**Growth and mortality of the exploited mangrove crab *Ucides cordatus* (Ucididae) in N-Brazil**

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**Abstract**

Reliable estimates of growth and mortality parameters are crucial for understanding how populations of exploited species may respond to shifts in fishing pressure. Results of previous studies on growth of the ecologically and economically important mangrove crab *Ucides cordatus* in Brazil differ strongly and age estimates for minimum legal capture size (60 mm carapace width) range between less than one and 6-10 years. These discrepancies are probably due to inherent problems of the applied methods, namely laboratory based observations and cohort-analyses. The present paper takes a new approach by measuring individual growth increments of *U. cordatus* in situ. Crabs were measured, tagged, released into 100 m² field enclosures and periodically recaptured. There was no indication of an enclosure effect and 209 growth increments were obtained from specimens measuring 20.5 to 89.5 mm in carapace width (CW). For improving the size coverage of the von Bertalanffy growth curve, first instar juveniles were reared in the laboratory up to an age of six months. Their average percent size increase (PI) was 22.57 ± 6.75% during biweekly measurements, resulting in a CW of

7.8 to 11.5 mm after six months. Average PI of the enclosure crabs ranged between

10.87 ± 1.17% (indiv. < 40 mm CW) and 1.43 ± 0.87% (indiv. > 80 mm CW) per moult

and two large females had moulted without growing. Growth analysis revealed a larger

asymptotic size in males than in females (89 mm versus 72 mm) while the growth

parameter K of the von Bertalanffy growth function (VBGF) was lower in males (0.17

versus 0.25), resulting in similar growth performance of the two sexes (males: 1.16;

females: 1.10). Age at legal minimum capture size estimated by the inversed VBGF was

6.13 years in males and 7.38 years in females, corroborating the mid to upper range of

earlier growth estimates. Mortality parameters (Z, M and F) were calculated using length

converted catch curves. Z in males was higher than in females (0.69 versus 0.49), as

expected from the male-biased fishery. M, F and the exploitation rate E were estimated

for three different scenarios taking into account the uncertainty of the age/size of

functional maturity. Our study provides key information for the sustainable management

of the *U. cordatus* fishery and confirms that the species is relatively slow growing and

long lived (> 10 yrs), suggesting a high vulnerability to overfishing.

## 1. Introduction

Knowledge of growth and mortality parameters is fundamental to understand how exploited species respond to fishery and how a shift in fishing pressure may affect populations and ecological performances. This paper aims at determining growth and mortality parameters for the mangrove crab *Ucides cordatus cordatus (*hereafter referred to as *U. cordatus*) in N-Brazil. This large species (carapace width, CW: males > 90 mm; females > 70 mm) is the main leaf litter feeder in Brazilian mangroves and plays an important ecological role by processing up to 81% of the litter production in some areas (Nordhaus et al. 2006). Artisanal fishermen have been harvesting *U. cordatus* for decades along the Brazilian coast, and in recent years several crab populations have experienced strong declines due to deforestation, a fungal disease and overfishing (Nordi, 1994; Botelho et al., 2000; Alves et al., 2005; Boeger et al., 2007). The fishery targets mostly large males and in some areas yields are still six to eight tons per km² per yr (e.g. Caeté estuary, N-Brazil, Diele et al., 2005, Diele et al. in press). Current national minimum legal capture size (MLCS) is 60 mm CW (IBAMA N° 034/03-N, 24.06.2003).

To our knowledge, no data on mortality parameters of *U. cordatus* have been published as yet. While several studies investigated the growth of the species, large discrepancies exist among measured growth rates. Extrapolations from juvenile growth studied in the laboratory indicate that the species is slow growing, with an age of 6 to 10 years at 60 mm MLCS (Geraldes and Calventi, 1983; Ostrensky et al., 1995). Cohort-studies from NE-Brazil based upon size-frequency distributions of field-sampled specimens contradict these estimates. They indicate a manifold faster growth of *U. cordatus* with less than a year of age at 60 mm MLCS (Ivo et al., 1999; Vasconcelos et al., 1999; Monteiro and Coelho Filho, 2000). Pinheiro et al. (2005) also applied cohort-analyses, but derived

almost five folds higher age estimates at 60 mm MLCS for a southern Brazilian crab population compared to the NE-Brazilian cohort studies. The large differences among the published growth estimates suggest that methodological problems inherent to cohort analyses rather than biogeographic differences may be the cause: According to Hartnoll (1982), it is improbable that year classes can be reliably discriminated in later growth of large long-lived crustaceans, where clearly distinguishable cohorts are generally lacking, thus complicating growth analyses. This could well be the case in *U. cordatus*, where all cohort analyses were based upon size-frequency in which larger specimens were more frequent than smaller ones. Laboratory growth studies (see above) on the other hand, may not adequately represent the growth performance of free-living crabs. Clearly, the strongly diverging growth estimates so far available for *U. cordatus* would result in completely different management scenarios of this ecologically and economically important species. Therefore alternative methods are needed to help estimate the species' growth more reliably.

Here we take a new approach by calculating growth parameters of *U. cordatus* from direct size increment measurements of a wide range of different sized crabs in the field. Data were obtained from tagged and recaptured specimens that were kept in 100m² enclosures in a N-Brazilian *Rhizophora mangle* dominated forest stand. In addition to these field studies, growth of first instar crabs up to an age of six months was monitored in the laboratory to ensure good coverage of the whole growth curve. Mortality parameters (Z, M and F) were estimated using length converted catch curves derived from the calculated growth parameters and population census data (Diele et al., 2005). Furthermore the exploitation rate (E) of the males was estimated. We compare our results with previous studies and provide important information for the sustainable management of the fishery of *U. cordatus*.

**2. Material and Methods**

2.1 Study area

The study area is located in northern Brazil, where approx. 65% of the countries

mangrove forests occur. Field experiments were performed in a *Rhizophora mangle*

dominated mangrove stand in the northern part of Bragança peninsula, Caeté estuary

(W 46° 76´- W 46°52´and S 0°80´- S1°07´). The region experiences semidiurnal macro-

tides with amplitude of up to 5m. Rainfall is approx. 2,500mm per year, mostly falling

between January and June, the rainy season. Average air (24-28°C) and water (27-

30°C) temperatures vary little over the year (INMET, 1992; unpublished data of the

research project "Mangrove Dynamics and Management", MADAM). *U. cordatus* is

artisanally fished year round in the study area (Diele et al., 2005; Diele et al. in press).

2.2 Growth studies

A combination of laboratory studies (focussing on first instar crabs) and field studies

(focussing on larger/older crabs) was used to obtain growth estimates for specimens of a

wide size range.

2.2.1 Laboratory experiments

The growth of seven first instar crabs cultivated from field captured megalopae that had

metamorphosed in the laboratory (day of metamorphosis = age 0) was monitored for 16

to 28 weeks in 1998 (size of first instars between 1.37 - 1.55 mm CW). The crabs were

kept under ambient light (12 h light / 12 h dark) and temperature conditions (26.0 ± 1.3

°C) in a shaded outdoor laboratory at the University of Bragança (UFPa). Each crab was

placed in a 500ml plastic container filled to one side with mangrove sediment and to the

other side with estuarine water. The sediment contained infauna, such as the abundant

capitellid polychaete *Notomastus lobatus*, that served as a food source. *R. mangle* leaf litter and shredded particles thereof were placed on the sediment surface as additional food. When crabs had reached a size of approx. 3 mm CW, they were transferred to individual 10ltr buckets filled two thirds with mangrove sediment and one third with estuarine water. Water was changed every second day. Approx. every two weeks the sediment was carefully sieved and the crabs' carapace width measured to the nearest 0.1mm under a dissection microscope. Growth increment was calculated by comparing the CW's between subsequent measurements. Due to the small size of the juveniles, their sex was not determined. For reducing mortality, sieving was postponed when burrow entrances were plugged (as an indicator of moulting activities) and crabs thus possibly soft-shelled. Sieving was only performed the day after a closed burrow had been re-opened by the inhabitant to ensure that the crabs' integuments had hardened.

2.2.2 Field experiments

For obtaining growth increment data from free-living crabs, 125 larger burrows plugged over several days, abundant during the dry season, were excavated. According to local fishermen, such burrows are typically occupied by moulting crabs. Seasonal moulting, at least in larger *U. cordatus* specimens, is also known from other areas in Brazil (Nascimento, 1993) while the crabs reproduce during the rainy season only (Alves, 1975; Castro, 1986; Diele et al., 2005). The excavated burrows were carefully searched for recently moulted crabs and their exuviae. Only in five cases (three males, two females) sufficient parts of the old exoskeleton were found to allow reconstruction of the pre-moult size and to compare it with the new size of the already hardened crab. Due to the low success rate of the above approach, several in situ capture-recapture experiments were conducted between 1997 and 2000/2001, with crabs kept in 100m$^2$ field enclosures. The enclosures were erected in a *R. mangle* dominated mangrove

stand, the favoured habitat type of the crabs. Enclosure walls were made of interlocking wooden (1997 and 1998) or PVC laths (1999 – 2000/2001, see Fig. 1) that reached 1.0 to 1.2 m into the sediment and measured 1.5 m above the surface. Every 10 cm, 15 mm holes were drilled into the walls to allow for unimpeded water flow. Food for the enclosed crabs was provided by natural litter falling from the *R. mangle* canopy above, as well as by younger *R. mangle* trees planted inside the enclosure. Behavioural observations of free-living crabs have shown that *U. cordatus* is very territorial and does not move far away from its burrows during foraging (average: 19cm, max: 1m; Nordhaus et al., 2009). Daily *R. mangle* leaf litter fall in the forest was approx. 3 g DW m$^{-1}$ (Nordhaus et al., 2006).

INSERT FIGURE 1

To facilitate recapture, the enclosures were subdivided into one 75 m² compartment for larger specimens and two 12.5 m² compartments for smaller crabs (Fig. 1). Several runs of capture-recapture experiments were performed between 1997 and 2000/2001 (Table 1 and 2). Prior to the onset of each experiment, a professional crab collector removed all specimens inside the enclosures. These were then stocked with males and females measuring between 20.5 to 89.2 mm CW. To compensate for the edge effect, crabs were released at densities slightly below natural (75m² compartment: approx. 1.4 indiv. m$^{-2}$ versus natural average densities of 1.65 indiv. m$^{-2}$ for larger crabs; 12.5m² compartments: 2.24 to 3.2 indiv. m$^{-2}$ versus natural densities of 4.38 indiv. m$^{-2}$ for smaller crabs, Diele et. al., 2005). Preliminary observations had indicated that the enclosure walls did not fully prevent movements in and out of the enclosures; therefore only tagged specimens were released for enabling later identification (Table1). Two different tagging methods were applied, depending on the size of the crabs:

(i) Smaller specimens were heatbranded with a soldering iron for approx. 2 seconds on the carpus of the larger cheliped, leaving a small white dot. After crabs had moulted, the dot had faded but was still visible. In contrast to PIT-tagging (see below) branding did not allow identifying crabs individually. However, only specimens belonging to specific size classes and/or identical handedness per size class were released (Table 1), so that average growth increment per size class could still be reliably measured. Between 1997 and 1999 a total of 189 heatbranded crabs with a CW between 20.5 and 45.5 mm were released into the two 12.5 m² compartments of the enclosures (Table 1). Recaptured crabs were not used again for subsequent capture-recapture experiments.

INSERT TABLE 1

(ii) Crabs > 40 mm were large enough for carrying individual passive transponders (PIT-tags). These tags were implanted into the ventral basis of the merus of the third pereiopod. Legs were rarely shed during or after injection of the tag and the wound healed within two weeks (as observed in 25 test animals kept in the laboratory up to 3 months after marking). The PIT tag (Trovan ID 100, AEG / Telefunken) consists of a glass-encapsulated cylinder measuring 2.2 mm in diameter and 11 mm in length and was injected with a pre-sterilised needle using a hand injector. The tag has an operating frequency of 128 kHz and provides a unique 12-digit code when energised by a 128 kHz external power source provided by the Trovan LID 500 hand-held reader exciter (maximum reading distance 16 cm). PIT tags have also been successfully applied for monitoring growth in other crustaceans (*Macrobrachium rosenbergii* and *Cancer magister*: Prentice, 1990; *Paralithodes camtschaticus*: Donaldson et al., 1992; Pengilly and Watson, 1994). Between 1999 and 2000 altogether 134 different PIT-tagged males (40.0 – 89.2 mm CW) and 114 different PIT-tagged females (40.0 – 69.7 mm CW) were

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released into the enclosures (Table 2). Recaptured specimens were set free again for subsequent capture-recapture runs if they had no injuries or limb losses.

For testing the impact of tagging on the survival of the crabs, 12 heatbranded, 12 PIT-tagged and 12 untreated specimens were kept in the laboratory for 8 weeks, during which none of the crabs died. In all field experiments only specimens with a full set of pereiopods were used in order to avoid bias in growth increment due to regeneration. All heatbranded and PIT-tagged crabs were tagged and released within two days after their first collection. Only crabs in intermoult stage with fully hardened carapaces were released. Colouration and integrity of their integuments indicated whether they had moulted recently (early intermoult: dorsally shiny blue, ventrally bright white, smooth surface, no injuries) or were in later intermoult stage (dorsally faint blue carapace, ventrally darker white, large specimens often with injuries).The carapace width of both released and recaptured crabs was measured with a calliper rule to the nearest 0.1 mm.

2.2.3 Growth models

Growth per moult was calculated (i) as percentage size increment (PI = postmoult CW – pre-moult CW / pre-moult CW x 100) and (ii) as absolute increment (AI = post-moult CW – pre-moult CW). The relationship between PI or AI and pre-moult CW was calculated by simple linear, log-linear or quadratic equations.

The von Bertalanffy growth function (VBGF) (von Bertalanffy, 1934; Ricker, 1975) was used to describe the growth of the crabs:

$$CW_t = CW_\infty \cdot (1-e^{-(K \cdot (t-t0))}) \tag{1}$$

where $CW_t$ is the length at time t, $t_0$ is the age at zero length and K is the curving

parameter of the growth function. Growth parameters were estimated using a non-linear

iterative fitting algorithm (Generalized Reduced Gradient – GRG2) (Fylstra 1998),

provided in a spreadsheet developed by Brey (2001). The optimum combinations of K

and $CW_\infty$ values were obtained by varying $CW_\infty$ until the coefficient of variation for K was

minimized. $t_0$ was set to -0.08 as larval development until moulting to juvenile comprises

approx. one month in *U. cordatus* (Diele 2000, Diele and Simith 2006). Munro´s $\Phi'$

(Pauly and Munro, 1984) was used to calculate the growth performance of the fiddler

crabs:

$$\Phi' = \log_{10}(K) + 2 \cdot \log_{10}(CW_\infty) \tag{3}$$

This index allows for comparison of the growth potential of different species and thus

serves to evaluate patterns along latitudinal gradients and/or among taxonomic groups.


Age estimates were calculated by using the inversed VBGF. The maximum lifespan or

longevity was estimated by the equation of Taylor (1958): $tmax = (3/K)$ and as the age

where 95% $CW_\infty$ is reached.


2.3 Mortality

Total mortality rate (Z) for males and females was calculated using length converted

catch curves (Ricker, 1975; Sparre et al., 1989) assuming type III survivorship (Caddy

and Sharp, 1986) and single exponential mortality. To calculate the model, size

frequency distributions of the *U. cordatus* population of the Caeté estuary were taken

from Diele et al. (2005), and the parameters of the VBGF described above were used.

For the regressions only the right, descending arm of the catch curve was considered as

the left arm represents smaller animals that might not have been sampled quantitatively.

Z equals the negative slope of the regression line. An Excel spreadsheet provided by Brey (2001) was used for the catch curve analysis.

Natural mortality (M) was calculated after the empirical formula of Rikhter and Efanov (1976):

$M = 1.521 / (T_{CW50}{}^{0.72}) - 0.155$

Where $T_{CW50}$ is the age at which 50% of the population is mature. $T_{CW50}$ was calculated by transforming the size at gonadal maturity data of the local crab population (Vale, 2003) to age using the inverse VBGF. As it is common that specimens are physiologically mature but do not yet reproduce, M was also calculated using $T_{CW75}$ and $T_{CW100}$, thus the age at which 75% and 100% of the population reaches gonadal maturity. Fishing mortality (F) was calculated by subtracting M from Z for the exploited males and by dividing F by Z, their exploitation rate (E) was estimated. As females are hardly ever harvested, their M should equal Z.

## 3. Results

3.1 Growth increment

3.1.1 Laboratory data

During the first two weeks after metamorphosis, the small juveniles built burrows at or just above the water surface. Thereafter they burrowed in more elevated areas. Crabs and/or their walking tracks were rarely seen on the sediment surface during the first 16 weeks and the leaf material offered showed no feeding marks during this time. Instead it was observed that the small crabs feed upon the infaunal polychaete *Notomastus lobatus* (n = 5 observations during sieving for CW measurements). The number of

walking tracks increased after week 16 and feeding marks on plant matter indicated that crabs began to forage on the sediment surface.

The carapace width (CW) of the seven crabs cultivated for 16 to 28 weeks in 1998 continuously increased during the first three biweekly measurement intervals. Thereafter size did not always increase at subsequent measurements indicating a decrease in moulting frequencies (Fig. 2). At 10 to 11 weeks the crabs had reached a CW of 3.7 to 4.6 mm. Size differences between individuals augmented with age and at week 27/28 the largest specimens was 32% larger than the smallest still alive (11.5 versus 7.8 mm CW) (Fig. 2), despite similar sizes at first instar (1.51 and1.52 mm CW, respectively).

INSERT FIGURE 2

INSERT TABLE 3

The relationship between pre-moult size and percent growth increment (PI) or absolute increment (AI) was fitted with a linear, log-linear and quadratic model. The coefficient of determination ($R^2$) was highest when the quadratic model was applied (Table 3) and significant both in PI (P<0.01) and AI (P<0.001). PI ranged between 10.4% and 47.4% between two measurements, which, in the latter case, probably referred to more than one moult, given that the value is well outside the other measures (Fig. 3). Average PI was 22.57 ± 6.75%. PI decreased significantly with size, while AI increased until a pre-moult size of approx. 7.5 mm, when it began to decrease (Fig. 3).

INSERT FIGURE 3

3.1.2 Field data

50% of the crabs tagged and released into the field enclosures were recaptured at least once (n = 217) yielding a total of 244 recaptures, when including multiple recaptures of the same specimens (Table 4). From the heatbranded crabs, 52 males and 54 females were recaptured. In the case of the PIT-tagged crabs, 72 and 39 different males and females were recaptured (including two recaptures made 0.9m and 1.3m outside the enclosure wall), yielding 73 and 30 size increment data, respectively (Table 4). In total 125 growth increments from males (pre-moult CW 20.5 to 82.4 mm) and 84 from females (pre-moult CW 20.5 and 69.6 mm) were obtained from the capture recapture experiments.

INSERT TABLE 4

From the PIT-tagged crabs, 56 males were recaptured once. Eight had not yet moulted at the time of recapture, as indicated by the appearance of their carapace, while the remaining ones had obtained a new and larger exoskeleton. Another 15 males were recaptured two or three times with one or two increases in size. In females, 32 PIT-tagged specimens were captured once. 13 had not yet moulted at the time of recapture, two had moulted without attaining a larger size (66.0 and 66.7 mm CW; their cephalothorax and all limbs were intact) and 17 had increased in size. Another seven females were caught two or three times having attained one or two size increments.

The relationship between growth increment and pre-moult size was determined using 189 data sets for which the observed increase in size could confidentially be attributed to one single moulting event, according to the appearance of the crab's carapaces at release and recapture and their specific times at free (males: 113 increments; females

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75). Linear, log-linear and quadratic models were used to fit the relationships. The coefficient of determination ($R^2$) was highest when the quadratic model was applied (Table 3). Maximum percent increment (PI) per moult was 17.4% and 16.4 % in males and females, respectively, and occurred in small crabs with a pre-moult CW of 30.5 mm (Fig. 4A and B). Minima were observed in large crabs: The lowest PI value, aside of the two cases of zero growth (see above), was 0.5% increment in a male with 82.4 cm pre-moult CW and 0.9 % in a female with a pre-moult CW of 64.7. In both sexes there was a significant, generally inversely proportional relationship between pre-moult size and percent growth increment (PI) (males: $R^2 = 0.612$; $P<0.0001$; females: $R^2 = 0.618$; $P<0.0001$; Fig. 4A and B, Table 5). The relationship was also significant for absolute growth (AI) (males: $R^2 = 0.400$; $P<0.0001$; females: $R^2 = 0.401$; $P<0.0001$, Fig. 4C and D), where largest increments were found in intermediate size classes. Observed maximum increments were 6.9 mm in males (pre-moult CW: 61 mm) and 5.8 mm in females (pre-moult CW: 35.5 mm). The smallest AI values per moult occurred in larger crabs, with minima of 0.4 mm (pre-moult CW: 82.4) and 0.6 mm (pre-moult CW: 64.7mm) in males and females, respectively (Fig. 4C and D). PI and AI data from new and old exoskeletons of five excavated free-living crabs (two females, three males, all untagged) fit well into the growth pattern observed for tagged crabs of corresponding size kept in the enclosures (Table 5).

INSERT FIGURE 4

INSERT TABLE 5

3.1.3 Moulting frequency

Several individual capture-recapture data sets give an indication of the frequency of moulting of *U. cordatus*:

Indication for at least two moulting events per year in intermediate-sized crabs, one in the dry and one in the rainy season:

(i)      All smaller males and females released into the 12.5m² enclosure compartments in June/July 1997 (31.00 to 33.00 mm CW cohort) had recently moulted as indicated by the early intermoult (EI) stage of their carapaces (Table 1). Five to six months after their release, 18 males (60%) and 17 females (65%) were recaptured. All had grown and their carapaces were in EI stage again.

(ii)     An intermediate-sized male measuring 48.2 mm CW released in May 2000 had grown by 2.7 mm when recaptured in November 2000. Both at release and recapture the crab's carapace was in EI stage.

(iii)    Three intermediate-sized males with a CW of 41.5 mm, 44.4 mm and 48.8 mm, all in EI stage when first released in November 2000, had increased in size by 4.0, 4.45 and 3.1 mm, respectively, when recaptured in May 2001.

(iv)    Another intermediate-sized male with a CW of 44.9 mm was released in June 2000 and recaptured 11 months later. Both times the crab was in EI. Its carapace had grown over proportionally by 10.8 mm CW suggesting that this male may have moulted at least twice during time at free.

Indication for variable moulting frequencies of similar sized crabs:

(i)      A male in EI stage measuring 48.2 mm CW released in May 2000 had grown by 2.7 mm when recaptured in November 2000, while another male in EI stage with 50 mm CW had not moulted during the same time span.

(ii)     Two males with a CW of 48.8 mm and 54.0 mm released in November 2000

(both in EI stage) had already grown when recaptured in May 2001, while two

other males of similar size (46.5 mm CW; 50.9 mm CW, EI stage) showed no

size increase during the same time at free.


Sex-specific differences

(i)  None of 13 females in EI stage released in November 2000 (pre-moult size 44.7

to 63.5, average size 52.3 ± 6.0 mm) had grown until their recapture in May

2001, whereas 5 out of 10 males in EI stage (41,5 to 69.0 mm, average 55.8 ±

8.7 mm) had increased in size during the same time span. The largest male

having moulted again had a CW of 62.7 mm.


Large crabs with a CW of approx. 60mm rarely moulted outside the dry season, as

indicated by the capture-recapture experiments as well as fishermen´s and own

observations on the appearance of their carapace throughout the year (Diele,

unpublished).


3.2.  Von Bertalanffy growth parameters and age at size estimates

Most of the species' size range was included in the assessment of the von Bertalanffy

parameters, resulting in a good coverage of the calculated growth curve with true

measurements (Fig. 5). The growth parameters show a good fit with $R^2$ values > 0.9

(Table 6). Females have a 23% smaller asymptotic size ($CW_\infty$) than males,

compensated by a 32% higher K-value, resulting in only minor variation in growth

performance between sexes (1.9%). The calculated asymptotic sizes ($CW_\infty$) in males

and females were 7 and 2 mm lower than the maximum size observed in the field

($CW_{max}$), respectively (Table 6).

INSERT TABLE 6

INSERT FIGURE 5

Age estimates calculated by the inversed VBGF for maximum sizes and the size at 50%, 75% and 100% gonadal maturity indicate an overall slow growth and long lifespan of *U. cordatus* (Table 7). Males and females reach 95% of the asymptotic size ($CW_{\infty 95}$) in 17.54 and 11.90 years, respectively. Age at the legal minimum capture size of 60 mm CW is 6.13 years in males (34.75% $CW_{\infty 95}$) and 7.38 years in females (60.02% $CW_{\infty 95}$). On Bragança peninsula, average CW of the commercially exploited males is 74 mm (Diele et al., 2005; Diele et al., in press; last data collection in December 2005), which corresponds to an age of approx. 9.5 years according to the VBGF parameters.

INSERT TABLE 7

3.3 Mortality and exploitation rates

The instantaneous rate of mortality (Z) estimated from the catch curve of the crab population sampling (Diele et al., 2005) was 0.69 ± 0.077 (95% confidence range) in males and 0.49 ± 0.086 (95% confidence range) in females (Fig. 6). Natural mortality estimates range between 0.58 and 0.35 for males, and 0.49 and 0.26 for females, depending upon the underlying age estimate for the three different sizes of gonadal maturity (Table 8). Based upon the Z and M-values, the fishery mortality (F) and exploitation rate (E) of males was calculated for each of the three M estimates ranging between 0.16 and 0.5 (Table 8).

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**4. Discussion**

4.1. Early juvenile behaviour and growth in the laboratory

The first instar crabs of *U. cordatus* cultivated in the laboratory stayed mostly below the sediment surface during the first four months of their post metamorphic life. Their cryptic lifestyle explains why we rarely found early juveniles in the field, unlike the juveniles of sympatric species, such as fiddler and grapsid crabs. Larger numbers of small *U. cordatus* specimens were recently found in NE-Brazil dwelling in burrow walls or sediment plugs of conspecific burrows (Schmidt and Diele, 2009). In contrast to older juveniles and adults who collect leaf litter on the forest floor (Nordhaus et al. 2009), early juveniles were observed to feed on infaunal polychaetes in the present work. The mangrove sediment of the Caeté estuary contains > 600 capitellid polychaetes (*Notomastus lobatus*) per m² (Beasley et al., in press), and nutrient-rich infaunal food is thus available for the young recruits. Foraging below ground reduces the risk of encountering predators and unfavourable abiotic conditions can also be avoided inside the sediment. Juveniles are generally less tolerant to environmental extremes than adults (Wolcott and Wolcott, 1988) and their comparably higher surface to volume ratio renders them more susceptible to desiccation. Hence, the humid underground habitat seems to offer many advantages for *U. cordatus* juveniles during their first months of life. Future research (including stomach content analyses of free living juveniles) will focus on the intrinsic and extrinsic factors triggering the switch from a life below ground as a carnivore to feeding above ground on very abundant plant food that is however comparably poor in nutrients, especially nitrogen.

Average relative size increment during the biweekly measurement intervals of the early juveniles was 22.6 ± 6.6 % and decreased with increasing size, as was also observed in

other crustaceans (e.g. Hartnoll, 1982 and 1983; Fletcher et al., 1990). Up to ten individual size increments per crab were noted within the six month of laboratory study. Whether this number equalled the number of moults or whether crabs moulted even more often is not clear as their size was checked every other week only. The young crabs varied considerably in size at same age, despite equal handling and similar initial carapace width (CW): A 1.51 mm first instar crab measured 11.53 mm after approx. 6 months, whereas a former 1.52 mm crab of the same cohort grew to only 7.83 mm within the same time span. A similar variation in size after 6 months was observed for a cohort of free-living crabs of the land crab *Gecarcinus ruricula* (Hartnoll et al., 2006). It is unlikely that variations in food quantity or quality have caused the diverging growth rates in our study, as crabs were supplied with equal amounts of well mixed sediment taken from the same location. The same holds true for sex specific differences in growth, these are generally negligible in crustaceans prior to the onset of maturity (Ehrhardt and Restrepo, 1989; Methot, 1989; Wolff and Soto, 1992). Alternatively we assume that genetic differences and/or differences in maternal fitness or larval "histories" have caused the diverging growth rates.

Clearly, growth is influenced by the amount (and quality) of food offered. For example, early *Ucides* juveniles cultivated in preliminary trials without sediment change for more than 50 days (Diele, unpubl.) grew distinctly slower than those in the present study that experienced biweekly sediment renewal and consequently more abundant food. Early juveniles kept without sediment by Pinheiro et al. (2005) grew also much slower, despite being offered small pieces of fish. The frequent moulting of the small laboratory crabs in the present study suggests that they were not food limited. To which extent, however, their size increments are representative for free-living specimens is unknown, even though the laboratory effect was minimized by cultivating them only during their first 6

months of their life, when being still relatively small and thus easy to handle. Since the natural habitat of early juveniles was recently discovered in the field, future studies should now try to monitor their growth in the field.

4.2 In situ growth rates, age at size estimates and longevity

The present study provides first direct in situ growth increment measurements of *U. cordatus* obtained from larger tagged specimens kept in field enclosures. Free living crabs showed a similar size increment after moulting as enclosed crabs of same size, suggesting that growth was not influenced by the applied experimental procedures. Our data show that *U. cordatus* is a slow growing species with a life span exceeding 10 years. Its growth can be well described by the von Bertalanffy function (VBGF), which yielded asymptotic sizes ($CW_\infty$) within the range of maximum crab sizes found in the field. The growth performance indices of the two sexes were similar (less than 2 % variation) as the higher K-value of the females was compensated for by the larger $CW_\infty$ of the males (see below). Crabs attain sexual maturity at a relatively small size. The smallest berried female found in the Caeté mangroves measured only 29.0 mm CW (Diele unpubl.), while massive gonadal maturity ($CW_{50\%}$) was estimated to occur at 40.0 and 35.1 mm CW for females and males, respectively (Vale, 2003). Early sexual maturity reduces the risk of dying without having reproduced, but the trade-off is slower growth as energy allocation to reproduction reduces the amount available for somatic growth (Hartnoll, 1985). In two Southern Brazilian *Ucides* populations, massive maturity occurs at a similar size in females (43 mm $CW_{50\%}$), but males mature later than in the Caeté estuary (44 mm $CW_{50\%}$: Dalabona et al., 2005; 51.3 mm $CW_{50\%}$: Hattori, 2002; values refer to morphological maturity). Attaining sexual maturity is a lengthy process rather than a precise moment (Luppi et al., 2004), as morphological, gonadal and functional maturity (e.g. courtship behaviour) are rarely synchronized (López-Greco and Rodriguez,

1999). For estimating natural mortality with the formula of Rikhter and Efanov (1976) (see below), we therefore not only applied the age at 50% maturity, but also at 75% and 100% maturity.

*U. cordatus* has an indeterminate growth pattern, continuing to moult after reaching maturity. Our capture-recapture study provides for the first time unambiguous data that some males moult more than once per year until a size of at least 62.7 mm. Multiple moulting was however much more common in intermediate sized males (until approx. 50 mm carapace width) than in larger ones and it was more frequent in intermediated sized males than in females. Our results confirm earlier studies that large males and females moult mostly once during the dry season (Nascimento et al.,1982, Nascimento, 1993). Annual moulting also occurs in the large gecarcinid land crab *Cardisoma guanhumi* (Felicano, 1962 cited after Wolcott, 1988; Taissoun, 1974).

In the Caeté estuary, *U. cordatus* males grow considerably larger than females. Maximum size was 17% greater in males captured during population sampling than in females (87.5 mm CW versus 73 mm CW, respectively). Fishermen that target only the uppermost size classes even catch larger males (maximum CW 99 mm, Diele et al., 2005). The sexual dimorphism in body size of crabs in our study area is also reflected by estimates obtained with the VBGF, which gave a 23% higher asymptotic size value for males (males: $CW_\infty = 92.00$ mm; females: $CW_\infty = 71.00$ mm). A similar trend is known from other *U. cordatus* populations (for review see Pinheiro et al., 2005) and many other crab species (Hartnoll, 1982). A larger male size may result from smaller energy investment into reproduction, allowing them to allocate more energy into growth compared to females (see also Hartnoll, 1985; Hartnoll et al., 2006). However, observed maximum sizes of crabs in other exploited Brazilian *U. cordatus* populations differ much

less between sexes than in the Caeté estuary (for review see table 3 in Pinheiro et al., 2005). For example in Iguape (Sao Paulo State), the largest captured male was only 6.4% larger than the largest female. In contrast, in the state of Amapá the intersexual size difference of *U. cordatus* was similar to our study (20%; Viera, 1997). If, irrespective of site-specific differences (see below), a distinct sexual size dimorphism is the natural state of (unexploited) *U. cordatus* populations, similar male-female sizes in exploited stocks would point to a high intensity of a given fishery and vice versa, as only large males are typically targeted. The unexploited females, on the other hand, are ideal for comparing natural intrasexual differences in maximum sizes across different locations, as their size distribution is relatively unaffected by fishery. Female maximum sizes range between 61 (Ceará: Mota Alves, 1975), 83 mm CW (Ceará: Ivo et al., 1999) and even > 91mm CW (Amapá: Viera, 1997). A clear latitudinal trend is not detectable (see also Pinheiro et al., 2005, Table 3) and the reason for the large intraspecific differences is unclear. Possibly, variations in nutritional composition of the leaf litter or sediment promote different maximum sizes of *U. cordatus* in different locations.

Age at size estimates for *Ucides cordatus* in the Caeté estuary calculated by the inverse VBGF indicate 3.26 and 2.76 years of age at massive maturity ($CW_{50\%}$) and of 6.13 and 7.38 years at 60 mm minimum legal capture size (MLCS) for males and females, respectively. There are several factors that may result in over- or underestimation of true age at a given size. For instance, specimens with greater genetic fitness may grow faster, likewise those from locations with better food quantity or quality (Hartnoll, 1982; Wenner et al., 1985). In crabs having suffered limb loss, age is probably underestimated due to energy allocation into regeneration, which reduces overall growth increment (Hartnoll, 1988). Nevertheless, age at size estimates are valuable tools for extrapolating

the overall growth of a species, despite individual variability, especially when based

upon a large set of data as in the present study.


Previous studies of growth in *U. cordatus* gave highly controversial estimates concerning

age at size and longevity. The in situ growth increment data of this work does not

support former results that the species is very fast growing with less than 1 year of age

at 60 mm MLCS and a maximum life span of only two to three years (Ivo et al., 1999;

Vasconcelos et al., 1999; Monteiro and Coelho-Filho, 2000). Such fast growth is not very

likely for *U. cordatus*, given the combination of the species' large size, nutrient-poor diet

(see below) and slow metabolism (Diele and Koch, in press). The studies mentioned

above applied cohort-analyses basing upon size-frequency distributions. The

distributions were dominated by larger crabs, monthly sample sizes were relatively small

(sometimes < 100 specimens per sex) and visually detectable polymodal peaks

progressing over time were lacking. The latter is typical for long-living crustaceans

rendering cohort analysis highly subjective in such cases. This was clearly demonstrated

by different researchers analysing a set of identical length-frequency data of the slow

growing spanner crab *Ranina ranina*, resulting in large discrepancies (Boullé, 1995, cited

after Kirkwood et al., 2005). Another cohort-analysis, performed by Pinheiro et al. (2005)

for *U. cordatus* in southern Brazil, indicated much slower growth than the former cohort-

studies, with a maximum life span of > 10 yrs. Hence, their results are much closer to

our estimates than the ones from NE-Brazil. The southern Brazilian crabs, however,

seem to attain 60 mm MLCS faster than the crabs at our northern Brazilian study site

(3.8 and 4.7 years at 60 mm CW in males and females respectively versus 6.13 and

7.38 years). It remains open whether this discrepancy is method-based (see above) or

the result of different environments. For example, S-Brazil experiences less rainfall and

smaller salinity fluctuations than our Amazonian study site and crabs may thus need to spend less energy for osmoregulation, leaving more energy for growth.

Slow growth and long life spans as in *U. cordatus* are also known from other large land crabs: The gecarcinid crab *Cardisoma guanhumi* for example, is estimated to be around 13 years old at 98 mm CW (Henning, 1975) and *Gecarcinus ruricola* 10 to 15 years at 70 to 100 mm CW (Hartnoll et al., 2006). As in *U. cordatus*, these species mainly feed upon plant material poor in nitrogen. In some species, additional protein may be derived from occasional cannibalism, as was observed in *Cardisoma carnifex* (Diele, unpubl.). Protein supplementation also enhances growth in *C. guanhumi* and *Gecarcinus lateralis* (Wolcott and Wolcott 1984 and 1987). *U. cordatus* is also nitrogen limited as crabs fed with additional proteins grew twice as much as those supplied with pure mangrove leave diet (Ostrensky et al., 1995). In contrast, large carnivorous and scavenging crabs grow much faster: Male *Cancer polyodon* (Wolff and Soto, 1992) and *Chionecetes bairdi* (Donaldson et al., 1981) attain 65 mm CW in 1.2 and 3.9 and years, respectively, and the mud crab *Scylla serrata* reaches 80 to 160 mm CW in only one year (Hill, 1975). The strongly diverging growth pattern and life spans of large carnivorous versus herbivorous crabs thus appear to result from their different diets and metabolism. Slow growth of land crabs seems to be an adaptive response to limited nitrogen (Wolcott and Wolcott 1987 and 1992).

4.3 Mortality and exploitation rates

The estimates of total, natural and fishing mortality given in this study are the first published for any *U. cordatus* population to our best of knowledge. Total mortality in males was 30% higher than in females ($Z = 0.69$ and $0.49$, respectively), as was

expected from the sex-selective impact of the male-only fishery realized in the study area. As total mortality (Z) equals production (P) per biomass (B) (Z = P/B) under equilibrium conditions (Allen 1971), the turnover ratio of *U. cordatus* is probably low (Z= P/B = 0.69 in males) when compared to carnivorous aquatic crabs such as *Callinectes arcuatus* ($Z_{males}$ = 2.49 (Fischer and Wolff, 2006). Former calculations of the P/B ratio of *U. cordatus* in the Caeté estuary resulted in an even lower value (P/B = 0.16; Koch and Wolff 2002) than in the present study, but were probably underestimates as these calculations were based upon size-frequency distributions dominated by older and thus less productive crabs.

Natural mortality estimates (M) for females could be obtained by two independent methods, due to their unexploited state. M should equal Z derived from the catch curve analysis (F = 0; Z = M = 0.49) and did so as demonstrated by the very similar M value obtained by the formula of Rikhter and Efanov (1976) from the age at first maturity at $t_{CW50}$ (M = 0.49) and $t_{CW75}$ (M = O.44). M calculated from $t_{CW100}$ was however distinctly lower (M = 0.26). The similarity of M derived from the catch curve with the first two values of the second method suggests that these estimates are reasonable. For the exploited male population M could only be calculated by the Rikhter and Efanov formula. Their M values were higher than the females' values for all maturity scenarios. Based on the results of the females derived from two independent methods, the estimates from age at massive maturity at $t_{CW50}$ (M = 0.58) and $t_{CW75}$ (M = 0.53) are more realistic than the estimate derived from $t_{CW100}$ (0.35). Pinheiro et al. (2005) estimated age at functional maturity as 3 and 2.8 yrs in males and females, respectively, for which M values of 0.53 and 0.56 are calculated here for his SE-Brazilian crab population. These results match well with the M estimates for the Caeté crab population, at least for males. At our study site predation is probably the most significant natural mortality factor as crab racoons,

crab hawks and cancrivorous fishes are very abundant in the mangroves. The lethargic crab disease, caused by fungi, which recently caused dramatic mass mortalities of *U. cordatus* in several locations of NE-Brazil, has not yet reached N-Brazil. In males considerable mortality further occurs during synchronized mate searching activities. During the 3 to 4 days of mass mating events ("andança"-events, Diele and Koch, in press) males heavily fight for females and we frequently observed seemingly exhausted and dying specimens in the mangroves around this time. In addition to these natural mortality factors, male crabs, particularly the large ones, are targeted by fishermen (Diele et al., 2005). Our estimate for fishery mortality (F= Z-M) of the male population in the Caeté estuary, however, is rather low (F = 0.11 and 0.24 in scenario 1 and 2, respectively) and suggests that the rate of exploitation (E = 0.16 and 0.24 in scenario 1 and 2, respectively) is as yet relatively low in the study area. This corresponds with the finding that (i) large males are still relatively abundant in the Caeté mangrove forests, (ii) fisheries landings are 22% below the calculated maximum sustainable yield (Diele et al., in press), (iii) the size of the captured crabs has not decreased in recent years (data series 1997-2005, Diele et al., 2005 and Diele et al., in press) and only legal artisanal fishing techniques are applied.

In summary, by providing in situ growth increment data for the first time, our study ascertained that the mangrove crab *U. cordatus* is a slow growing species. This is in line with other large herbivorous land crabs worldwide. Slow growth suggests a high vulnerability to overfishing, calling for reliable fisheries monitoring and careful management of this resource. It also underlines that compliance of laws that ban capture techniques facilitating high exploitation rates are crucial for the sustainability of the fishery of this slow growing crab (Diele et al 2005, Diele et al in press). In the future, post-settlement mortality and growth of early juveniles should be studied in the field,

given that the natural habitat of this important stage in the species' life cycle is now

known (Schmidt and Diele 2009).

Table 1. Release size, handedness, number and intermoult status of heatbranded *U. cordatus* crabs released into two 12.5 m² compartments inside 100 m² field enclosures each year between 1997 and 1999. Recapture Date: Date when the enclosure was searched for the tagged crabs. CW: Carapace width; H: handedness; L: Left-handed; R: Right-handed; EI: Early intermoult; LI: Later intermoult.

| Release Date | Size at release CW in mm | H | Males Released | Females Released | Recapture Date |
|---|---|---|---|---|---|
| 1997, June/July | 31.0/32.0/33.0 | L/R | 30 (EI) | 26 (EI) | 1997, Nov/Dec |
| 1998, April | 30.0/31.0 | L/R | 26 (LI) | 27 (LI) | 1998, August |
| 1999, May | 20.5 | R | 2 (LI) | 2 (LI) | 1998, August |
| 1999, May | 25.0/26.0 | L | 6 (LI) | 6 (LI) | 1998, August |
| 1999, May | 30.0/31.0 | R | 8 (LI) | 11 (LI) | 1998, August |
| 1999, May | 35.0/36.0 | L | 12 (LI) | 14 (LI) | 1998, August |
| 1999, May | 45.5 | R/L | 10 (LI) | 9 (LI) | 1998, August |
| **Total** | | | **94** | **95** | |

Table 2. Release / recapture dates and number of PIT-tagged *U. cordatus* crabs released into a field enclosure each year between 1999 and 2000. Recapture Date: Date when the enclosure was searched for the tagged crabs. Number in brackets: Renewed release of recaptured crabs.

| Release Date | Males Released | | Females Released | | Recapture Date |
|---|---|---|---|---|---|
| 1999, April | 61 | | 41 | | 1999, October |
| 1999, August | 0 | ( 6) | 0 | | 1999, October |
| 1999, October | 0 | (13) | 0 | (7) | 2000, May/June |
| 2000, May/June | 28 | (12) | 29 | (5) | 2000, October/Nov |
| 2000, October/Nov | 45 | (17) | 44 | (10) | 2001, May |
| **Total** | **134** | | **114** | | |

Table 3. Relationship (R² values) between percent (PI) or absolute growth increment (AI) and pre-moult carapace width of early juveniles cultivated in the laboratory and crabs kept in the field enclosure.

| | Laboratory | Field enclosure | |
|---|---|---|---|
| | Unsexed | Males | Females |
| Linear model | | | |
| PI | 0.141 | 0.568 | 0.617 |
| AI | 0.708 | 0.051 | 0.341 |
| log-linear model | | | |
| PI | 0.086 | 0.523 | 0.601 |
| AI | 0.799 | 0.025 | 0.306 |
| Quadratic model | | | |
| PI | 0.213 | 0.612 | 0.618 |
| AI | 0.820 | 0.400 | 0.401 |

Table 4. Number of tagged *U. cordatus* crabs recaptured from the field-enclosure between 1999 and 2001, total number of recaptures resulting from multiple recaptures of the same individuals and number of observed growth increments. Brackets indicate the number of initially released crabs.

| Sex and tagging method | Recaptured specimens | | Total number of recaptures | Growth increments |
|---|---|---|---|---|
| Heatbranded males | 52 | (94) | 52 | 52 |
| PIT-tagged males | 72 | (134) | 89 | 73 |
| **Total males** | **124** | | **158** | **125** |
| Heatbranded females | 54 | (95) | 54 | 54 |
| PI-tagged females | 39 | (114) | 49 | 30 |
| **Total females** | **93** | | **103** | **84** |
| **All crabs** | **217** | **(437)** | **244** | **209** |

Table 5. Average values and standard deviation of percent (PI) and absolute growth increment (AI) per moult per size class of crabs kept in the field enclosure. Only increments that could confidentially be attributed to one single moulting event within a specific time at free were considered (males: n = 113; females: n = 75). CW: Carapace width. CW with *: Growth increments of excavated free-living specimens.

| CW (mm) | | Males | | CW (mm) | | Females | |
|---|---|---|---|---|---|---|---|
| | n | PI (%) | AI (mm) | | n | PI (%) | AI (mm) |
| < 40 | 40 | 10.87 ± 3.28 | 3.54 ± 1.17 | < 40 | 39 | 11.67 ± 3.16 | 3.75 ± 1.09 |
| 40 < 50 | 12 | 9.88 ± 2.50 | 4.34 ± 1.03 | 40 < 50 | 8 | 7.07 ± 2.58 | 3.28 ± 1.12 |
| 50 < 60 | 14 | 8.27 ± 2.16 | 4.56 ± 1.08 | 50 < 60 | 11 | 4.52 ± 1.27 | 2.38 ± 0.66 |
| 60 < 70 | 27 | 5.82 ± 1.81 | 3.69 ± 1.03 | 60 < 70 | 15 | 2.88 ± 1.24 | 1.79 ± 0.76 |
| 70 < 80 | 14 | 3.61 ± 1.11 | 2.59 ± 0.76 | | | | |
| > 80 | 3 | 1.43 ± 0.87 | 1.17 ± 0.71 | | | | |
| | | | | | | | |
| 59.2* | 1 | 6.93 | 4.1 | 52.8* | 1 | 4.55 | 2.40 |
| 60.4* | 1 | 5.79 | 3.5 | 62.0* | 1 | 3.23 | 2.00 |
| 63.3* | 1 | 5.37 | | | | | |

Table 6. Parameters of the von Bertalanffy growth function ($CW_\infty$, K), the curve fit ($R^2$) and the growth performance value ($\Phi'$; basing upon $CW_\infty$ cm ). Size range: Pre-moult size of the crabs for which growth increment data were obtained (laboratory and field data joined); $CW_{P\text{-}max}$: Largest crab captured during population sampling (Diele et al., 2005; Females: n = 1997; Males n = 2552); $CW_{F\_max}$: Largest crab encountered in catch of fishermen (Diele et al., 2005, Diele unpublished, n = 81708) as well as average of the 2% largest crabs ($CW_{2\%}$). In males $CW_{2\%}$ refers to the catch of fishermen, in females to the population sampling.

| | Size range (mm) | $CW_\infty$ (mm) | K ($y^{-1}$) | $R^2$ | $\Phi'$ | $CW_{P\text{-}max}$ (mm) | $CW_{F\_max}$ (mm) | $CW_{2\%}$ (mm) |
|---|---|---|---|---|---|---|---|---|
| Males | 1.37-82.4 | 92 | 0.17 | 0.993 | 1.16 | 87.5 | 99.0 | 83.8 ± 1.4 |
| Females | 1.37-69.6 | 71 | 0.25 | 0.992 | 1.10 | 73.0 | - | 68.8 ± 1.3 |

Table 7. Age at size estimates (yrs). $t_{CW50}$, $t_{CW75}$, $t_{CW100}$: age at size of 50, 75 and 100% gonadal maturity, number in brackets: CW in mm (Vale, 2003). $t_{max}$: maximum age after calculated afterTaylor; $t_{max95}$: maximum age where 95% of $CW_\infty$ is reached. $t_{60}$: age at legal minimum capture size (60 mm CW); $t_{74}$: age at average capture size realized on the Bragança peninsula (74 mm CW, Diele et al., 2005). No value is given for female crabs as they are only very sporadically harvested in the Caeté estuary.

| | $t_{CW50}$ | $t_{CW75}$ | $t_{CW100}$ | $t_{max}$ | $t_{max95}$ | $T_{60}$ | $t_{74}$ |
|---|---|---|---|---|---|---|---|
| Males | 2.75 (35.1) | 3.04 (37.9) | 4.67 (51.0) | 17.64 | 17.54 | 6.13 | 9.52 |
| Females | 3.26 (40.02) | 3.64 (43.00) | 6.06 (55.70) | 12.00 | 11.90 | 7.38 | - |

Table 8. Mortality parameters (Z, M and F) and exploitation rates (E). M, F and Z were calculated from crab population sampling data (Diele et al., 2005) for three scenarios basing upon the age at 50%, 75% and 100% of gonadal maturity (1: $t_{CW50,}$ 2: $t_{CW75,}$ 3: $t_{CW100,}$; see Table 7). No F and E values are given for female crabs as they are only sporadically harvested in the Caeté estuary.

| | | Scenario 1 | | | Scenario 2 | | | Scenario 3 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Z | M | F | E | M | F | E | M | F | E |
| Males | 0.69 | 0.58 | 0.11 | 0.16 | 0.53 | 0.16 | 0.24 | 0.35 | 0.35 | 0.50 |
| Females | 0.49 | 0.49 | - | - | 0.45 | - | - | 0.26 | - | - |

Figure 1



Figure 2

## Figure 3

**PI (% growth increment)**



$$y = 20.72 + 2.011x - 0.298x^2$$
$$R^2 = 0.213$$
$$n = 53$$

**AI (mm growth increment)**



$$y = -0.195 + 0.389x - 0.025x^2$$
$$R^2 = 0.782$$
$$n = 53$$

Pre-moult carapace width (mm)

## Figure 4

**Males**

**Females**



A
$$y = -7.255 + 0.242x - 0.004x^2$$
$$R^2 = 0.612$$
$$n = 113$$

B
$$y = -17.535 - 0,161x - 0.001x^2$$
$$R^2 = 0.618$$
$$n = 75$$

C
$$y = -4.702 + 0.379 x - 0.004 x^2$$
$$R^2 = 0.400$$
$$n = 113$$

D
$$y = -0.048 + 0.2 x - 0.003 x^2$$
$$R^2 = 0.401$$
$$n = 75$$
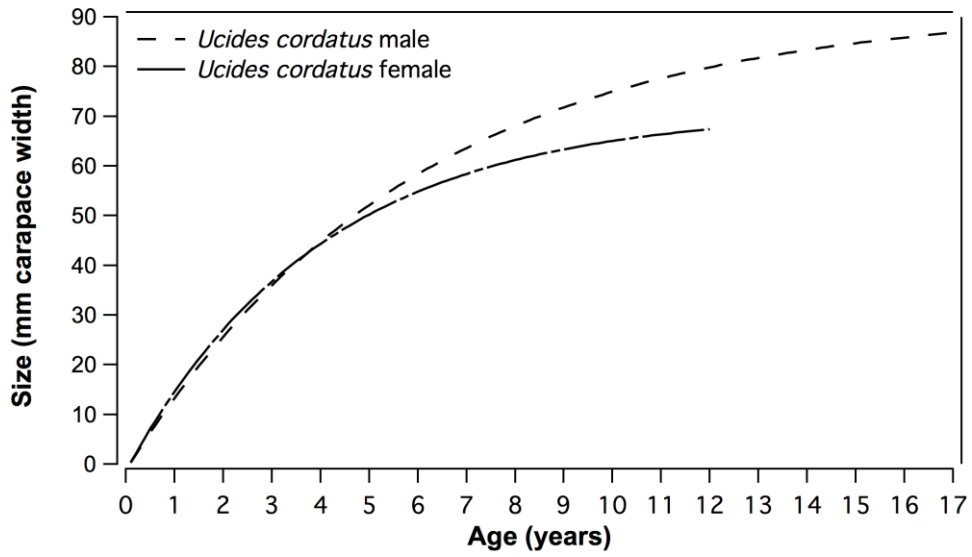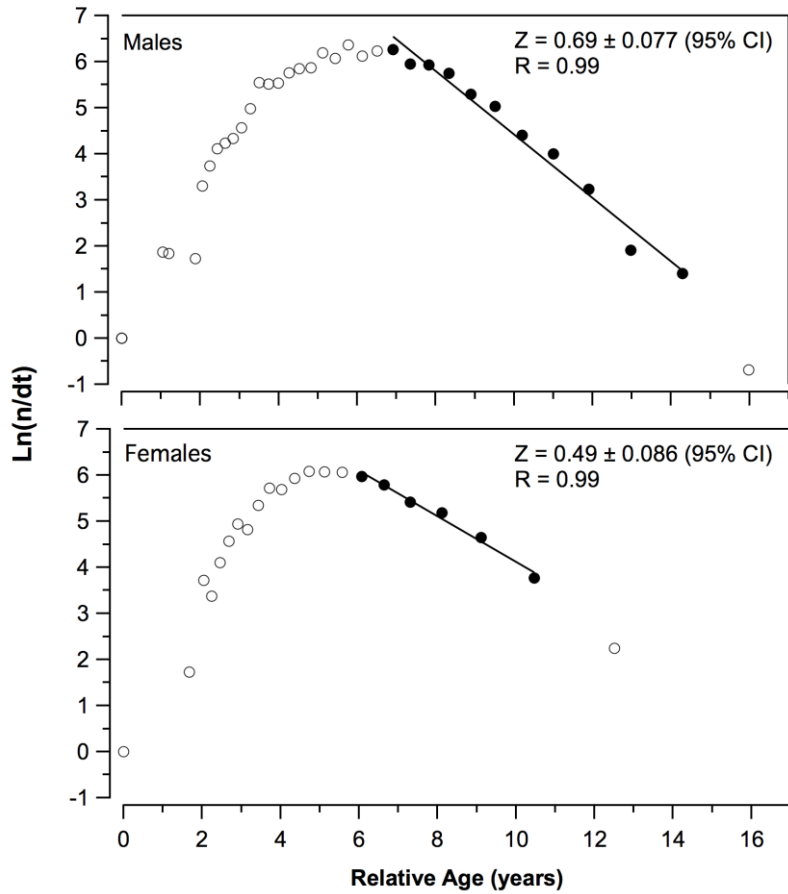
Pre-moult carapace width (mm)
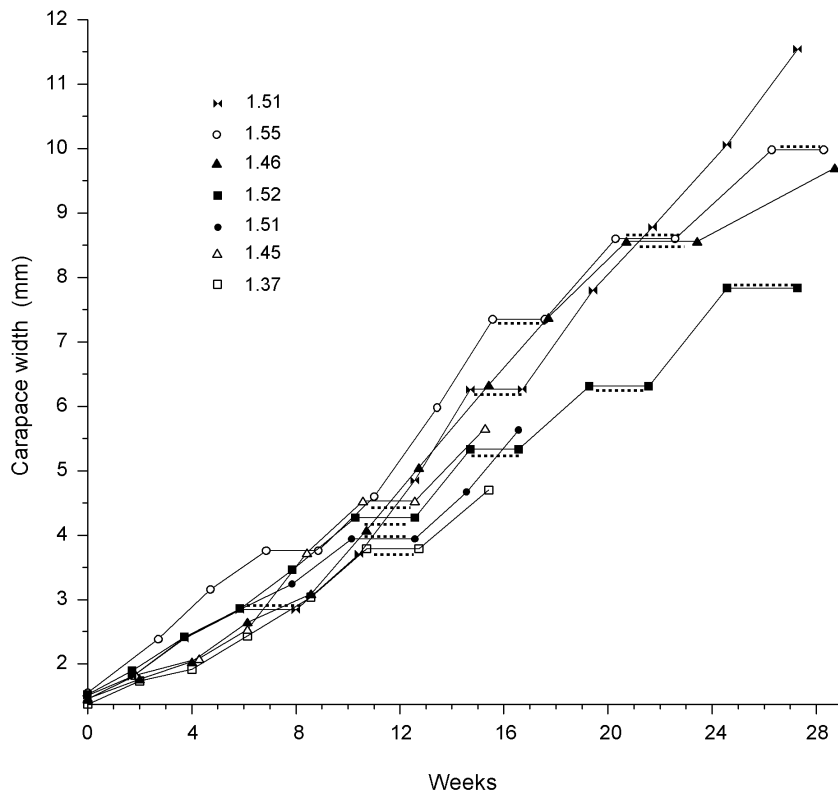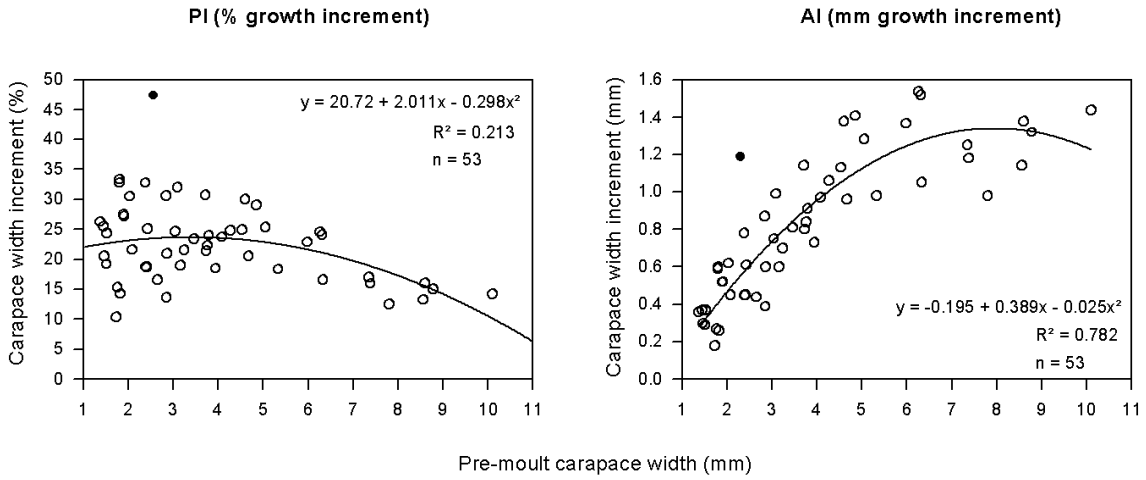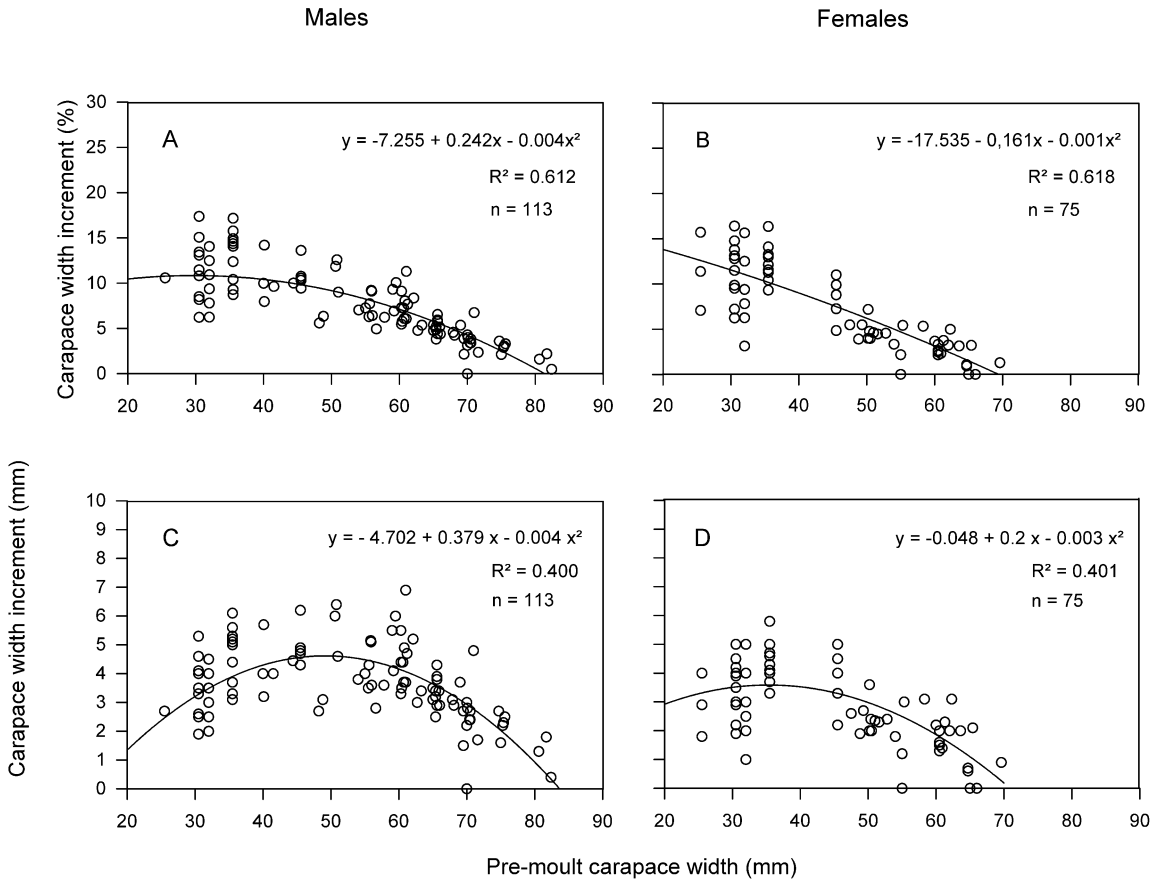
Figure 5



Figure 6

**References**

Allen, K.R., 1971. Relation between production and biomass. J. Fish Res. Bd. Can. 28, 1573–1581.

Alves, M.M.I. ,1975. Sobre a reprodução do caranguejo, *Ucides cordatus* (Linnaeus), em mangues do estado Ceará (Brasil). Arq. Cien. Mar. 15, 85-91.

Alves, R.R.N., Nishida, A.K., Hernández, M.I.M., 2005. Environmental perception of gatherers of the crab "caranguejo-uçá (*Ucides cordatus*, Decapoda, Brachyura) affecting their collection attitudes. J. Ethnobiol. Ethnomed. 1(10), http://www.ethnobiomed.com/content/1/1/10

Beasley, C.R., Fernandes, M.E.B., Figueira, E.A.G., Sampaio, D.S., Melo, K.R., Barros, R.S., 2001. Mangrove infauna and sessile epifauna. In: Saint-Paul, U. and Schneider, H. (Eds.), MADAM – Mangrove Dynamics and Management. Ecological Studies, Springer, Berlin, Heidelberg.

Boeger, W.A., Pie, M.R., Vicente, V., Ostrensky, A., Hungria, D.,Castilho, G.G., 2007. Histopathology of the mangrove land crab *Ucides cordatus* (Ocypodidae) affected by lethargic crab disease. Dis. Aquat. Organ. 78(1), 73-81.

Boullé, D.P., 1995. Seychelles krab giraf (*Ranina ranina*) fishery: the status of the stock. Report to the Seychelles Fishing Authority, Mahé.

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

Brey, T., 2001. Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. Germany. Alfred Wegener Institute for Polar and Marine Research. http://www.thomas-brey.de/science/virtualhandbook/

Caddy, J., Sharp, G., 1986. An Ecological Framework for Marine Fishery Investigations. FAO Fisheries Technical Paper, 382.

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, Ma. Bol. Lab. Hidrob. 7, 7-26.

Dalabona, G.; Silva, J. L.; Pinheiro, M. A. A., 2005. Size at morphological maturity of *Ucides cordatus* (Linnaeus, 1753) (Brachyura, Ocypodidae) in the Laranjeiras Bay, Southern Brazil. Braz. Arch. Biol. Tech. 48 (1), 139-145.

Diele, K., 2000. Life history and population structure of the exploited mangrove crab *Ucides cordatus cordatus* (L.) (Decapoda: Brachyura) in the Caeté estuary, North Brazil. Center for Tropical Marine Ecology, Contribution 9, ZMT Bremen, 103 pp.

Diele, K., Koch, V., Saint-Paul, U., 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus*: Indications for overfishing? Aquat. Living Resour. 18, 169-178.

Diele, K., Simith, D., 2006. Salinity tolerance of northern Brazilian mangrove crab larvae, *Ucides cordatus* (Ocypodidae): Necessity for larval export? Estuar. Coast. Shelf Sci. 68, 600-608.

Diele, K., Araújo, A.R., Glaser, M., Salzmann, U., in press 2010. Artisanal fishery of the mangrove crab *Ucides cordatus* and first steps towards a successful co-management in N-Brazil. In: Saint-Paul, U. and Schneider, H. (Eds.), Mangrove Dynamics and Management in North Brazil. Ecological Studies, Springer, Berlin, Heidelberg. Vol. 211.

Diele, K., Koch, V., in press 2010. Comparative population dynamics and life histories of N-Brazilian mangrove crabs, genera *Uca* and *Ucides* (Ocypodoidea). In: Saint-Paul, U. and

Schneider, H. (Eds.), Mangrove Dynamics and Management in North Brazil. Ecological Studies, Springer, Berlin, Heidelberg. Vol. 211.

Donaldson, W.E, Cooney, R.T., Hilsinger, J.R., 1981. Growth, age and size at maturity of Tanner crab, *Chionoecetes bairdi*, in the Northern Gulf of Alaska (Decapoda, Brachyura). Crustaceana. 40(3), 286-302.

Donaldson, W. E., Schmidt, L., Watson, L., Pengilly, D., 1992. Development of a technique to tag adult red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), with passive integrated transponder tags. J. Shellfish Res. 11 (1), 91-94.

Ehrhardt, N. M., Restrepo, V. R., 1989. The Florida stone crab fishery: A reusable resource? In: Caddy, J. F (Ed.), Marine invertebrate fisheries: Their assessment and management, John Wiley & Sons.

Fischer, S., Wolff, M., 2005. Fisheries assessment of *Callinectes arcuatus* (Brachyura, Portunidae) in the Gulf of Nicoya, Costa Rica, with remarks on its socioeconomic relevance. Fish. Res. 77, 301-311.

Fletcher, W. J., Brown, I. W., Fielder, D. R., 1990. Growth of the coconut crab *Birgus latro* in Vanuatu. J. Exp. Mar. Biol. Ecol. 141, 63-78.

Fylstra, D., 1998. Design and use of the Microsoft Excel Solver, Interfaces 28: 29-55.

Geraldes, M. G., de Calventi, I. B., 1983. Estudos experimentales para el mantenimiento en cautiverio del cangrejo *Ucides cordatus*. Centro de Investigaciones de Biología Marina (CIBIMA), Rebublica Dominicana.

Giarrizzo, T., Saint-Paul, U. ,2008. Ontogenetic and seasonal shifts in the diet of Pemeceu sea catfish *Sciades herzbergii* (Siluriformes: Ariidae) from a macrotidal mangrove creek in the Curuçá estuary (North Brazil). Rev. Biol. Trop. 56,861-873.

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

Hartnoll, R.G., 1983. Strategies of crustacean growth. Austral. Mus. Memoir 18: 121-131.

Hartnoll, R. G., 1985. Growth, sexual maturity and reproductive output. In: Wenner, A.M. (Ed.), Factors in adult growth. Crustacean Issues 3: 101-128.

Hartnoll, R.G., 1988. Growth and molting. In: Burggren, W. W., McMahon, B. R. (Eds.), Biology of the land crabs. Cambridge University Press, pp. 186-210.

Hartnoll, R.G., Baine, M. S. P., Grandas, Y., James, J., Atkin, H., 2006. Population biology of the black land crab, *Gecarcinus ruricola*, in the San Andres Archipelago, Western Caribbean. J.Crust. Biol., 26: 316-325.

Hattori, G. Y., 2002. Biologia populacional do caranguejo de mangue *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ocypodidae) em Iguape (SP). Master's Thesis, Faculdade de Ciências Agrárias e Veterinárias – UNESP Jaboticabal. 82 pp.

Henning, H. G., 1975. Kampf-, Fortpflanzungs- und Häutungsverhalten, Wachstum und Geschlechtsreife von *Cardisoma guanhumi* Latreille (Crustacea, Brachyura). Forma et Functio. 8, 463-510.

Hill, B.J., 1987. Abundance, breeding and growth of the crab *Scylla serrata* in two South African estuaries. Mar. Biol. 32(2), 1432-1793.

IBAMA - Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, 2003. N° 034/03-N, 24.06.2003

INMET - Instituto Nacional de Meterologia, 1992. Technical Report - Normais climatológicas (1961-1990).

Ivo, C. T C., Dias, A.F., Mota, R.I., 1999. Estudo sobre a biologia do caranguejo Uçá, *Ucides cordatus cordatus* (Linnaeus, 1763), capturado no Delta do Rio Parnaíba, Estado do Piauí. Bol. Tec. Cient. CEPENE. 7,153–84.

Kirkwood, J.M., Brown, I.W., Gaddes, S.W., Hoyle, S. (2005). Juvenile length-at-age data reveal that spanner crabs (*Ranina ranina*) grow slowly. Mar. Biol. 147, 331-229.

Koch V., Wolff M., 2002. Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Mar. Ecol. Prog. Ser. 22, 119-130.

López-Greco, L.S., Rodríguez, E.M., 1999. Size at the onset of sexual maturity in *Chasmagnathus granulata* Dana, 1851 (Grapsidae, Sesarminae): a critical overall view about the usual criteria for its determination. In: Schram, R., Vauplen, K.F. (Eds.), Crustaceans and the biodiversity crisis. Leiden. pp. 676-689.

Luppi, T.A., Spivak, E.D., Bas C.C., Anger K., 2004. Molt and growth of an estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae), in Mar Chiquita coastal lagoon, Argentina. J. Appl. Icht. 20, 333–344.

Mehtot, R. D., 1989. Management of a cyclic resource: The dungness crab fisheries of the Pacific coast of North America. In: Caddy, J. F. (Ed.), Marine invertebrate fisheries: Their assessment and management. John Wiley & Sons.

Monteiro, B.R., Coelho-Filho, P.A., 2000. Estrutura populacional e crescimento do caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763), no estuário do Rio Paripe (Itamaracá, Pernambuco, Brasil). Resumos do I Congresso Brasileiro sobre Crustáceos, São Pedro, Brazil. 1, 95.

Mota-Alves, M. I., 1975. Sobre a reprodução do caranguejo-uçá, *Ucides cordatus* (Linnaeus), em mangues do Estado do Ceará – Brasil. Arq. Ciên. Mar. 15, 85–91.

Nascimento S.A., 1993. Biologia do caranguejo-uçá (*Ucides cordatus*). ADEMA, Aracajú

Nascimento S.A., Rosas dos Santos E., Bomfim L., Saraiva da Costa R., 1982. Estudo bio-ecológico do caranguejo-Uça (*Ucides cordatus*) e do manguezal do estado de Sergipe -Nordeste do Brazil. Sinopse, Governo do Estado de Sergipe, Brazil. pp. 1-12.

Nordhaus, I., Diele, K., Wolff, M., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuar. Coast.Shelf Sci. 67, 239-250.

Nordhaus, I., Diele, K., Wolff, M., 2009. Activity patterns, feeding and burrowing behaviour of the mangrove crab *Ucides cordatus* (Ocypodidae). J. Exp.Mar. Biol. Ecol. 374, 104-112.

Nordi, N., 1994. A produção dos catadores de caranguejo-uçá (*Ucides cordatus*) na região de Várzea Nova, Paraíba,Brazil. Rev. Nordest. Biol. 9, 71-77.

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., Munro, J.L., 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2, 21.

Pengilly, D., Watson, L.J., 1994. Automated detection of internally injected tags in red king crabs at crab processing facilities. Fish. Res. 19, 293-300.

Pinheiro, M.A.A., Fiscarelli, A.G., Hattori, G.Y., 2005. Growth of the mangrove crab *Ucides cordatus* (Brachyura, Ocypodidae). J.Crust.Biol. 25(2), 293-301.

Prentice, E. F., 1990. A new internal telemetry tag for fish and crustaceans. In: Sparks, A. K. (Ed.), Marine farming and enhancement; Proc. 15th U.S.-Japan meeting on aquaculture, Kyoto, Japan, 22-23 October 1986. NOAA Tech. Rep. NMFS 85, Seattle, WA.

Rikhter, V.A., Efanov, V.N., 1976. On one of the approaches to estimation of natural mortality of fish populations. International Commission for the Northwest Atlantic Fisheries (ICNAF) Research Document 76/IV/139. pp. 1-6.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Canada. 191, 1-382.

Schmidt, A.J., Diele, K., 2009. First field records of mangrove crab *Ucides cordatus* recruits associated with conspecific burrows. Zoologia. 26(4), 792-794.

Sparre, P.U., Venema, S.C., 1989. Introduction to tropical fish stock assessment. Part I-Manual. Tech. Rep., FAO, Rome, Fish. Tech. Paper 306/1.

Taissoun, E., 1974. El cangrejo de tierra *Cardisoma guanhumi* (Latreille) en Venezuela: Distribuicon, ecologia, biologia y evaluacion populacional. Bol. Cent. Invest. Biol. 10, 1-36.

Taylor, C.C., 1958. Cod growth and temperature. J. Cons. Int. Explor. Mer. 23,366–370.

Vale, do, P.A.A., 2003. Biologia reprodutiva do caranguejo *Ucides cordatus cordatus* (Linnaeus 1763), num manguezal do estuário do rio Caeté. Master thesis, Universidade Federal do Pará, Belém, Brazil. 47 pp.

Vasconcelos, E. M S., Vasconcelos, J. A.,. Ivo, C. T C.,1999. Estudo sobre a biologia do caranguejo Uçá, *Ucides cordatus cordatus* (Linnaeus, 1763), capturado no estuário do Rio Curimatau (Canguaretama) no Estado do Rio Grande do Norte. Bol. Tec. Cient. CEPENE. 7, 85–116.

Viera, I.M., 1997. Bioecologia, captura e esforço de pesca do caranguejo-uça, *Ucides cordatus cordatus* (Linnaeus) em Sucuriju-AP. I workshop do programa institucional de estudos costeiros PEC do Museu Paraense Emilio Goeldii. 07-12.12.1997, Salinopolis, Brazil. Programa de resumos, pp.31-33.

von Bertalanffy, L., 1934. Untersuchungen über die Gesetzlichkeiten des Wachstums. 1. Allgemeine Grundlagen der Theorie. Roux`Arch. Entwicklungsmech. Org. 131, 613-653.

Wenner, A.M., Page, H.M., Siegel, P.R., 1985. Variation in size at onset of egg production. In: A.M. Wenner (Ed.), Factors in adult growth. Crustacean Issues 3, 149-164.

Wolcott, D.L., Wolcott, T.G., 1984. Food quality and cannibalism in the red land crab, *Gecarcinus lateralis*. Physiol. Zool. 57 (3), 318-324.

Wolcott, D. L., Wolcott, T.G., 1987. Nitrogen limitation in the herbivorous land crab *Cardisoma guanhumi*. Physiol. Zool. 60 (2), 262-268.

Wolcott, T.G., 1988: Ecology. In: Burggren, W.W., McMahon, B.R. (Eds.), Biology of the land crabs. Cambridge University Press, pp. 55-96.

Wolcott, T.G., Wolcott, D. L., 1988. When limiting factors aren´t: Lessons from land crabs. In: Chelazzi, G., Vannini, M. (Eds.), Behavioural adaptions to intertidal life. NATO ASI Series, Ser. A: Life Science. 151,135-15.

Wolcott, D.L., Wolcott, T.G., 1992. Herbivory in crabs: Adaptations and ecological considerations. Amer. Zool. 32, 370-381.

Wolff, M., Soto, M., 1992. Population dynamics of *Cancer polyodon* in La Herradura Bay, northern Chile. Mar. Ecol. Prog. Ser. 85, 69-81.

**Figure Captures**

Fig. 1. 100 m² PVC field enclosure for *U. cordatus* capture-recapture experiments in mangroves of Braganca peninsula, N-Brazil. The enclosure comprises one 75 m² and two 12.5 m² compartments. See text for explanations.

Fig. 2. Growth of juvenile *U. cordatus* cultivated for 16 to 28 weeks in the laboratory after metamorphosis from the megalopal stage (n = 7; 1998). Broken lines highlight size constancy between subsequent measurements. Legend indicates size (CW in mm) of crabs at first instar.

Fig. 3. Percent (PI) and absolute growth increment (AI) of juvenile *U. cordatus* (n = 7) during approx. biweekly measurement intervals with moulting events occuring. The crabs were cultivated in the laboratory for 16 to 28 weeks in 1998. Dark data points were excluded for regression analysis.

Fig. 4. Percent growth increment (A and B) and absolute growth increment (C and D) per moult of male and female *Ucides cordatus* kept in field enclosures.

Fig. 5. Von Bertalanffy growth curves of male and female *Ucides cordatus*, Bragança peninsula, N-Brazil (see Table 6 for growth parameters). The curves base upon 125 male and 84 female growth increments of specimens kept in field enclosures and on 17 growth increments from first instar crabs kept in the laboratory. The growth curves are plotted up to the age at which 95% of the maximum asymptotic size ($CW_\infty$) is reached.

Figure 6. Total mortality (Z) assessed with the catch curve analysis for males and females captured during population sampling (Diele et al., 2005).