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Temporal variation in the weight-size relationship of the mangrove crab *Ucides cordatus* L. (Decapoda: Ucididae) in relation to its life cycle phases

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Abstract

The relationship between weight and size of individuals can be used to evaluate the status of a population, which is particularly useful for natural populations that are being exploited. *Ucides cordatus* occurs on the Atlantic coast of the American continent, from Florida (USA) to Santa Catarina (Brazil). This species is economically very important, most of all in the Northeastern area of Brazil, as well as in the Dominican Republic and Suriname. The objective of this study was to analyze life phases ('fattening', 'matumba', 'milk-crab', 'maturation' and 'walking') by use of the weight-length relationships, as well as temporal variations in this condition factor for each sex of *U. cordatus*. For this purpose, individuals were sampled monthly for twenty-four months at the Jaguaribe River estuary, Ceará State, Northeastern Brazil. The relationship between total weight and cephalothorax width was established using regression analysis, adjusted by a power equation. The dynamics of the condition factor were analyzed for each sex using the variation of its averages related to annual life cycle; this was done for each of the previously-mentioned phases. The relationship between total weight and cephalothorax width showed an isometric growth in males and negative allometric growth in females suggesting that, for the same reference size, males are heavier than females. When considering the average of the female condition factors, these were greater than those for males during the annual life cycle, except during the 'maturation' phase, which is the phase with a higher demand of energetic reserves for males. Annual variation of the condition factor in females presented no significant difference.

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Allometry; brachyuran; sexual dimorphism; trade off

Introduction

The mangrove crab, *Ucides cordatus* (Decapoda: Ucididae), is one of the most important components of the Brazilian mangrove fauna (Melo, 1996). It occurs from Florida (USA) to Santa Catarina (Brazil; Melo, 1996) and is an important economic resource, mainly in the northeastern Brazilian estuaries (Ivo & Gesteira, 1999; Glaser & Diele, 2004).

The life cycle of Decapoda can be described in an annual cycle based on the molt cycle (Gonzalez-Gurriaran et al., 1995), reproduction (Mantelatto & Fransozo, 1997; Kumar et al., 2003; Doi et al., 2007) or both (Sumpton et al., 1994; Vinuesa, 2007), as well as by taking observations made by local communities into account (Souto, 2007). *U. cordatus*' molt cycle occurs, in general, between August and November (Pinheiro & Fiscarelli, 2001; Wunderlich et al., 2008), when it is observed as a phase called 'milk-crab' by local, traditional fishers communities (Souto, 2007). This phase occurs as a result of high contents of carbonates being retained in the hemolymph, giving the internal organs a whitish milky-like color (Pinheiro & Fiscarelli, 2001).

During ecdysis this crustacean burries itself to change its exoskeleton (Alves & Nishida, 2002), closing the opening of its galleries in order to diminish the risks of dissection and predation (Hartnoll, 1988). Besides molting, reproduction in *U. cordatus* also occurs in a seasonal cycle (Ivo & Gesteira, 1999; Pinheiro & Fiscarelli, 2001; Wunderlich et al., 2008), which varies throughout its range of distribution from December to May. The mating season of this species is commonly known as 'walking' (Souto, 2007). This phase is characterized by behavior in which individuals leave the burrows and walk, roaming around the mangrove area in search of mating partners, and by agonistic interactions among males (Pinheiro & Fiscarelli, 2001).

While Pinheiro & Fiscarelli (2009) studied the condition factor – representing the weight-size relationship – of *U. cordatus* and evaluated it monthly and seasonally, we propose that this species' annual life cycle should be studied considering five phases: 'walking', 'fattening', 'matumba', 'milk-crab' and 'maturation'. The 'walking' phase, corresponding to the beginning of the mating season, occurs from January to March. This is followed by a 'fattening' phase from April to June, when animals have been observed to spend more time in feeding habits (Souto, 2007). During July and August, males and females remain inside the burrows for longer periods of time and close the entrance of the galleries, herein called the 'matumba' phase. The next phase, the 'milk-crab', corresponds to a pre-molt stage during which animals are internally milky-like, lasts from September to October. During November and December a 'maturation' phase is observed in which gonads develop and animals prepare for reproduction or the 'walking' phase.

Energetic investments in life cycle phases, such as reproduction and molting, can be reflected in changes in the individuals' weight. Such change is better described by the relationship between size (e.g., carapace width) and total wet weight. Biometric relationships between weight and size can be used to provide important information about sexual dimorphism, ontogenetic changes related to sexual maturity, proximity to ecdysis and growth (Baptista et al., 2003). Weight is also useful in evaluating a populations status, especially for exploited species, as the recording of this variable allows the monitoring of these populations regarding structure and biomass, which ensures the biocoenosis equilibrium (Fonteles-Filho, 2011).

The analysis of the weight-size relationship allows the estimation of a constant that represents the degree of fattening of a species, called condition factor. This parameter indicates the level of fattening or physiological well-being of an organism (Encina & Granado-Lorencio, 1997). The evaluation of this parameter allows the establishment of relationships between environmental conditions and the organism's behavioral aspects (Santos et al., 2006) and it can vary with gonadal development, season and among different populations of the same species (Pinheiro & Fiscarelli, 2009). The present study aims to study the weight-cephalothorax width relationship in *U. cordatus* males and females and to identify which phases of its annual life cycle demand higher energetic reserves storage by use of the condition factor dynamics.

Materials and methods

Animals were collected at Jaguaribe River mangrove (4°26′15″S-37°48′45″W) which is located in Aracati City, Ceará State, Northeastern Brazil. The study area presents a mild tropical semi-arid climate with an average of 26 to 28°C (Ipece, 2010). Regarding precipitation, the region presents two well established seasons, although there might be some years above mean annual precipitation, with the highest precipitation period from January to May (maximum monthly mean of 237.8 mm in March). From June to December, the average is never higher than 47.7 mm (minimum monthly mean of 2.4 mm in September).

Ucides cordatus was sampled monthly from July 2010 to June 2012, during low tide using 'forjo' traps, which are not considered size-selective traps (Carvalho & Igarashi, 2009), aiming to capture animals of all size classes. Sampled animals were sacrificed by immersion in ice and transported to the laboratory where they were sexed according to abdomen morphology (Pinheiro & Fiscarelli, 2001). These individuals were also measured regarding cephalothorax width (CW) using a vernier caliper (0.05 mm) and weighted using a scale (0.01 g) (TW = total wet weight). Specimens with loss of appendages were discarded from analysis. In order to test differences between mean weight of the sexes we performed a Student t-test, to a 5% level (Zar, 2010).

The relationship TW/CW was established for all sampled males and females. The empirical points of the relationship TW/CW for each sex were submitted to analysis of the adjusted regression by the power function ($y = ax^b$), where TW is the dependent variable (y) and CW is the independent variable (x), 'a' is the condition factor and 'b' is the growth in weight (Hartnoll, 1982; Pinheiro & Fiscarelli, 2009). The kind of growth (isometric, $b = 3$; positively allometric, $b > 3$; and negatively allometric, $b < 3$) was evaluated using a t-test towards reference value 3 with a significance level of 5% (Zar, 2010).

The condition factor, for each individual, was established from the equation $a = \mathrm{TW}/(\mathrm{CW})^b$, where TW represents total weight, CW represents carapace width, a is condition factor, and b the allometric constant obtained through the relationship TW/CW for each. The difference between the mean condition factor of the sexes was tested using a Student t-test, to a 5% level (Zar, 2010). Temporal variations in the condition factor were analyzed for each phase of the annual life cycle of mature *U. cordatus*, classified into the five proposed phases: 'walking' (January to March); 'fattening' (April to June); 'matumba' (July to August); 'milk-crab' (September to October) and 'maturation' (November to December). According to Leite et al. (2013), who studied the same population as used in the present study, these animals reach maturity at 52 mm CW for males and 45 mm for females. Therefore, we considered males larger than 52 mm CW and females larger than 45 mm CW as mature and individuals smaller than these values as immature. Despite our efforts to equally sample mature and immature animals, for two of the life cycle phases a low number of immatures was captured. Therefore, the analysis of the condition factor in relation to each phase of the annual life cycle was performed using only mature individuals. Before testing for differences, data was tested for normality and homoscedasticity. Data were not normally distributed and thus compared using non-parametric tests. Condition factor, grouped according to the life cycle phase, had its mean compared through Kruskal-Wallis test (Zar, 2010).

Statistical analyses were performed using R Development Core Team (2011).

Results

A total of 521 individuals (296 males and 225 females) were used in the TW/CW relationship. On average, males were heavier than females (97.46 ± 47.85 g $>$ 74.68 ± 40.25 g; t-test $= 5.89$; $P < 0.00001$). This relationship had a significant positive correlation for males ($r = 0.992$; $P < 0.0001$) and females ($r = 0.993$; $P < 0.0001$). The relationships between weight and carapace width were represented using the equations $\mathrm{TW} = 0.0006\mathrm{CW}^{2.950}$ and $\mathrm{TW} = 0.0007\mathrm{CW}^{2.894}$, for males and females, respectively. Growth in males was isometric ($b = 2.950$; $t_{\mathrm{cal}} = -0.78$; $t_{\mathrm{crit\ bilateral}} = \pm 1.96$) while females exhibited a negative allometric growth ($b = 2.894$; $t_{\mathrm{cal}} = -2.35$; $t_{\mathrm{crit\ bilateral}} = \pm 1.96$) (fig. 1).

Condition factor

The mean condition factor for females ($7.04 \times 10^{-4} \pm 0.54 \times 10^{-4}$) was around 1.2 times higher than for males ($5.72 \times 10^{-4} \pm 0.59 \times 10^{-4}$; t-test $= -26.11$; $P < 0.0001$). When analyzing mature individuals, the mean condition factor of

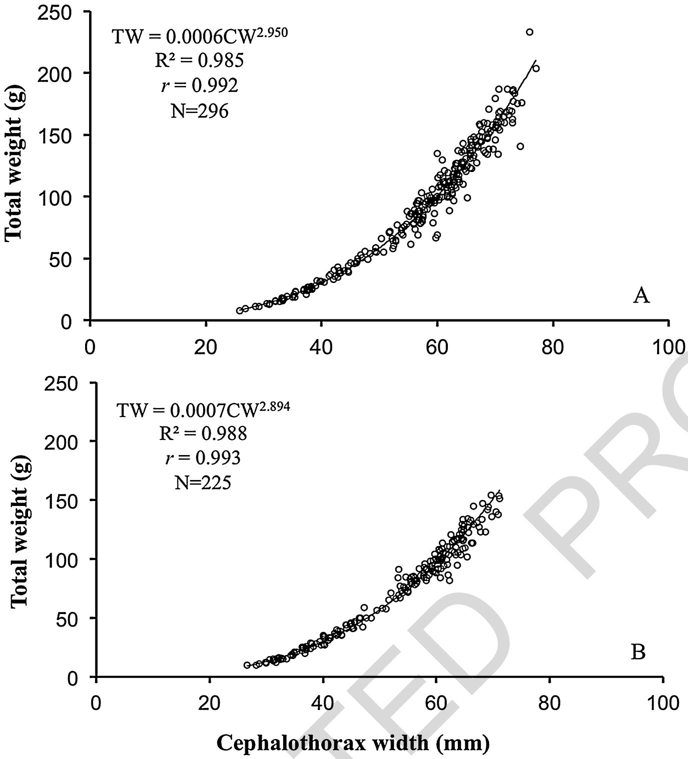

Figure 1. Total weight versus cephalothorax width of *Ucides cordatus* males (A) and females (B).

males varied through an annual life cycle, with the lowest values observed during 'fattening', then increasing until it reached a peak during the maturation period, to drop again at the beginning of the reproduction phase ('walking'; table 1). The condition factor in females also varied through the annual life cycle, but less so than for males. From the 'fattening' phase the decrease in the condition factor was gradual until it reached the lowest value during 'milk-crab'. From there, an increase in the condition factor was observed until it closed the cycle, reaching its highest value during the 'fattening' phase (table 1). Maximum and minimum values, means, and standard-deviations of the condition factor of mature individuals are presented in table 1.

The analysis of the mean condition factor of male *U. cordatus* for each phase was significantly different between 'maturation' (the highest mean value) and the other life cycle phases ($H = 75.104$; d.f. $= 4$; $P < 0.0001$). For females, although fluctuations were observed in the condition factor, the means did not differ significantly.

Discussion

The values of the growth constant in weight (b) of the TW/CW relationship indicated that males exhibited an isometric growth pattern while females showed

Table 1.
Maximum and minimum values, means and standard deviations of the condition factor for mature males and females of *Ucides cordatus*, separated by phase of the annual life cycle.

Annual life cycle	Condition factor							
	Males				Females			
	N	Min	Max	Mean ± SD	*N*	Min	Max	Mean ± SD
Matumba	45	3.86	7.07	5.52 ± 0.70	28	5.61	7.68	6.83 ± 0.54
Milk-crab	19	3.81	9.45	6.76 ± 2.00	24	5.22	7.57	6.82 ± 0.59
Maturation	47	5.37	12.99	8.95 ± 2.20	24	5.94	7.94	6.99 ± 0.50
Walking	56	3.66	10.51	6.60 ± 1.77	37	6.06	9.14	7.04 ± 0.57
Fattening	53	3.17	10.69	5.58 ± 1.51	42	4.44	8.48	6.90 ± 0.62
Total	220				155			

Abbreviations: Max, maximum condition factor; Min, minimum condition factor; *N*, number of individuals; SD, standard deviation.

negative allometric growth, with males being heavier than females. In Brachyuran, the kind of growth in weight can vary between sexes, as there is a greater energetic investment in females for gametogenesis, while for males there is a greater investment in somatic growth (Mantellato & Martinelli, 1999) and the development of secondary sexual characters. In some semi-terrestrial crabs, such as *U. cordatus*, the larger cheliped in males has important functional roles as a secondary sexual character as it is used to defend territory and in cohort and mating behavior (Hartnoll, 1988). Corresponding in this manner to a factor that influence the growth pattern, as well as mean weight, since the chelipeds in males are larger and heavier than in females (Pinheiro & Fiscarelli, 2009; Leite et al., 2013). As a consequence of the energetic investment in it, this appendages can perform its functions during reproduction.

Although a decrease in the mean condition factor from the ‘fattening’ phase to a minimum value in ‘matumba’ was observed for males in a population from South Brazil (Pinheiro & Fiscarelli, 2009), *U. cordatus* in the northeast area may be spending all its energetic reserves during reproduction (‘walking’ phase). However, for females there might be a general pattern in *U. cordatus*, with the mean condition factor reaching its lowest point during the ‘milk-crab’ phase. According to Pinheiro & Fiscarelli (2009) this decrease occurs in the beginning of the ecdysis process, in which the animals go inside their burrows and block the opening as well as stop feeding. Therefore, the variation from the ‘fattening’ phase to ‘milk-crab’ in females can correspond to an allocation and assimilation of energetic reserves that are accumulated during ‘fattening’ to activities related to molt (Herreid II & Full, 1988). In Brachyuran, growth requires the accumulation of resources before ecdysis and also to complete the growth of tissue during intermolt (Hartnoll, 1985).

The significant difference in mean condition factor during maturation that was observed only in males suggests that these individuals must accumulate and allocate a greater amount of resources during molt than females (Pinheiro et al., 2005; Diele & Koch, 2010). The theory of life history predicts that reproduction and growth compete for limited resources (Gadgil & Bossert, 1970; Glazier, 1999; Lika & Kooijman, 2003). As a result, these processes are considered antagonistic or mutually exclusive (Adiyodi, 1988). Based on this theoretical prediction, it is suggested that similar values in the condition factor, observed in the transition from 'fattening' to annual life cycle phases related to growth in females, indicate that in these individuals the energetic ballast must be kept at higher levels. Besides somatic growth and metabolic activity maintenance, the available energy in their body must be allocated to gonadal development (Watt, 1986), which requires a higher energy demand when compared to males (Adiyodi, 1988).

The significant increase in the condition factor between "matumba" and "maturation" for males reflects the accumulation of energetic reserves. This process could be related more directly to reproductive behavior than to gonadal development. In Brachyuran, agonistic interactions such as fighting behavior in males competing for females as well as the elaborated cohort behavior, are common (Dunham & Gilchrist, 1988), and similar behavior have been observed in *U. cordatus* males during 'walking' (Pinheiro & Fiscarelli, 2001). Therefore, it is possible that these aspects connected to the reproductive behavior of this species have a high energetic cost. As a result, the strategy in which individuals accumulate reserves during 'maturation' in preparation for mating, is related to maximization of reproductive success.

The mean condition factor of females was significantly higher than that for males for four phases of the annual life cycle. This difference can be attributed to a greater weight and size of ovaries as a result of the accumulation of yolk (Adiyodi, 1988). In addition, the period in which gonads are preparing for reproduction is characterized by elevated energetic concentrations in the organisms that aim to supply for the necessary demand for gamete fertilzation and to ensure the offspring's survival (Vismara et al., 2004). During 'maturation', however, the males' condition factor was higher, which may reflect an investment in accumulating energy to be used during the next life phase, 'walking', when males must roam, court and guard females. Also, the condition factor between males and females differs due to the fact that in Brachyuran, females refrain from eating during egg incubation (Hartnoll, 2006). As a result, it is likely that there is a higher demand in accumulating energetic reserves to maintain the metabolism during this phase. When analyzing the females condition factor it is likely that the lack of variation in this parameter is closely related to physiological needs related to reproduction (i.e., gametogenesis). We suggest that the need to maintain an energetic ballast in equilibrium to minimize the conflicting trade-offs between reproduction and growth is reflected in a stable condition factor.

The general 'well-being' of a species and its environment's suitability, being correlated to external (e.g., availability of food, latitudinal gradient) and internal factors (e.g., gonad cycle, rate of feeding and growth) can be indicated by the condition factor. By comparing the condition factor in different populations under a different climate or fishing pressure, it is possible to estimate which population presents a better general fitness. Therefore, we suggest that the population of *U. cordatus* in northeastern Brazil is in a better condition, as demonstrated by the condition factor, than its counterpart in southeastern Brazil where the mean condition factor was lower for both males and females (Pinheiro & Fiscarelli, 2009). This aspect can be a consequence of the great anthropogenic impact on the environment and low conservation status observed in Brazilian Southeast mangrove areas.

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Queries to the Authors:

Please check if "Development Core Team" was changed to "R Development Core Team" correctly (page 4, line 26).

Please check if last page of Glazier (1999) reference is correct now.