

# Reproductive aspects of *Cyrtograpsus angulatus* Dana, 1851 (Brachyura, Grapsidae) in the Lagoa do Peixe, Rio Grande do Sul State, Brazil.

Castiglioni, D. S.<sup>1,2</sup> and Santos, S.<sup>1,3</sup>

<sup>1</sup> NEBECC (Group of Studies on Crustacean Biology, Ecology and Culture)

<sup>2</sup> Curso de pós-graduação em Ciências Biológicas – área de Zoologia – IBB – UNESP 18.618-000 Botucatu, SP, Brasil.  
e-mail: danielacastiglioni@bol.com.br.

<sup>3</sup> Laboratório de Carcinologia, Departamento de Biologia, Universidade Federal de Santa Maria, 97.105-900 - Santa Maria/RS, Brasil. e-mail: ssantos@ccne.ufsm.br.

## Abstract

The aim of this study was to analyze some aspects of the reproductive biology of *Cyrtograpsus angulatus* such as sexual maturity, breeding period, and fecundity. The crabs were monthly sampled during one year (August 94 to July 95) in seven distinct areas of Lagoa do Peixe, Rio Grande do Sul State, Brazil (31°13'S/50°55'W - 31°26'S/51°09'W). A total of 2,646 specimens were collected and analyzed in laboratory, where they were sexed. The carapace width (mm) of each crab was also registered. The carapace width at which 50% of the population of *C. angulatus* was considered mature was 20.26 mm for males and 16.17 mm for females. The reproductive period extended from July to February, with highest frequency of ovigerous females in November, characterizing a seasonal reproduction. Carapace width of ovigerous females varied from 15 to 43.9 mm, and the average fecundity was  $27,851.14 \pm 14,897.27$  eggs, reaching a maximum value of 60,323.01 eggs and minimum of 3,110.5 eggs. The great variation of fecundity may be related to multiple spawning in this species resulting from a single copulation. The relationship between crab size (L) and number of eggs laid by each female in an egg batch (F) can be expressed by the equation:  $F = 0.9808 L - 7651.4$  ( $r^2 = 0.69$ ,  $N=35$ ,  $p<0.05$ ), which indicates that the fecundity is directly proportional to size of the animal.

**Key words:** *Cyrtograpsus angulatus*, Grapsidae, sexual maturity, breeding period, fecundity.

## Introduction

The study of reproductive biology in Crustacea, involving aspects as sexual maturity, breeding period and fecundity, can facilitate the understanding of the adaptative strategy and of the reproductive potential of each species, and also its relationship with the environment and other animals.

Sexual maturity is understood as the set of morphological and physiological changes whereby young or immature individuals reach the ability to produce gametes and to copulate successfully and by this way they begin to act directly in the population fluctuation (Mantelatto and Fransozo, 1996).

Crustaceans exhibit various patterns of life history and reproductive strategies, mainly when habitat is considered. The breeding period of the Decapoda representatives can be continuous if they lay eggs with approximately the same intensity throughout the year, or seasonal, if the spawn is more intense during a certain time of the year (Sastry, 1983).

Fecundity in Decapoda Pleocyemata corresponds to the total number of eggs per female during only spawn, in determinate period of its reproductive cycle (Negreiros-Fransozo *et al.*, 1992). Fecundity of one species may be related to the size or weight of an animal (Ogawa and Rocha, 1976; Du Preez and McLachlan, 1984), to the environmental factors (Jensen, 1958), to the latitudinal variation (Jones and Simons, 1983) and also to the survival rate of the species larvae (Branco and Aylar, 1992).

The family Grapsidae encloses a group of very diversified crabs, since it has representatives at sea, mangrove areas living on wood and rocks around estuaries, and fresh water. According to Sastry (1983), their habitats can reflect the success in the diversity of reproductive strategies in such crustaceans.

*Cyrtograpsus angulatus* Dana, 1851 is a representative of Grapsidae and it can be found concentrate in tide zones (Buckup and Bond-Buckup, 1999). According to Melo (1996), this species presents a geographic distribution that extends from Occidental Atlantic - Brazil (from Rio de Janeiro to Rio Grande do Sul State), Uruguay and Argentina (including Patagonia) to Eastern Pacific - Peru and Chile.

The species *C. angulatus* has been studied under sexual aspects: analysis of molt and growth by Spivak (1988); role played by *C. angulatus* in *Microphallus szidati* and *Falsicollis chasmagnathi* life cycles by Martorelli (1989); quantitative analysis of the relationship between the female's body size and egg production at Marchiquita Lagoon, Argentina by Luppi *et al.* (1997); effect of salinity reduction in juvenile growth by Spivak (1999).

Individuals of family Grapsidae, Ocypodidae and Portunidae (Brachyura), Diogenidae (Anomura) and Penaeidae (Penaeidea) were captured in Lagoa do Peixe, Rio Grande Sul State, Brazil. Crabs of family Grapsidae dominates the lagoon in number of specimens (84% of the total), being *C. angulatus* the dominant species in such place. It is found in great concentrations, mainly in the channel that links the lagoon to the ocean (Santos *et al.*, 2000). This paper aims to analyze some aspects of the reproductive biology of *C. angulatus* in Lagoa do Peixe, Rio Grande do Sul State, such as sexual maturity, breeding period and fecundity.

## Material and Methods

The Lagoa do Peixe is connected to the sea through a channel so that this lagoon presents salt water, good conditions for the development of many organisms such as crabs, shrimps, fishes and birds. This lagoon is located 120 km north of Rio Grande county, Rio Grande do Sul State, southern Brazil. It presents 30 km of extension, 500m of width and its mean depth is about 40 cm (Santos *et al.*, 2000).

Monthly samples were taken during one year (August 94 to July 95) in seven distinct areas of Lagoa do Peixe, defined in a previous sampling in July 1994. The sites were chosen mainly in function of the salinity gradient established between the mouth and the extremity of the lagoon (Figure 1). Samplings were performed with a "coca net" (mouth = 3m, length = 8 m, side mesh = 15 mm).

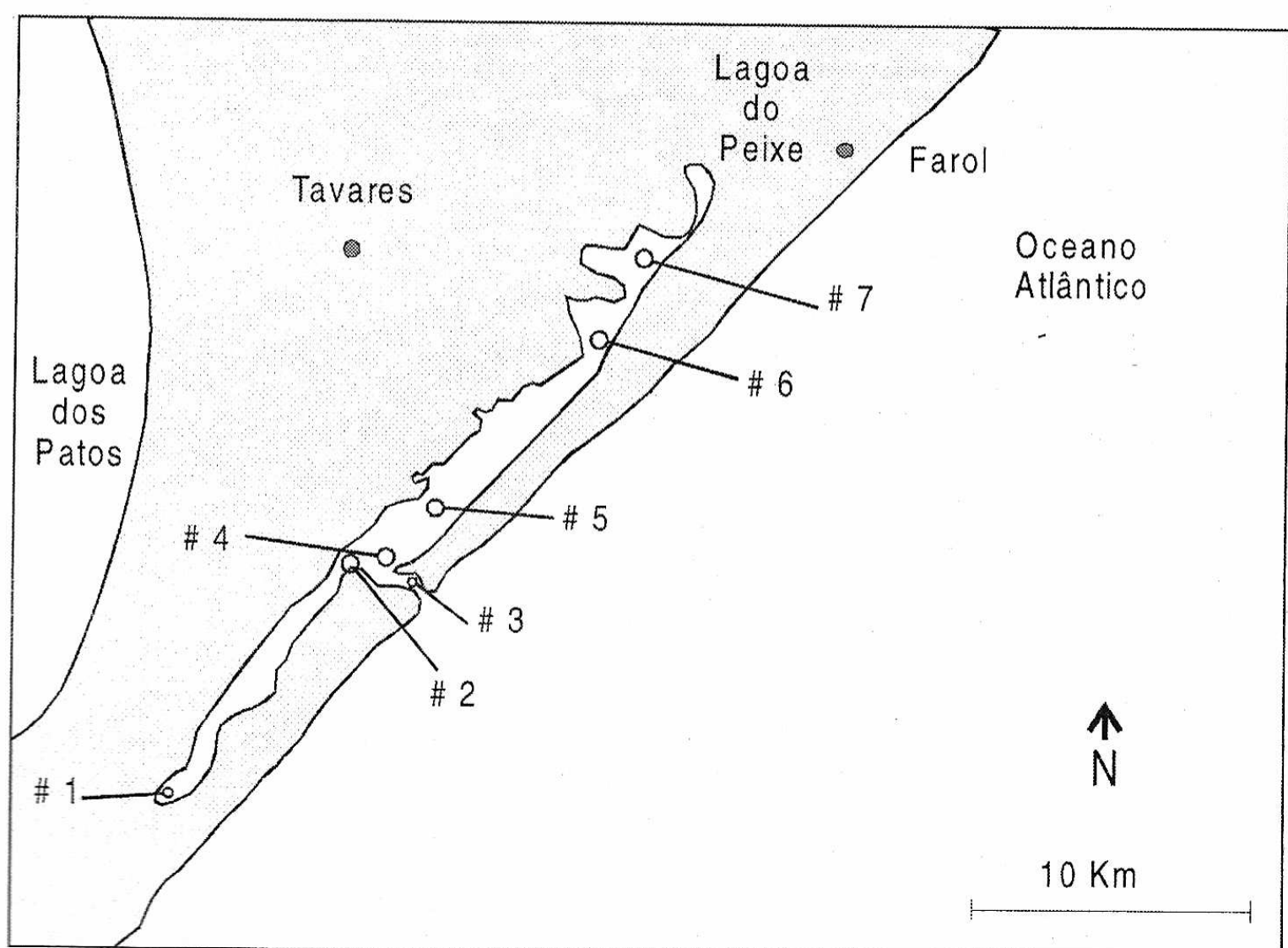


Figure 1: *C. angulatus*, Lagoa do Peixe, RS: Localization of the seven sampling areas.

The following data of each animal were registered: 1) Carapace width (CW): the greatest distance between the lateral margins of the carapace. The measures were taken with a vernier caliper (0.01 mm). 2) Sex: young males - few filamentous setae in the first thoracic sternites, abdomen segmentation few clear, first and second pleopods are translucent; adult males - many filamentous setae in the first thoracic sternites, abdomen segmentation is very clear, the first pleopod is white and the second is translucent; young females - triangular abdomen; adult females - semicircle shaped abdomen; ovigerous female. 3) Maturity stage: the animals were dissected and the gonad development was registered according to table I. The standardization of the gonad development periods was based on the collected animals in a previous sampling in July 1994, where five developmental stages were adopted in females and four in males, characterized on shape, coloration and volume occupied by ovaries and testes, following a modification of the methods proposed by Haefner (1976), Johnson (1980), Choy (1988), Wenner (1989), Costa and Negreiros-Fransozo (1998) and Mantelatto and Fransozo (1999).

Table I: *C. angulatus*, Lagoa do Peixe, RS: Description of the gonadal development stages.

Stages	Characteristics
<b>Females</b>	
Immature (IM)	Gonads could not be seen
Rudimentary (RU)	Gonad filamentous and yellow-orange colored, almost indistinguishable from the hepatopaneas.
Developing (DG)	Gonad orange colored with a small volume; gonad/hepatopaneas ratio is 1:3.
Intermediary (INT)	Brown-red gonad; gonad/hepatopaneas ratio is 1:1.
Advanced (AV)	Bright brown gonad. Gonad volume is superior to the hepatopaneas volume (3:1).
<b>Males</b>	
Immature (IM)	Gonad unrecognizable.
Rudimentary (RU)	Gonad is visible and looks opaque coloration. Hepatopaneas is well developed.
Developing (DG)	Gonad is recognized, however it presents a small volume; coloration between brown and transparent without entanglement.
Intermediary (INT)	Upper vas deferent with a volume close to DG stage, but the inner substance is transparent, without entanglement.
Developed (DE)	Upper vas deferent filled with a white substance (spermatophores) and voluminous. Vas deferent tends to entangle and with clear divisions.

Females and males were considered mature from DG stage. Considering the percentage of mature individuals in size classes, the size of first maturation was determined based on CW in which 50% (median) of the individuals were matures (Somerton, 1980). The curve obtained were adjusted according the Galton Ogiva (Fonteles-Filho, 1989).

The reproductive period was determined analyzing the proportion of ovigerous females in the population throughout the year. Goodman's test (1964, 1965) was used to compare the numbers of ovigerous females among the studied month.

To determine the *C. angulatus* fecundity, 35 ovigerous females from 16.2 to 36.3 mm of CW, carrying eggs in initial stage of embryonic development were analyzed. Pleopods from those females were cut off to facilitate egg removal. Each egg mass was dried at 30°C for 48h and weighted. Three sub-samples were randomly taken from each egg mass, weighed and their eggs were counted under a

dissecting microscope. The individual fecundity was determined by the arithmetic mean of three sub-samples extrapolated to the total weight of the egg mass of each ovigerous female. The average number of eggs from females in each size class was correlated to the third power of carapace width, because according to Hines (1982) this dimension is recommended since it reflects the body's volume available to produce eggs.

Results

A total of 2.646 animals were sampled during 12 collections; 962 males and 1,681 females (including 1.367 ovigerous females) and 3 juveniles crabs of undefined sex based on their external morphology.

Based on the external morphology, the size of first maturation was 10.4 and 15.1mm for males and females (Figure 2), respectively. It was observed that 73.2% and 92.4% of the males and females captured, respectively, were matures. The smallest male and female individuals presented immature stages of gonad development. Animals with the greatest variation in size were found in stage DG (Developed) (Table II).

Table II: *C. angulatus*, Lagoa do Peixe, RS: Mean ( $\pm$  sd), minimum and maximum values of the carapace width (mm) in each stage of gonad development.

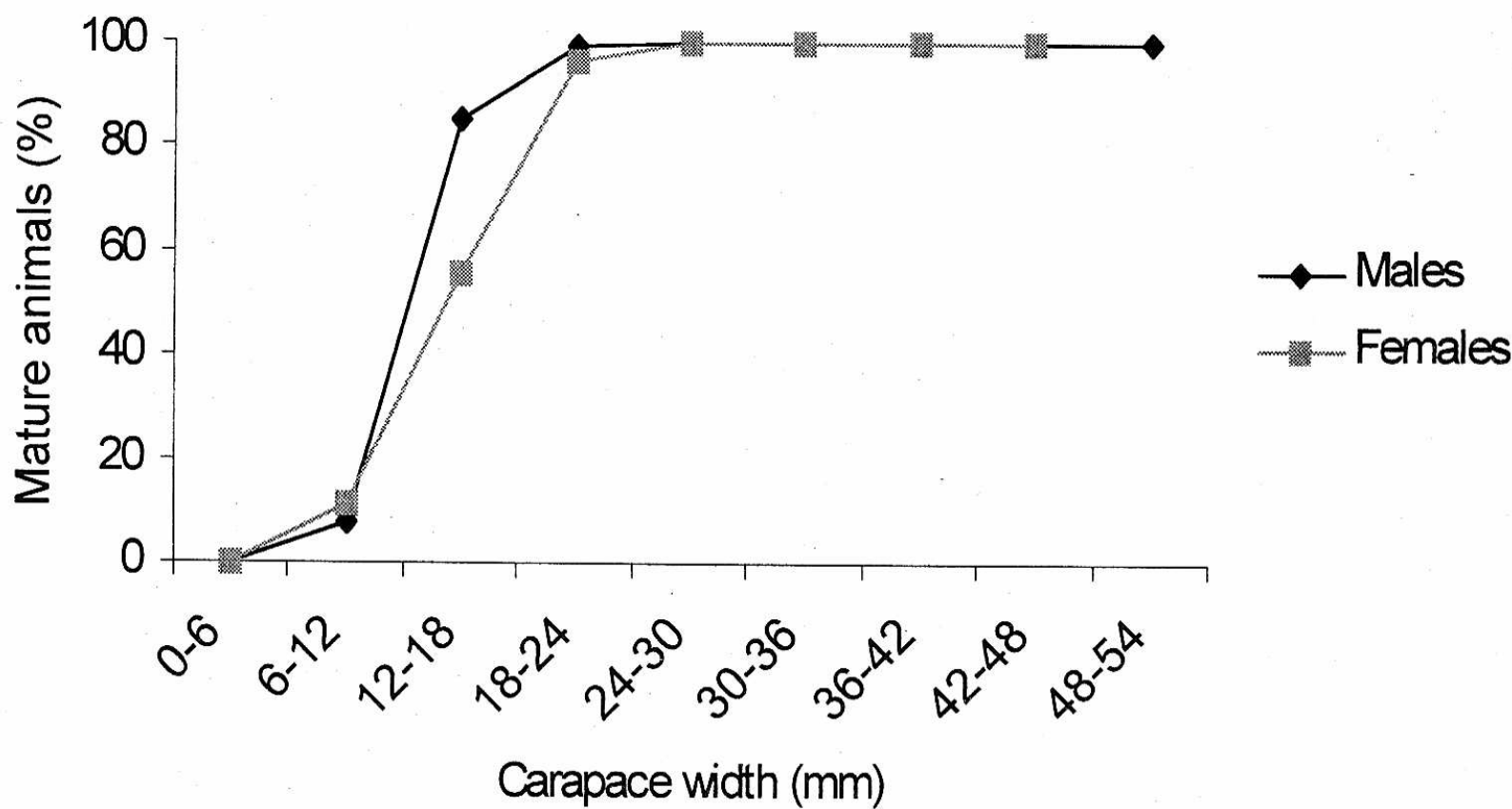
Stage of gonad	N	Minimum	Maximum	Mean $\pm$ sd
Males				
Immature	49	2.8	31.8	14.4 $\pm$ 7.8
Rudimentary	208	12.2	44.0	26.5 $\pm$ 5.9
Developing	527	16.1	51.1	28.1 $\pm$ 6.2
Developed	178	21.4	47.7	32.8 $\pm$ 6.6
Females				
Immature	34	2.7	26.3	13.4 $\pm$ 6.6
Rudimentary	62	14.9	33.5	22.7 $\pm$ 3.9
Developing	119	15.2	45.6	25.7 $\pm$ 4.1
Intermediary	77	19.4	35.5	28.3 $\pm$ 3.2
Advanced	22	24.1	43.2	30.4 $\pm$ 5.4
Ovigerous females				
Rudimentary	506	15.0	42.3	32.4 $\pm$ 4.5
Developing	628	18.2	43.5	28.0 $\pm$ 3.6
Intermediary	191	21.4	43.9	28.4 $\pm$ 3.9
Advanced	42	23.0	32.5	27.6 $\pm$ 3.2

Concerning the gonad development, 50% of the males and females presented mature gonads from 20.26 mm and 10.17 mm of CW, respectively (Figure 3).

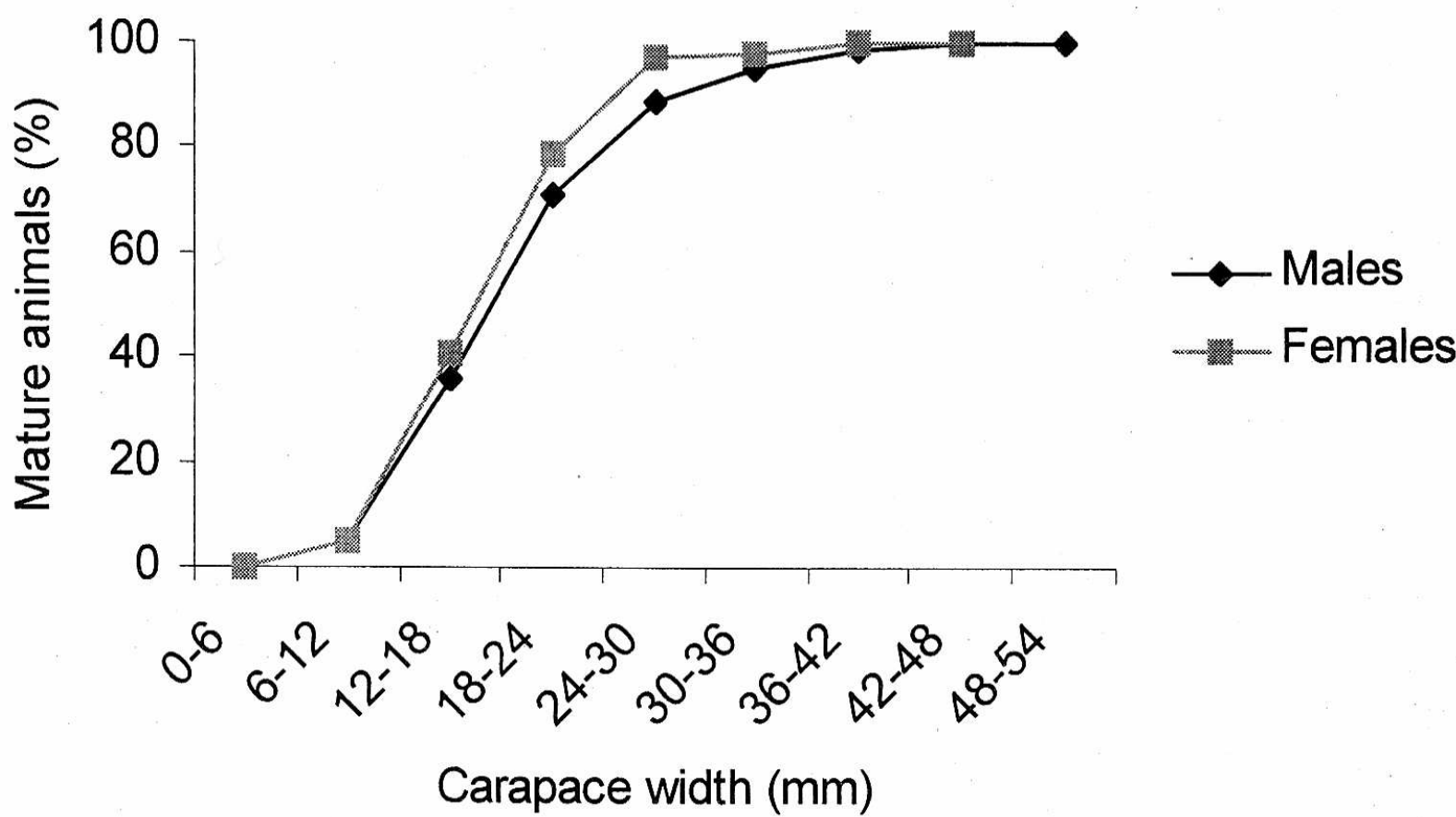
From 1.681 adult females sampled, 1.367 were ovigerous (81.32%). Ovigerous females represented 51.6% of the total of sampled individuals. The reproductive period occurred from July to February, with the highest frequency of ovigerous females in November ( $p<0.05$ ). Figure 4 shows the relative frequency of ovigerous females, in each collection month. In August, September, October and November 1994, the ovigerous females represented 75.9, 94.2, 78.1 and 86.9%, respectively, of the sampled females.

Nauplius

Fecundity in *C. angulatus* varied from 3,110.45 (CW=16.2 mm) to 60,323.01 (CW= 36.3mm) eggs. The average  $\pm$  standard deviation fecundity was  $27,851.14 \pm 14,897.27$  eggs. The relationship between crab size and number of eggs can be expressed by the equation:  $F= 0.9808L-7651.4$  ( $r^2= 0.69$ ,  $N=35$ ), in which,  $F$ = individual fecundity,  $L$ = carapace width raised to the third power ( $\text{mm}^3$ ),  $r^2$ = determination coefficient.



**Figure 2.** *C. angulatus*, Lagoa do Peixe, RS: Cumulative frequency of the sexual maturity, based on the external morphology in males and females.



**Figure 3.** *C. angulatus*, Lagoa do Peixe, RS: Cumulative frequency of the sexual maturity, for males and females, based on crabs with gonads developed.

The analysis of the gonadal development of the ovigerous females registered the presence of crabs with gonads from Rudimentary to Advanced stages. This fact suggests that those females are able to spawn more than one egg mass in one reproduction season, i.e., multiple spawning.

The fecundity data obtained can be fitted into 2 distinct equations: one, probably of female at first spawning, and the other, of female at second spawning. Separating the data, the following equations for first and second spawning were obtained:  $F=1,8688L-1463.7$  ( $r^2=0.87$ ) and  $F=1,4302L-13076$  ( $r^2=0.86$ ), respectively (Figure 5). The analysis of covariance (ANCOVA, Zar, 1996) showed that the straight lines are significantly different ( $p<0.05$ ).

## Discussion

Lopez *et al.* (1997) analyzed sexual maturity of *Chasmagnathus granulata* Dana, 1851, in the Bay of Samborombon, Argentina, based on the relative growth and histological analyses of testicles and ovaries. The gonad maturity in both sexes occurred before the changes in external morphology. In the present study it was observed that *C. angulatus* reached the morphological maturity before the physiological maturity.

According to González-Gurriarán (1985), it is necessary to compare different methods for the determination of sexual maturity to obtain more secure estimates. The accurate estimation of size at maturity should include examination of external morphological modifications and gonad development. This fact is confirmed in the present study, in which the registered values for females and males in the external morphological analysis and gonad development were different, showing that the morphological maturity does not coincide with the physiological maturity in *C. angulatus*, as proposed by other authors (Sastry, 1983; Conan and Comeau, 1986 and Choy, 1988).

If a crab only becomes able to reproduce when it acquires the morphological and physiological conditions, it can be inferred that the size in which such conditions are verified in *C. angulatus*, in the Lagoa do Peixe, is 16.17 and 20.26 mm of CW for females and males, respectively.

Some species of Brachyura concentrate their breeding period in few months of the year, as *Plagusia dentipes* De Haan (1835) studied by Tsuchida and Watanabe (1997); *Sesarma reticulatum* (Say, 1817) and *Sesarma cinerum* (Bosc, 1802) by Seiple (1979); *Metopograpsus messor* (Forsk., 1775) by Sudha and Anilkumar (1996), while others reproduce the whole year, with peaks in some months, as *Callinectes danae* Smith, 1869 by Costa and Negreiros-Fransozo (1998), and *Portunus spinimanus* Latreille, 1819 by Santos and Negreiros-Fransozo (1999).

Fukui (1988), studying seven species of grapsids from the north hemisphere, found three periods of reproduction: 1) reproduction from spring to autumn during eight months; 2) summer reproduction, with four months duration; and 3) autumn to spring reproduction, extending for six months from October to April. Based on the Fukui scheme (*op cit.*) reproductive season of *C. angulatus* is from spring to autumn, with a peak of ovigerous females in October and November. Reproductive period from the spring to the autumn, with peak in October-November was found for *Armases angustipes* (Dana, 1852), another grapsid crab, in the Ilha do Farol, Paraná, Brazil (Kowalczyk and Masunari, 2000).

Ovigerous females of *Pachygrapsus transversus* (Gibbes, 1850) studied by Flores and Negreiros-Fransozo (1999), in Ubatuba (Brazil), occur in greatest percentages in summer months, also characterizing a seasonal reproduction. The adult females of the grapsid *Paragrapsus laevis* (Dana, 1852) studied by Gemmel (1979), in the Sidney Cove (Australia), also present a seasonal reproduction, however with two reproductive seasons – a long one, from April to September, and another brief one, occurring from December to January. As the reproductive period of *C. angulatus* is more intense at certain periods of the year, this species presents a seasonal reproduction (figure 4), and the females probably synchronize the spawning period at times when best ambient conditions for the offspring development are available. This seasonality can be attributed to the fact of this species to inhabit the intertidal region, where it is more susceptible to the influences of climatic changes than the one that inhabit sublittoral regions. According to Mantelatto and Garcia (1999) some species extend their reproductive period when they laid fewer eggs per spawning.

According to Costa and Negreiros-Fransozo (1996), the study on fecundity is an important parameter used for the determination of the reproductive capacity of a species and of the size of its population. Moreover, fecundity associated to the sexual maturity and reproductive period provide a better knowledge of the reproductive strategies used by a species (Sastry, 1983). The variability in number of eggs in a species can also come from the physiological conditions in which the females are found, the latitudinal and environmental factors as light, temperature, salinity, availability of food, pressure of parasites and predators. Based on the mean fecundity of *C. angulatus* in Lagoa do Peixe – Brazil (present study) and in Marchiquita – Argentina (Luppi *et al.*, 1997), those factors can explain the differences between the two

populations, 27,851.14 and 35,456 respectively. The number of eggs produced by brachyurans varies widely between species: the grapsid crab *Aratus pisonii* (H. Milne Edwards, 1837), studied by Conde and Diaz (1989), presented mean fecundity of 16,379 eggs; the females of the portunid *P. spinimanus*, analyzed by Santos and Negreiros-Fransozo (1997) presented mean fecundity of 429,676 eggs and in the study carried out by Mantelatto and Fransozo (1997), *Callinectes ornatus* Ordway, 1863, another portunid, presented mean fecundity of 171.570 eggs.

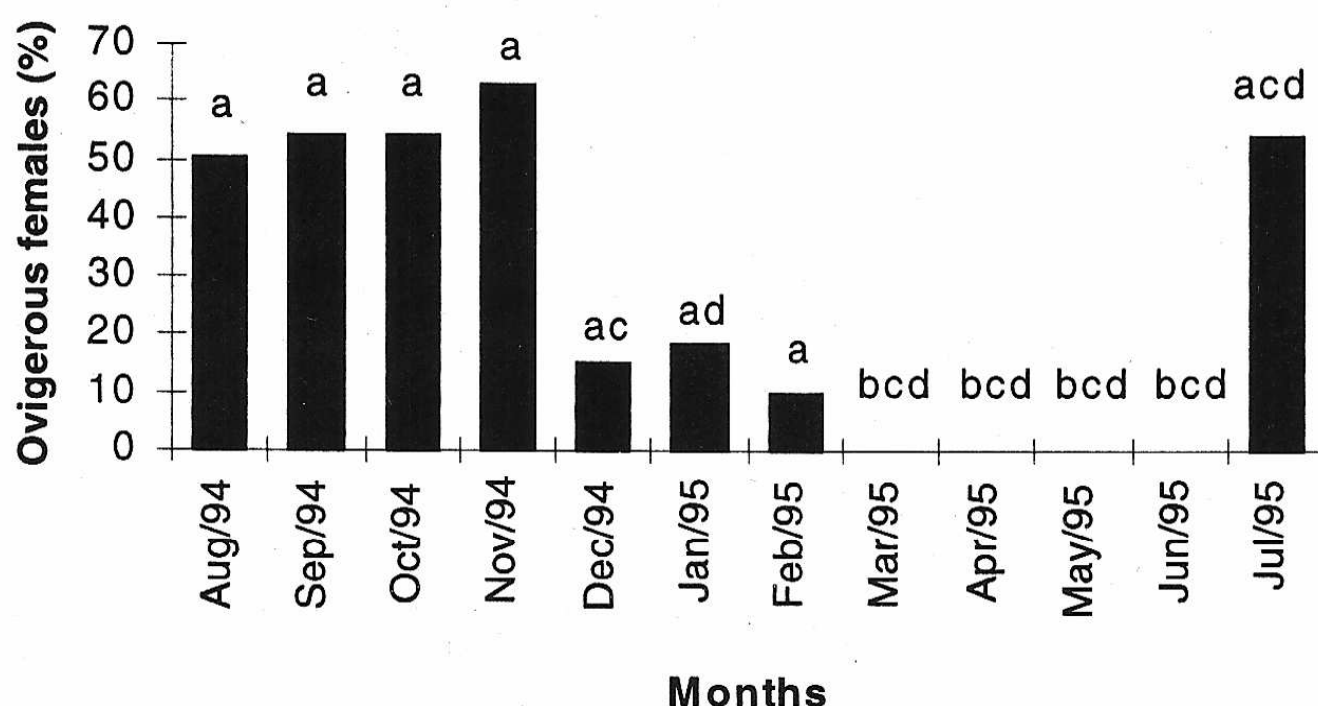


Figure 4. *C. angulatus*, Lagoa do Peixe, RS: Frequency of ovigerous females along the months of studies. Same letters above bars indicate no statistical differences among months.

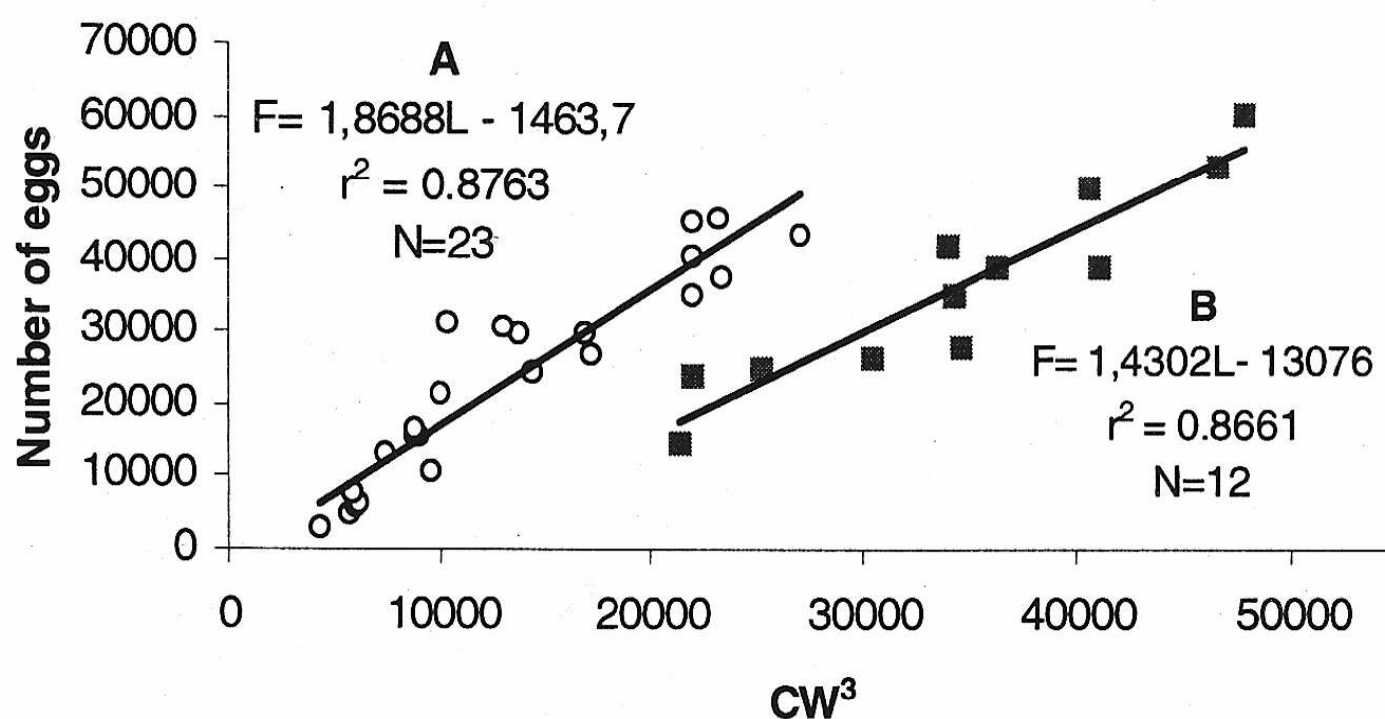


Figure 5. *C. angulatus*, Lagoa do Peixe, RS: Linear regressions between the number of eggs and the third power of carapace width ( $\text{mm}^3$ ) for the first (A) and second (B) posture ( $F$ = fecundity;  $L = \text{CW}^3$ ;  $r^2$ = determination coefficient;  $N$ = number of ovigerous females).

Analyzing the figure 5, it can be observed that females with similar sizes can produce egg masses with very different numbers, probably indicating a process of multiple spawning within the same reproductive season (Mantelatto and Fransozo, 1997; Santos and Negreiros Fransozo, 1997 and Mantelatto and Garcia, 1999). Greco and Rodriguez (1999), studying *C. granulata*, in the Samborombón Bay, Argentina, verified that the females possess multiple spawns, being able to have more than four spawns during the reproductive season, extending from September to March (spring-summer), with one month of incubation. The occurrence of *C. angulatus* ovigerous females with developed ovaries suggests that they are able to produce multiple spawns in the same season reproductive. This fact has also been found in other brachyurans (Choy, 1988; Abelló, 1989; Costa and Negreiros-Fransozo, 1998; Santos and Negreiros-Fransozo, 1999).

The species *C. angulatus* presents a fecundity rate moderate (based in the present study and Luppi *et al.* 1997), when compared with other species of Grapsidae family, as *P. transversus*, studied by Ogawa and Rocha (1976), *C. granulata* by Ruffino *et al.* (1994) and Stella *et al.* (1996), *A. pisonii* by Leme and Negreiros-Fransozo (1998) and *Goniopsis cruentata* (Latreille, 1803) by Cobo and Fransozo (1999) (Table III).

Table III: *C. angulatus*, Lagoa do Peixe, RS: Comparison of fecundity mean between species of the family Grapsidae.

Species	Authors	Mean CW	Mean of eggs
<i>Aratus pisonii</i>	Leme and Negreiros-Fransozo (1998)	18.7	15,197.1
<i>Chasmagnathus granulata</i>	Stella et al. (1996)	25.2	26,790.0
<i>Chasmagnathus granulata</i>	Ruffino et al. (1994)	16.5	19,205.5
<i>Goniopsis cruentata</i>	Cobo and Fransozo (1999)	33.6	57,235.0
<i>Pachygrapsus transversus</i>	Ogawa and Rocha (1976)	10.6	9,222.0
<i>Cyrtograpsus angulatus</i>	Luppi et al. (1997)	29.9	35,456.0
<i>Cyrtograpsus angulatus</i>	Present study	26.2	27,851.1

Acknowledgements

The authors are grateful to Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS), proc. nº 9560076-0/95) for financial support. To Dr. Paulo Juarez Rieger (FURG) for providing good infrastructure. To the Instituto Brasileiro do Meio Ambiente e Recursos Naturais (IBAMA) for permission and facilities during sampling work at Parque Nacional da Lagoa do Peixe.

References

Abelló, P. 1989. Reproductive biology of *Macropipus tuberculatus* (Roux, 1830) (Brachyura: Portunidae) in the Northwestern Mediterranean. *Ophelia*, 30(1): 47-53.

Branco, J. O. and Aylar, M. G. 1992. Fecundidade em *Callinectes danae* Smith (Decapoda, Portunidae) da Lagoa da Conceição, Florianópolis, Santa Catarina, Brasil. *Revista Brasileira de Zoologia*, 9(3/4): 167-173.

Buckup, L. and Bond-Buckup, G. 1999. Os Crustáceos do Rio Grande do Sul. Porto Alegre, Ed. da Universidade, UFRGS. 503 p.

Choy, S. C. 1988. Reproductive biology of *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae) from the Gower Peninsula, South Wales. *Marine Biology*, 9(3): 227-241.

Cobo, V. J. and Fransozo, A. 1999. Fecundity and reproduction period of the red mangrove crab *Goniopsis cruentata* (Brachyura, Grapsidae), São Paulo State, Brazil. The Biodiversity Crisis and Crustacea: Proceedings of the fourth international crustacean congress, Amsterdam, the Netherlands: 527-533.

Conan, G. Y. and Comeau, M. 1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. *Canadian Journal of Fisheries and Aquatic Science*, 43: 1710-1719.

Conde, J. E. and Diaz, H. 1989. The mangrove tree crab *Aratus pisonii* in a tropical estuarine lagoon. *Estuarine Coastal and Shelf Science*, 28: 639-650.

Costa, T. M. and Negreiros-Fransozo, M. L. 1996. Fecundidade de *Callinectes danae* Smith, 1869 (Crustacea, Decapoda, Portunidae) na região de Ubatuba (SP), Brasil. *Arquivos de Biologia e Tecnologia*, 39(2): 393-400.

Costa, T. M. and Negreiros-Fransozo, M. L. 1998. The reproductive cycle of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) in the Ubatuba Region, Brazil. *Crustaceana*, 71(6): 615-627.

Du Preez, H. H. and McLachlan, A. 1984. Biology of three-spot swimming crab *Ovalipes punctatus* (De Hann). III. Reproduction, fecundity and egg development. *Crustaceana*, 47(3): 285-297.

Flores, A. A. V. and Negreiros-Fransozo, M. L. 1999. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. *Bulletin of Marine Science*, 65(1): 59-73.

Fonteles-Filho, A. A. 1989. Recursos Pesqueiros, Biologia e Dinâmica Populacional. Fortaleza, Imprensa oficial do Ceará, 296p.

Fukui, Y. 1988. Comparative studies on the life history of the Grapsidae crabs (Crustacea: Brachyura) inhabiting intertidal cobble and boulder shores. *Publications of the Seto Marine Biological Laboratory*, 33(4/6): 121-162.

Gammel, P. 1979. Reproductive cycle and feeding behavior of the estuarine shore crab – *Paragrapsus laevis* (Crustacea, Brachyura, Grapsidae). *Zoologischer Anzeiger*, 202 (1/2): 1-8.

- González-Gurriarán, E. 1985. Reproducción de la nécora *Macropipus puber* (L) (Decapoda, Brachyura), y ciclo reproductivo en la Ría de Arousa (Galicia, NW España). Boletín del Instituto Español de Oceanografía, 2(1): 10-32.
- Goodman, L. A. 1964. Simultaneous confidence intervals for contrasts among multinomial populations. Annals of Mathematics, 35(2): 716-725.
- Goodman, L. A. 1964. On simultaneous confidence intervals for multinomial proportions. Technometrics, 7(2): 247-254.
- Greco, L. S. L. and Rodriguez, E. M. 1999. Annual reproduction and growth of adult crabs *Chasmagnathus granulata* (Crustacea, Brachyura, Grapsidae). Cahiers de Biologie Marine, 40(2): 155-164.
- Haefner, Jr, P. A. 1976. Distribution, reproduction and moulting of the rock crab, *Cancer irroratus* Say, 1917, in the mid-Atlantic bight. Journal of Natural History, 10: 377-397.
- Hines, A. H. 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. Marine Biology, 69: 309-320.
- Jensen, G. C. 1958. The relation between body size and number of eggs in marine malacostrakes. Meddelelser Fra Danmarks Fisheri Havundersogelser, 2: 1-25.
- Johnson, P. T. 1980. Histology of the blue crab *Callinectes sapidus*: a model for the Decapoda: 1-440. (Praeger Scientific Publishing Co, New York).
- Jones, M. B. and Simons, M. J. 1983. Latitudinal variation in reproductive characteristics of a mud crab *Helice crassa* (Grapsidae). Bulletin of Marine Science, 33(3): 656-670.
- Kowalczyk, V. G. L. and Masunari, S. 2000. Crescimento relativo e determinação da idade na fase juvenil de *Armases angustipes* (Dana) (Decapoda, Brachyura, Grapsidae). Revista Brasileira de Zoologia, 17(1): 17-24.
- Leme, M. H. A. and Negreiros-Fransozo, M. L. 1998. Fecundity of *Aratus pisonii* (Decapoda, Grapsidae) in Ubatuba region, State of São Paulo, Brazil. Iheringia, Série Zoologia, 84: 73-77.
- López, L. S.; Stella, V. S. and Rodríguez, E. M. 1997. Size at onset of sexual maturity in *Chasmagnathus granulata* (Decapoda, Brachyura). Nauplius, 5(2): 65-75.
- Luppi, T. A.; Bas, C. C.; Spivak, E. D. and Anger, K. 1997. Fecundity of two grapsid crab in the Laguna Mar Chiquita, Argentina. Archives of Fishery and Marine Research, 45(2):149-166.
- Mantelatto, F. L. M. and Fransozo, A. 1996. Size at sexual maturity in *Callinectes ornatus* (Brachyura, Portunidae) from the Ubatuba region (SP), Brazil. Nauplius, 4: 29-38.
- Mantelatto, F. L. M. and Fransozo, A. 1997. Fecundity of the crab *Callinectes ornatus* Ordway, 1863 (Decapoda, Brachyura, Portunidae) from the Ubatuba Region, São Paulo, Brazil. Crustaceana, 70(2): 214-225.
- Mantelatto, F. L. M. and A. Fransozo. 1999. Reproductive biology and moulting cycle of the crab *Callinectes ornatus* (Decapoda, Portunidae) from the Ubatuba region, São Paulo, Brazil. Crustaceana, 72(1): 64-76.
- Mantelatto, F. L. M. and Garcia, R. B. 1999. Reproductive potential of the hermit crab *Calcinus tibicen* (Anomura) from Ubatuba, São Paulo, Brazil. Journal of Crustacean Biology, 19(2): 268-275.
- Martorelli, S. R. 1989. The role of *Cyrtograpsus angulatus* (Crustacea, Brachyura) in the life-cycles of *Microphallus szidati* (Digenea, Microphallidae) and *Falsificollis chasmagnathi* (Acanthocephala, Filicollidae) – some aspects of their ecological parasitology. Memórias do Instituto Oswaldo Cruz, 84(4): 567-574.
- Melo, G. A. S. 1996. Manual de identificação dos Brachyura (caranguejos, siris) do litoral brasileiro. São Paulo, Plêiade, FAPESP. 604p.
- Negreiros-Fransozo, M. L.; Fransozo, A.; Mantelatto, F. L. M.; Nakagaki, J. and Spilborghs, M. C. F. 1992. Fecundity of *Paguristes tortugae* Schmitt, 1933 (Crustacea, Decapoda, Anomura) in Ubatuba (SP) Brazil. Revista Brasileira de Biologia, 52(4): 547-553.
- Ogawa, E. F. and Rocha, C. A. S. 1976. Sobre a fecundidade de crustáceos decápodos marinhos do estado do Ceará, Brasil. Arquivos de Ciências do Mar, 16(2): 101-104.
- Ruffino, M. L.; Telles, M. D. and D'Incao, F. 1994. Reproductive aspects of *Chasmagnathus granulata* Dana, 1851 (Decapoda, Grapsidae) in the Patos Lagoon Estuary – Brazil. Nauplius, 2: 43-52.
- Santos, S. and Negreiros-Fransozo, M. L. 1997. Fecundity in *Portunus spinimanus*, 1819 (Crustacea, Brachyura, Portunidae) from Ubatuba, São Paulo, Brazil. Interciência, 22(5): 259-263.
- Santos, S. and Negreiros-Fransozo, M. L. 1999. Reproductive cycle of the swimming crab *Portunus spinimanus* Latreille (Crustacea, Decapoda, Brachyura) from the Ubatuba, São Paulo, Brazil. Revista Brasileira de Zoologia, 16(4): 1183-1193.
- Santos, S.; Rieger, P. J.; Vieira, R. R. R. and Barutot, R. A. 2000. Composição e distribuição dos Crustacea (Decapoda) na Lagoa do Peixe, Rio Grande do Sul, Brasil. Revista Brasileira de Zoologia, 17(1): 213-223.

- Sastry, A. N. 1983. Ecological aspects of reproduction. In: Vernberg, W. B. (Ed). The Biology of Crustacea: environmental adaptations. New York. Academic Press, inc. 8: 179-270.
- Seiple, W. 1979. Distribution, habitat preferences and breeding periods in the crustaceans *Sesarma cinerum* and *S. reticulatum* (Brachyura, Decapoda, Grapsidae). Marine Biology, 52: 77-86.
- Spivak, E. D. 1988. Molt and growth in *Cyrtograpsus angulatus* Dana (Decapoda, Brachyura). Journal of Natural History, 22(3): 617-629.
- Spivak, E. D. 1999. Effects of reduced salinity on juvenile growth of two co-occurring congeneric grapsid crabs. Marine Biology, 134(2): 249-257.
- Somerton, D. A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Canadian Journal of Fisheries and Aquatic Science, 37(10): 1488-1494.
- Stella, V. S.; López, L. S. and Rodriguez, E. M. 1996. Fecundity and brood biomass investment in the estuarine crab *Chasmagnathus granulata* Dana, 1851 (Decapoda, Brachyura, Grapsidae). Crustaceana, 69: 309-312.
- Sudha, K. and Anilkumar, G. 1996. Seasonal growth and reproduction in a highly fecund brachyuran crab, *Metapograpsus messor* (Forsk.) (Grapsidae). Hydrobiologia, 319(1): 15-21.
- Tsuchida, S. and Watanabe, S. 1997. Growth and reproduction of the grapsid crab *Plagusia dentipes* (Decapoda: Brachyura). Journal of Crustacean Biology, 17(1): 90-97.
- Wenner, E. L. 1989. Incidence of insemination in female crabs *Callinectes sapidus*. Journal of Crustacean Biology, 9(4): 587-594.
- Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall, Upper Saddle River. 941p.

Received: 15<sup>th</sup> Dec 2000  
Accepted: 15<sup>th</sup> Dec 2001