

GROWTH OF THE MANGROVE CRAB *UCIDES CORDATUS* (BRACHYURA, OCYPODIDAE)

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A B S T R A C T

During monthly samplings between September 1998 and August 2000, 3,660 specimens of *Ucides cordatus* (Linnaeus, 1763) (2054 males and 1606 females) were obtained and examined for size (CW = carapace width) to determine growth-age equations for each sex. This species showed a slower growth, with a marked seasonal oscillation, in females as compared to males, suggesting application of the seasonal and nonseasonal von Bertalanffy growth model, respectively. CW_{∞} and k constant were closely similar for the two sexes ($CW_{\infty \text{ male}} = 90.3$ mm; $CW_{\infty \text{ female}} = 88.6$ mm; $k_{\text{male}} = 0.28$; $k_{\text{female}} = 0.26$). The age at sexual maturity was estimated to be around 3 years, while the age at legal size ($CW = 60$ mm) was 3.8 and 4.7 years for males and females, respectively. In the laboratory, juvenile stages did not show differences in growth rates under the same temperature and photoperiod conditions.

Ucides cordatus (Linnaeus, 1763) is associated with the mangrove areas of the Western Atlantic, occurring from Florida (U.S.A.) to the State of Santa Catarina, Brazil (Melo 1996). In Brazilian mangroves, it is the second largest brachyuran after the gecarcinid *Cardisoma guanhumi*, and is important for its abundance and use as human food (Fausto-Filho, 1968). A large number are captured in various regions of Brazil, especially the northeast, where it occurs in an artisanal fishery. The importance of this resource has also been reported in a study of crab-meat processing (Ogawa *et al.*, 1973b) and the utilization of its processing residues (Ogawa *et al.*, 1973a). Nevertheless, the Brazilian Institute of the Environment and of Renewable Natural Resources (Ibama, 1994) has indicated a need for further study of this species to ensure proper enforcement of harvest regulations established in 1998.

The growth of *U. cordatus* has been little studied, but some information is available on its growth in captivity (Geraldes and Calventi, 1983; Ostrensky *et al.*, 1995), and it is considered to be extremely slow growing. These laboratory growth data agree with those from field studies conducted by Diele (2000), but contrast with those obtained for the population field studies in northeast Brazil, where rapid growth rate was reported (Botelho *et al.*, 1999; Ivo and Gesteira, 1999; Ivo *et al.*, 1999; Vasconcelos *et al.*, 1999). Rapid growth has also been reported by Poma-Sánchez (1995) for the congener *U. occidentalis* in Peru.

Crustaceans have asymptotic growth because of the molt increment and because of growth seasonality. The identification and temporal monitoring of population size modes and the application of mathematical models such as that of von Bertalanffy (1938) have provided reliable estimates of the age of individuals of many crustaceans. The relatively few studies of variation in growth rates among decapods has included studies of portunid species in various regions of the world (González-Gurriarán, 1985; Fernández *et al.*, 1991), as well as in Brazil (Branco and Masunari, 1992; Branco and Lunardón-Branco, 1993). In these studies, size increase has

been influenced by temperature, salinity, and photoperiod (Costlow and Bookhout, 1968; Leffler, 1972; Du Preez and Mclachlan, 1984).

The first objective of the present study was to determine the growth curves (size and weight) for *U. cordatus* males and females in Iguape (SP), Brazil, and to estimate age at sexual maturity ($CW_{50\%}$), at maximum asymptotic size (CW_{max}) and at commercial size (CW_{com}). The second objective was to determine the increase in size of captive juveniles under rigidly controlled temperature, salinity, and photoperiod.

MATERIALS AND METHODS

Field Growth

Ucides cordatus specimens were collected monthly from September, 1998 to August, 2000 in mangroves near Barra de Icapara (24°41'S), Iguape (SP), Brazil, by digging burrows by hand or by using baited traps. The species was identified by diagnostic characters reported by Melo (1996).

The specimens were placed in individual plastic bags to avoid the loss of appendages and stored frozen. At the time for analysis, specimens were thawed at room temperature, washed for mud removal, and sexed by abdominal morphology and number of pleopods (Pinheiro and Fiscarelli, 2001).

Carapace width (CW) of adult specimen was measured using a venier caliper (to nearest 0.05 mm). Carapace width of juveniles was measured using a stereomicroscope coupled to a computer image analysis system (to nearest 0.01 mm) based on the KS-100 3.0 software (Carl Zeiss, GMBH). Excess water was absorbed with paper towels and the total wet weight (WT) of each specimen was recorded with a precision balance (0.01g).

Growth was analyzed by sex, and the specimens were grouped into 5-mm size classes (Santos, 1978), with the individuals being grouped on a four-month basis. Size modes were determined by the method of Bhattacharya (1967) and confirmed using the NORMESP routine of the FiSAT software (Gayanilo *et al.*, 1996). The mean of each normal curve was plotted graphically; it was linked to each age-cohort identification, and monitored in function of time. The data for size increase within the same age-cohort were used for the determination of asymptotic size (CW_{∞}) and growth constant (k) (Santos, 1978; Fonteles-Filho, 1989), with confirmation by the FiSAT program. Seasonal variation of growth was tested by analysis of residuals, with identification of the semester characterized by maximization of the mean residual (t -test; $\alpha = 0.05$). In this case, the model used to represent growth was the seasonal von Bertalanffy model

$$(CW_t = CW_\infty [1 - e^{-k\Delta t - (Ck/2\pi)\{sen[2\pi(t-t_s)] - sen[2\pi(t_0-t_s)]\}}]),$$

and in the opposite case, the model used was the nonseasonal von Bertalanffy model

$$(CW_t = CW_\infty [1 - e^{-k\Delta t}]),$$

which have the following parameters: CW_t = carapace width at time t ; CW_∞ = asymptotic size of the growth curve, k = growth constant (in years); C = constant of the amplitude of seasonal growth oscillation (ranging from 0 = low seasonal influence, to 1 = high seasonal influence); WP = parameter calculated for the period of lowest growth rate (Winter Point); and t_s = seasonal oscillation parameter, calculated by $t_s = WP - 0.5$.

Because *U. cordatus* has an insignificant hatching size, the initial age (t_0) was not considered in the growth model (Fonteles-Filho, 1989), although it was determined for the first juvenile stage (t_{j1}) ($CW_{j1} = 1.51$ mm according to Diele, 2000) using the growth curves for each sex. According to Moreau (1987) and D'Incao *et al.* (1993), the similarity of these ages validates the use of the von Bertalanffy model to represent growth during the larval phase.

Maximum age or longevity (t_{max}) was estimated by the equation of Taylor (1958): $t_{max} = (3/k) + t_0$, where k is the growth constant and t_0 the initial age (in years). Because this equation does not consider the time of larval development (from hatching to the first juvenile stage), this value was added to the analyses. Longevity was also determined by the inverse formula of the von Bertalanffy for $CW_{99\%}$, and by the size of the largest specimens of each sex captured, and the two methods were compared.

The maximum size (CW_{max}) of males and females in the field was compared to the confidence interval of the extreme values per each sample (FiSAT; $\alpha = 0.05$). Ages at maximum size (CW_{max}), at minimum legal size for the commercial fishery (CW_{com}), and at the beginning of functional maturity (CW_{mf}) were also estimated. In the last case, the sizes of 51.3 mm for males and of 43.0 mm for females were used, as established by Hattori (2002).

The weight growth curve was established by determining the asymptotic weight of each sex (WT_∞) with the substitution of CW_∞ in the equations $WT_{male} = 0.0004CW^{2.99}$ and $WT_{female} = 0.0007CW^{2.86}$ determined by Pinheiro and Fiscarelli (2001). The weight growth curve as a function of age was established for each sex using

$$WT_t = WT_\infty [1 - e^{-k\Delta t - (Ck/2\pi)\{sen[2\pi(t-t_s)] - sen[2\pi(t_0-t_s)]\}}]^b$$

(seasonal growth) and $WT_t = WT_\infty [1 - e^{-k\Delta t}]^b$ (non-seasonal growth), where: WT_t is weight at age t , WT_∞ is asymptotic weight, b is the allometric growth constant obtained for the WT/CW ratio, and the remaining terms have been defined earlier. The growth and weight performance rates were calculated for each sex by the equations $\Phi = \log_{10}(k) + 2/3 \cdot \log_{10}(WT_\infty)$ and $\Phi' = \log_{10}(k) + 2 \cdot \log_{10}(CW_\infty)$, respectively.

Published information on the cephalothoracic size of males and females of *U. cordatus* from different Brazilian locations, and parameters of the growth curves and performance indices, were compared to determine possible influence of latitude on growth.

Growth in the Laboratory

Young *U. cordatus* specimens were captured in the same mangrove area during the period from December 1999 to September 2000 and placed in individual 100-mL acrylic flasks containing $15 \pm 1\%$ salinity water, treated with 0.02% potassium phenoxymethylpenicillin. The flasks were stored in a climatic chamber under controlled temperature ($27 \pm 2^\circ\text{C}$) and photoperiod (12h:12h) conditions, with constant aeration. Each flask contained a PVC tube (2 cm \times 1.3 cm diameter) to be used by the animal as shelter.

The animals were fed small portions of fish muscle daily, with ground eggshells added for the specimens in postmolt; ecdysis and mortality were recorded daily. Exuviae and dead specimens were preserved in glycerinated alcohol (1:1) for later CW measurement with a stereomicroscope coupled to a computer image analysis system using the KS-100 3.0 program (Carl Zeiss, GMBH). Analysis of size increase was conducted using all data obtained during the study period, while molting frequency analyses (MF) were calculated using data from crabs that molted at least twice. Molt frequency (MF), metric increment, and percent size increase (ΔCW) were recorded for each specimen, and the means for each 3-mm size class were established. The data for each parameter were analyzed with ANOVA in a fully randomized design with a different number of replicates, and the means were compared by the Tukey's test ($\alpha = 0.05$).

RESULTS

Growth in the Field

A total of 3660 *U. cordatus* specimens (2054 males and 1606 females) were obtained from September 1998 to August 2000. Grouping crabs into size classes at 4-month intervals revealed polymodal population size-structure, with two to three normal curves for each time period (Figs. 1, 2). Monitoring temporal shifts of the modal values for each sex revealed two to three annual age-cohorts for males (Fig. 2A) and females (Fig. 2B).

The ordered pairs of the $CW_{t+\Delta t}/CW_t$ ratio for each sex were subjected to linear regression analysis and the following equations were obtained: $CW_{t+\Delta t} = 9.66 + 0.88CW$ ($n = 11$; $r^2 = 0.96$; $P < 0.01$) for males and $CW_{t+\Delta t} = 8.37 + 0.86CW$ ($n = 10$; $r^2 = 0.86$; $P < 0.01$) for females. The linearity of these equations confirms the possibility of using the von Bertalanffy model. The goodness of fit of the equation for females was lower than for males because of two ordered pairs with an extremely high weight increase that occurred during the transition from the September–December to the January–April four-month periods (see Fig. 3B). When these two points were removed from the analysis, the fit of the regression line was increased ($r^2 = 0.95$), indicating a certain seasonality for female growth. This was confirmed by the greater amplitude of oscillation of female seasonal growth when the spring/summer semester was compared with the fall/winter semester ($C \geq 1.0$), whereas this amplitude was smaller for males ($C < 0.3$). Therefore, the nonseasonal model was used for male growth, while the seasonal model was used for females ($WP = 0.324$ and $C = 1$).

The growth curves for males and for females were expressed by the equations $CW_t = 90.32[1 - e^{-0.28t}]$ and $CW_t = 88.55[1 - e^{-0.26t - 0.041\{sen[2\pi(t+0.18)] - sen[2\pi(0.18)]\}}]$, respectively (Fig. 4), and the growth rate ($k = 0.28$) and asymptotic size of males ($CW_\infty = 90.32$ mm) were similar to those for females ($k = 0.26$ and $CW_\infty = 88.55$ mm).

The age estimated for the first juvenile stage of male *U. cordatus* (t_{j1}) was 22 days (0.0602 years), slightly higher than that for females (19 days = 0.052 years). Longevity (t_{max}) calculated by the method of Taylor (1958) was estimated at 10.8 years for males and 11.6 years for females, corresponding to maximum sizes (CW_{max}) of 83.5 and 77.9 mm, respectively. Considering the size of the largest specimens captured ($CW_{male} = 83.4$ mm and $CW_{female} = 78.1$ mm), longevity was slightly lower (9.2 and 8.3 years), and increased to 16.5 and 17.4 years when sizes corresponding to 99% of the asymptotic size ($CW_{99\%}$) were used. According to the FiSAT program, the maximum predicted size was 86.9 mm ($84.7 \leq CW \leq 89.1$ mm; $P < 0.05$) for males and 79.2 mm ($75.1 \leq CW \leq 83.2$ mm; $P < 0.05$) for females, with longevity estimated at 11.8 and 8.7 years, respectively.

Functional maturity occurred at 2.8 years in females and at 3 years in males, with a mean age of 2.9 years. The minimum capture size in Iguape, established at 60 mm by the Ibama Law 122/2001, occurred at 3.8 years in males and at 4.7 years in females, corresponding to 42% and 55.4% of the maximum longevity for the species, respectively.

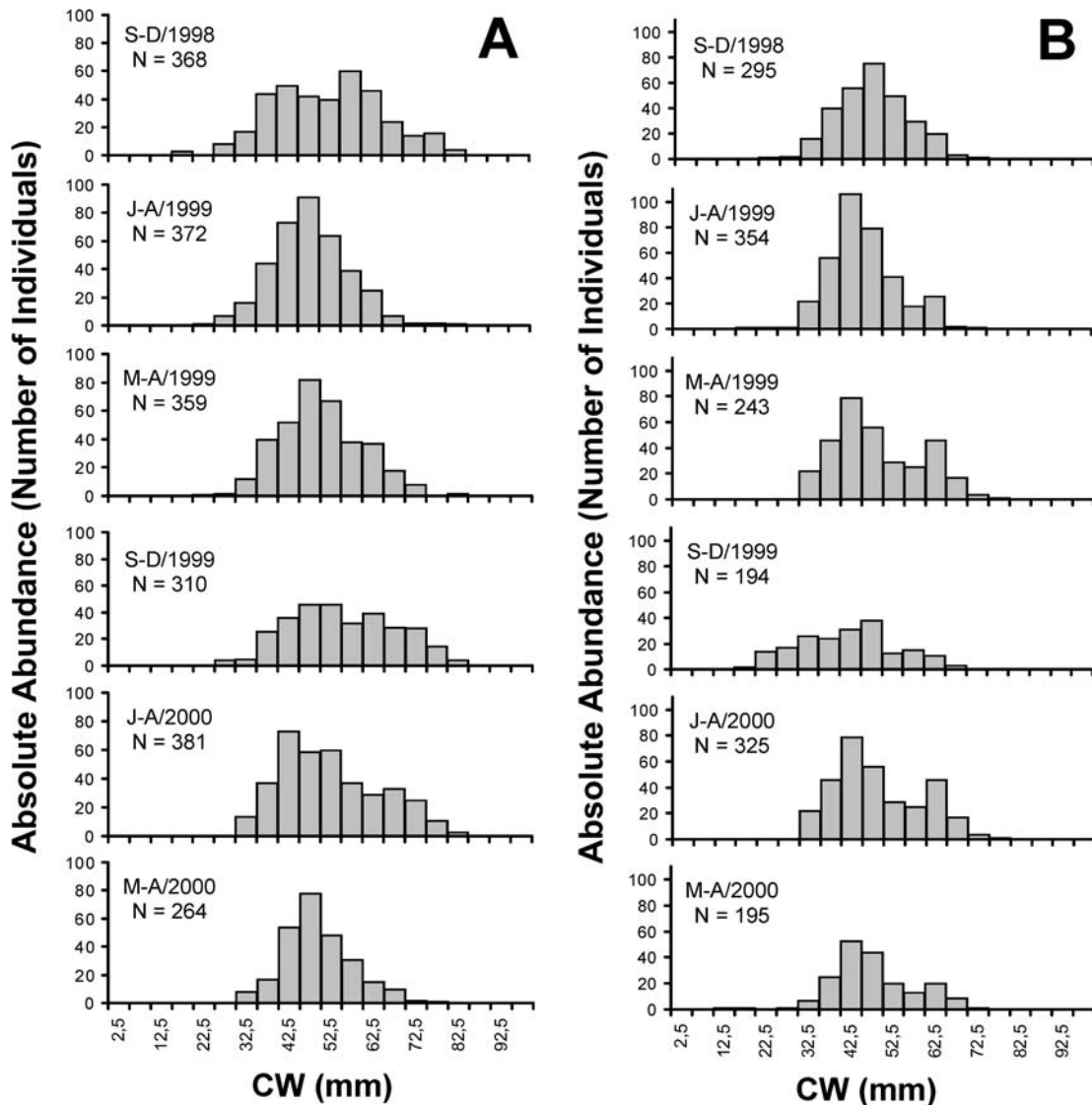


Fig. 1. *Ucides cordatus* (Linnaeus, 1763). Frequency distribution of males (A) and females (B) into size classes (CW = carapace width) during the study period at Iguape (SP), Brazil.

Weight growth curves for males ($WT = 281.74[1 - e^{-0.28t}]^{2.99}$) and females ($WT = 259.45[1 - e^{-0.26t-0.041\{sen[2\pi(t+0.18)]sen[2\pi(0.18)]\}}]^{2.86}$) indicate a maximum weight relative to maximum age (t_{max}) of 222.38 g and 180.39 g, respectively (Fig. 4).

The size growth performance index differed little between sexes ($\Phi'_{males} = 1.36$ and $\Phi'_{females} = 1.31$), as also observed for the weight growth performance index ($\Phi_{males} = 1.08$ and $\Phi_{females} = 1.02$).

Growth in the Laboratory

From December 1999 to September 2000, a total of 49 juvenile specimens were captured, with size range from 2.75 mm to 19.38 mm CW (9.61 ± 3.35 mm), and no significant difference was observed between the monthly mean CW values.

In the present study, 59.2% of the specimens kept in the laboratory died after capture. Of the 20 remaining speci-

mens, 65.0% underwent one molt ($n = 13$), 25.0% underwent two molts ($n = 5$), and only 10.0% ($n = 2$) underwent three molts during the experiment.

Twenty-five measurements for the analysis of increase in size as a function of time were obtained. Mean size increment (mm and percent), and molt frequency (days) per size class did not differ significantly from one another, although this occurred among the mean CW values ($P < 0.05$) (Table 1). For the variation in size analyzed (5.63 mm to 13.00 mm), the individuals had a mean increase in size of 0.52 mm (0.12 mm to 1.50 mm), with a 5.6% mean rate in increase in size (1.5% to 17.5%). Ecdysis occurred on average every 74 days (2.5 months), ranging from 28 d to 128 d.

Discussion

Growth in the Field

In crustaceans, growth and reproduction are antagonistic processes competing for the same energy resources

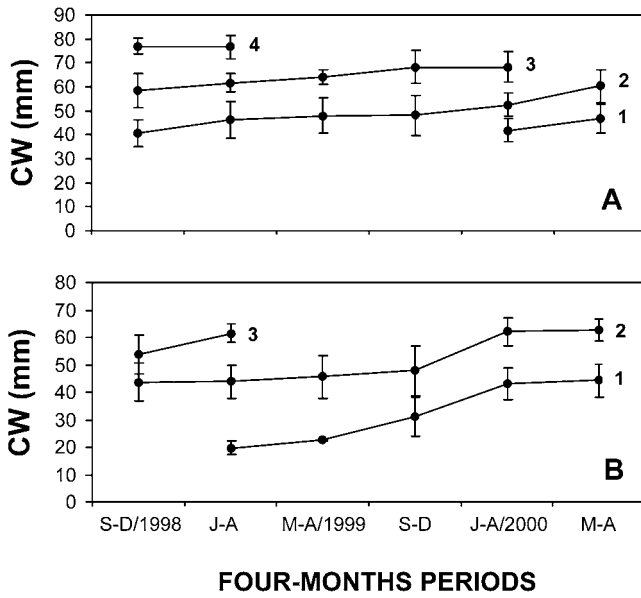


Fig. 2. *Ucides cordatus* (Linnaeus, 1763). Age-cohorts of males (A) and females (B) during the study period at Iguape (SP), Brazil (CW = carapace width; points = means; vertical lines = standard deviations).

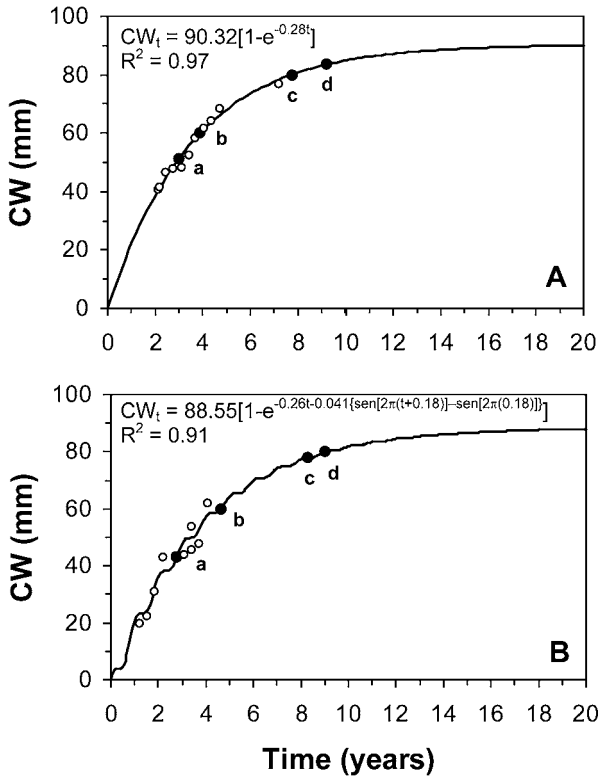


Fig. 3. *Ucides cordatus* (Linnaeus, 1763). Adjustment of the von Bertalanffy curve to the empirical points between cephalothoracic width (CW) and age for males (A = nonseasonal model) and females (B = seasonal model), during the study period, at Iguape (SP), Brazil (a = size at functional maturity; b = minimum legal size for harvest, CW 60.0 mm; c = longevity or estimated CW_{max} ; d = commercial size at Iguape, CW 80.0 mm).

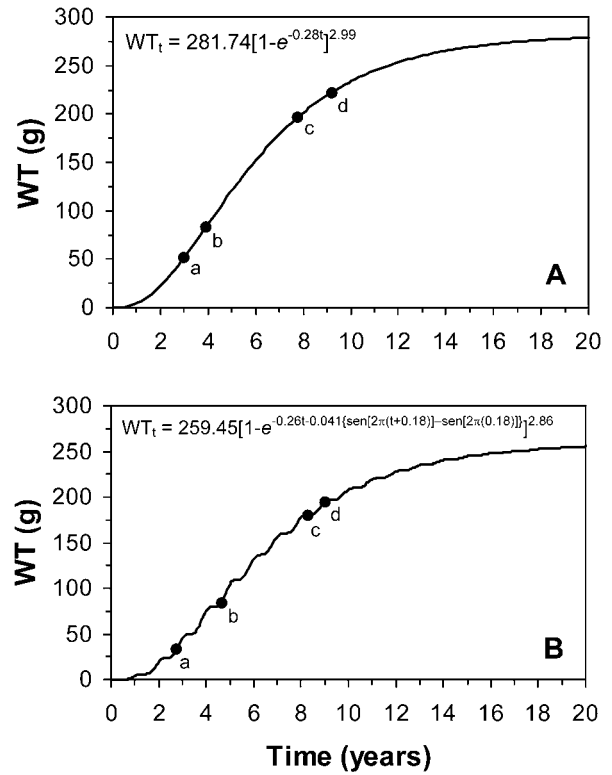


Fig. 4. *Ucides cordatus* (Linnaeus, 1763). Adjustment of the von Bertalanffy curve to the empirical points between total wet weight (WT) and age for males (A = nonseasonal model) and females (B = seasonal model), during the study period, at Iguape (SP), Brazil (a = size at functional maturity; b = minimum legal size for harvest, CW 60.0 mm; c = longevity or estimated CW_{max} ; d = commercial size at Iguape, CW 80.0 mm).

(Hartnoll, 1985). Thus, the energy demand for reproduction may interrupt the sequence of molts necessary for somatic growth, an obligatorily event occurring in females during egg incubation and in males during courtship and copulation.

In the Infraorder Brachyura, adult males usually reach a larger size and higher weight than adult females. For *U. cordatus* this size difference was small (males, 80–85 mm CW; females, 75–80 mm CW), as shown by the data obtained for various Brazilian locations (Tables 2 and 3). This sex dimorphism in size is more marked in aquatic brachyurans than in semiterrestrial and terrestrial ones and has an adaptive function of protection against predators that male crabs of some aquatic species provide for females during or after copulation, when the female's exoskeleton is still decalcified (Hartnoll, 1969; Gleenson, 1991; Pinheiro and Fransozo, 1999). The asymptotic size estimated for *U. cordatus* was slightly larger than that of the largest specimens captured in Iguape ($CW_{males} = 83.4$ mm; $CW_{females} = 78.1$ mm), corresponding to a 7.6% difference for males and an 11.8% difference for females. These sizes are confirmed when compared to the maximum size of this species at locations close to Iguape (see Tables 2 and 3), with a reduction of this difference to 5.0% (males) and 7.1% (females) when compared with 95% CW_{∞} . Similar percent differences (0.7% to 9.8%) were also observed by others

Table 1. *Ucides cordatus* (Linnaeus, 1763). Growth of juveniles reared in the laboratory according to size class (n = number analyzed; Min = minimum carapace width; Max = maximum carapace width; \bar{x} = mean; s = standard deviation; ΔCW = increase in size; MF = molt frequency).

CLASS CW (mm)	CW (mm)				ΔCW		MF	
	n	Min.	Max.	$\bar{x} \pm s$	mm	Percent	n	(days)
5–8	9	5.63	8.00	7.36 \pm 0.45 a	0.36 \pm 0.32 a	4.66 \pm 3.49 a	7	64 \pm 19 a*
8–11	11	8.12	10.88	9.44 \pm 0.97 b	0.60 \pm 0.47 a	6.21 \pm 4.88 a	9	81 \pm 21 a
11–14	5	11.50	13.00	12.17 \pm 0.56 c	0.71 \pm 0.46 a	5.70 \pm 3.50 a	4	75 \pm 42 a
Total	25	5.63	13.00	9.26 \pm 2.07	0.52 \pm 0.38	5.55 \pm 4.07	20	74 \pm 25

* Means for the same parameter followed by the same letter did not differ significantly ($P > 0.05$).

(Tables 3, 4) when comparing the estimated parameter to the size observed in the field.

The growth rates and the data concerning increase in size obtained in the present study indicate an extremely slow growth for *U. cordatus*, confirming the results obtained by Geraldes and Calventi (1983), Ostrensky *et al.* (1995), and Diele (2000). These results, however, contrast with those reported by Ivo *et al.* (1999), Vasconcelos *et al.* (1999), and Monteiro and Coelho-Filho (2000), who obtained k values five-fold higher, on average, than those obtained in the present study. In view of this wide variation, mainly between close latitudes (see Table 4), we may deduce a possible error in the determination of this parameter. In addition, the longevity values obtained in the studies indicating a slow growth for *U. cordatus* were extremely high. Fonseca (1998) stated that the k constant has been underestimated in studies on crustaceans, with a consequent overestimate of longevity to biologically unreasonable maximum values. However, our study consistently indicated slow growth, both in the field and in the laboratory, as well

as reduced molting frequency and an increase in size as a function of time, suggesting that our estimates are correct.

According to Fonseca (1998), the absence of structures in crustaceans that may be used to estimate age (e.g., otoliths and scales) requires that growth analyses be based on frequency distribution in size classes, requiring greater biological knowledge and experience on the part of the investigator. Temporal simulations of the life cycle of the species are important to ensure reliability of results. *Ucides cordatus* has seasonal reproduction, with ovigerous females occurring only between November and March. Larval and eclosion recruitment follow a lunar (Diele, 2000) or semilunar schedule (Freire, 1998), permitting the prediction of subsequent biological events. Thus, a female that extrudes her eggs at the end of November will have larval and eclosion recruitment associated with the new or full moon of the following month (Diele, 2000), with the following hypothetical chronologic sequence: spawning (November 27, 1998) + full embryonic development at 25°C (15 days according to Pinheiro and Hattori, 2003;

Table 2. *Ucides cordatus* (Linnaeus, 1763). Review of variation in cephalothoracic width (CW) and total wet weight (WT) of males from various Brazilian locations (\bar{x} = mean; s = standard deviation).

Author (year)	Locality	Latitude	CW (mm)				WT (g)			
			n	Min.	Max.	$\bar{x} \pm s$	n	Min.	Max.	$\bar{x} \pm s$
Alcantara-Filho (1982)	Pará River (PA)	00°43'S	10	75.0	89.4	84.4 \pm 3.8	—	—	—	—
Alcantara-Filho (1982)	Marcanã River (PA)	00°45'S	60	41.0	82.5	59.1 \pm 9.9	—	—	—	—
Diele (2000)	Caeté River (PA)	01°00'S	2487	17.0	87.5**	60.8	2487	5.0	245.0	92.5 \pm 48.6
Alcantara-Filho (1982)	Pau Deitado River (MA)	02°30'S	69	23.4	79.3	61.7 \pm 12.4	—	—	—	—
Castro (1986)	São Luís (MA)	02°35'S	—	31.0	82.6	69.1	—	—	—	—
Ivo <i>et al.</i> (1999)	Parnaíba River (PI)	02°48'S	2807	23.4	89.8	58.9 \pm 9.5	1684	8.0	284.0	87.1 \pm 38.6
Alcantara-Filho (1982)	Portinho River (PI)	02°55'S	65	45.7	77.6	64.7 \pm 7.4	—	—	—	—
Costa (1972)	Caucaia (CE)	03°40'S	976	27.0	74.0	55.4	976	9.0	184.0	77.8
Alcantara-Filho (1978)	Ceará River (CE)	03°40'S	796	44.0	81.0	60.3 \pm 5.8	—	—	—	—
Alcantara-Filho (1982)	Ceará River (CE)	03°40'S	45	30.9	71.4	49.2 \pm 12.6	—	—	—	—
Mota-Alves (1975)	Caucaia (CE)	03°40'S	229	46.7	61.0	—	—	—	—	—
Vasconcelos <i>et al.</i> (1999)	Curimatau River (RN)	06°20'S	1579	29.0	82.0	60.8 \pm 9.9	1380	9.0	240.0	10.11 \pm 49.4
Alcantara-Filho (1982)	Canal Santa Cruz (PE)	07°49'S	62	32.5	85.4	68.7 \pm 13.1	—	—	—	—
Botelho <i>et al.</i> (1999)	Formoso River (PE)	08°42'S	426	22.8	79.5	51.9 \pm 10.3	1684	8.0	284.0	87.1 \pm 38.6
Botelho <i>et al.</i> (1999)	Ilhetas River (PE)	08°48'S	483	14.1	76.1	44.6 \pm 11.7	331	1.2	173.4	44.6 \pm 29.0
Monteiro and Coelho-Filho (2000)	Paripe River (PE)	07°45'S	231	—	—	46.4 \pm 11.2	231	—	—	52.9 \pm 34.3
Alcantara-Filho (1982)	Mundaú Lagoon (AL)	09°42'S	49	29.4	77.0	53.7 \pm 8.7	—	—	—	—
Alcantara-Filho (1982)	Pomonga River (SE)	10°40'S	58	29.7	82.2	52.8 \pm 11.6	—	—	—	—
Souza (1999)	Sepetiba Bay (RJ)	22°55'S	177	35.5	89.5	—	—	—	—	—
Souza and Oshiro (1996)	Barra de Guaratiba (RJ)	23°04'S	—	41.6	89.5	—	—	—	—	—
Present Study	Iguape (SP)	24°41'S	1522	16.7	83.4	50.5 \pm 11.1	1522	2.1	259.1	64.3 \pm 43.2
Nakamura (1979)	Paranaguá Bay (PR)	25°33'S	422	38.3	71.5	—	—	—	—	—
Branco (1993)	Itacorubi (SC)	27°35'S	142	53.0	96.0	—	142	77.0*	383.8*	—
Total			12,695	14.1	96.0	—	10,437	1.2	383.8	—

* Data interpreted by graphical methods; **Mentions one specimen with CW = 91 mm obtained from the analysis of specimens sold by fishermen.

Table 3. *Ucides cordatus* (Linnaeus, 1763). Review of variation in cephalothoracic width (CW) and total wet weight (WT) of females from various Brazilian locations (\bar{x} = mean; s = standard deviation).

Author (year)	Locality	Latitude	CW (mm)				WT (g)			
			<i>n</i>	Min.	Max.	$\bar{x} \pm s$	<i>n</i>	Min.	Max.	$\bar{x} \pm s$
Alcantara-Filho (1982)	Marcanã River (PA)	00°45'S	40	33.3	71.7	51.5 ± 8.3	—	—	—	—
Diele (2000)	Caeté River (PA)	01°00'S	1945	14.0	73.0	54.6	1945	10.0	145.0	49.5 ± 22.8
Alcantara-Filho (1982)	Pau Deitado River (MA)	02°30'S	30	35.5	63.5	51.6 ± 8.6	—	—	—	—
Castro (1986)	São Luís (MA)	02°35'S	—	46.0	79.3	59.2	—	—	—	—
Ivo <i>et al.</i> (1999)	Parnaíba River (PI)	02°48'S	3303	25.5	83.0	56.1 ± 7.5	2063	25.5	83.0	56.1 ± 7.5
Alcantara-Filho (1982)	Portinho River (PI)	02°55'S	36	48.4	73.2	59.2 ± 6.5	—	—	—	—
Costa (1972)	Caucaia (CE)	03°40'S	1574	32.0	68.0	54.5	1574	14.0	120.0	72.2
Alcantara-Filho (1978)	Ceará River (CE)	03°40'S	1092	34.0	75.0	56.9 ± 4.6	—	—	—	—
Alcantara-Filho (1982)	Ceará River (CE)	03°40'S	40	29.9	62.1	46.2 ± 10.0	—	—	—	—
Mota-Alves (1975)	Caucaia (CE)	03°40'S	276	45.7	60.6	—	—	—	—	—
Vasconcelos <i>et al.</i> (1999)	Curimatau River (RN)	06°20'S	1443	24.0	81.0	58.9 ± 10.9	1186	4.1	216.0	85.6 ± 48.9
Monteiro and Coelho-Filho (2000)	Paripe River (PE)	07°45'S	154	—	—	40.6 ± 7.9	154	—	—	35.1 ± 20.7
Alcantara-Filho (1982)	Canal Santa Cruz (PE)	07°49'S	13	41.5	73.7	62.0 ± 10.7	455	8.5	125.2	56.6 ± 24.4
Botelho <i>et al.</i> (1999)	Formoso River (PE)	08°42'S	532	26.2	70.0	50.9 ± 7.7	331	3.5	110.6	39.2 ± 19.6
Botelho <i>et al.</i> (1999)	Ilhetas River (PE)	08°48'S	470	4.3	66.6	43.8 ± 8.5	—	—	—	—
Alcantara-Filho (1982)	Mundaú Lagoon (AL)	09°42'S	51	31.6	63.4	52.5 ± 7.2	—	—	—	—
Alcantara-Filho (1982)	Pomonga River (SE)	10°40'S	42	34.7	63.2	51.5 ± 6.0	—	—	—	—
Souza (1999)	Sepetiba Bay (RJ)	22°55'S	83	41.4	68.6	—	—	—	—	—
Souza and Oshiro (1996)	Barra de Guaratiba (RJ)	23°04'S	—	29.6	89.5	—	—	—	—	—
Present Study	Iguape (SP)	24°41'S	1199	14.8	78.1	46.0 ± 8.6	1199	1.5	173.3	44.9 ± 25.0
Nakamura (1979)	Paranaguá Bay (PR)	25°33'S	390	38.3	71.5	—	—	—	—	—
Branco (1993)	Itacorubi (SC)	27°35'S	16	48	77	—	16	44.7*	175.3*	—
Total			12,729	4.3	89.5	—	8,923	1.5	216.0	—

* Data interpreted by graphical methods.

Rodrigues, 1982) = larval eclosion one day before the new moon (December 17, 1998) + full larval development (30 days according to Rodrigues and Hebling, 1989; Diele, 2000) = recruitment of megalopae (CW = 1.51 mm according to Diele, 2000) at the new moon of the following month (January 16, 1999) + a 22.6% increase in size/fortnight (Diele, 2000) = 17.4 mm young on July 3, 1999; therefore, eight months after spawning, explaining the occurrence of a 13 mm juvenile in August, 1999.

The longevity of crustaceans may be overestimated by the equation of Taylor (1958) because it depends on the estimate of the k constant, usually underestimated by most authors (Fonseca, 1998). In addition, Taylor's equation was

developed for teleost fish, which reach their maximum age at 95% of the asymptotic size. Nevertheless, our estimate of the k constant for *U. cordatus* generated biologically compatible longevity values, in contrast to the values obtained for $CW_{99\%}$, which resulted in 50% older ages (16.5 to 17.4 years). The longevity estimated by FiSAT resulted in ages more compatible with larger specimens previously recorded at other Brazilian locations (see Tables 2 and 3), showing similarity with the largest animals captured in the field for both sexes (males, 9.2 years; females, 8.3 years). Even though the data reported by Diele (2000) indicate a slow growth for *U. cordatus*, the estimated longevity generated extremely long life spans (males, 27.2 years;

Table 4. Review of the parameters estimated for the size and weight growth curves for species of the genus *Ucides* (CW = cephalothoracic width; CW_{∞} = asymptotic size of the growth curve; k = growth constant; t_0 = age soon after eclosion; Φ' = size growth performance index; WT = wet weight; WT_{∞} = asymptotic weight of the weight growth curve; b = constant of the power function for the WT/CW relationship; Φ = size weight performance index; M = males; F = females; VB = nonseasonal von Bertalanffy model; VBS = seasonal von Bertalanffy model).

Species	Author (Year)	Local	Latitude	Sex	Model	CW_{∞} (mm)	k (years)	t_0 (years)	Φ'	WT_{∞} (g)	b	Φ
<i>Ucides cordatus</i>	Diele (2000)	Caeté River (PA)	01°00'S	M	VB	89.0	0.15	—	1.07**	283.7	2.95	0.81**
				F	VB	72.5	0.18	—	0.97**	147.3	2.86	0.70**
	Ivo <i>et al.</i> (1999)	Parnaíba River (PI)	02°48'S	M	VB	94.3*	1.22	—	4.04*	333.9*	2.91	1.77*
				F	VB	85.2*	1.20	—	3.94*	224.9*	2.85	1.65*
	Vasconcelos <i>et al.</i> (1999)	Curimatau River (RN)	06°20'S	M	VB	90.8*	1.20	—	3.99*	381.3*	3.12	1.80*
				F	VB	87.9*	0.90	—	3.84*	267.9*	3.15	1.57*
Monteiro and Coelho-Filho (2000)	Paripe River (PE)	07°45'S	T	VB	77.8*	0.96	—	3.76*	—	—	—	
Present study	Iguape (SP)	24°14'S	M	VB	90.3	0.28	—	1.36	281.7	2.99	1.08	
			F	VBS	88.6	0.26	—	1.31	259.5	2.86	1.02	
<i>Ucides occidentalis</i>	Poma-Sánchez (1995)	Tumbes (Peru)	03°30'S	M	VB	119.51	1.20	0.712	4.16*	—	—	—
				F	VB	112.75	0.90	0.749	4.08*	—	—	—

* Data not cited by the author but calculated from his published data; **The data were converted because the author used a Neperian logarithm (nl) to represent the index.

females, 27.6 years), perhaps indicating an underestimate of the k constant (see Fig. 5). According to the authors who propose a rapid growth for this species, the estimated ages ranged from 1.9 to 2.8 years (Ivo *et al.*, 1999; Vasconcelos *et al.*, 1999), values that are not consistent with schedules for each consecutive stage of the life history, as previously demonstrated.

Koch (1999) classified *Ucides cordatus* as herbivorous, mainly feeding on senescent leaves available on the mangrove swamp substrate, in agreement with other investigators (Geraldine and Calventi, 1983; Nascimento, 1993). The biochemical composition of senescent leaves may be one of the main causes of the reduced growth rate of *U. cordatus*, since Wolcott and Wolcott (1987) detected a limitation of *Cardisoma guanhumi* growth when the species was submitted to low nitrogen concentrations. High tannin concentrations may also cause the same effect, with reports of growth reduction or even interruption in some arthropods (Fleck and Layne, 1990).

The seasonal model of von Bertalanffy was effective in representing the growth of *U. cordatus* females in response to reduced feeding, acting in synergy with environmental factors limiting reproduction. Despite the statistical significance of the seasonal oscillation growth constant for males ($C < 0.3$), its magnitude was negligible to represent seasonality, making this model similar to the nonseasonal one.

Larger specimens undergo only one molt per year after the pubertal molt (Nascimento, 1982). This molt event (reproductive or nuptial molt) was observed mainly in October–November before the “crab walk” behavior (or “andada”), when all the crabs leave their burrows, and form pair-bonds and copulate (Góes *et al.*, 2000). This fact explains the reduced mean increase in size of adults of the same age range, with signs of a second annual molt appearing to be present for males measuring 40 mm to 65 mm (for example, during the transition from January–April to May–August), implying a greater growth rate for females.

The greater size increase rate occurred during the transition from September–December to January–April (Fig. 3A, B), and was evident among females starting from 30 mm. Below this size, females have a greater increase in size (for example, cohort 1 in the transition between May–August and September–December), in agreement with Diele (2000), who observed a 13% mean increase in specimens ranging 20 mm to 30 mm in size, reduced three-fold from 50 mm. The cohort 1 of females (Fig. 3B) indicates that females measuring 35–45 mm become adults after the puberty molt in the transition between September–December and January–April, when they acquire morphological and physiological maturity (Hattori, 2002). Starting from this size, the females show a reduced growth rate, which increases again two years later between September–December and January–April, when a subsequent significant increase in size indicates the allometric alteration of the cephalothorax of this species (45–65 mm). For males, the higher increments in size also occurred during the transition between September–December and January–April, although during the first year there was a change in the growth rate of the first gonopod pair, followed by the puberty molt in the

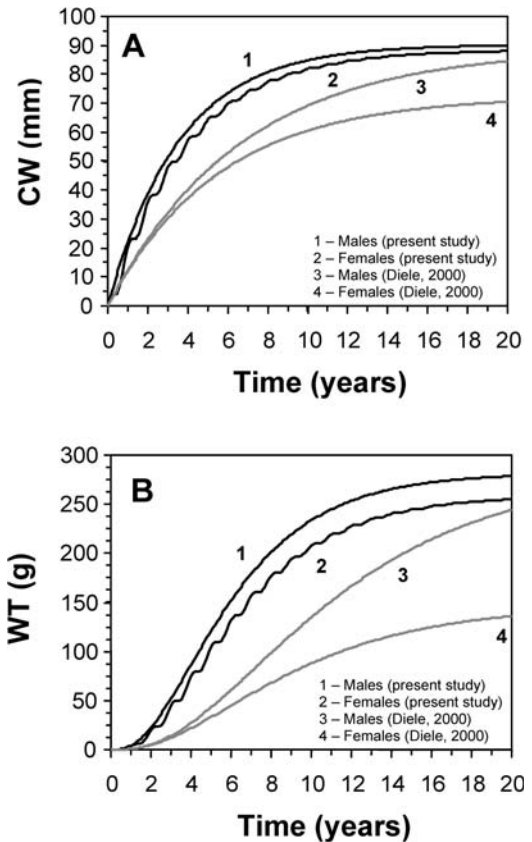


Fig. 5. *Ucides cordatus* (Linnaeus, 1763). Comparison of curves of the growth of size (A) and weight (B) obtained for each sex at Iguape (SP), Brazil ($24^{\circ}14'S$ = present study) and Caeté (PA), Brazil ($01^{\circ}00'S$ = Diele, 2000).

following year, when the male acquires functional maturity (Hattori, 2002).

Ucides cordatus reached functional maturity at an age about 81% higher than that of species of the genus *Callinectes* (Branco and Masunari, 1992; Branco and Lunardón-Branco, 1993) and six times higher than that of *Arenaeus cribrarius*, which reaches sexual maturity at six months of age (Pinheiro and Fransozo, 1998). In *U. occidentalis*, studied by Poma-Sánchez (1995) and Rujel-Mena (1996), physiological maturity occurs at nine months; therefore, it is four times quicker than that obtained in the present study for *U. cordatus*. This is due to the large growth constant of *U. occidentalis*, which was four-fold higher than that of *U. cordatus* in Iguape (Table 4), showing the importance of the k constant in these estimates.

The similar t_0 values obtained for the first juvenile stage on the basis of the growth curves for each sex indicate that the mathematical models represent the growth of the species during the larval phase, in contrast to the data reported by other investigators who studied shrimp (D’Incao, 1984) and brachyurans (D’Incao *et al.*, 1993; Pinheiro and Hattori, unpublished data). This was possibly due to the similarity of the growth rates (k) and asymptotic size (CW_{∞}) for *U. cordatus* in a comparison between the sex, in contrast to the data obtained by the authors cited above.

The reduced growth rate of *U. cordatus* in terms of size and weight is a source of concern because of the continued intensity of the harvest, which has been increasing every year. The absence of a plan for the management of the species, especially where its harvesting rate is high, has already caused a reduction in size in specimens from the Brazilian North (Gondim and Araújo, 1996). The difficulty in optimizing the larval production of this species in the laboratory, because of a high mortality caused by the need for specific live food in this phase, has been a limiting factor. In this respect, the management of natural populations of these species still seems to be the best solution for the sustained exploitation of this resource.

Growth in the Laboratory

The juvenile phase of crustaceans is characterized by a greater increase in size and molting frequency, followed by a gradual decrease after the pubertal molt (Hartnoll, 1982). In the present study, due to the controlled environmental conditions and the reduced size amplitude of the specimens analyzed (5.63–13.00 mm), this did not occur, in contrast to the data reported by Diele (2000), who showed different size increase rates both in captivity (1.2–11.5 mm \approx J_I to J_{XIII}) and in the field (20.5–82.4 mm).

In crustaceans, the greater increase in size during the juvenile phase reduces the time for the critical phase of development. In the present study, the mean increment rate for the same amplitude of size variation was about four times lower than that obtained by Diele (2000), with a molting frequency about twice lower. These differences were due to the different types of management used in these experiments, because Diele (2000) reared his specimens in containers with mangrove sediment and kept them under natural temperature/photoperiod conditions, feeding them *Rizophora mangle* leaves. Certainly, Diele (2000) used mangrove sediment to reduce animal stress, while in the present study, and in the study presented by Geraldès and Calventi (1983), PVC tubes were used to this purpose.

The nutritional aspect of a diet has an important effect on the growth of an organism. Despite the high specificity of *U. cordatus* for senescent mangrove leaves, offering an alternative diet to optimize the growth in size and weight is a common procedure that was used in previous studies (Geraldès and Calventi, 1983; Ostrensky *et al.*, 1995). Ostrensky *et al.* (1995) observed that a mixed diet consisting of vegetables, mangrove leaves, and fish quadrupled the growth rate when compared to a diet consisting only of mangrove leaves. These authors recorded a 1.7-fold higher growth rate using larger specimens (mean size of 47.8 mm), in contrast to Geraldès and Calventi (1983) who worked with smaller animals (16.0–24.8 mm), with an increment rate four times lower than that detected in the present study. The method used by Geraldès and Calventi (1983) differed from that used in the present study only in terms of diet (vegetables, banana leaves, and mangrove leaves) and by the fact that the animals were reared under conditions of light deprivation. Thus, in addition to the nutritional component, photoperiod seems to have a negative effect on the growth of *U. cordatus*, confirming the results reported by Costlow and Bookhout (1968) and Leffler (1972). Comparison of the data obtained shows that constancy of photoperiod may lead to

homogeneity in animal size, in addition to minimizing the rate of increase in size.

On the basis of the information obtained, rearing *U. cordatus* in captivity still depends on the development and testing of potential diets that will optimize their growth and weight gain.

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