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AGE AND GROWTH OF *CALLINECTES DANAE* (BRACHYURA: PORTUNIDAE) IN A TROPICAL REGION

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ABSTRACT

Some 2178 male and 2109 female *Callinectes danae* Smith, 1869 were caught in Northeastern Brazil, from March 2009 through February 2010; we reared 24 males and 24 females for 6 months. The relative growth (relation between weight and cephalothorax width) showed negative allometry, except in adult males. The females presented marked changes in relative size of the fifth pleomere as they matured, while the males showed changes in chela size. As rearing progressed, the females underwent ecdysis five times while the males underwent ecdysis six times. The puberal molt was the last to occur. The von Bertalanffy growth model (with t_0) provided the best fit, when compared to the von Bertalanffy (with CW_0), von Bertalanffy (with $t_0 = 0$), Gompertz, and Richard models. The following growth functions for reared individuals were obtained: $CW_t = 9.88(1-\exp(-0.0228(t+14.27)))$ and $CW_t = 8.02(1-\exp(-0.0158(t+26.23)))$. For wild individuals the growth functions were as follows: $CW_t = 12.12(1-\exp(-0.0052(t+29.36)))$ and $CW_t = 9.48(1-\exp(-0.0036(t+59.04)))$, for males and females, respectively. The individuals reached smaller sizes in the rearing system; however, the growth rate was higher. The mean longevity ranged from 375 to 429 days for males and from 458 to 553 for females. The maximum longevity ranged from 550 to 860 and from 764 to 1205 days, for males and females, respectively.

KEY WORDS: growth, longevity, rearing, swimming crab, von Bertalanffy

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INTRODUCTION

Crabs from the family Portunidae are characterized by a paddle-shaped pair of fifth pereiopods. This family is distributed throughout the Western Atlantic coast from North America to the extreme south of South America (Melo, 1996).

Callinectes danae Smith, 1869 is the most abundant species of portunid in Venezuela (Carmona-Suárez and Conde, 2002) and throughout the Brazilian coast (Teixeira and Sá, 1998; Severino-Rodrigues et al., 2001; Branco and Freitas-Junior, 2009; Nevis et al., 2009). This species is distributed from Florida (United States) to southern Brazil (Melo, 1996). It is found from the intertidal zone to 75 m depth, showing great tolerance to salinity variation. It can also occupy estuarine areas, particularly those with muddy sediments (Melo, 1996).

The analysis of growth and age structure in crustaceans is complicated by the absence of permanent rigid structures that might record age. Therefore, the study of crustacean growth is usually performed by analysis of the progression of modes in size-frequency distributions through time, field or laboratory rearing experiments, mark-recapture studies or by quantifying lipofuscin accumulation in nerve tissue (Vogt, 2012).

The study of growth is extremely important because the biological parameters obtained through the use of growth models are the basis for fisheries management. Additionally, morphometric analyses are valuable for inferring size-at-maturity which is a necessary input to conservation measures (Mantelatto and Fransozo, 1992).

A large effort has been made to characterize the age and growth of many species of portunid such as *C. danae* (Branco and Masunari, 1992; Keunecke et al., 2008; Castillo et al., 2011), *Callinectes ornatus* Ordway, 1863 (Branco and Lunardon-Branco, 1993; Keunecke et al., 2008), *Portunus pelagicus* (Linnaeus, 1758) (Sumpton et al., 1994; Josileen and Menon, 2005), *Arenaeus cribrarius* (Lamarck, 1818) (Pinheiro and Hattori, 2006), *Charybdis bimaculata* (Miers, 1886) (Doi et al., 2008) and *Callinectes sapidus* (Rathbun, 1896) (Ferreira and D'Incao, 2008). However, there is a lack of information regarding the growth of *C. danae* in tropical regions and the validation in rearing system. To fill this gap, the present study sought to estimate *C. danae* growth curves using biological parameters and ages based on analyses of wild specimens and validate the growth under reared condidtions.

MATERIAL AND METHODS

Data Collection

Specimens of *Callinectes danae* Smith, 1869 were caught in the Santa Cruz Canal (08°47′30″S, 34°53′20″W – Fig. 1),

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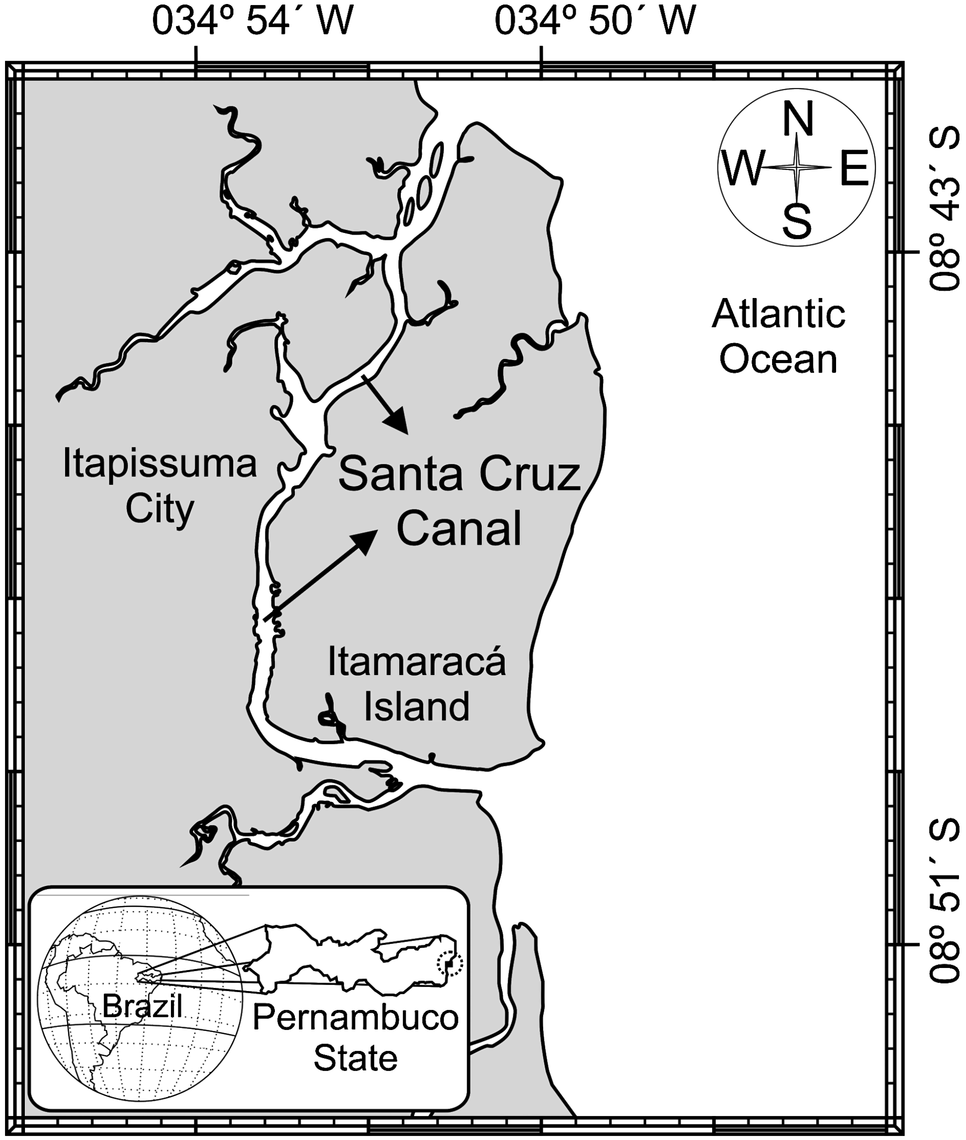

Fig. 1. Geographical location of the collection area of *Callinectes danae*, the Santa Cruz Canal, Pernambuco state, Brazil.

Northeastern Brazil, from March 2009 through February 2010. Crabs were sampled every month at low tide using a beach seine (with 2 or 3 efforts by day, once a month, totaling 12 months) with a 12-mm mesh aperture and line with fish bait, mainly Engraulidae (once a month, totaling 12 months). The beach seine caught mainly the juveniles that are on the margin of Canal due their low selectivity and the line caught mainly the adults that are in adjacent area due to deeper waters and high selectivity (Shinozaki-Mendes, 2012). Temperature and salinity of the surface water were recorded on each occasion and are reported as mean ± standard deviation of all values.

The specimens were identified according to the identification key for Brachyura proposed by Melo (1996). The gender and maturity of *C. danae* were determined from the shape and adherence of the pleon. Juvenile females have a triangular pleon locked distally to the thoracic sternites. Adult females have a semicircular, unlocked pleon. The male pleon has the shape of an "inverted T" and is locked (juvenile) or unlocked (adult) distally to the thoracic sternites (Van Engel, 1990).

The following measurements were made: width of cephalothorax (CW, in cm), at the end of lateral spines; width of fifth pleomere (W_5, in cm), measured in the middle portion; right chela length (CL, in cm), from the end of the immovable finger to the opposite end, using a vernier calliper with precision to nearest 0.01 cm and total wet weight (TW, in g) using balance with precision to nearest 0.01 g. Individuals with missing appendages were not weighed.

The relationship between TW and CW was modeled by the equation

$$\mathrm{TW} = \beta_0 \mathrm{CW}^{\beta_1},$$

where β_0 is the intercept and β_1 is the allometric coefficient (the relationship is allometrically positive when $\beta_1 > 3$, allometrically negative when $\beta_1 < 3$, and isometric when $\beta_1 = 3$). The student's t test was used to compare the β_1 from models (Zar, 1984). The linear models

$$1)\ W_5 = \beta_0 + \beta_1 CW \quad \text{and}$$
$$2)\ CL = \beta_0 + \beta_1 CW$$

were used to describe the relationships between W_5 and CW and between CL and CW, respectively. These relationships were established separately for the two sexes, as well as for juveniles and adults. The "W" test was used to compare models; this test is based on maximum likelihood and uses the chi-squared distribution (Mendes, 1999), as follow:

$$W = ((n1 + n2)\ln((RS1, 2)/(n1 + n2))) - (n1 \ln((RS1)/(n1))) - (n2 \ln((RS2)/(n2)))$$

where n is the number of points observed, RS is the residual sum of squares, 1 is the model number1, 2 is the model number 2, and ln is the logarithm neperian.

The computational package FISAT II (Gayanilo et al., 2005) was used for the modal progression analyses. Males and females were analyzed separately. Size-frequency distributions with size classes of 0.5 cm CW were constructed for each sample date with the aim of defining the mean CW of modes representing supposed age groups using the Bhattacharya (1967) method. The "Linking of means" tool was applied to identify the increase in size throughout the growth. The "linking of means" tool generates a file containing the increase in size with age that was used in the estimations of growth curves described below.

Rearing (Validation)

In July 2010, we selected 48 specimens (24 of each sex) of *C. danae* caught in Santa Cruz Canal with the beach seine described above. The smaller individuals caught (mean of 2 cm) were designated as "age zero" as they represent crabs recruited to the population in the current year, based on Hines (1986), who reported that the average size of the first crab is 2.89 cm.

The specimens were randomly distributed into experimental aquarium units. Each unit contained sand substrate, 40 liters of water with a mean salinity of $23.5 \pm 0.2‰$ and a mean temperature of $27.3 \pm 0.1°C$, a biological and mechanical filter and an aeration system. The animals were reared for 180 days and fed daily with alternating rations of fish, shrimp and mollusks.

Biometry was performed at the beginning of the experiment and at each molt. The CW was measured and the increase in size was computed for each specimen. The sizes (CW) at which males and females underwent ecdyis under reared condidtions were analyzed for the normality using Shapiro-Wilk test ($p < 0.05$). Then the mean and standard deviation were calculated.

Growth Model

Growth parameters based on the growth data were calculated using five models:

1) von Bertalanffy (1938) (VB1):
$CW_t = CW_\infty(1 - \exp(-kt))$;

2) von Bertalanffy com t_0 (Beverton and Holt, 1957) (VB2): $CW_t = CW_\infty(1 - \exp(-k(t - t_0)))$;

3) von Bertalanffy com CW_0:
(Simpfendorfer et al., 2002) (VB3):
$CW_t = CW_0 + (CW_\infty - CW_0)(1 - \exp(-kt))$;

4) Richards (1959) (RGF):
$CW_t = CW_\infty/(1 + \exp(-k't + b))^m$;

5) Gompertz (1875 *apud* Campana and Jones, 1998) (GGF): $CW_t = CW_\infty \exp(-a \exp(-k''t))$;

where: CW_t = cephalothorax width (cm) at age "t"; CW_∞ = mean theoretical CW that a species can reach (asymptotic size); k = growth constant, in days; t = age, in days; t_0 = age at $CW_t = 0$; CW_0 = the first crab size (was used the smallest individual size); k', b, m, k'' and a are the coefficients of the model.

To evaluate which growth curve better described the data, we used the Akaike Information Criterion (AIC) (Akaike, 1974) defined as: $AIC = 2\text{Log}(\theta) + 2K$, where θ = minimum likelihood and K = number of parameters from the model. Then was calculated the variation from the smallest value of AIC (Δ_i) and the importance of each model (W_i), defined as: $W_i = \exp(-0.5\Delta_i)100/\sum \Delta_i$.

The next step was to define the upper and lower limits of the 95% confidence interval using likelihood and bootstrap analyses, both with 1000 iterations (Hood, 2006). We used the previously mentioned "W"-test to compare models between males and females and between wild and reared individuals.

The mean longevity was estimated using: 1) the estimated age of the oldest cohort identified by the Bhattacharya (1967) method, and 2) the average CW_t of adults. Maximum longevity was calculated considering the time (t_x) to reach 95% and 99% of CW_∞ proposed by Cailliet et al. (2006): $t_x = 1/k \ln(CW_\infty - CW_0)/(CW_\infty(1 - x))$ where x was replaced by 0.95 and 0.99.

RESULTS

Morphometry and Growth of Wild Crabs

Between March 2009 and February 2010, 4287 specimens of *C. danae* were caught, of which 2109 were females (49%) and 2178 were males. For males, the CW ranged from 1.4 to 11.2 cm in juveniles (n = 1897) and from 4.8 to 12.4 cm in adults (n = 281). For females, the CW ranged from 1.1 to 8.4 cm in juveniles (n = 2004) and from 7.1 to 10.0 cm in adults (n = 105) (Fig. 2). The water temperature ranged from 27.0 to 31.5°C, with a mean of $29.4 \pm 1.2°C$. The salinity ranged from 18.5 to 31.9‰ with a mean of $26.6 \pm 3.5‰$.

The relative growth of juvenile and adults, as well as of males and females, showed statistically significant differences in all comparisons, based on the W-test (all p-values were inferior to 0.018). The models presented a high correlation (Fig. 3). Only adult males showed positive allometry ($\beta_1 = 3.2$) between TW and CW, significantly different from juveniles males, juveniles females and adult females (p-values inferior to 0.0001). While adult and juvenile female showed no different alometry ($p = 0.4824$), the juve-

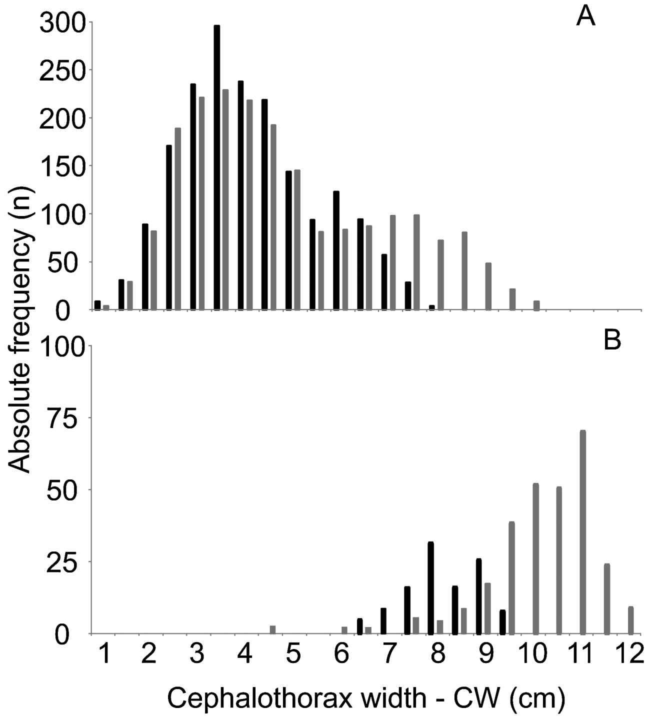

Fig. 2. Absolute frequency of males (grey) and females (black), juveniles (A) and adults (B) of *Callinectes danae* by CW class. The CW class indicates the mean class value.

nile male and juvenile female showed statistically difference ($p = 0.0058$) although both are negative allometric.

Upon examining the relationship of W_5 on CW, it was observed that females had a remarkable morphometric differentiation of the pleon at adulthood, whereas the change was barely noticeable in males (Fig. 4). When examining the relationship between CL and CW, the opposite occurs. The males have a prominent morphometric differentiation of chelae at adulthood whereas the change is subtle in females (Fig. 4).

From the mean sizes (CW) found using the Bhattacharya Method it was possible to identify the modal (age) groups throughout the year. Five groups of males and 4 groups of females were identified (Fig. 5). Groups of smaller individuals showed similar sizes (male and female) but the females reach smallest size than males.

Rearing Experiment (Validation)

During the rearing experiment, the females performed five molts and the males performed six molts, in which the latter is the puberty molt, where there is a noticeable change in the shape and adherence of the abdomen. The size of the individuals in each molt follows the normal distribution (*p*-values from 0.0512 to 0.6626). The mean initial size (CW) ranged from 2.1 to 2.5 cm and the females reached smaller sizes than males. The time between two consecutive molts increased (Table 1) until the animals reached puberty and then there were no new molts. The general molt increments and intermolt periods were greater in females than in males. The average time elapsed between last molt and end of experiment was 52 days for females and 37 for males.

Growth

Growth parameters of the models were calculated based on data from the wild population and reared individuals (Table 2 and Fig. 6). In all models, the CW_∞ is larger for males than it is for females. The growth constant "k" from the von Bertalanffy growth model is also larger for males than it is for females.

The models from the wild population were most superimposed except near the origin. The variation in origin is caused by the CW_0 that is a fixed value in VB1 and VB3. Reared individuals showed a greater variation on the growth curves and CW_∞ values. Reared individuals of both sexes reached smaller asymptotic sizes but had higher growth rates than wild crabs.

Based on biological parameters (Table 2) and on AIC (Table 3), the VB1 does not represent the smallest size; the CW_∞ was lower than the mean maximum size and presented a wide confidence interval (CI) although it had the best AIC values for males. The VB2 presented biological parameters consistent with the observations; a narrow CI and a median value of AIC. The VB3 presented a low AIC for female meantime presented a high AIC for males and

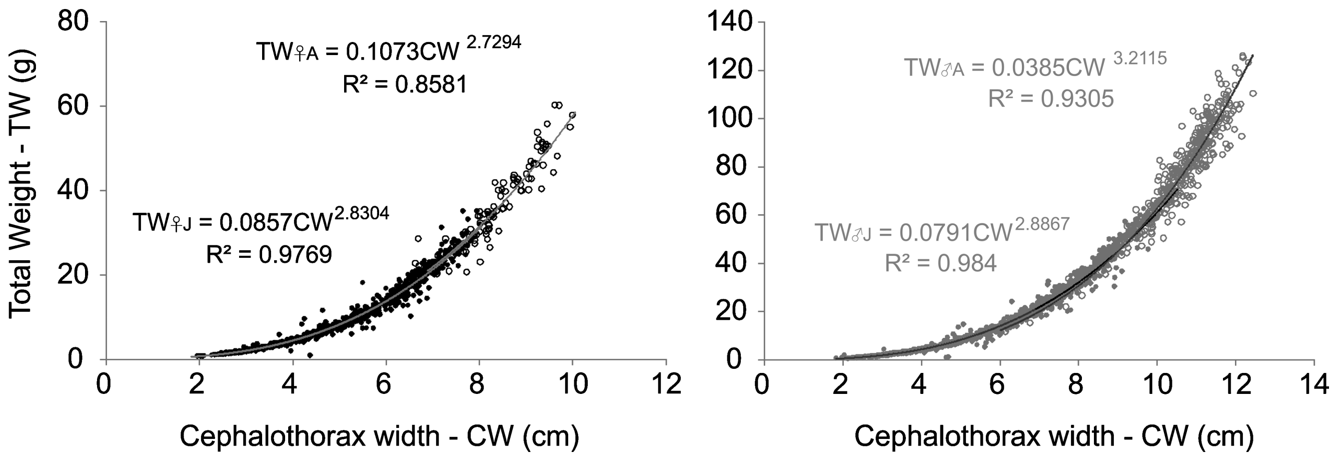

Fig. 3. Relationship between TW and CW from females (♀, Black symbol) and males (♂, grey symbol), juveniles (J, solid fill) and adults (A, no fill) of *Callinectes danae* and their respective models and correlation coefficient (R^2).

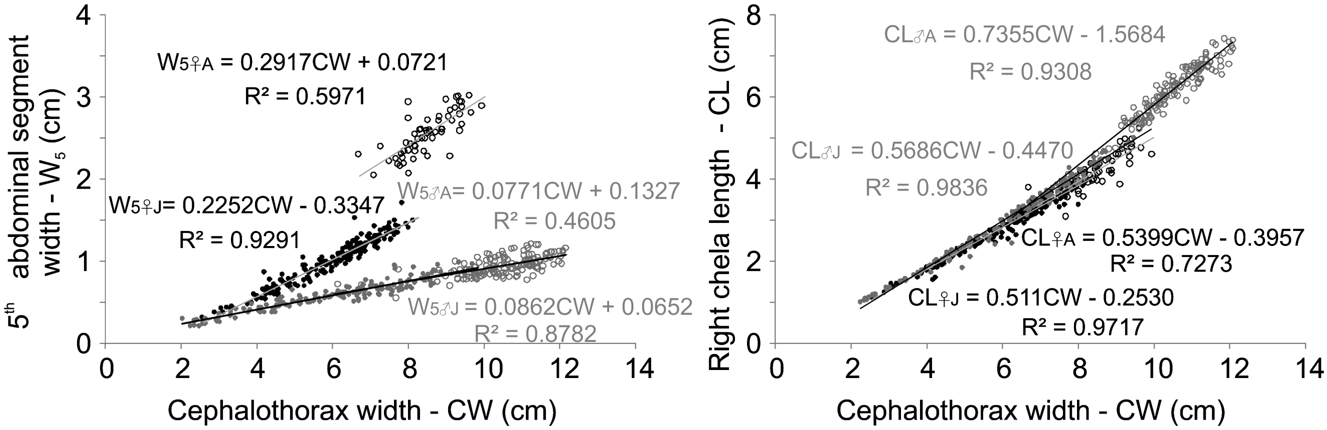

Fig. 4. Relationship between $W_5 \times CW$ and $CL \times CW$ from females (♀, Black symbol) and males (♂, grey symbol), juveniles (J, solid fill) and adults (A, no fill) of *Callinectes danae* and their respective models and correlation coefficient (R^2).

a wide confidence interval. The GGF presented biological parameters consistent with the observations; a narrow CI and a median value of AIC, similar to VB2. The RGF showed a very high AIC and CW_∞ very low. From this analysis, models VB2 and GGF showed the best fit to data. Thus, the VB2 model was selected for calculating the longevity and for comparative purposes, since the data available in crustacean literature use the von Bertalanffy model.

All the growth models differed significantly between "reared" and "wild" crabs and between the sexes ($p < 0.0001$ in all pairwise comparisons). Thus, the growth curves were analyzed separately; the upper and lower limits of the 95% CI on parameters are shown in Table 2.

From VB2 model parameters, the average lifespan of wild crab is estimated to be 429 days for males and 458 days for females based on the most long-lived cohort. If instead the average size of adults is considered (males: 10.6 cm; females: 8.4 cm), the lifespan is estimated to be 375 for males and 553 days for females. The maximum lifespan was estimated based on 95% and 99% of CW_∞ to be 550 to 860 days (1.5 to 2.4 years) in males and from 764 to 1205 days (2.1 to 3.3 years) in females. "Wild" catches are

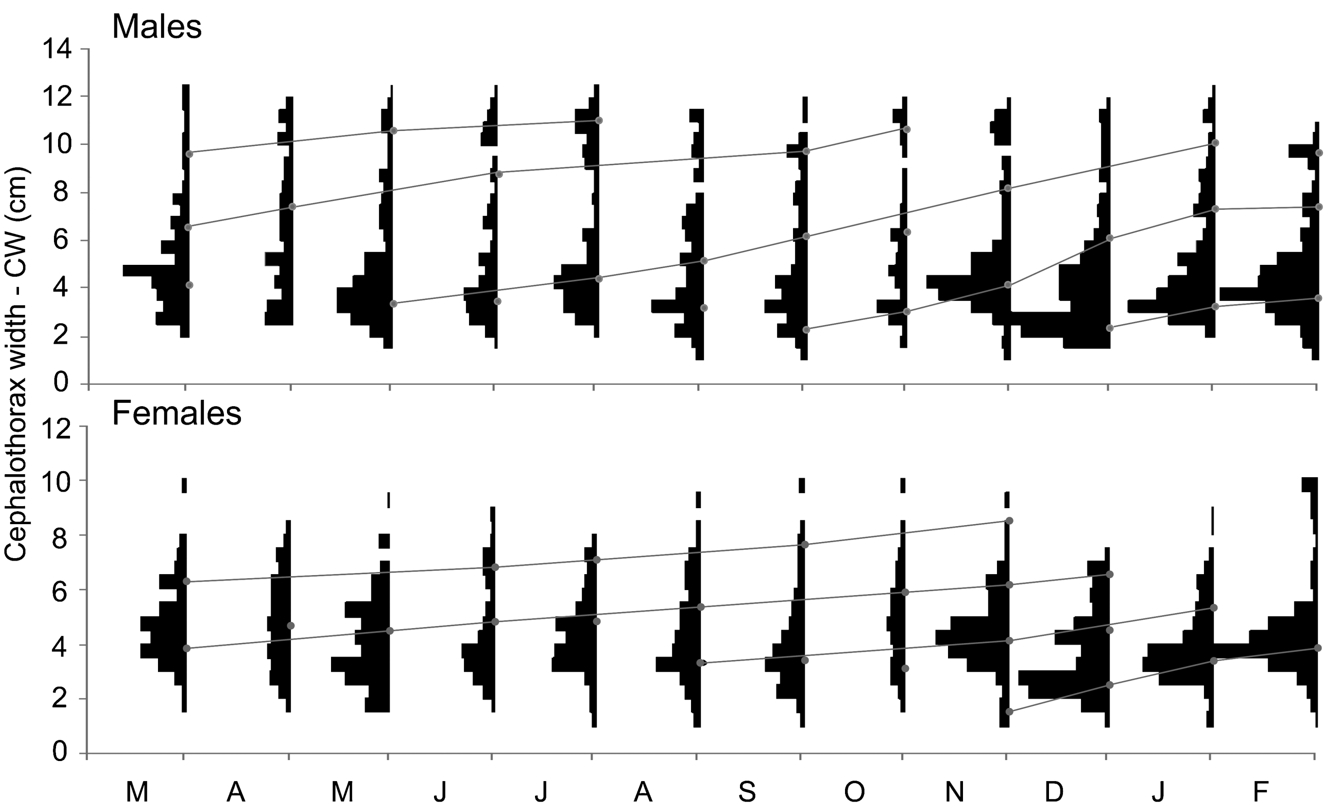

Fig. 5. Absolute frequency of males and females and the modal groups, identified by Bhattacharya method and selected by the "Linking of means" tool, of *Callinectes danae* caught in Northeastern Brazil from March 2009 to February 2010.

Table 1. Sizes (CW) at which males and females of *C. danae* underwent ecdysis under reared conditions, the mean number of days of the intermolt period and the percentage of increment. SD: standard deviation.

Ecdisys	Females			Males		
	CW ± SD	Days	Increment	CW ± SD	Days	Increment
Initial	2.1 ± 0.3	08	40.5%	2.5 ± 0.1	09	24.9%
1st	2.9 ± 0.1	18	25.3%	3.1 ± 0.1	17	20.3%
2nd	3.6 ± 0.1	29	32.6%	3.7 ± 0.1	21	26.6%
3th	4.8 ± 0.1	36	28.5%	4.7 ± 0.1	23	26.4%
4th	6.2 ± 0.2	37	26.9%	5.9 ± 0.2	32	18.7%
5th	7.8 ± 0.2			7.0 ± 0.2	41	24.5%
6th	–			8.7 ± 0.2		

composed primarily of juvenile individuals (Fig. 7). Only half of the female population reaches 105 days, while half of the males do not live past 75 days. Given that the size of first maturity for this study population is 8.4 cm for males and 7.4 cm for females (Shinozaki-Mendes, 2012); we estimate that maturity is reached at 198 and 366 days, respectively.

DISCUSSION

Somatic growth was faster in males than in females. This is related to the difference in energy use between the sexes. Females direct energy towards the production of large numbers of eggs and towards spawning migrations, while males primarily invest in somatic growth (Hartnoll, 1974). In the case of *C. danae*, during reproduction the males hold the females in pre- and post-copulatory embraces; therefore, it is imperative that they reach a larger size than the females.

Males had a higher relative chela growth than females (CL × CW). The difference was even more pronounced when males became adult, making chela size a feature distinguishing the sexes in this species. Nevertheless the chela alometry is barely perceptible if compared with *Ucides cordatus* (Linnaeus, 1763) (Diele and Koch, 2010) and *Cardisoma guanhumi* Latreille, 1825 (Shinozaki-Mendes et al., 2012). Larger male chelae confer advantages such as superiority in combat (Hartnoll, 1974) and in offering protection female during their puberty molt (Guerrero-Ocampo et al., 1998).

The sharp increase in the ratio of W_5 to CW in females is due to a change in the shape of the abdomen from triangular to semicircular at the puberty molt. This is an important feature, as females need to increase the area of their abdomen to better incubate the eggs. A natural advantage in studying the growth of crustaceans is the ecdysis and pubertal molt. These characteristics become advantages for making growth a discrete variable, and not continuous,

Table 2. Growth parameters for wild and reared males and females of *C. danae* using the von Bertalanffy growth function (VB1, VB2 and VB3), Gompertz growth function (GGF) and Richards growth function (RGF). The values in brackets indicate the upper and lower limits of the confidence interval at 95%. CW_∞: asymptotic size; k: Constant growth, on a daily basis; t_0: age at size $CW_t = 0$; k′, k″, a, b and m are the coefficients of the model.

		Wild		Rear	
		♂	♀	♂	♀
VB1	CW_∞	10.9 (4.2; 26.2)	7.6 (3.4; 18.0)	7.8 (0.1; 19.4)	6.3 (1.1; 14.4)
	k	0.008 (0.004; 0.020)	0.009 (0.002; 0.019)	0.064 (0.009; 0.040)	0.073 (0.017; 0.140)
VB2	CW_∞	12.1 (6.7; 20.0)	9.5 (8.4; 11.7)	9.9 (4.8; 16.2)	8.0 (4.4; 14.0)
	k	0.005 (0.002; 0.009)	0.004 (0.002; 0.005)	0.023 (0.013; 0.047)	0.016 (0.009; 0.031)
	t_0	−29.4 (−48.9; −14.7)	−59.0 (−91.8; −38.2)	−14.3 (−23.7; −7.0)	−26.2 (−45.4; −13.2)
VB3	CW_∞	11.8 (2.8; 23. 6)	8.3 (2.6; 18.1)	8.7 (1.0; 19.1)	6.6 (3.0; 14.0)
	k	0.006 (0.000; 0.012)	0.006 (0.002; 0.012)	0.039 (0.004; 0.146)	0.045 (0.021; 0.149)
GGF	CW_∞	11.02 (5.23; 18.68)	8.55 (4.74; 15.08)	9.13 (4.50; 15.28)	7.43 (3.75; 12. 52)
	k′	−0.0095 (−0.0172;- 0.0051)	−0.0064 (−0.0094;-0.0028)	−0.0389 (−0.0335; −0.0096)	−0.0258 (−0.0444;-0.0131)
	a	1.65 (0.82; 2.84)	1.40 (0.70; 0.2.34)	1.18 (0.57; 2.07)	0.99 (0.50; 1.65)
RGF	CW_∞	10.7 (6.6; 16.1)	8.5 (5.3; 12.9)	7.7 (4.6; 11.7)	7.4 (4.4; 11.6)
	k″	0.012 (0.008; 0.020)	0.006 (0.004; 0.010)	1.275 (0.638; 1.933)	0.026 (0.014; 0.040)
	b	1.8900 (1.3200; 2.8400)	0.0035 (0.0021; 0.0050)	10^{20} (10^{19}; 10^{20})	0.0005 (0.0003; 0.0008)
	m	−0.6950 (−1.0424; −0.4219)	−0.0020 (−0.0051; −0.0021)	−48.62 (−75.02; −30.39)	−0.0006 (−0.0008; −0.0003)

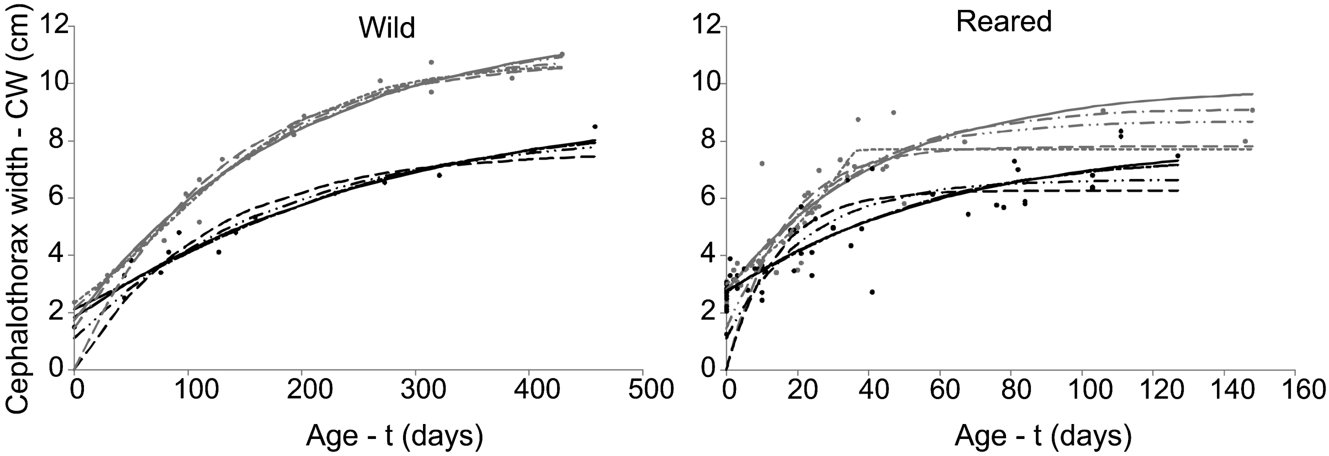

Fig. 6. Growth functions for males (grey) and for females (Black) of *Callinectes danae* in reared conditions and in the wild. Dashed line: von Bertalanffy (VB1); continuous line: von Bertalanffy with t_0 (VB2); dashed line with two dots: von Bertalanffy with CW_0 (VB3); dotted line: Richards (RGF) and dashed line with one dot: Gompertz (GGF).

as occurs for the fish. Thus, there is a great accuracy in the measurement of growth, since reproducibility is clearly feasible (Campana, 2001).

Hilborn and Walters (1992) cited that the problem in modal progression analyses is the superposition of modal classes of old individuals. There are some other notorious limitations listed by Lessa and Duarte-Neto (2004): 1) is overlapping fashion to age underestimated; 2) the formation of groups is based on size, and non-age; 3) the spawning does not occur in a discrete period of the year; 4) may be cohorts subjected to different environmental conditions and thus have different growth rates; 5) some size classes are under-represented; and 6) is usually selectivity of fishing gear. However, when performing validation using another method of growth, these limitations can be overcome. In this study, the validation showed that the number of molts estimated by modal progression analysis is equal to the observed in the laboratory. Meanwhile the size and age showed differences between the cultivation and natural conditions.

Table 3. Analysis of the Akaike information criterion for von Bertalanffy growth function (VB1, VB2 and VB3), Gompertz growth function (GGF) and Richards growth function (RGF) for males and females, reared and wild, variation from the smallest value of AIC (Δ_i) and the importance of each model (W_i) in %.

Sex		Wild			Rear		
		AIC	Δ_i	w_i	AIC	Δ_i	w_i
♂	VB1	9.1	0.0	49.2	9.9	0.0	48.3
	VB2	12.0	2.9	11.5	12.0	2.1	16.9
	VB3	14.0	4.9	4.2	14.4	4.5	5.1
	GGF	10.4	1.3	25.7	11.5	1.6	21.7
	RGF	12.4	3.3	9.4	13.5	3.6	8.0
♀	VB1	8.5	0.4	29.5	10.1	0.2	31.7
	VB2	9.8	1.7	15.4	11.9	2.0	12.9
	VB3	8.1	0.0	36.0	9.9	0.0	35.0
	GGF	10.0	1.9	14.0	11.6	1.7	14.9
	RGF	12.0	3.9	5.1	13.6	3.7	5.5

One of the pre-requisites for using the method of Bhattacharya (1967) is to use a single fishing gear or fishing gear with the same selectivity. Meantime, the population of *C. danae* in Santa Cruz Canal presents a spatial segregation (Shinozaki-Mendes, 2012). Thus, the combination of two fishing gear is the only way to caught juveniles and adults in a representative way. Thereby it is important to highlight the possibility of bias in the analysis.

In this study, males displayed larger growth parameter values than females, based on the von Bertalanffy model. This result was also observed for *C. danae* in Venezuela (11°N) (Castillo et al., 2011) and at lower latitudes, between 22° and 27°S, in Brazil (Keunecke et al., 2008 and Branco and Masunari, 1992, respectively). An important feature of the growth curves is that the CW_∞ and k act in opposing ways, i.e., a model can be fitted to the same data with lower values of CW_∞ if values of k are higher and vice versa. Therefore, we chose to perform a comparison of the curves instead of considering the only growth parameters separately. Thus, we plotted the values of the growth curves of *C. danae* known to date (Fig. 8). All authors used the von

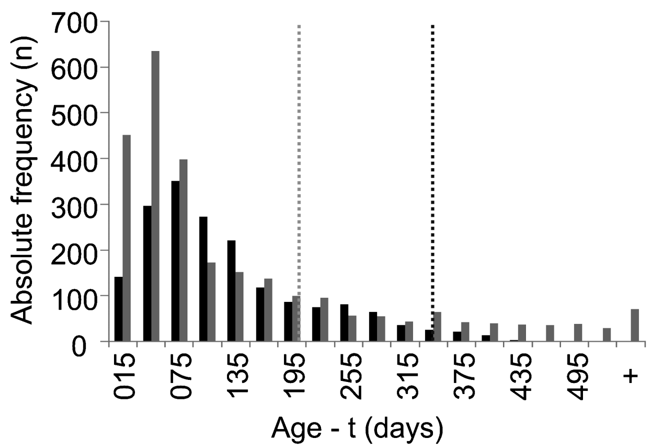

Fig. 7. Frequency of males (grey) and females (Black) of *Callinectes danae* by age. The age indicated on the figure represents the average value of the class. The dotted line indicates the age of first maturation.

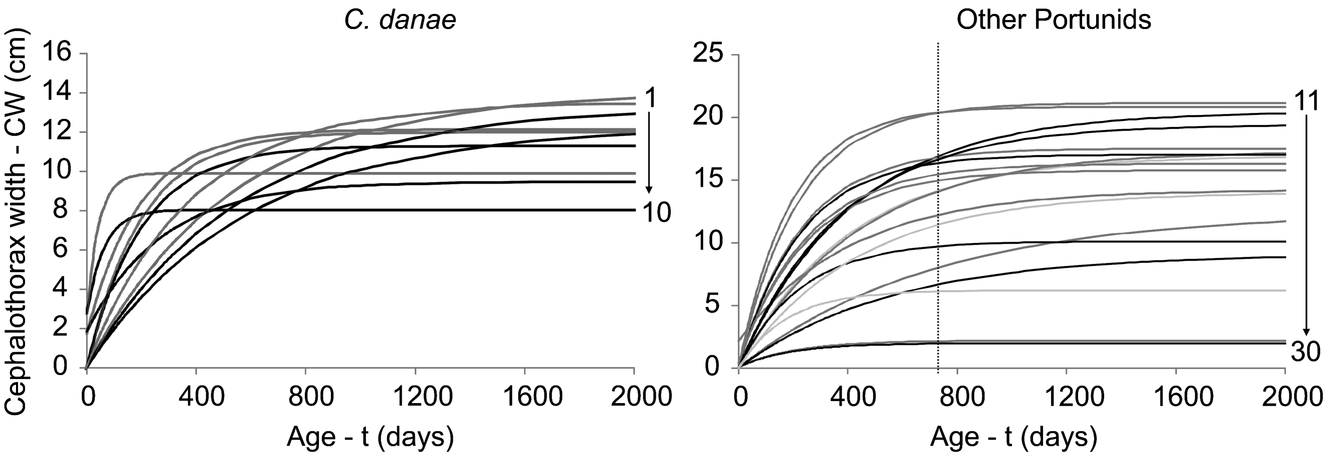

Fig. 8. Growth models for *Callinectes danae* (curve 1 to 10) and other Portunids (11 to 30). Males (grey), females (black) and grouped sex (light grey) in the wild and reared, given by various authors. Branco and Masunari (1992): 1 and 3; Castillo et al. (2011): 2 and 6; Present study: 4, 8, 9 and 10; Keunecke et al. (2008): 5 and 7; Josileen and Menon (2005): 11 and 12; Lee and Hsu (2003): 13 and 14; Sumpton et al. (1994): 15 and 17; Dineshbabu (2011): 16 and 19; Hernández and Arreola-Lizárraga (2007): 18 and 23; Ferreira and D'Incao (2008): 20 and 21; Fischer and Wolff (2006): 22; Pinheiro and Hattori (2006): 24 and 26; Branco and Lunardon-Branco (1993): 25 and 27; Abowei et al. (2009): 28; Doi et al. (2008): 29 and 30.

Bertalanffy curve, some authors have adopted the original formula of von Bertalanffy (1938) and others used the model proposed by Beverton and Holt (1957).

The growth curves of reared individuals (curves 8 and 10, Fig. 8) had k values larger than those of wild individuals. This observation indicates an influence of rearing conditions on the rate of growth. An explanation is their limited movement. The animal expends less energy and additionally has an unlimited food supply, conditions which usually do not occur in the natural environment. While the limited space available to reared individuals contributes to lower energy expenditure, it can also be a growth-limiting factor if too small (Ferreira and D'Incao, 2008). Another possibility is the temperature difference: the rearing experiment was not exposed to full sun, reaching lower temperature than in wildlife.

Among the growth curves of wild *C. danae*, individuals from the Northeast (the present work) and southeastern Brazil (Keunecke et al., 2008) (22°S) showed very similar growth rates, with k between 0.004 and 0.005. The individuals from higher latitudes (27°S) from southern Brazil (Masunari and White, 1992) clearly show smaller growth rates ($k = 0.002$) and higher asymptotic values. This fact can be explained by the low temperatures recorded in the South, which result in slower growth and allow the animals to reach greater sizes. However, Vogt (2012) states that the longevity achieved by individuals at high latitudes is not simply the result of temperature influencing growth rate, but rather is an adaptation of the whole life history to different environments. Different from this trend, Castillo et al. (2011) in Venezuela (11°N) found values similar to southern Brazil (27°S). These authors suggest that the differences can be due the geographical areas, method of analysis or sampling plan.

By comparing von Bertalanffy growth curves for several species of portunids, adjusted by various authors, and without taking into account the seasonal variability in the models (Fig. 8), we can draw some conclusions. First, we note that for most species the growth of males and females was based on different models, where the females reach sizes smaller than the males. Secondly, most species of portunid reach the asymptote of the curve before two years of age (Fig. 8). This indicates a rapid growth rate compared to other tropical brachyurans, such as *Ucides cordatus* (Linnaeus, 1763), which takes more than 10 years to reach 95% asymptotic size (Diele and Koch, 2010). Species that grow rapidly may recover more easily from overfishing (Longhurst and Pauly, 2007), however, regardless of the growth strategy of the specie, the maximum sustainable yield should be respected, because populations of fast-growing species may also decline due to fishing effort above sustainable levels (Gulland, 1983).

Longevity data in the literature may indicate the age of the oldest specimen on record, the largest modal size (age) group, or the maximum age estimated by growth models (Vogt, 2012). Thus, these data may vary considerably for the same species. For *C. danae*, Keunecke et al. (2008) estimated the lifespan as 2.3 years for males and 2.5 years for females, using 99% of CW_∞. This value is close to that found in the present study (2.4 and 3.3 years). Although females have greater longevity than males, they have fewer cohorts. This feature may be related to the longer period of intermolt performed by females that must be added to the possibility of a longer lifespan after pubertal molt.

Note that in the studies cited above, the female has a longer lifespan. According to Vogt (2012), this observation may be associated with the greater stress incurred by males, as they defend females and cater to the nutritional requirements of themselves and the female during the period preceding copulation. However this is not a rule. There are certainly species of brachyuran where males live much longer than females, e.g. tanner crab *Chionoecetes bairdi* Rathbun, 1893 (Donaldson et al., 1981) and snow crab *Chionoecetes opilio* (Fabricius, 1788) (Godbout et al., 2002).

Longevity is a factor intrinsic to the species, which adds to geographical variations and ecological adaptations (Vogt, 2012). One should also consider the different data sources and methods of analysis, since the estimates of longevity of the same population can fluctuate widely depending on the method of analysis, including the specimens used to make these estimations.

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