



## Population features of the spider crab *Acanthonyx scutiformis* (Dana 1851) (Crustacea, Majoidea, Epialtidae) associated with rocky-shore algae from southeastern Brazil

GUSTAVO MONTEIRO TEIXEIRA<sup>1,2</sup>, VIVIAN FRANZOZO<sup>1,2</sup>, VALTER JOSÉ COBO<sup>1,3</sup>  
& CÉLIA MARY HIYODO<sup>1</sup>

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

<sup>2</sup>Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista. Caixa Postal 510, 18618-000 Botucatu, São Paulo, Brasil. E-mail: gmteixeira@ibb.unesp.br

<sup>3</sup>Laboratório de Zoologia, Departamento de Biologia, Universidade de Taubaté. Praça Marcelino Monteiro 63, 12030-010, Taubaté, São Paulo, Brasil.

**Abstract.** *Acanthonyx scutiformis*, an endemic species in the Brazilian coast, is commonly found in intertidal rocky-shore algal communities. This study analyzes the population biology of *A. scutiformis* from Ubatuba region. A total of 371 specimens were collected over one year. Size range was 4.2–12.7 mm CW (carapace width) for females and 3.7–15.8 mm CW for males. Females predominated in intermediate size classes, whereas males prevailed in the largest ones. The estimated size when 50% crabs were mature was 10.7 mm CW for males and 8.9 mm CW for females. Sex ratio varied among the demographic groups. The processes that influence *A. scutiformis* population structure can be related to the different times males and females reach sexual maturity and probably to the distinct predation pressures on each sex during the adult phase.

**Key words:** *Acanthonyx*, spider crab, population structure, sex ratio, sexual maturity, growth.

**Resumo.** Aspectos populacionais do caranguejo-aranha *Acanthonyx scutiformis* (Dana 1851) (Crustacea, Majoidea, Epialtidae) associado às algas de costões rochosos no sudeste do Brasil. *Acanthonyx scutiformis* é uma espécie endêmica da costa brasileira, comumente encontrada na zona entre-marés de praias rochosas junto aos bancos de algas. Este estudo analisou a biologia populacional de *A. scutiformis* na região de Ubatuba. Um total de 371 espécimes foi coletado, durante o período de um ano. A amplitude de tamanho encontrada para as fêmeas foi de 4,2 a 12,7 mm de CW (largura da carapaça) e para os machos de 3,7 a 15,8 mm de CW. As fêmeas predominam nas classes de tamanho intermediárias enquanto os machos predominam nas maiores classes. O tamanho estimado em que 50% dos caranguejos encontram-se maduros sexualmente foi de 10,7 e 8,9 mm de CW para machos e fêmeas, respectivamente. A razão sexual variou entre os grupos demográficos. Os processos que atuam na determinação da estrutura populacional de *A. scutiformis* podem estar relacionados à aquisição diferencial da maturidade sexual entre machos e fêmeas e, provavelmente, à pressões de predação distintas sobre machos e fêmeas durante a fase adulta de suas vidas.

**Palavras-Chave:** *Acanthonyx*, Caranguejo-aranha, estrutura populacional, razão sexual, maturidade sexual, crescimento.

### Introduction

In the southeast-south of the Brazilian coast, a region that extends from the border of Rio de Janeiro and Espírito Santo States to the extreme south of Rio Grande do Sul State, Brachyurans account for 189 species, of which 47 belong to the

Majidae family (Melo 1996). According to Ng *et al.* (2008), the taxon Majidae was transferred to the superfamily Majoidea, and up to eight families can be recognized, especially in the Americas. Thus, the genus *Acanthonyx* Latreille, 1825 is included in the family Epialtidae. Coelho & Torres (1994)

mentioned that the genus *Acanthonyx* is represented in the Western Atlantic by three species: *A. petiverii* in Florida, Antilles and north of South America, and *A. scutiformis* (Dana 1851) and *A. dissimulatus* Coelho, 1991-1993, in Brazil.

In the northern coast of São Paulo State, the spider crabs *A. scutiformis* and *Epialtus brasiliensis* are commonly found on algal banks including the genus *Sargassum*, *Padina*, *Laurencia* and *Hypnea* (Negreiros-Fransozo *et al.* 1994, Hiyodo & Fransozo 1995, Negreiros-Fransozo & Fransozo 2001). According to Howard (1981), crustaceans and gastropods frequently constitute the major densities of the benthic epifauna in algal and phanerogam communities.

The features on brachyuran populations from the northern coast of São Paulo State has been increasingly reported in the last decades both for species from non-consolidated sublittoral areas (Negreiros-Fransozo & Fransozo 1995, Mantelatto *et al.* 1995, Santos *et al.* 1995, Negreiros-Fransozo *et al.* 1999) and for estuarine species (Leme 2002, Costa & Negreiros-Fransozo 2003, Colpo & Negreiros-Fransozo 2004, Castiglioni & Negreiros-Fransozo 2005, Castiglioni *et al.* 2006, Silva *et al.* 2007). However, data on rocky-shore species are still scarce (*e.g.* Hiyodo & Fransozo 1995, Flores & Negreiros-Fransozo 1999, Fransozo *et al.* 2000). The available literature concerning the population biology of spider crab species from hard bottoms in São Paulo coast includes the studies of Negreiros-Fransozo *et al.* (1994) and Teixeira *et al.* (2008) with *Epialtus brasiliensis*, and Mantelatto *et al.* (2003) and Cobo (2006) with *Mithraculus forceps*.

Functional maturity can be assumed as the minimum size for each sex to be morphologically and physiologically able to reproduce (Mura *et al.* 2005). Generalizations about the dimensions of males and females of certain species when they reach sexual maturity are based on allometric technique, macroscopic gonad analysis, microscopic gonad analysis (histology), development of secondary sexual characters, or functional criterion, including behavioral patterns related to gamete transference.

Among brachyurans, spider crabs are mature only after the terminal molt (Hartnoll 1963). Thus, mature specimens cannot grow and their size distribution may depend mainly on some factors that influence the growth, survival and maturation of juveniles (Hartnoll *et al.* 1993).

In this study, the population biology of *A. scutiformis* from Ubatuba region was analyzed with emphasis on size distribution, sex ratio, and morphologic sexual maturity based on the

development of secondary sexual characters. *A. scutiformis* has a restrict distribution along the Brazilian southeastern coast, ranging from Espírito Santo to São Paulo States (Melo 1996). Features of natural populations are fundamental to the conservation of species such as this Brazilian endemic species, *A. scutiformis*.

## Material & Methods

Spider crabs were manually sampled every month during low tide periods, from March/2003 to February/2004, by scanning the algae (*Sargassum* and *Hypnea*) on the rocky shores in Ubatuba (23°28'24"S; 45°04'00"W), São Paulo State, Brazil. The collected specimens and some algal portions were kept cold in thermo boxes during transportation. In the laboratory, crabs were counted, sexed, and checked for the presence of eggs on female's pleopods. Carapace width was measured under microscope stereoscope or using a caliper (0.1 mm accuracy).

All the obtained crabs were distributed into five demographic groups: young males, adult males, young females, adult females, and ovigerous females. Juvenile and adult specimens were sorted based on the examination of the secondary sexual characters such as pleopod morphology, free abdomen (*i.e.* the abdomen does not adhere to the thoracic sternites), convex abdomen (forming an incubator chamber) in the females, and distinct cheliped development in adult males when compared with juvenile males. Such changes associated with the sexual maturity attainment are similar to those described for the epialtid *Epialtus brasiliensis* by Negreiros-Fransozo *et al.* (1994). The identification of juvenile specimens based on the abdominal condition (sealed or not) has been widely used for Portunoidea (*e.g.* Taissoun 1969, Williams 1974, Pinheiro & Fransozo 1993, Santos & Negreiros-Fransozo 1996) and useful for the representatives of the superfamily Majoidea.

The present results were compared with those obtained by Hiyodo & Fransozo (1995), who analyzed the allometric patterns of the same *A. scutiformis* population. Although they used carapace length instead of width, the allometric relationship between carapace width and carapace length presented isometry. Utilizing the equations determined by those authors ( $CW=0.71*CL^{0.99}$  for males and  $CW=0.74*CL^{0.98}$  for females) and converting the CL data into CW, we could found the following values: 12.8 mm for the largest juvenile males; 8.9 mm for the smallest adult males; 10.8 mm for the largest juvenile females; and 8 mm for the smallest adult females. Such findings agree with the

separation of adults and juveniles already done in the analysis of secondary sexual characters. Crabs were distributed into 13 size classes of 1 mm amplitude. The male:female proportions in each size class were compared through the chi-square ( $\chi^2$ ) test ( $\alpha = 0.05$ ). The population structure was analyzed by plotting in histograms the number of individuals per demographic category and size class. To determine sexual maturity, the relative frequency was expressed in percentage for each sex and size class and plotted in graphs. Data were fit to a sigmoid curve, according to the results of the logistic equation:

$$Y = \frac{1}{1 + e^{r(CW - CW_{50})}} ;$$

$CW_{50}$  = carapace width when 50% of the crabs were

sexually mature;  $r$  = the curve slope. The equation was fitted by the least-squares regression method (Aguilar *et al.* 1995, Vazzoler 1996).

Specimens were deposited in the NEBECC (Crustacean Biology, Ecology and Culture Study Group), Department of Zoology, Institute of Biosciences, Unesp, Botucatu, São Paulo State, Brazil.

## Results

A total of 371 *A. scutiformis* specimens were sampled during the study period, of which 165 were males (68 adults and 97 juveniles) and 206 females (63 non-ovigerous adults, 72 ovigerous adults, and 71 juveniles). The distribution of crab demographic groups into 13 size classes is presented in Table I. Size range was 3.7–15.8 mm CW in males and 4.2–12.7 mm CW in females.

**Table I.** *Acanthonyx scutiformis*. Distribution of individuals in size classes and demographic groups. N values in bold represent the size classes in which both adult and juvenile crabs can occur. ns = not significant.

Size class (mm)	Immatures			Matures			Total of crabs		
	Males	Females	$\chi^2$	Males	Females	$\chi^2$	Males	Females	$\chi^2$
3.0--]4.0	3	0	* oos	0	0	-	3	0	* oos
4.0--]5.0	8	1	p<0.05	0	0	-	8	1	Ns
5.0--]6.0	10	3	ns	0	0	-	10	3	Ns
6.0--]7.0	13	13	ns	0	0	-	13	13	Ns
7.0--]8.0	17	<b>18</b>	ns	0	<b>1</b>	* oos	17	19	Ns
8.0--]9.0	<b>12</b>	<b>20</b>	ns	<b>5</b>	<b>8</b>	ns	17	28	Ns
9.0--]10.0	<b>17</b>	<b>14</b>	ns	<b>3</b>	<b>40</b>	p<0.05	20	54	p<0.05
10.0--]11.0	<b>9</b>	<b>2</b>	p<0.05	<b>11</b>	<b>37</b>	p<0.05	20	39	p<0.05
11.0--]12.0	<b>6</b>	0	* oos	<b>10</b>	41	p<0.05	16	41	p<0.05
12.0--]13.0	<b>2</b>	0	* oos	<b>15</b>	8	ns	17	8	Ns
13.0--]14.0	0	0	-	17	0	* oos	17	0	* oos
14.0--]15.0	0	0	-	4	0	* oos	4	0	* oos
15.0--]16.0	0	0	-	3	0	* oos	3	0	* oos
<b>Total</b>	<b>97</b>	<b>71</b>	<b>p&lt;0.05</b>	<b>68</b>	<b>135</b>	<b>p&lt;0.05</b>	<b>165</b>	<b>206</b>	<b>p&lt;0.05</b>

\* oos = only one sex

For females, the highest frequencies obtained for juveniles and adults were 8-9 mm and 11-12 mm CW, respectively (Fig. 1). For males, the highest frequencies obtained for juveniles and adults were from 7-8 to 10-11 mm and from 12-13 to 13-14 mm CW, respectively (Fig. 2).

The result of the logistic equation indicates that approximately 50% male crabs were sexually mature in the 10–11 mm CW size class, whereas for females this proportion was found in the 8–9 mm CW size class (Fig. 3).

Sex ratio for the total number of collected crabs was 0.8:1 (M:F); 0.5:1 for adult and 1.3:1 for

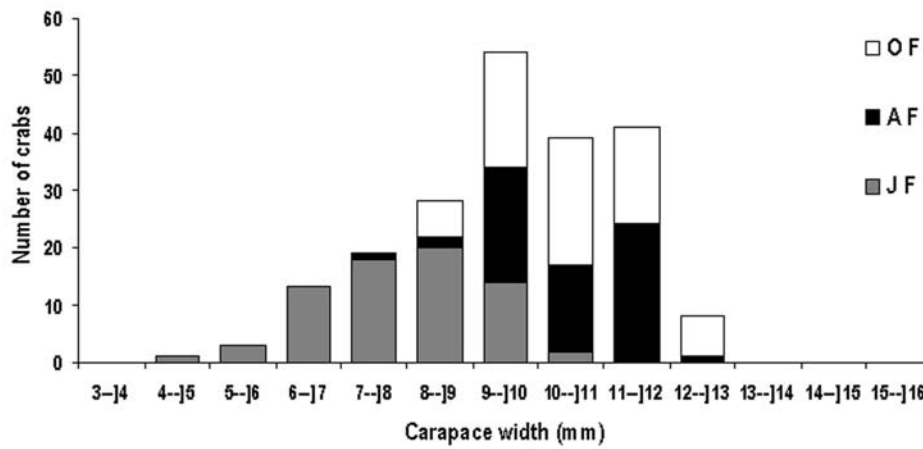
juvenile crabs ( $p < 0.05$ ). In the sex ratio analysis according to size class, the  $\chi^2$  test indicates significant differences ( $p < 0.05$ ) for adult animals in the size classes from 9-10 to 11-12 mm CW, with predominance of females. For juveniles, there were significant differences for males in the classes 4-5 and 10-11 mm CW (Table I and Fig. 4 a, b and c).

## Discussion

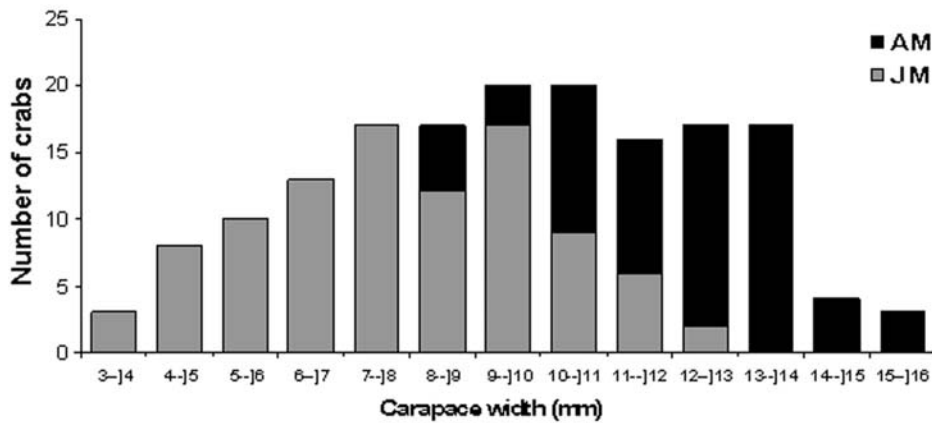
In spider crabs, growth is interrupted when sexual maturity is reached (Elner & Beninger 1992). Thus, the age, stage and size at morphologic sexual

maturity are coincident events for a certain specimen (Orensanz *et al.* 2007). Such pattern is described as “determined growth”, remarkably differing from the

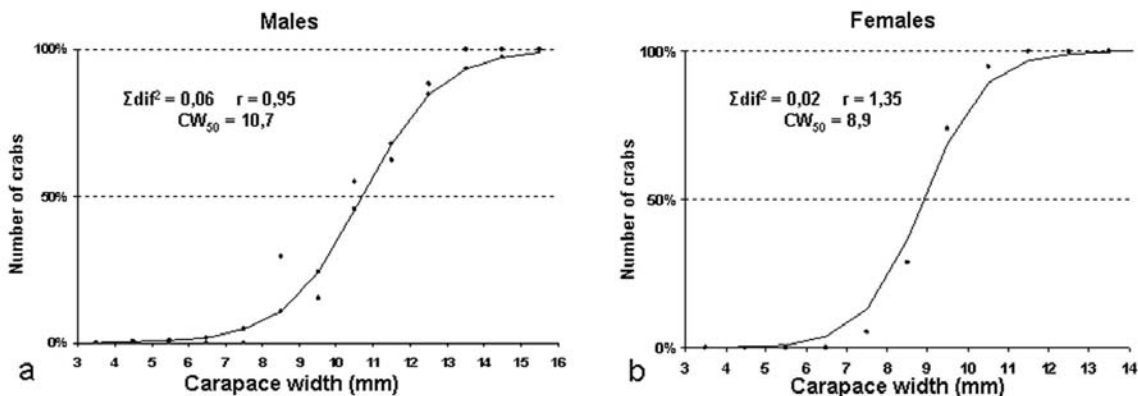
“undetermined growth”, in which successive molts, even after sexual maturity, allow the specimens to gradually grow until death (Hartnoll 1985).



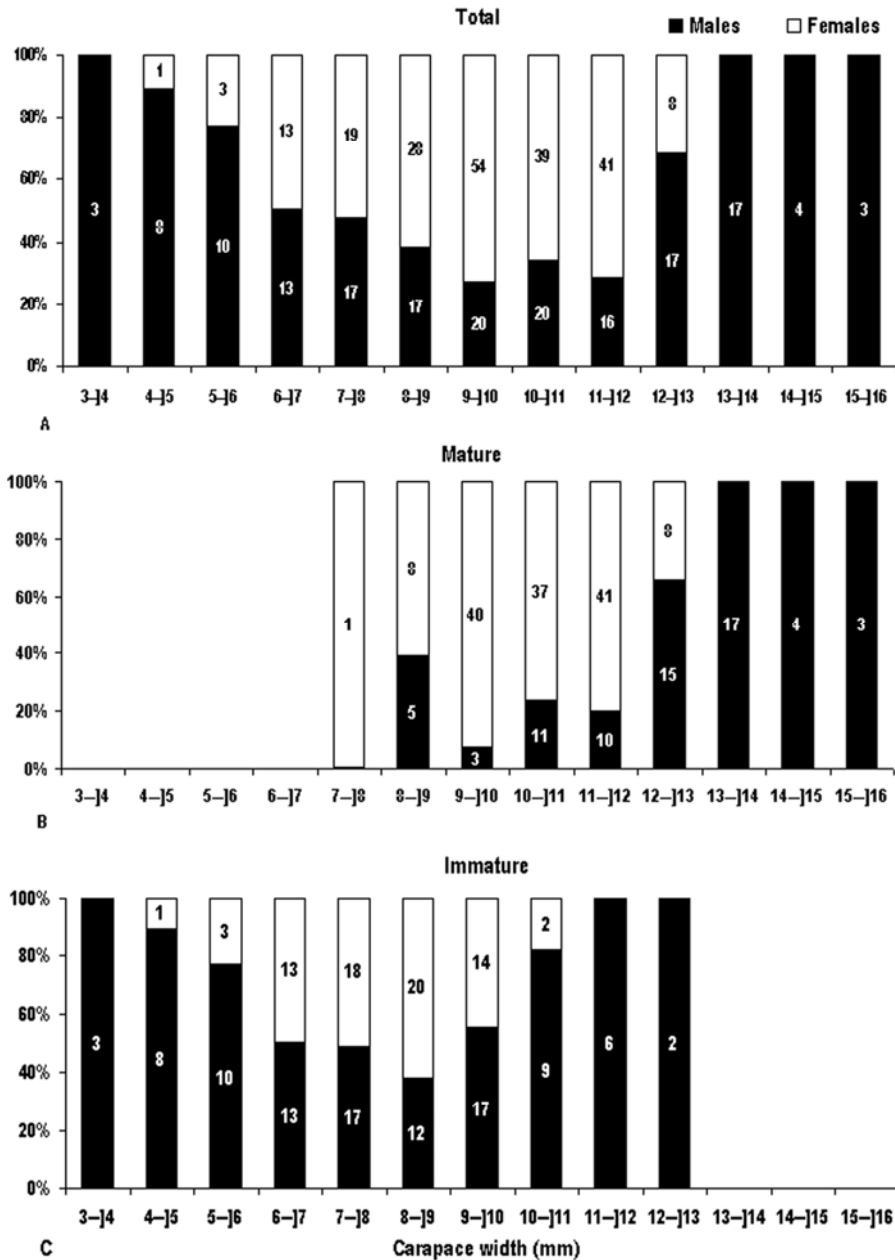
**Figure 1.** *Acanthonyx scutiformis*. Size frequency distribution of females (71 juveniles, 63 non-ovigerous adults and 72 ovigerous females). OF: Ovigerous Females; AF: Non-Ovigerous Adult females; JF: Juvenile females.



**Figure 2.** *Acanthonyx scutiformis*. Size frequency distribution of males (97 juveniles and 68 adults). AM: Adult males; JM: Juvenile males.



**Figure 3.** *Acanthonyx scutiformis*. Maturation curve for males (a) and females (b). According to the logistic equation,  $CW_{50}$  is 10.7 mm CW for males and 8.9 mm CW for females.



**Figure 4.** *Acanthonyx scutiformis*. Percentage of males and females per size class. 4a. Total of crabs; 4b. Adults; and 4c. Immatures.

The size of mature individuals of a certain spider crab species varied due to their size at terminal molt or puberty molt, which can be different for each specimen, but in a wide extension range of body size (Hartnoll *et al.* 1993).

Three growth stages can be recognized in Majoidea crabs: immature, pre-pubertal, and mature (Hartnoll 1963). Such stages are identified based on two important events during the animal's growth (Teissier 1935): pre-puberty molt, in which immature crabs begin their changes to become adults, and puberty molt or terminal molt (Carlisle 1957), in which crabs are completely mature.

Negreiros-Fransozo *et al.* (1994) analyzed in detail the morphologic changes that occur in *Epialtus brasiliensis* (Majoidea, Epialtidae) during its puberty molt and described a remarkable increase in the size of chelipeds and gonopods. Such size differences can be associated with necessary male behaviors during the adult life, such as territory defense, agonistic behavior against other individuals for food or females to copulate, and also mating. In this sense, the present results on the predominance of males in the largest size classes could be an advantage during many behavioral displays.

The considerable adult size extension in

both sexes was already recorded for a number of Majoidea species (Teissier 1960, Winget *et al.* 1974, Aldrich 1974, Hartnoll *et al.* 1993, Negreiros-Fransozo *et al.* 1994, Hiyodo & Fransozo 1995, Hartnoll & Bryant 2001). For males, such wide extension requires three successive molts, two of which are optional, as in certain crab species they can occur in several size categories, even before sexual maturity (Aldrich 1974).

The present analysis showed that mature females have from 7 to 8 mm CW, whereas males from 8 to 9 mm CW, although the latter reach larger size classes than females. For many brachyuran species, females can attain reproductive stages by accumulating energetic resources in size classes that are better for reproduction, delaying the somatic growth (Colby & Fonseca 1984, Conde & Diaz 1989, Diaz & Conde 1989).

The  $CW_{50}$  calculated for *A. scutiformis* females (8.9 mm CW) was lower than that obtained for males (10.7 mm CW). Such finding corroborates the results obtained by Hiyodo & Fransozo (1995). Studying another spider crab species, *E. brasiliensis*, in the same geographic area, Negreiros-Fransozo *et al.* (1994) also found smaller maturity sizes for females than for males.

As stated by Bernardo (1993), the phenotypic plasticity in the maturity transition can be associated with age, development (expressed by stage) and growth (expressed by body size). Such plasticity can be influenced by the interaction between the growth and the reproduction process, which compete for energetic resources and are thus antagonistic events. In this sense, the crabs could begin their reproductive season with reduced sizes due to a slow growth, providing reproduction in a situation of high mortality rate at the largest size classes (life-history tactics *r*, as mentioned by Stearns (1976)). The opposite strategy could be a rapid growth if the crab can only reproduce at larger sizes (life history tactics *k*, as mentioned by Stearns (1976)), providing a higher ability to produce gametes (Hartnoll & Gould 1988). In this last case, however, the animals would be more susceptible to predation before reproducing.

A different number of juvenile specimens between sexes was also verified by Negreiros-Fransozo *et al.* (1994) in *E. brasiliensis*. As regards adult crabs, females were more numerous than males, which can be explained by the higher survival rate of the former, whereas males with larger chelipeds could be more easily identified by predators (Diesel 1986). Besides, males are more active and present more notable behaviors when searching or fighting for females (Wirtz & Diesel

1983). Such factors can considerably increase their susceptibility to predation

Small herbivores usually look for shelter among algae and frequently choose those structurally complex or with morphologic or chemical features that prevent the presence of some predator fishes (Hay 1997). Cruz-Riviera (2001) described the decoration habit of the spider crab *Acanthonyx lunulatus* and other two Majoidea species as a strategy to reduce predation. The presently studied species, *A. scutiformis*, does not have an evident decoration habit; however, its coloration and body ornaments make it very misidentified with the algae and difficult to see with the naked eyes. Such behavior might have interfered in the number of collected specimens for each sex, which was reduced mainly in the two first classes (N= 12). However, this differential distribution should not be disregarded, as discussed by Fransozo *et al.* (2000) concerning the Xanthoidea crab *Menippe nodifrons*. Such species has a differentiated habitat occupation during its juvenile phase as the young lives in worm colonies and the adults are found in the fissures and under rocks of the intertidal region.

Warner (1967) reported that, during the reproductive period of *Aratus pisonii* (H. Milne Edwards 1837), females migrate from the interior of the mangrove to the water edge, increasing the relative frequency of females. Thus, the deviation in the sex ratio per size class found in *A. scutiformis* could be due to the cryptic habit of such crabs, as they live among the branches of algae, which makes capturing difficult.

In marine crustaceans, as mentioned by Wenner (1972), sex-ratio patterns can vary with the size, and some inferences can be done about anomalous patterns based on the sexual reversion (disregarded in the case of *A. scutiformis*), besides the differences between sexes in relation to their longevity, migration, mortality and growth rate.

There is no report in literature about majid migration in the Brazilian coast. However, Furbock & Patzner (2005) observed non-directional maximum movements as far as 16 m in a 9-day period for *Maja crispata*. González-Gurriarán *et al.* (2002), studying *M. squinado*, detected directional movements as far as 100 m in short periods of time for adult crabs and more restricted and non-directional movements for juveniles. It is interesting to note, however, that such majid specimens are very large, relative to the genera *Epialtus* and *Acanthonyx*.

*A. scutiformis* dependence on algae for a favorable habitat can constitute an increasing

protection factor, favoring sex encounters for mating. On the other hand, the algal bank can easily be removed by strong marine currents during storms and crabs may present increased mortality risk or modified density due to seasonal variation in environmental factors.

The sex ratio obtained for the total sampled *A. scutiformis* was similar to that obtained by Negreiros-Fransozo *et al.* (1994) for *E. brasiliensis*, close to 1:1. However, those authors found more males in the immature demographic group and more females in the adult group. Both species of the Epialtidae family occur in sympatry and syntopy; they also present a great overlap of juveniles and adults in some size classes, and the same sex-ratio pattern, sexual dimorphism and life habits. Such data corroborate the hypothesis that population features are mainly determined based on the differential sexual maturity attainment between sexes and on the major predation susceptibility of adult males in algal banks on the rocky shores of the northern littoral of São Paulo State.

### Acknowledgements

The authors are grateful for the financial support during the collections (Fapesp #94/4878-8 and # 98/3134-6). We also thank the colleagues from the NEBECC group who helped in sampling and laboratory analysis, and the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) for allowing wild animal sampling.

### References

- Aguilar, A.T., Malpica, Z. C. & Urbina, B. V. 1995. **Dinamica de poblaciones de peces**. Primera Edición, Ed. Libertad, 304pp.
- Aldrich, J. C. 1974. Allometric studies on energy relationships in the spider crab *Libinia emarginata* (Leach). **Biological Bulletin**, 147: 257-273.
- Bernardo, J. 1993. Determinants of maturation in animals. **Trends in Ecology and Evolution**, 8: 166-173.
- Carlisle, D. B. 1957. On the hormonal inhibition of moulting in decapod crustacea. II. The terminal anecdyosis in crabs. **Journal of the Marine Biological Association of the United Kingdom**, 36: 291-307.
- Castiglioni, D. S. & Negreiros-Fransozo, M. L. 2005. Comparative population biology of *Uca rapax* (Smith, 1870) (Brachyura, Ocypodidae) from two subtropical mangrove habitats on the Brazilian coast. **Journal Natural History**, 39(19):1627-1640.
- Castiglioni, D. S., Negreiros-Fransozo, M. L. & Mortari, R. C. 2006. Biologia populacional do caranguejo violinista *Uca rapax* (Smith, 1870) (Crustacea, Ocypodoidea), proveniente de uma área de manguezal degradado em Paraty, RJ, Brasil. **Atlântica**, 28(2): 73-86.
- Cobo, V. J. 2006. Population biology of the spider crab, *Mithraculus forceps* (A. Milne-Edwards, 1875) (Majidae, Mithracinae) on the southeastern Brazilian coast. **Crustaceana**, 78(9): 1079 – 1087.
- Coelho, P. A. & Torres, M. F. A. 1994. Taxonomia e distribuição das espécies do gênero *Acanthonyx* Latreille, no Brasil (Crustacea, Decapoda, Majidae). **Trabalhos Oceanográficos da Universidade Federal de Pernambuco**, 22: 221–224.
- Colby, D. R. & Fonseca, M. S. 1984. Population dynamics, spatial dispersion and somatic growth of the sand fiddler crab *Uca pugilator*. **Marine Ecology Progress Series**, 16: 269–279.
- Colpo, K. D. & Negreiros-Fransozo, M. L. 2004. Comparison of the population structure of the fiddler crab *Uca vocator* (Herbst, 1804) from three subtropical mangrove forests. **Scientia Marina**, 68(1): 139-146.
- Conde, J. E. & Díaz, H. 1989. The mangrove tree crab *Aratus pisonii* in a tropical estuarine coastal lagoon. **Estuarine Coastal Shelf Sci**, 28: 639–650.
- Costa, T. M. & Negreiros-Fransozo, M. L. 2003. Population biology of *Uca thayeri* (Rathbun, 1900) (Brachyura, Ocypodidae) in a subtropical South American mangrove area: Results from transect and catch-per-unit-effort techniques. **Crustaceana**, 75(10): 1201-1218.
- Cruz-Rivera, E. 2001. Generality and specificity in the feeding and decoration preferences of three Mediterranean crabs. **Journal of Experimental Marine Biology and Ecology**, 266(1): 17-31.
- Dana, J. D. 1851. On the classification of the Majoid Crustacea or Oxyrhynga. *American Journal of Science and Arts*, ser. 2, 11: 425-434.
- Diaz, H. & Conde, J. E. 1989. Population dynamics and life history of the mangrove crab *Aratus pisonii* (Brachyura, Grapsidae) in a marine environment. **Bulletin of Marine Science**, 45: 148–163.
- Diesel, R. 1986. Population dynamics of the commensal spider crab *Inachus phalangium* (Decapoda: Majidae). **Marine Biology**, 91: 481–489.
- Elner, R. W. & Beninger, P. G. 1992. The productive biology of snow crab *Chionoecetes*

- opilio*: a synthesis of recent contributions. **American Zoologist**, 32: 524-533.
- Flores, A. A. V. & Negreiros-Fransozo, M. L. 1999. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. **Bull. Marine Science**, 65(1): 59-73.
- Fransozo, A., Bertini, G. & Correa, M. O. D. 2000. Population biology and habitat utilization of the stone crab *Menippe nodifrons* in the Ubatuba region, São Paulo, Brazil. In: Klein J. C. V. V. & Schran, F. R. (eds.) **The biodiversity crisis and Crustacea, Crustacean Issues**, 12: 275-281.
- Furbock, S. & Patzner, R. A. 2005. Daily movement patterns of *Maja crispata* Risso 1827 (Brachyura, Majidae). **Acta Adriatica**, 46(1): 41-45.
- González-Gurriarán, E., Freire, J. & Bernadez, C. 2002. Migratory patterns of female spider crabs *Maja squinado* detected using electronic tags and telemetry. **Journal of Crustacean Biology**, 22: 91-97.
- Hartnoll, R. G. 1963. The biology of Manx spider crabs. **Proceedings of the Zoological Society of London**, 141: 423-496.
- Hartnoll, R. G. 1985. Growth, sexual maturity and reproductive output. In: Wenner AM, Ed **Factors in Adult Growth**. AA Balkema, Rotterdam, 101-128.
- Hartnoll, R. G. & Gould, P. 1988. Brachyuran life history strategies and the optimization of egg production. **Symposium of the Zoological Society of London**, 59: 1-9.
- Hartnoll, R. G., Bryant, A. D. & Gould, P. 1993. Size distribution in spider crab populations – spatial and temporal variation. **Journal of Crustacean Biology**, 13(4): 647-655.
- Hartnoll, R. G. & Bryant, A. D. 2001. Growth to maturity of juveniles of the spider crabs *Hyas coarctatus* Leach and *Inachus dorsettensis* (Pennant) (Brachyura: Majidae). **Journal of Experimental Marine Biology and Ecology**, 263: 143-158.
- Hay, ME. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. **Coral Reefs** 16 Suppl., 67-76.
- Hiyodo, C. M. & Fransozo, A. 1995. Relative growth of spider crab *Acanthonyx scutiformis* (Dana, 1851) (Crustacea, Decapoda, Majidae). **Brazilian Archives of Biology and Technology**, 38(3): 969-981.
- Howard, R. 1981. The ecology and trophic role of caridean shrimps in the eelgrass community of Western Port, Victoria. **Ph.D. Thesis**, University of Melbourne, pp. 196.
- Leme, M. H. A. 2002. A comparative analysis of the population biology of the mangrove crabs *Aratus pisonii* and *Sesarma rectum* (Brachyura, Grapsidae) from the north coast of São Paulo State, Brazil. **Journal of Crustacean Biology**, 22(3):553-557
- Mantelatto, F. L. M., Fransozo, A. & Negreiros-Fransozo, M. L. 1995. Populational structure of *Hepatus pudibundus* (Herbst, 1785) (Decapoda, Brachyura, Calappidae) in the Fortaleza Bay, Ubatuba, SP. **Revista Biología Tropical**, 43(1-3): 265-270.
- Mantelatto, F. L. M., Faria, F. C. R. & Garcia R. B. 2003. Biological aspects of *Mithraculus forceps* (Brachyura: Mithracidae) from Anchieta Island, Ubatuba, Brazil. **Journal of the Marine Biological Association of the United Kingdom**, 83: 798 – 791.
- Melo, G. A. S. 1996. Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. **Plêiade\ FAPESP**. ED. São Paulo, 603p.
- Mura, M., Orru, F. & Cau, A. 2005. Size at sexual maturity of the spider crab *Anamathia rissoana* (Decapoda: Majoidea) from the Sardinian sea. **Journal of Crustacean Biology**, 25(1): 110 -115.
- Pinheiro, M. A. A. & Franzoso, A. 1993. Análise da Relação Biométrica do peso úmido pela largura da carapaça para o siri *Arenaeus cribarius* (Lamarck, 1818) (Crustacea, Brachyura, Portunidae). **Arquivos de Biologia e Tecnologia**, 36(2): 331-341.
- Negreiros-Fransozo, M. L. & Fransozo, A. 1995. On the distribution of *Callinectes ornatus* Ordway, 1863 and *Callinectes danae* Smith, 1869 (Brachyura, Portunidae) in the Fortaleza Bay Ubatuba, Brazil. **Iheringia**, Série Zoológica, 79: 13-25.
- Negreiros-Fransozo, M. L. & Fransozo, A. 2001. Larval development of *Epialtus bituberculatus* H. Milne Edwards, 1934 (Crustacea: Decapoda: Brachyura: Majidae) with comments on majid larvae from the southwestern Atlantic. **Proceedings of the Biological Society of Washington**, 114(1): 120-138.
- Negreiros-Fransozo, M. L., Fransozo, A. & Reigada, A. L. D. 1994. Biologia populacional de *Epialtus brasiliensis* Dana, 1852 (Crustacea, Majidae). **Revista Brasileira Biologia**, 54(1): 173-180.
- Negreiros-Fransozo, M. L., Mantelatto, F. L. M. &



- Fransozo, A. 1999. Population biology of *Callinectes ornatus* Ordway, 1863 (Decapoda, Portunidae) from Ubatuba (SP) State, Brazil. **Scientia Marina**, 63(2): 157-163.
- Ng, P. K. L., Guinot, D. & Davie, P. J. F. 2008. Systema Brachyurorum: part I. An annotated checklist of extant brachyuran crabs of the world. **The Raffles Bulletin of Zoology**, 17: 1-286.
- Orensanz, J. M., Ernst, B. & Armstrong, D. A. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering sea. **Journal of Crustacean Biology**, 27(4): 576-591.
- Santos, S., Negreiros-Fransozo, M. L. & Fransozo, A. 1995. Estructura poblacional de *Portunus spinimanus* Latreille, 1819 (Crustacea, Brachyura, Portunidae) en la ensenada de la Fortaleza, Ubatuba (SP), Brasil. **Revista de Investigaciones Marinas**, 16 (1-3): 37-43.
- Santos, S. & Negreiros-Fransozo, M. L. 1996. Maturidade fisiológica em *Portunus spinimanus* Latreille, 1819 (Crustacea, Brachyura, Portunidae) na região de Ubatuba, SP. **Papéis Avulsos de Zoologia**. 39(20): 365-377.
- Silva, S. M. J., Hirose, G. L. & Negreiros-Fransozo, M. L. 2007. Population dynamic of *Sesarma rectum* (Crustacea, Brachyura, Sesarmidae) from a muddy flat under human impact, Paraty, Rio de Janeiro, Brazil. **Iheringia, Sér. Zool.**, 97(2): 207-214.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. **The Quarterly Review of Biology**, 51:3-47.
- Taissoun, E. N. 1969. Las especies de cangrejos del género *Callinectes* (Brachyura) em el Golfo de venezuela y Lago de Maracaibo. **Boletín de Centro de Investigaciones Biológicas. Universidade Zulia**, 2: 1-101.
- Teissier, G. 1935. Croissance des variants sexuelles chez *Maja squinado*. **Travaux de la Station Biologique de Roscoff**, 13: 93-130.
- Teissier, G. 1960. Relative Growth. In: Wateman TH Ed, **The physiology of Crustacea**, Vol. I. Academic Press, New York and London, pp. 537-560.
- Teixeira, G. M., Fransozo, V., Castilho, A. L., Costa, R. C. & Freire, F. A. M. 2008. Size distribution end sex ratio in the spider crab *Epiplatys brasiliensis* (Dana 1852) associated with seaweed on a rocky shore in southeastern Brazil (Crustacea, Decapoda, Brachyura, Majoidea, Epiplatidae). **Senckenbergiana Biologica**, 88(2): 169-176.
- Vazzoler, A. E. M. 1996. Biologia da reprodução de peixes teleosteos: teorias e prática. **Ed. EDUEM**, Maringá. 169pp.
- Warner, G. F. 1967. The life history of the mangrove tree crab *Aratus pisonii*. **Journal of Zoology**, 153: 321-335
- Wenner, A. M. 1972. Sex ratio as a function of size in marine crustacean. **American Naturalist**, 106(949): 321-350.
- Williams, A. B. 1974. The swimming crab of the genus *Callinectes* (Decapoda: Portunidae). **Fish. Bulletin**, 72(3): 683-768.
- Winget, R. R., Maurer, D. & Seymour, H. 1974. Occurrence, size composition and sex ratio of the rock crab, *Cancer irroratus* and the spider crab *Libinia emarginata* Leach in Delaware Bay. **Journal of Natural History**, 8: 199-205.
- Wirtz, P. & Diesel, R. 1983. The social structure of *Inachus phalangium*, a spider crab associated with the sea anemone *Anemonia sulcata*. **Zeitschrift fur Tierpsychologie**, 62:209-234

Received April 2008

Accepted November 2008

Published online March 2009