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Fecundity of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ocypodidae)

MARCELO ANTONIO AMARO PINHEIRO*, MARISTELA D'ANDRÉA BAVELONI and OSWALDO DA SILVA LEME TERCEIRO
Departamento de Biologia Aplicada, FCAV, Universidade Estadual Paulista (UNESP) Campus de Jaboticabal, Via de Acesso Prof. Paulo Donato Castellane, s/n CEP 14884-900, Jaboticabal, SP, Brazil
Tel. +55 (16) 3209-2620; Fax +55 (16) 3202-4275; email: pinheiro@fcav.unesp.br

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Summary

Females of the mangrove crab *Ucides cordatus* were collected in a monthly basis along a 2-year period at the mangrove areas of Iguape, SP, Brazil. Ovigerous individuals were measured (CW, carapace width) and weighed (WW, wet weight). Each brood was weighed (WWE, wet weight of eggs), dried (DWE, dry weight of eggs) and the number of eggs (EN) was recorded. Scatter plots for the relationships EN/CW, EN/WW and EN/WWE were produced, and the data were subjected to regression analysis. Relative average fecundity ($\overline{F'}$) was calculated in different seasons and compared to verify if there were any temporal variation of reproductive intensity. Fecundity in *U. cordatus* varied from 36.081 to 250.566 eggs according to the size-dependent relationship EN = $15.27CW^{2.24}$ ($N = 66$; $R^2 = 0.69$; $p<0.001$). The other expressions obtained for the relationships were: EN = $3797.6WW^{0.813}$ ($N = 56$; $R^2 = 0.72$; $p<0.001$); EN = $29226WWE^{0.775}$ ($N = 54$; $R^2 = 0.70$; $p<0.001$); and EN = $1093586DWE^{0.769}$ ($N = 66$; $R^2 = 0.86$; $p<0.001$). Ovigerous females were found only during spring and summer, and relative average fecundity differed between these seasons. Relative average fecundity was higher in spring and relative frequency of ovigerous females was higher during summer. Overall reproductive intensity was similar between these seasons. The observed trends are regarded to be related to temperature and photoperiod variations.

Key words: Fecundity, reproduction, *Ucides*, Ocypodidae, crab

Introduction

The reproductive strategy of brachyuran crustaceans is extremely diversified, ultimately shaped to maximize egg production and offspring survivorship, thus favoring the preservation of the species (Hartnoll and Gould, 1988). The estimation of fecundity and the delimitation of the breeding season are important tasks to achieve forecasting of the turnover capacity of natural populations (Mantelatto and Fransozo, 1997), providing essential information for studies of environmental impact, management of stocks exposed to fishing pressure and to evaluate the potential of a given species for aquaculture production.

Fecundity is a species-specific factor, not only regarding the number of eggs extruded in a single batch but also the frequency of brood production

*Corresponding author.

during the breeding season or life span (Sastry, 1983). According to Bourdon (1962), fecundity is defined as the number of eggs produced in each batch, usually increasing with the female body size (Pinheiro and Fransozo, 1995; Costa and Negreiros-Fransozo, 1996; Pinheiro and Terceiro, 2000) and decreasing with egg size or volume (Hines, 1982). Fecundity may also be affected by exogenous and/or endogenous factors (Jensen, 1958; Sastry, 1983), varying interspecifically among populations from different areas.

Size-specific fecundity has been assessed by using different regression models, including non-linear relationships, such as the power function $y = ax^b$ (Thomas, 1964; Haynes et al., 1976; Somerton and Meyers, 1983; Pinheiro and Fransozo, 1995; Pinheiro and Terceiro, 2000), and the volumetric model $y = a+bx^3$ (Jensen, 1958; Almaça, 1987; Flores, 1993; Leme and Negreiros-Fransozo, 1998). Therefore, intraspecific fecundity comparisons, either seasonal within a given population or spatial among different populations, are not always possible. The structure of the compared populations should be similar and the mathematical and statistical treatment of data need to be standardized (Pinheiro and Terceiro, 2000).

There is a general lack of information on the fecundity patterns of seniterrestrial mangrove brachyurans from which grapsids were more frequently studied (Pillay and Ono, 1978; Seiple and Salmon, 1987; Kyomo, 1988; Díaz and Conde, 1989; Ruffino et al., 1994; Schuh and Diesel, 1995a, 1995b; Cobo and Fransozo, 1998; Leme and Negreiros-Fransozo, 1998). Regarding ocypodids, there are a few accounts on species of the genus *Uca*, e.g., a revision by Hines, 1982, and *Ucides* (e.g., Rujel-Mena, 1996 on *U. occidentalis* and Mota-Alves, 1975, and Costa, 1979, on *Ucides cordatus*).

Ucides cordatus (Linnaeus, 1763) is a semiterrestrial crab belonging to the Ocypodidae family, distributed along the western Atlantic from Florida (USA) to Santa Catarina (Brazil) (Melo, 1996). This species is restricted to mangrove areas, where it feeds on leaves and digs galleries in the sediment, being considered one of the key-role mangrove species (Koch, 1999).

The purpose of the present study is to estimate the potential fecundity, the relative average seasonal fecundity ($\overline{F'}$) and the reproductive intensity (IR) of *U. cordatus* as a means to evaluate its reproductive strategy. In addition, it is also presented a revision of the literature containing information on the egg production of this species, which is compared to the values obtained for other mangrove brachyurans.

Materials and Methods

Specimens of *U. cordatus* were monthly collected at the mangrove areas of Barra de Icapara (24°41′9.2″S), Iguape (SP), during the period from September, 1998, to August, 2000. In each month the individuals were captured manually in their open and closed burrows by two crab men in a rectangular mangrove area (50×10 m = 500 m^2), disposed perpendicularly from the shore to mangrove apicum. Individual females (nonovigerous and ovigerous) were put in plastic bags to avoid the loss of eggs and appendages, and frozen until further analysis.

Approximately ten eggs from each individual brood were examined under a dissecting microscope to determine the embryonic stage of eggs, classified whether as initial, intermediate or final, corresponding, respectively, to the stage ranges 1–4, 5–8 and 9–10 proposed by Boolootian et al. (1959). Only females incubating initial broods (late blastula to early gastrula) were used for egg counts to minimize the error due to egg loss during subsequent stages (Pinheiro and Terceiro, 2000).

The wet weight (WW) of each ovigerous female and their brood (WWE) was recorded using an analytical balance to the nearest 0.01 g. The carapace width (CW) of examined females was measured with a vernier caliper to a precision of 0.05 mm. For each specimen, the relative brood weight (BW%) was obtained by the percentage of egg wet weight in comparison with total wet weight of the female. The correlation between BW% and CW was tested at the 5% significance level.

The pleopods of each female were removed with scissors and stored in 70% ethanol, which was replaced with absolute ethanol 24 h after for better dehydration. For analysis, the excess of ethanol was discarded and the broods were placed in Petri dishes to separate the eggs. After isolation, the egg mass of each female was dried in a stove at 60°C for 48 h to achieve weight stability.

The dry weight of eggs (DWE) of each female was recorded in an analytical balance to the nearest 0.0001 g, and three subsamples of about 3 mg were separated to estimate fecundity. In each subsample, eggs were counted under a microscope supplied with a computer analysis system (software KS-100 3.0, Zeiss). To determine the fecundity of each female (EN), the mean of the three subsamples was extrapolated to DWE, resulting in individual fecundity.

After the input of data, the scatterplots of the relationships EN×CW, EN×WW, EN×WWE and

EN×DWE were visually analyzed to observe the shape of the scatter and then choose the mathematical model providing the best fit. Since in most relationships the power function $y = ax^b$ renders an excellent fit (Pinheiro and Fransozo, 1995), it was possible to calculate the relative average seasonal fecundity ($\overline{F}'$), according to Pinheiro and Terceiro (2000),

$$\overline{F}' = \frac{1}{n}\sum_{i=1}^{n} \frac{NE_i}{CW_i^{\,b}}$$

where $\overline{F}'$ is relative average fecundity, n is the total number of ovigerous females in the sample, NE_i is the number of eggs of the ith female, b is the constant of the function $y = ax^b$ for the relationship EN×CW, and CW_i is the carapace width of the ith female.

$\overline{F}'$ was calculated for each season to assess reproductive potential and intensity. Data were subjected to an ANOVA and the contrast among average values was tested by a Tukey test ($\alpha = 0.05$).

The percentage of ovigerous females was calculated for each season based on the relative frequency of breeding individuals within the total female in each season. The proportions were compared at the 5% statistical significance level by the χ-square test, according to Zar (1999).

The reproductive intensity (IR) was calculated for each season as the $\overline{F}'$ value multiplied by the seasonal proportion of ovigerous females.

Results

During the period from September, 1998, to September, 2000, 276 *U. cordatus* ovigerous females were captured. Size range of collected crabs ranged from 30.9 and 72.9 mm (50.6 ± 8.7 mm) CW. Females carrying early broods prevailed (39.1%), followed by crabs bearing intermediate (34.4%) and final clutches (26.5%). From the 108 females collected with early embryos, 66 crabs within the size range between 36.8 to 72.8 mm (50.9 ± 8.7mm) CW were used for fecundity analyses. Number of eggs varied from 36,081 to 250,565 (107,891 ± 46,399).

EN was positively correlated with female size (r = 0.83; p<0.001) and the resulting scatterplot shows a curvilinear trend (Fig. 1A), expressed by the function EN = 15.3 $CW^{2.24}$ (R^2 = 0.69, N = 66, p<0.001), which rendered a satisfactory fit. The same pattern was observed for the relationships between EN and weight (Fig. 1B, 1C), in which a positive and significant correlation at the 0.1% statistical significance level was

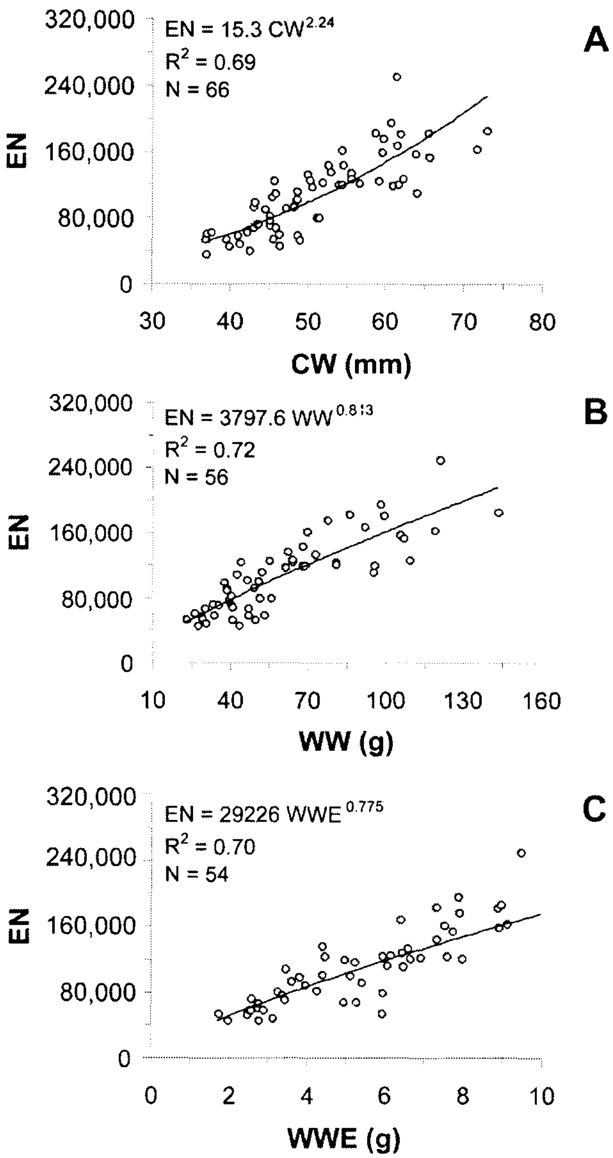

Fig. 1. *Ucides cordatus* (Linnaeus, 1763). Scatterplot and fitted power function for the relationships: A. Number of eggs (EN) vs. carapace length (CW). B. number of eggs (EN) vs. total wet weight (WW). C. Nmber of eggs (EN) vs. wet weight of eggs (WWE).

found (EN/WW, r = 0.85; EN/WWE, r = 0.84 and EN/DWE, r =0.93). Descriptive statistics of the variables involved are shown in Table 1, and the models adjusted to the data are listed in Table 2.

The variable BW% varied from 4.6 to 16.2% (8.7 ± 2.0%) and was not found to be correlated with female size (N = 146; r = -0.09, p>0.001).

Ovigerous females were only recorded in spring and summer during both sampled years (Fig. 2A). Their relative frequency was higher during summer (31.6% > 25.8%; χ^2=17.75, p<0.01), but their index of

Table 1. *Ucides cordatus* (Linnaeus, 1763). Descriptive statistics of biometric and biologic variables of ovigerous females used in fecundity and biometric analyses involving number of eggs

Variables	*N*	Min.	Max.	$\bar{x} \pm s$	CV, %
CW, mm	66	36.85	72.85	50.90 ± 8.68	17.1
EN	66	36,081	250,566	107,891 ± 46,339	43.0
WW, g	56	22.98	143.28	60.76 ± 28.34	46.7
WWE, g	54	1.75	13.72	5.45 ± 2.42	44.4
DWE, g	66	0.27	2.10	0.94 ± 0.46	48.9

Table 2. *Ucides cordatus* (Linnaeus, 1763). Equations of biometric relationships using number of eggs (EN) as the dependent variable and carapace width (CW), total weight of ovigerous female (WW), wet weight of eggs (WWE) and dry weight of eggs (DWE) as independent variables. All relationships were found significant at the 0.1% statistical significance level

Relationship	*N*	Power function ($y=ax^b$)	Linearized function ($\ln y = \ln a + b \ln x$)	R^2	*F*	*t*
EN × CW	66	$EN = 15.3\ CW^{2.24}$	ln EN = 2.72 + 2.24 lnCW	0.69	145.5	12.1
EN × WW	56	$EN = 3797.6\ WW^{0.813}$	ln EN = 8.24 + 0.813 ln WW	0.72	136.2	11.7
EN × WWE	54	$EN = 29{,}226\ WWE^{0.775}$	ln EN = 10.3 + 0.775 ln WWE	0.70	122.5	11.0
EN × DWE	66	$EN = 109{,}358\ DWE^{0.769}$	ln EN = 11.6 + 0.769 ln DWE	0.86	389.4	19.7

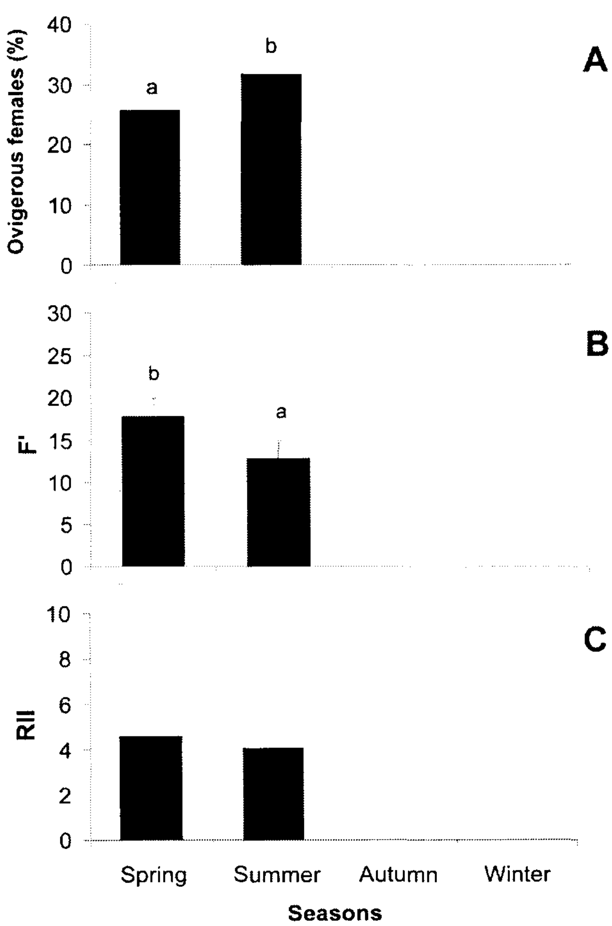

Fig. 2. *Ucides cordatus* (Linnaeus, 1763). Bar graph showing percentage of ovigerous females in the total female sample (A), relative average fecundity (B) and reproductive intensity (C) in each season during the study period from September, 1998, to August, 2000.

relative average fecundity was higher during spring (17.9 ± 3.0 > 12.9 ± 2.3; p<0.001) (Fig. 2B). The antagonism between the relative frequency of ovigerous females and the index of relative average fecundity ($\overline{F'}$) resulted in similar indices of IR in these seasons, i.e., 4.6 in spring and 4.1 in summer (Fig. 2C).

Discussion

The number of eggs produced by decapod crustaceans may vary widely according to phylogenesis, life style and habitat (Du Preez and Maclachlan, 1984).

In brachyurans, egg production is limited by internal cephalotoracic space for the accumulation of yolk, varying according to the cephalotorax shape and the volume occupied by branchial chambers (Hines, 1982). According to Hartnoll (1988), *U. cordatus* may be classified in the T_2 category of "terrestriality" because, although reduced, their branchial chambers allow the storage of air due to a dorsal dilatation at the branchial carapace region. As a result, the relative volume of gonads in this species is notoriously reduced compared to aquatic brachyurans such as portunids. The average relative weight of the brood in *U. cordatus* is 8.7%, thus contrasting with the 12.3% value observed for the swimming crab *A. cribrarius* (Pinheiro and Terceiro, 2000). On the other hand, Gifford (1962) reported a higher relative brood weight in *Cardisoma guanhumi*, a more terrestrial species, compared to the values obtained herein for *U. cordatus*. Yet, the author established this average value based on only seven specimens. The present account confirms the general trend observed by Hines (1988), who evidenced that relative weight of broods is constrained to about 10% of the body weight in brachyuran crustaceans.

The estimation of fecundity allows the evaluation of the reproductive capability and population turnover potential of a given species (Fonteles-Filho, 1979). Actual fecundity is not only given by the number of eggs produced but also by the percentage of fertilized eggs. In most crustaceans, the number of eggs is positively and significantly correlated to the size of the parental female, a rule followed by the mangrove crab *U. cordatus*. It is worth noting that all functions fitted in the present study can be used to predict egg production since determination coefficients indicate an adequate fit of data, a condition that is not verified in many fecundity studies published so far. By comparing the scatterplots produced for *U. cordatus*, it may be concluded that the model used in the present study is representative for the size range of ovigerous females (Fig. 3). According to Pinheiro and Terceiro (2000), lack of representativeness may result in a non-efficient model for the analysis of fecundity in pleocyemate crustaceans, therefore hampering the extrapolation between the analyzed variables. For instance, the results presented by Costa (1979) and Mota-Alves (1975) for *U. cordatus* are obtained from crabs within a rather narrow size range ($32 \leq CW \leq 54$ mm), thus not encompassing a representative sample of the size distribution of ovigerous females.

Even within a single species, the latitudinal variation of fecundity is evident, certainly due to the effect

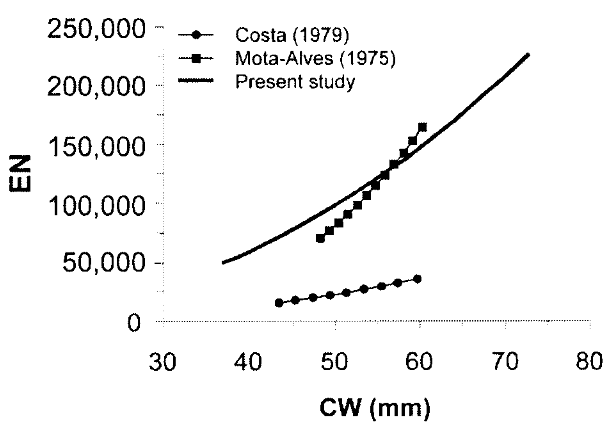

Fig. 3. *Ucides cordatus* (Linnaeus, 1763). Comparison of models fit to the relationship between number of eggs (EN) and carapace width (CW) for the three populations examined. Equations published by Costa (1979) and Mota-Alves (1975) were obtained from average number of eggs (EN) in each cephalotoracic length classes (CL), after extrapolation to carapace width values (CW).

of different environmental factors, mainly temperature and photoperiod (Hines, 1988). Such a trend does not seem to occur among *U. cordatus* populations, since size-specific fecundity functions at Iguape (24°42′S) and at a mangrove in Ceará Sate (3°40′S) (Mota-Alves, 1975) are remarkably similar, differing to those obtained by Costa (1979), probably because the latter have also used females carrying intermediate and final embryo stages which may be a source of bias leading to fecundity underestimation. Alternatively, a reduced reproductive potential may be due to specific environmental alterations not indicated by the author. This could be the case, since Costa's study was carried out at the same locality where Mota-Alves sampled the crabs.

The different reproductive patterns of crustaceans are the result of an interaction between endogenous and exogenous patterns. Water temperature and photoperiod are among the most important exogenous factors regulating reproduction (Payen, 1980). This seems to apply to *U. cordatus* since the relative frequency of ovigerous females is positively and significantly correlated to those environmental variables, and to rainfall as well (Pinheiro, 2001). This explains the seasonal reproductive pattern of this species, with the occurrence of breeding females during spring and summer, mainly during the latter when temperature is higher and the embryonic and larval development shorter favoring the survivorship of the offspring.

According to the classification proposed by Pinheiro and Fransozo (2001), *U. cordatus* follows a seasonal reproduction, always during the spring and summer months, regardless of latitude (Pinheiro, 2001). The length of the breeding period in this species does not differ between equatorial and intertropical populations (4–5 months), but the reproductive season starts 2 months before in regions close to the austral distribution boundary of this species. This is possibly due to differences of the climatic regime and synchronization of larval release, although the latter is known to be associated to periods of new and full moon (Freire, 1998; Diele, 2000).

Although multiple brooding is a common event in brachyuran crabs (Van Engel, 1958; Pinheiro and Fransozo, 1999), it does not seem to take place in *U. cordatus*. Costa (1979) states that females may produce up to two broods per year, but yearly unimodal distribution of females bearing mature gonads (Pinheiro, 2001) does not support that reproductive trend. According to Pinheiro (2001), the breeding period in this species is ensured by a mating season comprising several months, which actually time reproduction in this species.

Table 3. Revision of fecundity values in species of the genus *Ucides* examined so far and other semi-terrestrial brachyuran crabs

Species	Reference	Locality	Latitude	Fecundity equation	Carapace width, mm			Egg numbers		
					Min.	Max.	$\bar{x} \pm s$	Min.	Max.	$\bar{x} \pm s$
Ocypodidae:										—
U. cordatus	Costa (1979)	Caucaia, CE, Brazil	3°40′S	—	43.4*	59.7	—	17,600*	39,100**	—
	Mota-Alves (1975)	Caucaia, CE, Brazil	3°40′S	EN=0.028 $CW^{3.80}$ ($N = 50$; $R^2 = 0.81$)	48.2*	60.2*	—	64,000	195,000	
	Present study	Iguape, SP, Brazil	24°42′S	EN = 15.27 $CW^{2.24}$ ($N = 66$; $R^2 = 0.69$)	36.8	72.8	50.9± 8.7	36,081	250,566	107,891±46,399
U. occidentalis	Rujel-Mena (1996)	Trujillo, Peru	3°15′S	—	55.3	75.5		190,973	251,526	
Uca thayeri	Costa & Negreiros-Fransozo (1999)	Ubatuba, SP, Brazil	23°29′S	EN = 88.4 $CW^{1.91}$ ($N = 25$; $R^2 = 0.62$)	15.4	25.5	—	12,910	59,000	27,679±10,915
Gecarcinidae:										
Cardiosoma guanhumi	Silva & Oshiro (1998)	Baía de Sepetiba, RJ, Brazil	—	—	56.4	83.5		103,300	366,400	190,000
Grapsidae:										
Chasmagnathus granulata	Ruffino et al. (1994)	Lagoa dos Patos, RS, Brazil	31°00′S	EN = 13.61 $CW^{2.44}$ ($N = 30$; $R^2 = 0.78$)**	14.5	25.6	19.1± 2.0	—	—	19,250±6,816
Aratus pisonii	Leme (1995); Leme & Negreiros-Fransozo (1998)	Ubatuba, SP, Brazil	23°29′S	EN = 3714.6 + 1.67CW^3 ($N = 23$, $R^2 = 0.86$)	15.0	24.3	19.2± 2.2	7,448	27,500	15,197±5,771
	Conde & Diaz (1989)	Lagoa Taquariga, Venezuela	10°10′N	—	14.4	26.3	18.7	7,952	34,057	16,379
	Díaz & Conde (1989)	Parque Morrocoy, Venezuela	10°52′N	EN = −40,998.8 + 2846.6 CW ($N = 87$; $R^2 = 0.58$)	11.4	23.1	18.5	3,724	27,314	11,577
Sesarma curacaoense	Schuh & Diesel (1995a)	Trelawni, Jamaica	18°29′N	EN = −765 + 111 CW ($N = 49$; $R^2 = 0.80$)	7.5	15.8	—	112	980	—
Metasesarma rubripes	Capitoli et al. (1977)	Rio Grande, RS, Brazil	32°00′S	—	8.0	15.0	11.7± 2.6	2,500	4,350	3,790
Goniopsis cruentata	Cobo & Fransozo (1998)	Ubatuba, SP, Brazil	23°29′S	EN = 0.084 $CW^{3.80}$ ($N = 30$; $R^2 = 0.61$)	25.1	41.4	33.6± 4.0	12,249	169,400	57,235±35,235
	Silva & Oshiro (2000)	Mangue Itacuruçá, RJ, Brazil	—	EN = 5.54 $CW^{2.60}$ ($N = 51$; $R^2 = 0.42$)	34.4	47.2	38.0± 3.64	29,975	142,050	74,751±27,296

*In original article the number of eggs are represented by carapace length classes (CL), but converted to CW according to equation established by Alcantara-Filho (1978), in the same locatity. **Mean fecundity by size classes.

The higher percentage of ovigerous females takes place during summer, two months after the highest mating activity period which occurs in October, shortly after the nuptial molt when the carapace of crabs show a sky blue color (Pinheiro, 2001). However, the average relative fecundity is lower in summer than in spring, for what the reproductive potential is balanced over these seasons. In this point, *U. cordatus* contrasts to *A. cribrarius*, which shows a similar reproductive potential year round (Pinheiro and Terceiro, 2000) due to multiple brooding up to four viable clutches (Pinheiro and Fransozo, 1999).

Fecundity in *U. cordatus* may be regarded as intermediate compared to other brachyurans. Yet, its reproductive potential is higher than in other semi-terrestrial and terrestrial mangrove brachyurans (Table 3) where it is verified that the values reported in this contribution are similar to certain species of similar size and ecological role, as the congener *U. occidentalis*, examined by Rujel-Mena (1996), and the gecarcinid *Cardisoma guanhumi*, by Silva and Oshiro (1998). Although living in sandy, higher mangrove reaches, this latter species presents similar fecundity to that observed for *U. cordatus* in spite of being less abundant.

The results obtained may be used to predict reproductive potential of this species in estuaries, but there is still a need to gather information on this species fertility to achieve more reliable estimates.

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