringe (50 ml, diameter 2 cm) to a sediment depth of 10 cm. After mixing the samples and homogenising them, a sub-sample was analysed using the wet sieving method described by Holme and McIntyre (1984). Samples for determining the water content of the sediment were taken at the end of the ebb phase with a small corer at a sediment depth of 8−10 cm. The sediment was weighed wet, dried to constant weight and re-weighed, and its water content calculated from the difference between wet and dry weight. For the organic content analysis, samples were taken from the

Table 1. Mean and standard deviation for botanic and sediment parameters measured at the three *Rhizophora mangle* forest sites. All values in % of sampled area or sample weight, except for salinity (psu). RM: *R. mangle*; AG: *Avicennia germinans*.

Abiotic Parameters	Site A	Site B	Site C	Significance
Canopy coverage	62 ± 24	65 ± 25	62 ± 26	n.s.
Root coverage RM	44 ± 29	40 ± 23	50 ± 24	n.s.
Root coverage AG	8 ± 17	11 ± 19	11 ± 19	n.s.
Organic content	2.9 ± 1.4	2.8 ± 0.8	3.2 ± 1.2	n.s.
C/N ratio	14.9 ± 5.8	15.7 ± 8.1	12.4 ± 2.6	n.s.
Salinity	30.4 ± 6.9	30.3 ± 8.1	31.3 ± 6.4	n.s.
Silt/clay content	60.9 ± 26.3	76.5 ± 20.2	72.8 ± 19.8	$p < 0.01$
Water content	47.9 ± 9.1	53.5 ± 8.1	55.8 ± 7.4	$p < 0.001$

sediment surface and frozen. Inorganic carbon was removed with 0.02 M HCl. The samples were dried to constant weight, weighed to the nearest 0.1 mg and burned for six hours at 540 °C. The samples were then re-weighed and the organic content calculated. For the determination of the C/N ratio of the sediment, samples from the surface were dried at 100 °C for 24 h, crushed and then analysed using FISONS NA2100 elemental analyser. The C/N ratio was calculated by dividing the total organic content by total nitrogen.

2.4 Data analysis

A total of 162 plots (4050 m^2) were sampled at the three *R. mangle* forest stands during the bimonthly crab sampling. One way analysis of variance was used to test for differences between environmental parameters, size, abundance and biomass of crabs at the three sites. Although variance was heterogeneous in some cases despite data transformation, ANOVA was used anyway, following Underwood (1997 pp. 192-194), who states that this test is robust when comparisons include large and balanced sample sizes (as is the case in the present study). Post hoc comparisons were performed using Tukey's HSD-test.

3 Results

3.1 Environmental parameters

Canopy and root coverage were similar at the three *R. mangle* forest sites ($p > 0.05$). Average values ranged between 60 to 65% for the canopy, 40 to 50% for *R. mangle* stilt roots and 8 to 11% for *A. germinans* pneumatophores (Table 1). Values of organic matter content, the C/N ratio of the sediment and salinity were also similar at the three sites ($p > 0.05$). Differences existed in the silt/clay and water content of the sediment. With an average of 61% the silt/clay content was lowest at A ($p < 0.01$) while B and C had similar values (77% and 73%, $p > 0.05$). Water content was also lowest at site A (48%, $p < 0.001$), while B and C did not differ (54% and 56%, $p > 0.05$).

In contrast to the *R. mangle* forest sites, the peripheral sites had no canopy coverage and mangrove roots were rare (maximum of 5% coverage by *R. mangle* roots). Mean silt/clay content was 79% at the gap and 60% at the embankment of the road.

3.2 Population size structure

A total of 4549 crabs were caught at the three *R. mangle* forest sites and an additional 172 in the peripheral habitat. *CW* of the smallest and largest male was 1.7 and 8.75 cm *CW*, respectively, compared to 1.4 and 7.3 cm *CW* for females. Egg carrying females were encountered in February (Site A: 49%, B: 41% and C: 73% of total female catch) and in April (Site A: 2%, B: 25%, C: 35% of total female catch).

The size-frequency distributions of crabs at the three *R. mangle* sites were unimodal with few exceptions (Fig. 2). No clear progressions of the modal size-classes can be observed throughout the sampling period. In most months the distributions were negatively skewed (except site A, both sexes, in December 97 and site C, females, in October 97) (Fig. 2), while for the peripheral habitats the opposite holds true (Fig. 3). Only 4% of all captured crabs had a *CW* below 4 cm in the *Rhizophora* forest habitat, while 67% of all specimens sampled in the peripheral habitat were smaller than 4 cm.

Crabs at the two peripheral sites were of similar size ($p > 0.05$), while differences in mean *CW* existed between the *R. mangle* forest sites. Mean *CW* of both sexes (pooled over all months) was significantly larger at site C than at the other two sites ($p < 0.001$) where crab sizes were similar ($p > 0.05$) (Males, $n = 2552$; A: 5.97 ± 0.87; B 5.89 ± 1.14; C: 6.39 ± 1.04; Females, $n = 1997$; A: 5.49 ± 0.71; B: 5.25 ± 0.81; C: 5.65 ± 0.73) ($p < 0.001$). The highest proportion of large males ($CW \geq 6.5$ cm, see Sect. 3.5) was found at site C (53% of total male catch) followed by B (35%) and A (29%). Females with a $CW \geq 6.5$ cm also had the highest proportions at site C (14%), while the two other forest sites had lower values (7% and 6%, respectively). At the peripheral sites none of the captured males and only one female (<1%) had a size above 6.5 cm.

In both sexes the abundance of specimens in the uppermost size classes generally increased from A to B to C, however, this increase was much more pronounced in males (Table 2). The relative abundance of the largest males increased by a factor of 36 ($CW \geq 8.0$ cm) or 4.8 ($CW \geq 7.5$ cm) from A to C. The relative abundance of the largest females increased only by a factor of 2.3 ($CW \geq 6.5$ cm) or 1.9 ($CW \geq 6.0$ cm) (Table 2).

3.3 Sex ratio

In most study months males were more abundant than females at all thee *R. mangle* forest sites. The sex-ratio pooled

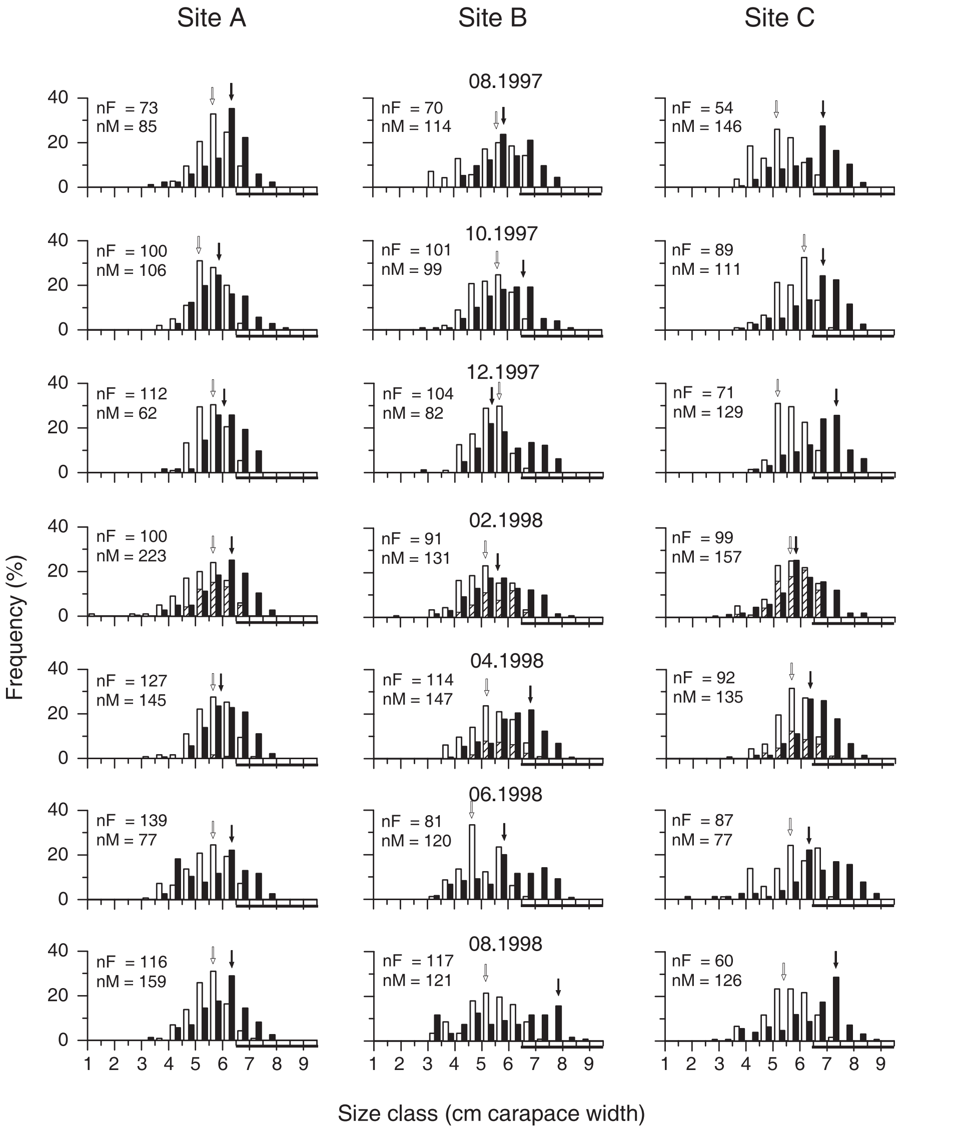

Fig. 2. Size-frequency distributions of *U. cordatus* sampled at *R. mangle* forest sites A, B and C from August 1997 to August 1998. Black bars: males; white bars: females, hatched bars: egg carrying females. nF and nM: number of females and males captured, respectively. Black rule on *x*-axis: size classes comprising crabs of commercial interest. Black and white arrows: strongest size class in males and females, respectively.

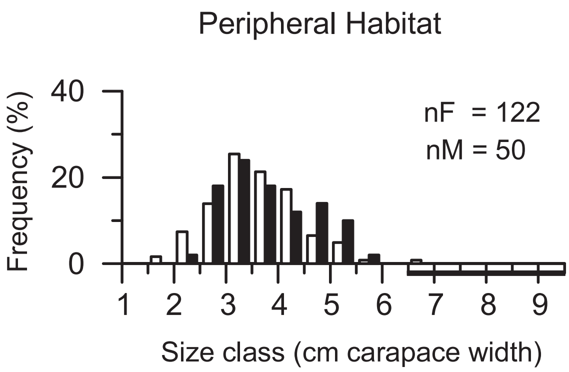

Fig. 3. Size-frequency distribution of *U. cordatus* sampled in May 1998 in the peripheral habitat (both study sites pooled, embankment and gap). Black bars: males; white bars: females; *nF* and *nM*: number of females and males captured, respectively. Black rule on *x-axis*: size classes comprising crabs of commercial interest.

Table 2. Number of crabs (*n*) in size group 1 (uppermost three size classes) and size group 2 (uppermost two size classes) at the study sites A, B, C and their proportion (%) of the total number of captured crabs per sex and site. *CW*: carapace width (cm).

Sex	Females				Males			
	Group 1		Group 2		Group 1		Group 2	
CW	≥ 6.0 cm		≥ 6.5 cm		≥ 7.5 cm		≥ 8.0 cm	
Site	*n*	%	*n*	%	*n*	%	*n*	%
A	206	26.9	51	6.6	21	2.5	1	0.1
B	138	20.4	41	6.0	63	7.7	7	0.9
C	203	38.8	77	13.9	106	12.0	32	3.6

Table 3. Number of male and female crabs and sex-ratio for the total catch obtained at the study site A, B and C. Data pooled over seven sampling occasions (August 1997-August 1998).

Site	Males	Females	% Males	Sex ratio	Chi² (1)
A	857	767	53	1.1:1	4.88 *
B	814	678	55	1.2:1	12.22 ***
C	881	552	62	1.6:1	75.08 ***

(1) Chi² test of goodness of fit testing the null hypothesis of equal proportions between sexes. * $p < 0.05$, *** $p < 0.001$.

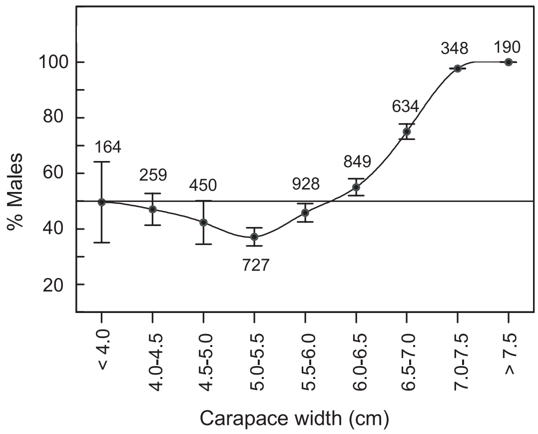

Fig. 4. Sex ratio as a function of size. Classes of the lower and upper limit of the size range were combined until a minimum of 20 crabs per *R. mangle* forest site were available for analysis. Indicated are average values ±1.96 standard deviations. Numbers: total amount of captured crabs in each size class.

over all sampling occasions deviated significantly from the hypothesised 1:1 ratio (Fisher 1930) (Table 3). Males dominated with increasing proportions from A to B to C. When regarding sex ratio as a function of size, females were generally more prominent in the smaller size classes (≤6.0 cm *CW*) with proportions of up to 66% in the 5.0 to 5.5 cm size class, whereas in the upper classes males dominated and resulting from their larger maximum size reached 100% (Fig. 4).

In the peripheral habitat females were more abundant than males. At the embankment of the road they dominated with 61% of the total catch ($n = 76$) with even higher proportions (79%) in the forest gap ($n = 96$).

3.4 Abundance and biomass

At the *R. mangle* forest sites mean total crab abundance and biomass (pooled over both sexes) was 1.65±0.5 indiv. m^{-2} and 142.0 ± 51.3 g freshmass m^{-2}, respectively. Total crab abundance was significantly higher at A than at the other two sites ($p < 0.05$) that had similar values ($p > 0.05$) (Fig. 5). Total biomass values however did not differ between A and C ($p > 0.05$), but both sites had a significantly higher total biomass than B ($p < 0.05$). Female abundance differed between all sites ($p < 0.0001$) with highest and lowest values at A and C, respectively. Female biomass was also higher at

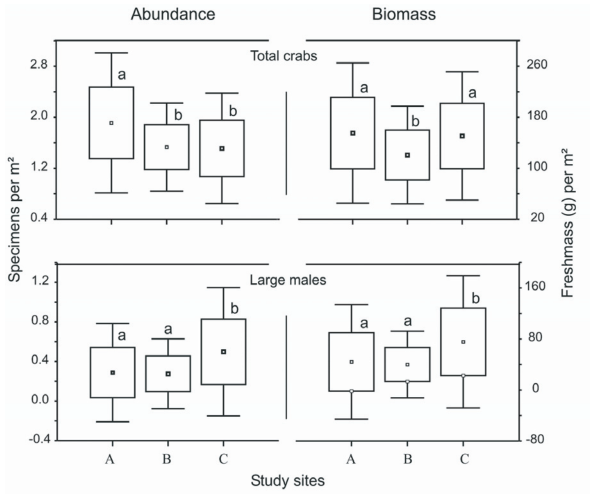

Fig. 5. Box and whisker plots of abundance and biomass of *U. cordatus* at the study sites A, B and C (for total crabs and large males with a *CW* ≥ 6.5 cm); Data pooled over all months. Whiskers: ±1.96 standard deviation; box: ±1.00 sd; small square: mean. Homogenous groups ($p > 0.05$) are indicated by equal letters.

A site than at the other two sites ($p < 0.05$), while the latter did not differ significantly ($p > 0.05$). Male abundance and biomass were similar between the three sites ($p > 0.05$). However, large marketable males (*CW* ≥ 6.5 cm, see 3.5) were significantly more abundant and had a higher biomass at C than at the other two sites ($p < 0.01$) which had similar values ($p > 0.05$) (Fig. 5). In the peripheral habitat mean total crab abundance was 4.38 ± 1.59 indiv. m^{-2}, with 4.61 ± 2.04 indiv. m^{-2} at the gap and 4.16 ± 1.17 at the embankment of the road.

3.5 Composition of the commercial catch and CPUE

Only males were landed at Furo Grande, destinated for whole crab sales. The largest and smallest specimens measured 9.9 and 5.0 cm *CW*, respectively. The size-frequency distributions show no distinct differences among years (Fig. 6). Annual mean size of the captured crabs (cm *CW*) varied between 7.23 ± 0.50 (1998) and 7.48 ± 0.42 (2002) (Fig. 6). Pooled over all years average landing size was 7.41 ± 0.44. Only 2% of the total catch (pooled data) had a *CW* of below 6.5 cm, the informal local limit for market-sized animals (Domingos de Araújo, pers. comm.). Even crabs measuring 6.5 to 7.0 cm were rarely landed (9%), whereas the percentage increased to 43% in the 7.0 to 7.5 size class. CPUE was similar in 1997 and 1998 (>0.05), while in 1999 and 2000 it decreased significantly by 6% and 8%, respectively ($p < 0.05$). Between 2000 and 2003 CPUE varied only little ($p > 0.05$).

4 Discussion

4.1 Population size structure

In both sexes larger crabs dominated the population at all *R. mangle* forest study sites and in all study months. Similar

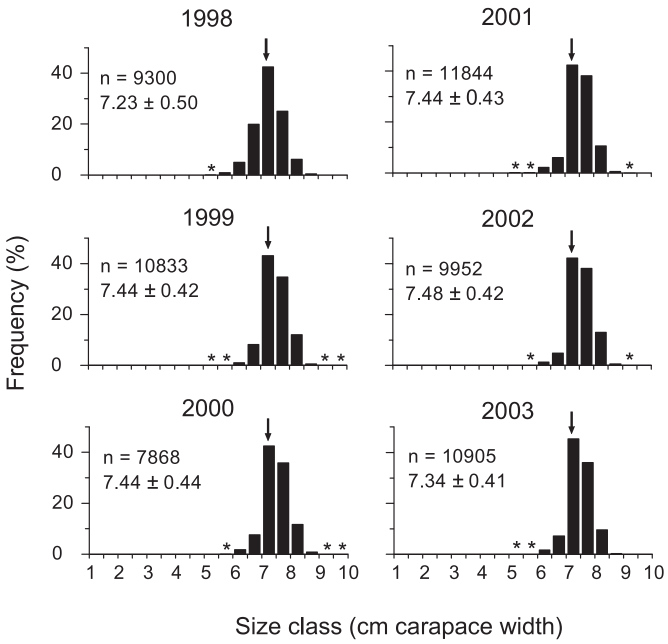

Fig. 6. Annual size-frequency distributions for the commercial catch of male *U. cordatus* at the landing point Furo Grande Bridge between 1998 and 2003; *n*: sample size; numbers below *n*: average and standard deviation; Black arrow: strongest size class. *: <0.1%.

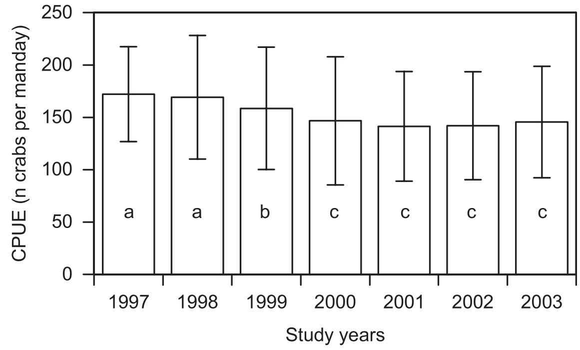

Fig. 7. CPUE – the number of crabs captured per fisherman per day – for the Furo Grande fishing area between 1997 and 2003 (average and standard deviation). Homogenous groups ($p > 0.05$) are indicated by equal letters.

distributions have also been reported from *U. cordatus* populations in other parts of Brazil (Alcântara-Filho 1978; Castro 1986). In contrast to smaller short-lived species such as *Uca* spp. (Koch et al. 2005), a dominance of large crabs is frequently found in large, long-living species, such as *U. cordatus*, where crabs accumulate in larger size classes as growth decreases with age (Hartnoll 1982; Hartnoll and Bryant 1990). Large crabs moult between June and November, and their growth increment is small and variable (Diele 2000). Consequently, progressions of modal size classes were not recognizable in the size frequency graphs. The low number of juveniles found in the forest samples may also relate to their small size and the difficulty of finding their burrows between the mangrove roots. In the samples of the root-bare peripheral habitat they were encountered much more frequent. The scarcity of larger crabs in the peripheral habitats near the road and in larger forest gaps indicates their preference for more shaded inner forest areas.

The size difference of crabs between the tree *R. mangle* sites appears to be influenced mostly by the crab fishery. Crabs were largest on average at the site that was furthest away from the departure and landing point in the Furo Grande fishing area, where fishing had commenced >10 years later than at the nearer sites (Domingos Pinho de Araújo, pers. comm.). Different fishing histories resulting from the different accessibility of the study sites thus probably explain why large marketable males ($CW \geq 6.5$ cm, see Sect. 3.5) and particularly the most intensively targeted crabs above 8.0 cm *CW* were up to 38 times more abundant at site C than at the other two more accessible sites. However, as relative abundance of large females was also highest at site C (if only by a factor of about two), the different exploitation histories of the three sites cannot be the only explanation for the observed pattern, as the fishery targets only males. Apparently, some habitat related factors and/or crab recruitment must also have influenced the population structure at the study sites differently, resulting in older age or faster growth of crabs at site C. Differences in food availability (leaf litter) and/or quality could have caused differential growth rates and thus crab sizes among areas, as has been reported for rock lobsters (McKoy and Estermann 1981) and for *Uca vocator* (Delevati Colpo and Negreiros-Fransozo 2004), but were not measured in this study. The measured environmental parameters do not explain the observed size pattern of crabs as except for the slightly lower silt/clay and water content of site A, values were similar at all sites.

In the Caeté estuary *U. cordatus* reproduces in the rainy season, reflected by the presence of egg-carrying females in the February and April samples. The entire reproductive season extends from January to June (Diele 2000). The peak of mating activities and subsequent fertilization rates is generally occurring in February (Diele 2000), which is well reflected by the distinctly higher percentage of egg-carrying females in this month, when compared to the April sampling. In other areas of Brazil, the reproduction of *U. cordatus* is also strictly seasonal (Alcântara-Filho 1978; Botelho et al. 1999; Ivo et al. 1999).

4.2 Sex ratio

A dominance of male crabs, as observed at the three *R. mangle* sites, was also reported for other *U. cordatus* populations in north-eastern Brazil (Castro 1986) and for *U. occidentalis* in Costa Rica (Cabrera Pena et al. 1994). In the present study there was no indication for sex-specific habitat partitioning in crabs of similar size, or for a reduced catchability of females in the *R. mangle* habitat. It is therefore unlikely that sex-biased sampling could have accounted for the observed deviation from the 1:1 ratio as expected by Fisher's theory (Fisher 1930; Willson and Pianka 1963). Instead, biological features such as differential growth and mortality, different maximum sizes and possibly longevity may account for the observed male biased sex-ratio. Wenner (1972) stated that in mature marine crustaceans a deviation from the expected 1:1 sex ratio seems to be the rule rather than the exception and stressed the importance of analysing sex ratio as a function of size. In the present study females clearly dominated in intermediate size classes with a peak at 5.0 to 5.5 cm (anomalous pattern; sensu Wenner 1972). From a *CW* of 6.0 cm males were more frequent until dominating 100% in the upper size classes due to their larger maximum size. The lower abundance of males in intermediate size classes was probably caused by differential growth rates of the two sexes. At a *CW* of approximately 4.5 cm males grow faster than females (Diele 2000; Diele, unpubl.), which reduces their "residence time" in these size classes. At the same time females accumulate in intermediate size classes due to their smaller maximum body size and slower growth, the latter often attributed to their higher energetic costs for reproduction (Conan 1985; Hartnoll and Gould 1988). The smallest egg carrying female found in the Caeté estuary had a *CW* of 2.9 cm and the size at which 50% and 75% of the females are physiologically mature is 4.0 and 4.3 cm *CW*, respectively (do Vale, unpubl.).

The male selectivity of the fishery in the Caeté estuary influences the sex ratio of the crab population, and it can be presumed that in an unexploited population the ratio would even be stronger male-biased. This is underlined by the fact that highest male proportions were found at the study site with the shorter fishing history (C) whereas the two more accessible sites that have been fished for a longer time span (A and B) had comparably higher proportions of females.

While differential growth, different maximum sizes and longevity between the two sexes may account for deviations from the 1:1 ratio in mature crabs (see above), juveniles should be equally represented by males and females (Wenner 1972). However, in the peripheral habitats and at the *R. mangle* sites small females ($CW \geq 4$ cm) were more abundant than similar sized males. As only relatively few juveniles were captured additional sampling is needed for ascertaining their sex ratio.

4.3 Abundance and biomass

In the *R. mangle* forest habitat, average abundance and biomass pooled over all sampling sites and dates was 1.7 indiv. m^{-2} and 142 g freshmass m^{-2}, respectively. In a Jamaican *Rhizophora* forest mean abundance of *U. cordatus* was 50% lower than in the Caeté estuary (Warner 1969), and lower densities were also recorded in Southern Brazil (1.1 indiv. m^{-2}, Branco 1993). However, in many other exploited populations in Brazil, higher abundance and biomass values were observed. In Maranhão, Castro (1986) recorded a mean density of 2.9 crabs m^{-2} in habitats dominated by large adults and biomass was about 2.5 times higher than in the Caeté estuary. The reason for the higher values, e.g. more favourable environmental factors (primary productivity) or a lower exploitation rate are not known (comparable harvest data are not available). In the present study high crab densities of more than 4 indiv. m^{-2} were observed only in areas where juveniles dominated.

Overall, the biomass of *U. cordatus* is very high when compared to other epibenthic species, in the Caeté estuary it accounts for 84% of the total epifaunal biomass (Koch and Wolff 2002). The crab population at Furo Grande is sustained by an average daily litter production of 4.5 g m^{-2} in the *R. mangle* dominated forest stands and it was estimated that the overall daily food intake by the *U. cordatus* population corresponds to 81% of the daily litter production (Nordhaus 2004). By retaining nutrients and energy within the forest and by enriching the detritus with shredded leaf material and faeces, *U. cordatus* acts as a keystone species in the mangrove forest ecosystem (Koch and Wolff 2002; Schories et al. 2003; Nordhaus 2004).

4.4 Commercial catch, CPUE and fisheries potential

The strong selectivity of the *U. cordatus* fishery for large males (for life-stock sales) has both a traditional and a commercial background. Crab collectors do not take females as they fear that otherwise the population will become extinct (pers. comm. J. Deus Dete and others). This traditional harvesting behaviour is enforced by consumers who typically choose the largest specimens (due to their higher meat content), which is reflected by our results: 98% of the catch was represented by males with a *CW* of ≥6.5 and mean capture size was 7.4 cm. In contrast to many other crustacean fisheries that are seriously affected by the non-compliance of fishermen with minimum capture sizes (Tewfik and Béné 2004) the Caeté fishermen (and consumers) only consider crabs larger than legal minimum capture size (6.0 cm *CW*) as being market-sized. The strong influence of the market on the size of the harvested crabs is also suggested by the finding that fishermen did not compensate the decrease in CPUE in 1999 and 2000 by capturing smaller crabs. This and the fact that the smallest landed specimens were always larger than the size at 50% male maturity (do Vale, unpubl.), suggests that the reproductive potential of the Caeté crab population is currently not being endangered by the fishery.

Given a mean freshmass of 53 g m^{-2} for market sized males (*CW* of ≥6.5 cm; pooled over all *R. mangle* sites) and a production to biomass ratio of 0.16 (Koch and Wolff 2002), an annual production of around 8.5 g m^{-2} of exploitable biomass or 1200 t is estimated for the Caeté mangroves. Extrapolating these data to the entire federal state of Pará and its eastern neighbour state Maranhão, which together comprise 889 400 h of mangrove forest (Kjerfve and de Lacerda 1993) and include 65% of the countries mangrove stands, gives an estimate of 76 000 t of annually exploitable *U. cordatus* biomass (males ≥6.5 cm *CW*) for this region. Despite the slow growth and low productivity of this species, its high biomass and abundance and the large extension of its habitat makes this semi-terrestrial crab a resource with a high fishery potential. The potential yield is comparable to or exceeds other important crab fisheries world-wide (e.g. USA 2001: 68 509 t hard blue crabs, 16 525 dungeness crabs, 11 246 t snow crabs; O'Bannon; Chesapeake Bay 1995: 33 500 t blue crabs, Rugolo et al. 1998; Europe 2001: 84 419 t crabs and sea-spiders; FAOstat-data 2004).

5 Conclusion

The *U. cordatus* population of the Caeté estuary shows no signs of overharvesting, despite de facto open access exploitation for over 30 years and the slow growth of the crabs. Recruitment overfishing does not occur as capture size was well above the size of first maturity and only large male specimens are harvested. This is due to market demands (large males only), to the large extension and relatively healthy state of the mangroves of the Caeté estuary and probably also to the way how *U. cordatus* is harvested. The local capture techniques (arm and hook) do not allow for total extraction of crabs in any given spot: areas with dense mangrove roots provide refugia as crabs cannot be harvested when their burrows are twisted around or blocked by roots. Therefore, the fishery has a high potential for sustainability. However, crab collectors could begin to use less sustainable capture techniques such as lassos and meshes. These entangle crabs when they emerge from their burrows and even those specimens burrowing between roots become fishable. Dense root patches would then no longer act as refugia and buffer against overexploitation. In other parts of Brazil, where these techniques are frequently used, fisheries yields have dropped significantly (Maneschy 1993; Botelho et al. 2000).

While CPUE has decreased by 15% between 1997 and 2003 in our study area, crab collectors have not counteracted this decline by harvesting smaller crabs, reflecting the strong market control on the size of the captured crabs. However, management plans are needed that particularly consider the economic and social sustainability of the *U. cordatus* fishery, which seem to run risk well before the biological one (Glaser and Diele 2004). Harvesting, processing, transporting and marketing of *U. cordatus* generate the main part of the income for over half of the rural households in the area (Glaser 2003). The Caeté estuary forms part of a recently proposed coastal co-management area that aims at turning the de facto open access to the region's natural resources, including *U. cordatus*, into effective common property management (Glaser and da Silva 2004). The importance of setting incentives in co-management so that participants acting in self interest will promote conservation and thus society's interest was stressed by Hilborn et al. (2004 and 2005).

Data upon growth, reproduction and recruitment are currently being analysed to model different exploitation scenarios and develop management strategies using matrix and length–based models (Miller 2001; Smith and Addison 2003; Zhang et al. 2004). Future works should also address the ecological sustainability of this fishery, i.e. the possible effects of the exploitation of this keystone species on the dynamics and functioning of the mangrove ecosystem.

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References

Alcântara-Filho P., 1978, Contribuição ao estudo da biologia e ecologia do caranguejo-uçá, *Ucides cordatus cordatus* (Linnaeus, 1763) (Crustacea, Decapoda, Brachyura), no manguezal do Rio Ceará (Brasil). Arq. Ciênc. Mar. 18, 1-41.

Boeger W.A., Pie M.R., Ostrensky A., Patella L., 2005, Lethargic crab desease: Multidisciplinary evidence supports a mycotic etiology. Mem. Inst. Oswaldo Cruz 100, 161-167.

Botelho E.R., Dias A.F., Ivo C.T.C., 1999, Estudo sobre a biologia do caranguejo-uçá, *Ucides cordatus cordatus* (Linnaeus, 1763), capturado nos estuários dos rios Formosos (Rio Formoso) e Ilhetas (Tamandaré), no estado de Pernambuco. Bol. Tec. Cient. Cepene 7, 117-145.

Botelho E.R., Santos M.C.F., Pontes A.C.P., 2000, Algumas considerações sobre o uso da redinha na captura do caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763), no litoral sul de Pernambuco-Brasil. Bol. Tec. Cient. Cepene 8, 55-71.

Branco J., 1993, Aspectos bioecológicos do caranguejo-uçá (Linnaeus 1763) (Crustácea, Decapoda) do manguezal do Itacorubi, Santa Catarina, BR. Arq. Biol. Technol. 36, 133-148.

Cabrera Pena J., Vives Jiminnez F., Solano Lopez Y., 1994, Size and sex ratio of *Ucides occidentalis* (Gecarcinidae) in a mangrove of Costa Rica. Uniciencia 11, 97-99.

Castro A. C. L., 1986, Aspectos bio-ecológicos do caranguejo-uçá, *Ucides cordatus cordatus* (Linnaeus, 1763), no estuário do Rio dos Cachorros e Estreito do Coqueiro, São Luís, Maranhão. Bol. Lab. Hidrobiol. 7, 7-26.

Cicin-Sain B., Knecht R.W., 1998, Integrated coastal and ocean management: Concepts and Practices. Island Press, Washington, DC.

Clark J.R., 1994, Integrated management of coastal zones. FAO Fish. Tech. Pap. Roma.

Conan G.Y, 1985, Periodicity and phasing of molting. In: Wenner A. M. (Ed.) Factors in adult growth. Rotterdam, A. A. Balkema, pp. 73-100.

De Boer W.F., Longamane F.A., 1996, The exploitation of intertidal food resources in Inhaca Bay, Mozambique, by shorebirds and humans. Biol. Conserv. 78, 295-303.

Delevati Colpo K., Negreiros-Fransozo M.L., 2004, Comparison of the population structure of the fiddler crab *Uca vocator* (Herbst, 1804) from three subtropical mangrove forests. Sci. Mar. 68, 139-146.

Diele K., 2000, Life history and population structure of the exploited mangrove crab *Ucides cordatus cordatus* (Linnaeus, 1763) (Decapoda: Brachyura) in the Caeté Estuary, North Brazil. ZMT Contrib. 9, Bremen.

Ehrhardt N.M., Die D.J., Restrepo, V.R., 1990, Abundance and impact of fishing on a stone crab (*Menippe merceneria*) population in Everglades National Park, Florida. Bull. Mar. Sci. 46, 311-323.

FAOSTAT data 2004, Fisheries Data, last accessed October 2004. (`http://faostat.fao.org/faostat/form?collection=Fishery.Primary&Domain=Fishery&servlet=1&hasbulk=0&version=ext`)

Feliciano C., 1962, Notes on the biology and economic importance of the land crab *Cardisoma guanhumi* Latreille of Puerto Rico. Spec. Contrib. Inst. Mar. Biol., Univ. of Puerto Rico, pp.1-29.

Fisher R.A., 1930, The genetical theory of natural selection. Clarendon Press, Oxford.

Foale S., 1999, Local ecological knowledge and biology of the land crab *Cardisoma hirtipes* (Decapoda: Gecarcinidae) at West Nggela, Solomon Islands. Pac. Sci. 53, 37-49.

Glaser M., 2003, Interrelations between mangrove ecosystems, local economy and social sustainability in the Caeté estuary, North Brazil. Wetl. Ecol. Manage. 11, 265-272.

Glaser M., Diele K., 2004, Asymmetric outcomes: Assessing central aspects of the biological, economic and social sustainability of a mangrove crab fishery, *Ucides cordatus* (Ocypodidae), in North Brazil. Ecol. Econ. 49, 361-373.

Glaser M., da Silva R., 2004, Prospects for the co-management of mangrove ecosystems on the North Brazilian coast: Whose rights, whose duties and whose priorities? Nat. Res. Forum 28, 224-233.

Hartnoll R.G., 1982, Growth. In: Abele L.G. (Ed.) The biology of Crustacea, Academic Press, New York, pp.11-196..

Hartnoll R.G., Gould P., 1988, Brachyuran life-history strategies and the optimisation of egg production. Symp. Zool. Soc. Lond. 59, 1-9.

Hartnoll R.G., Bryant, A.D., 1990, Size-frequency distributions in decapod crustacea - the quick, the dead, and the cast-offs. J. Crust. Biol. 10, 14-19.

Holme N.A., McIntyre A.D., 1984, Methods for the study of marine benthos. IBP Handbook no.16. Blackwell Scientific Publication.

Hilborne R., Punt A.E., Orensanz J., 2004, Beyond band-aids in fisheries management: fixing world fisheries. Bull. Mar. Sci. 74, 493-507.

Hilborne R., Orensanz J.M., Parma A.M., 2005, Institutions, incentives and the future of fisheries. Phil. Trans. R. Soc. B 360, 47-57.

INMET, 1992, Normais climatológicas (1961-1990). Tech. Rep., Instituto Nacional de Meterologia. http://www.inmet.gov.br.

Ivo C.T.C., Dias A.F., Mota I.R., 1999, Estudo sobre a biologia do caranguejo-uçá, *Ucides cordatus cordatus* (Linnaeus, 1763), capturado no Delta do Rio Parnaíba, estado Piauí. Bol. Tec. Cient. Cepene 7, 53-84.

Jennings S., Polunin N.V.C., 1996, Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. J. Appl. Ecol. 33, 400-412.

Jennings S. J.D., Reynolds D., Mills S.C., 1998, Life history correlates of responses to fisheries exploitation. Proc. R. Soc. London. 265, 333-339.

Jennings S.J.D., Reynolds J.D., Polunin N.V.C., 1999, Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conserv. Biol. 13, 1466-1475.

Koch V., Wolff M., 2002, Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Mar. Ecol. Prog. Ser. 228, 119-130.

Koch V., Wolff M., Diele K, 2005, Comparative population dynamics of four sympatric fiddler crab species (Ocypodidae, Genus *Uca*) for a North Brazilian mangrove ecosystem. Mar. Ecol. Prog. Ser. 291, 177-188.

Kjerfve B., de Lacerda L.D., 1993, Management and status of the mangroves in Brazil. In: de Lacerda, L.D. (Ed.) Conservation and sustainable utilisation of mangrove forests in Latin America and Africa regions, Part 1, Latin America, ISME, Inter.Soc. Mangrove Ecosystems, Okinawa, pp. 245-272.

Krause G, Schories D., Glaser M., Diele K., 2001, Spatial patterns of mangrove ecosystems: The Bragantinian mangrove of North Brazil (Bragança, Pará). Ecotropica 7, 93-107.

Maneschy M.C., 1993, Pescadores nos manguezais: Estratégias técnicas e relações sociais de produção na captura de caranguejo. In: Furtado L.G., Leitão W., de Mello A.F. (Eds.) Povos das Águas. Realidade e Perspectivas na Amazônia.. PR/MCT/CNPq. Museu Paraense E. Goeldi, Pará, Brazil, pp. 19-62.

McKoy J.L., Esterman D.B., 1981, Growth of tagged rock lobsters (*Jasus edwarsii*) near Stewart Island, New Zealand. New Zeal. J. Mar. Freshw. Res. 19, 457-466.

Mehlig U., 2001, Aspects of tree primary production in an equatorial mangrove forest in Brazil. ZMT Contrib. 14, Bremen.

Menezes M.P.M., Berger U., Worbes M., 2003, Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, north Brazil. Wetl. Ecol. Manage. 11, 233-242.

Miller T.J., 2001, Matrix-based modeling of blue crab population dynamics with applications to the Chesapeake Bay. Estuaries 24, 535-544.

Nordi N., 1994, A produção dos catadores de caranguejo-uçá (*Ucides cordatus*) na regiao de Várzea Nova, Paraíba, Brasil. Ver. Nordestina Biol. 9, 71-77.

Nordhaus I., 2004, Feeding Ecology of the semi-terrestrial crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in a mangrove forest in northern Brazil. ZMT Contrib. 18, Bremen.

O'Bannon B.K., 2002, Fisheries of the United States 2001. p. 18. National Marine Fisheries Service, Office of Science and Technology, Fisheries Statistics and Economics Division. U.S. Dept. Commerce. Silver Spring, Maryland. http://www.st.nmfs.gov/st1/fus/fus01/2001-fus.pdf

Ogawa M., Alves T.T., Caland-Noronha M.C, Araipe C.A.E, Maia E.L., 1973, Industrialização do caranguejo Uçá, *Ucides cordatus* (Linneaus). I – Técnicas para o processamento do carne. Arq. Ciênc. Mar. 13, 31-37.

Ostrensky A., Sternhain U.S., Brun E., Wegbecher, F.X., Pestana D., 1995, Technical and economic feasibility analysis of the culture of the land crab *Ucides cordatus* (Linnaeus, 1763) in Paraná coast, Brazil. Arq. Biol. Tecnol. 38, 939-947.

Pauly D., 1998, Tropical fishes: patterns and propensities. J. Fish Biol. A 53, 1-17.

Pinheiro M.A.A., Fiscarelli A.G., Hattori G.Y., 2005, Growth of the mangrove crab *Ucides cordatus* (Brachyura, Ocypodidae). J. Crust. Biol. 25, 293-301.

Rugolo L.J., Knott K.S., Lange A.M., Crecco V.A., 1998, Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun). J. Shellfish Res. 17, 493-517.

Schories D., Barletta-Bergan A., Barletta M., Krumme U., Mehlig U., Rademaker V. 2003, The keystone role of leaf-removing crabs in mangrove forests of North Brazil. Wetl. Ecol. Manage. 11, 243-255.

Smith M.T., Addison J.T., 2003, Methods for stock assessment of crustacean fisheries. Fish. Res. 65, 231-256.

Taissoun E., 1974, El cangrejo de tierra *Cardisoma guanhumi* (Latreille) en Venezuela. I. Métodos de captura, comercializacion e industrializacion. II. Medidas e recomendaciones para la conservacion de la espécie. Bol. Cent. Invest. Biol., Univ. del Zulia, 10, 1-36.

Underwood A.J., 1997, Experiments in ecology. Cambridge University Press.

Uphoff J.H. Jr., 1998, Stability of the blue crab stock in Maryland's portion of Chesapeake Bay. J. Shellfish Res. 17, 519-528.

Warner G.F., 1969, The occurrence and distribution of crabs in a Jamaican mangrove swamp. J. Anim. Ecol. 38, 379-389.

Wenner A.M., 1972, Sex ratio as a function of size in marine Crustacea. Am. Nat. 106, 321-350.

Willson M.F., Pianka E.R., 1963, Sexual selection, sex ratio and mating systems. Am. Nat. 97, 405-407.

Zhang Z., Hajas W., Phillips A., Boutillier J.A., 2004, Use of length-based models to estimate biological parameters and conduct yield analyses for male Dungeness crab (*Cancer magister*). Can. J. Fish. Aquat. Sci. 612, 2126-2134.