

REPRODUCTIVE ANALYSES OF THE SWIMMING CRAB *ACHELOUS SPINICARPUS* (STIMPSON, 1871) (CRUSTACEA: DECAPODA: PORTUNOIDEA) ON THE NORTHERN COAST OF SÃO PAULO, BRAZIL

THIAGO ELIAS DA SILVA^{*1}; VIVIAN FRANZOZO^{1,2}; FABIANO GAZZI TADDEI^{1,3}; ROGÉRIO CAETANO DA COSTA^{1,4}; ARIÁDINE CRISTINE ALMEIDA^{1,5} & ADILSON FRANZOZO¹.

¹NEBECC – Núcleo de Estudos em Biologia Ecologia e Cultivo de Crustáceos. Universidade Estadual Paulista “Júlio de Mesquita Filho” – UNESP, Departamento de Zoologia, Botucatu – SP, Brasil.

²Departamento de Ciências Naturais, Universidade Estadual do Sudoeste da Bahia - UESB, Vitória da Conquista - BA, Brasil.

³Laboratório de Estudos de Crustáceos Amazônicos - LECAM, Universidade do Estado do Amazonas/ Centro de Estudos Superiores de Parintins – UEA/CESP, Parintins – AM, Brasil.

⁴Laboratório de Biologia de Camarões Marinhos e de Água Doce – LABCAM, Universidade Estadual Paulista “Júlio de Mesquita Filho” – UNESP, Bauru – SP, Brasil.

⁵Universidade Federal de Uberlândia – UFU. Instituto de Biologia, Campus Umuarama. Uberlândia - MG, Brasil.

*Corresponding author: silva.t.e@hotmail.com.

ABSTRACT: The swimming crab *Achelous spinicarpus* can be considered an ‘indicator’ of cold-water environmental conditions in the northern coast of Sao Paulo, Brazil. In order to improve our understanding about this species, we examined size at sexual maturity, breeding period, and recruitment events of *A. spinicarpus* in the region. Swimming crabs were sampled by monthly trawling at seven depths in two locations (Ubatuba and Caraguatatuba) from July 2001 to June 2003. A total of 1057 specimens of *A. spinicarpus* were collected in Ubatuba (598 males and 459 females), from which only 15 females were ovigerous. Size at sexual maturity was estimated to be 24.2 and 23.8 mm carapace width (CW) in males and females, respectively. In Caraguatatuba, 5112 individuals were collected (3138 males and 1974 females), from which only 29 females were ovigerous. Size at sexual maturity was estimated to be 23.7 and 23.5 mm CW in males and females, respectively. Ovigerous females and juvenile recruitment occurred mostly during spring and summer seasons. Size at sexual maturity in *A. spinicarpus* differ from that previously reported for the species, suggesting certain reproductive plasticity.

Keywords: Brachyura, water mass, reproduction, recruitment, sexual maturity

INTRODUCTION

Portunidae, known as the swimming crabs, are an important source of food for human consumption. About 20 species occur in Brazilian marine waters, 17 of which are found along the northern coast of the State of São Paulo (MELO 1996; BERTINI *et al.* 2004). The genus *Portunus* WEBER, 1795 is clearly polyphyletic (MANTELATTO *et al.* 2007; NG *et al.* 2008); therefore, the actual number of species is still uncertain. Recently, nine species of this genus were reallocated to *Achelous* DE HAAN, 1833 by

MANTELATTO *et al.* (2009), including *Achelous spinicarpus* (STIMPSON, 1871), the target species of this study.

Achelous spinicarpus has a wide geographic distribution along the Western Atlantic coast, from North Carolina (USA) to Rio Grande do Sul (Brazil) (MELO 1996). This species inhabits shallow water to 550 m depth (WILLIAMS 1984), is associated with low water temperatures and is considered an indicator of the South Atlantic Central cold water mass in SE Brazil (PIRES 1992; DE LEO & PIRES-VANIN 2006).

Great abundance of *A. spinicarpus* has been reported for the northern coast of São Paulo (PIRES 1992; BERTINI & FRANSOZO 2004 and BRAGA *et al.* 2005), but its reproductive biology has been scarcely studied (CORBI-CORRÊA & FRANSOZO 2002; PARDAL-SOUZA & PINHEIRO 2013). These authors evaluated some morphometric relationships to estimate the size of the species at maturity in northern São Paulo and suggested the possibility of variations on the estimated size at sexual maturity.

Although a morphometric approach is still used to estimate sexual maturity in decapods crustaceans (SILVA *et al.* 2014), there are other procedures. The techniques usually employed to estimate sexual maturity are: 1) examination of the external abdominal morphology, with immature crabs having their abdomen sealed to the thoracic sternites (FLORES & NEGREIROS-FRANSOZO 1999); 2) physiological maturity evaluating mature gonad proportion in the population (REIGADA & NEGREIROS-FRANSOZO 1999).

Latitudinal variation in exogenous factors can influence reproduction in marine species (BERTINI *et al.* 2010 a; ANDRADE *et al.* 2015 a, b). Thus, it is expected that the reproductive characteristics of *A. spinicarpus* could also be influenced by environmental variations caused by the presence of South Atlantic Central Water. Both the size at sexual maturity and the reproductive period are basic data for the elaboration of conservation and environmental management strategies, which may be more relevant when dealing with ecologically important species such as portunids.

In addition, *A. spinicarpus* is part of the shrimp bycatch in *Farfantepenaeus paulensis* (PEREZ-FARFANTE, 1967) and *F. brasiliensis* (LATREILLE, 1817) fishery (SEVERINO-RODRIGUES *et al.* 2002, BERTINI *et al.* 2010 b). However, it is still unknown what effects such activity can cause in populations of this swimming crab.

The aim of the present study was to analyze reproductive pattern and recruitment of a population of *A. spinicarpus* present along the north coast of São Paulo during two years. Size of the sexual morphological maturity (carapace width₅₀), reproductive period and juvenile recruitment were therefore analyzed in localities near Ubatuba and Caraguatatuba.

MATERIAL AND METHODS

Study area

The sampled areas localities differ with reference to their hydrogeographic characteristics. Ubatuba littoral

(23°26'S, 45°02'W) presents a diverse combination of environmental variables such as texture and amount of organic matter available in the sediment, temperature and salinity of the water (MANTELATTO & FRANSOZO 1999 a). In contrast, the Caraguatatuba littoral area (23°51'S, 45°26'W) presents a homogeneous variation of these same environmental factors, because it is sheltered from the direct action of the waves and winds by the "São Sebastião" Island, with slight variations of the bottom morphology (BARROS *et al.* 1997).

Three water masses influence the studied region throughout the year (PIRES 1992): Coastal Water (Temperature > 20 °C and Salinity < 36), Tropical Water (T > 20 °C and S > 36), and South Atlantic Central Water (T < 18 °C and S < 36) (CASTRO-FILHO *et al.* 1987).

Biological data

Monthly samplings were carried out from July 2001 to June 2003 in both areas. Sampling was accomplished by means of a shrimp fishing boat equipped with double-rig trawls at seven depths: 5, 10, 15, 20, 25, 30 and 35 m (Fig. 1). The net opening was approximately 4.5 m; mesh aperture were 20 mm in the main net body and 15 mm in the cod end. Each trawl lasted 30 minutes, covering an estimated swept area of 18,000 m².

The swimming crabs were identified according to MELO (1996). All swimming crabs were sexed, measured at their maximum carapace width, excluding the lateral spine using a caliper to the nearest 0.01mm. Individuals were classified into five demographic groups according to HAEFNER (1990), differentiating juveniles (immature) and adults (mature) by shape and adherence of the abdomen to the thoracic sternites, and by the presence of eggs: juvenile males, adult males, juvenile females, adult females and ovigerous females.

Data analysis

Size at sexual maturity was estimated considering the size (CW, carapace width) at which 50% of specimens reached sexual maturity using a sigmoid curve based on the following equation:

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

where y is the estimated proportion of mature individuals, and r is the coefficient of angulation of the logistic curve. The equation was adjusted by the minimum squares method (VAZZOLER 1996).

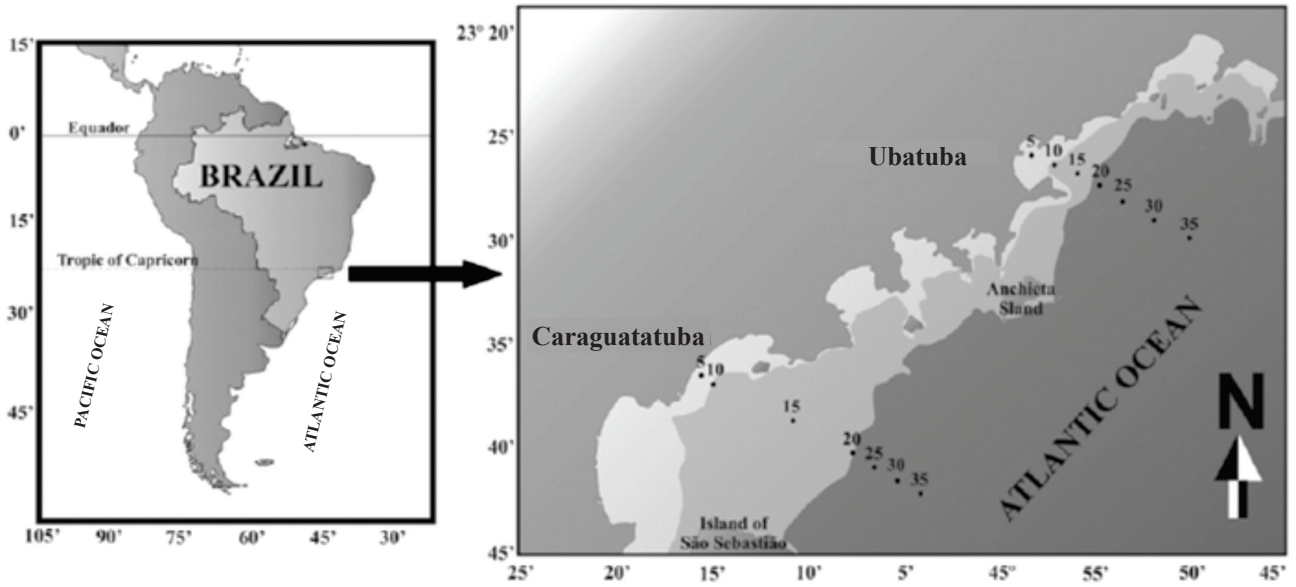


Fig. 1 - Map of the collection sites in the studied areas.

The reproductive period was verified by the presence of ovigerous females in the year four seasons, and the recruitment period by the proportion of juveniles in relation to the total abundance in each season. The proportion of juveniles was calculated in relation to the total of individuals in each locality (Ubatuba and Caraguatatuba), i. e., the expected proportion (calculated as: $J_{Ubatuba}/N_{Ubatuba}$ and $J_{Caraguatatuba}/N_{Caraguatatuba}$, where “J” is the total number of juveniles and “N” is the total number of individuals, in each locality) and expressed as percentage. Difference was tested with respect to its significance, i.e., between the expected and the observed juvenile proportion in each season of the year, by means of a binomial test (WILSON & HARDY 2002). The seasons when juvenile proportions were significantly higher ($\alpha = 0.05$) than expected were considered as recruitment periods.

RESULTS

During the study period, we obtained 1057 specimens of *A. spinicarpus* in Ubatuba: 598 males and 459 females (see Table 1). The estimated size (CW) at sexual maturity was higher in males (24.2 mm) than in females (23.8 mm) (Fig. 2). The largest juvenile male was 29.4 mm CW and the smallest adult male 21.2 mm. The largest juvenile female was 23.7 mm CW, the smallest adult female 20.9 mm, and the smallest ovigerous female 35.3 mm. In Caraguatatuba, we obtained 5112 specimens: 3138 males and 1974 females (see Table 1). The estimated size at

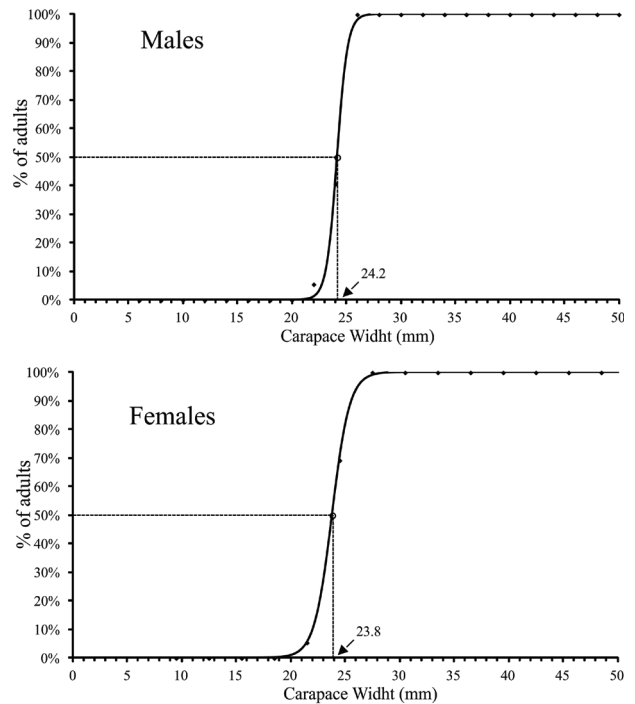


Fig. 2. *Achelous spinicarpus* (STIMPSON, 1871). Percentage of adult individuals (males and females) with the tendency line fitted to the logistic function for individuals collected in Ubatuba. The arrow indicates the estimated size at sexual maturity.

Table 1. *Achelous spinicarpus* (STIMPSON, 1871). Total number of specimens obtained in each locality.

	UBATUBA		CARAGUATATUBA	
	Males	Females	Males	Females
Total/sex	598	459	3138	1974
Adult	73	80*	500	228*
Juveniles	525	379	2638	1746
Ovigerous		15		29
Total/locality	1057		5112	

* these numbers include ovigerous females from each locality.

sexual maturity in this locality was 23.7 mm for males 23.7 mm CW, being the sizes of the largest juvenile 26.6 mm and the smallest adult 16.6 mm CW. For females, the size at sexual maturity was 23.5 mm CW, being the size of the largest juvenile female 23.8 mm and the smallest adult female 18.8 mm CW (Fig. 3). The smallest ovigerous female captured had 34.4 mm CW.

In both localities numbers of ovigerous females were low, but in Ubatuba (N=15) they were no significant and present in all seasons (Table 2). In Caraguatatuba,

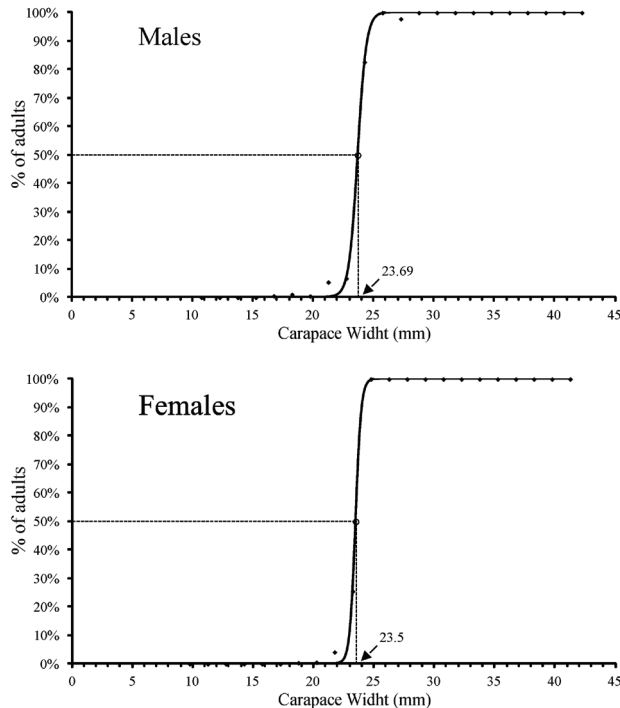


Fig. 3. *Achelous spinicarpus* (STIMPSON, 1871). Percentage of adult individuals (males and females) with the tendency line fitted to the logistic function for individuals collected in Caraguatatuba. The arrow indicates the estimated size at sexual maturity.

ovigerous females were observed only during spring (N = 1) and summer (N = 28) (Table 3). Juveniles constituted 85% of the sampled individuals in both areas and they were present in all seasons of the year. The proportion of juveniles was significantly higher (binomial test, $p < 0.05$) in the spring of 2001 and 2002 and in the summer of 2003 in Ubatuba (Fig. 4) and Caraguatatuba (Fig. 5).

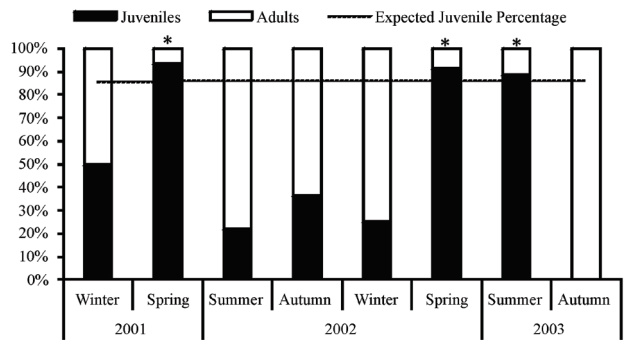


Fig. 4. *Achelous spinicarpus* (STIMPSON, 1871). Percentage of individuals (juveniles and adults) in Ubatuba. The “*” indicates seasons when observed juveniles proportion are significantly higher than the expected (binomial test, $p < 0.05$), indicating recruitment.

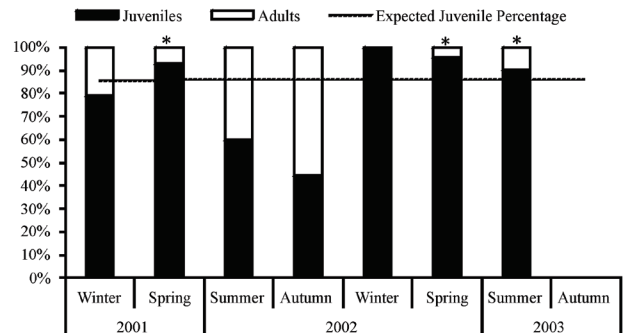


Fig. 5. *Achelous spinicarpus* (STIMPSON, 1871). Percentage of individuals (juveniles and adults) in Caraguatatuba. The “*” indicates seasons when observed juveniles proportion are significantly higher than the expected (binomial test, $p < 0.05$), indicating recruitment.

Table 2. *Achelous spinicarpus* (STIMPSON, 1871). Total number of individuals collected in all sampling points, during two years in Ubatuba.

	Juveniles	Adult Males	Non Ovigerous Adult Females	Ovigerous Females
Winter	5	2	2	3
Spring	372	11	16	4
Summer	523	56	45	6
Autumn	4	4	2	2
Total	904	73	65	15

Table 3. *Achelous spinicarpus* (STIMPSON, 1871). Total number of individuals collected in all sampling points, during two years in Caraguatatuba.

	Juveniles	Adult Males	Non Ovigerous Adult Females	Ovigerous Females
Winter	32	5	1	0
Spring	275	12	6	1
Summer	3985	314	145	28
Autumn	92	69	47	0
Total	4384	500	199	29

DISCUSSION

In natural environments, on the average males of brachyuran crabs usually reach sexual maturity at larger size than females. This has been reported for *Achelous spinimanus* (LATREILLE, 1819), *Callinectes ornatus* (ORDWAY, 1863), *Acantholobulus schmitti* (RATHBUN, 1860), *Persephona mediterranea* (Herbst, 1794) and *Hexapanopeus paulensis* Rathbun, 1930 (BRANCO *et al.* 2002; BRANCO & FRACASSO 2004; FUMIS *et al.* 2007; BERTINI *et al.* 2010a; SILVA *et al.* 2014). The larger body size of the males can represent an advantage while competing for access to receptive females, besides favoring protection during copulation.

Considering energy consumption, HARTNOLL (1985) found that growth and reproduction are competing processes. One of the basic causes of reduced growth is the diversion of energy to reproductive processes (HARTNOLL 2006). In this aspect, male crabs invest more energy in somatic growth, whereas females direct energy for reproduction (HARTNOLL 1982), since oocyte production requires more resources than sperm production (ALUNNO-BRUSCIA & SAINT-MARIE 1998).

The males' investment in growth is due to several factors related to reproduction, such as: visual displays, competition for females and protection of these during copulation (HARTNOLL 2006). Such behaviors were verified for *Arenaeus cribrarius* (LAMARCK, 1818) by PINHEIRO &

FRANZOZO (1999) in laboratory experiments. The copula behavior of *A. cribrarius* consists of the formation of a couple, usually with a male (in inter-molt) larger than the female (in pre-molt), after the courtship. To date, no cases have been reported in which females of portunids reach a maximum asymptotic size larger than the males.

The presence of ovigerous females in all seasons in Ubatuba is a common process in tropical regions, but in Caraguatatuba there was a tendency of reproductive activity in the months influenced by the South Atlantic Central Water. According to CASTRO-FILHO *et al.* (1987), the front of this water mass reaches the northern coast of São Paulo with greater intensity in the summer. It is important to emphasize that the low number of ovigerous females observed in this study, makes it difficult to formulate a definitive inference about the reproductive period. Therefore, it is necessary to combine information about the recruitment period that is the result of the reproductive activity.

Recruitment and breeding patterns of several species of decapod crustaceans are known to be linked in some way with the South Atlantic Central Water front, for instance: *C. ornatus*, *Mithraculus forceps* (A. Milne-Edwards, 1875), *Libinia spinosa* H. Milne Edwards 1834, *Persephona mediterranea* (Herbst, 1974), *Nematopalaemon schmitti* (Holthuis 1950), *Acantholobulus schmitti* and *Arenaeus cribrarius*

(MANTELATTO & FRANZOZO 1999 b; MANTELATTO *et al.* 2003; BRAGA *et al.* 2007; BERTINI *et al.* 2010 a; ALMEIDA *et al.* 2011; FRANZOZO *et al.* 2013; ANDRADE *et al.* 2015 b).

According to CASTRO-FILHO *et al.* (1987) and AIDAR *et al.* (1993), South Atlantic Central Water causes nutrient enrichment in the coastal region, increasing primary production and this may increase the availability of food for planktotrophic larvae. According to VEGA-PÉREZ (1993), the temporal variation of planktonic productivity may represent an essential factor in the reproductive activity of crustaceans, which is closely related to the availability of food (phytoplankton) for larvae. In addition, *A. spinicarpus* is considered by many authors as an indicator of South Atlantic Central Water on the Brazilian coast (PIRES 1992; DE LÉO & PIRES-VANIN 2006 and LIMA *et al.* 2014), being favored not only indirectly by the generated enrichment of nutrients, but also because it is adapted to withstand low temperatures ($T < 20^\circ$). Thus, spring and summer periods are apparently more favorable for the reproductive activities of this species.

According to ANDRADE *et al.* (2015 b) in a study of *A. cribrarius*, the reproductive activity of the species seems not only to be related to temporal variations in temperature, among other environmental factors (salinity, sediment characteristics), but also to an adaptive synchrony between a period of more intense larval dispersion and high availability of food in the water column. According to these authors, this reproductive plasticity is also reflected in changes in the size at sexual maturity and may have developed due to exogenous factors, both environmental and anthropic, such as: fishing and the introduction of exotic species.

Considering that the estimated values for size at sexual maturity of *A. spinicarpus*, in the present study, are different from those obtained by PARDAL-SOUZA & PINHEIRO (2013) (males, 37; females, 32 mm CW), sampled in the Brazilian Southeastern coast, from range depth of 95 to 100 m, with collections carried out about 5 years after the present study, it is likely that the size at maturity of this species is also being influenced by exogenous factors, both environmental and/or caused by human action, like it was early reported for the portunid *A. cribrarius* (ANDRADE *et al.* 2015b). However, it is worth mentioning that the technique used by PARDAL-SOUZA & PINHEIRO (2013) was based on the relative growth of secondary sexual characters, which may cause some variation in the results, and difficult a more precise comparison.

This study reinforces that the reproductive characteristics (sexual maturity, reproductive period and recruitment) of *A. spinicarpus* may be being modulated by two factors: dynamic of water masses (as suggested by PIRES *et al.* 1992 for the most of decapod crustaceans in this region) and anthropic effect. The effects of biotic interactions within the benthic community cannot be ruled out. However, studies are still needed to investigate the influence of such factors on the spatio-temporal distribution of this species, in order to correlate such variables with reproductive characteristics.

Although only a portion of the population of *A. spinicarpus* (5 to 35 m deep) was sampled in this study (taking into account that this species is distributed up to 500 m), it was verified that all benthic demographic groups were found. The high abundance (total number of individuals in 2 years = 6169) of this species in the shallow water indicates the use of this area (both Ubatuba and Caraguatatuba), through most of its life cycle, mainly, from juveniles to mature adults. In this sense, environmental changes caused directly or indirectly in these areas should be monitored to prevent damage to natural stocks and to marine organisms in general, particularly in the case of *A. spinicarpus* which may indicate important oceanographic processes such as South Atlantic Central Water input.

ACKNOWLEDGEMENTS

We are grateful for the financial support received by the BIOTA/FAPESP project (process number 1998/07090-3) and NEBECC co-workers for the collection. We are also grateful to Dr. Maria Lucia Negreiros-Franzo for her constructive comments and valuable grammar review of this manuscript.

REFERENCES

- AIDAR, E., S. A. GAETA, S. M. F. GIANESSELLA-GALVÃO, M. B. B. KUTNER & C. TEIXEIRA. 1993. Ecosistema costeiro subtropical: nutrientes dissolvidos, fitoplâncton e clorofila-*a* e suas relações com as condições oceanográficas na região de Ubatuba, SP. *Publicação esp. Inst. Oceanogr.* 10: 9-43.
- ALMEIDA, A. C., V. FRANZOZO, G. M. TEIXEIRA, M. FURLAN, K. A. N. HIROKI & A. FRANZOZO. 2011. Population structure and reproductive period of whitebelly prawn *Nematopalaemon schmitti* (Holthuis 1950) (Decapoda: Caridea: Palaemonidae) on the southeastern coast of Brazil. *Invertebr. Reprod. Dev.* 55(1): 30-39.

- ALUNNO-BRUSCIA, M. B. & B. SAINT-MARIE. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 55: 459-477.
- ANDRADE, L. S., I. F. FRAMESCHI, A. L. CASTILHO, R. C. COSTA & A. FRANZOZO. 2015a. Can the pattern of juvenile recruitment and population structure of the speckled swimming crab *Arenaeus cribrarius* (Decapoda: Brachyura) be determined by geographical variations? *Mar. Ecol.* 36(4), 950-958.
- ANDRADE, L. S., V. FRANZOZO, G. BERTINI, M. L. NEGREIROS-FRANZOZO & L. S. LÓPEZ-GRECO. 2015b. Reproductive plasticity in the speckled crab *Arenaeus cribrarius* (Decapoda, Brachyura, Portunidae) associated with a population decline. *J. Coast. Res.* 31(3): 645-652.
- BARROS, C. E., I. C. S. CORRES, R. BAITELL & A. R. D. ELIAS. 1997. Aspectos sedimentares da enseada de Caraguatatuba, litoral do Estado de São Paulo. *An. Acad. Bras. Cienc.* 69(1): 19-36.
- BERTINI G. & A. FRANZOZO. 2004. Bathymetric distribution of brachyuran crab (Crustacea, Decapoda) communities on coastal soft bottoms off southeastern Brazil. *Mar. Ecol. Prog. Ser.* 279: 193-200.
- BERTINI, G., A. FRANZOZO & G. A. S. MELO. 2004. Biodiversity of brachyuran crabs (Crustacea: Decapoda) from non-consolidated sublittoral bottom on the northern coast of São Paulo State, Brazil. *Biodiversity Conserv.* 13: 2185-2207.
- BERTINI, G., A. FRANZOZO & M. L. NEGREIROS-FRANZOZO. 2010b. Brachyuran soft-bottom assemblage from marine shallow waters in the southeastern Brazilian littoral. *Mar. Biodiversity* 40: 277-291.
- BERTINI, G., G. M. TEIXEIRA, V. FRANZOZO & A. FRANZOZO. 2010a. Reproductive period and size at the onset of sexual maturity of mottled purse crab, *Persephona mediterranea* (Herbst, 1794) (Brachyura, Leucosioidea) on the southeastern Brazilian coast. *Invertebr. Reprod. Dev.* 54(1): 7-17.
- BRAGA, A. A., A. FRANZOZO, G. BERTINI & P. B. FUMIS. 2005. Composition and abundance of the crabs (Decapoda, Brachyura) off Ubatuba and Caraguatatuba, northern coast of São Paulo, Brazil. *Biota Neotrop.* 5(2): <http://www.biotaneotropica.org.br/v5n2/en/abstract?article+BN002050220055>.
- BRAGA, A. A., A. FRANZOZO, G. BERTINI & P. B. FUMIS. 2007. Bathymetric distribution and recruitment of the spider crab *Libinia spinosa* H. Milne Edwards 1834 in the Ubatuba and Caraguatatuba regions, northern coast of São Paulo, Brazil (Crustacea, Brachyura, Majoidea, Pisidae). *Senckenb. Biol.* 87(1): 7-16.
- BRANCO, J. O. & H. A. A. FRACASSO. 2004. Biologia populacional de *Callinectes ornatus* (Ordway) na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. *Rev. Bras. Zool.* 21(1): 91-96.
- BRANCO, J. O., M. J. LUNARDON-BRANCO & F. X. SOUTO. 2002. Estrutura populacional de *Portunus spinimanus* Latreille (Crustacea, Portunidae) na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. *Rev. Bras. Zool.* 19(3): 731-738.
- CASTRO-FILHO, B. M., L. B. MIRANDA & S. Y. MYAO. 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. *Bol. Inst. Oceanogr.* 35(2): 135-151.
- CORBI-CORRÊA, E. & A. FRANZOZO. 2002. Growth patterns of *Portunus spinicarpus* (Stimpson, 1871) (Decapoda, Portunoidea) from Ubatuba region (SP), Brazil. *Nauplius* 10(2): 131-137.
- DE LÉO, F. C. & A. M. S. PIRES-VANIN. 2006. Benthic megafauna communities under the influence of the South Atlantic Central Water intrusion onto the Brazilian SE shelf: a comparison between an upwelling and a non-upwelling ecosystem. *J. Mar. Syst.* 60: 268-284.
- FLORES, A. & M. L. NEGREIROS-FRANZOZO. 1999. Allometry of the Secondary Sexual Characters of the Shore Crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae). *Crustaceana* 72(9): 1051-1066.
- FRANZOZO, V., T. E. SILVA, P. B. FUMIS, G. BERTINI & P. A. LIMA. 2013. Ecological distribution and population structure of *Acantholobulus schmitti* (Rathbun, 1930) (Crustacea, Decapoda, Xanthoidea) on the southeastern Brazilian coast. *Braz. J. Oceanogr.* 61(4): 277-287.
- FUMIS, P. B., A. FRANZOZO, G. BERTINI & A. A. BRAGA. 2007. Morphometry of the crab *Hexapanopeus schmitti* (Decapoda: Xanthoidea) in the northern coast of the state of São Paulo, Brazil. *Revista de Biologia Tropical* 55 (suppl. 1): 163-170.
- HAEFNER, P. A., JR. 1990. Morphometry and size at maturity of *Callinectes ornatus* (Brachyura, Portunidae) in Bermuda. *Bull. Mar. Sci.* 46(2): 274-286.

- HARTNOLL, R. G. 1985. *Growth, sexual maturity and reproductive output*. In: *Crustacean issues: factors in adult growth*. Ed. A. M. Wenner, AA Balkema, Rotterdam. 3: 101-128.
- HARTNOLL, R. G. 1982. *Growth*. In: *The Biology of Crustacea: embryology, morphology and genetics*. Ed. D. E. Bliss, New York Academic Press, New York. 2: 11-196.
- HARTNOLL, R.G. 2006. Reproductive investment in Brachyura. *Hydrobiologia* 557(1): 31-40.
- LIMA, P. A.; L. S. ANDRADE, C. E. R. D. ALENCAR, R. T. PEREIRA, G. M. TEIXEIRA & A. FRANSOZO. 2014. Two species of swimming crabs of the genus *Achelous* (Crustacea, Brachyura): environmental requirements determining the niche. *Hydrobiologia* 727: 197-207.
- MANTELATTO, F. L. M. & A. FRANSOZO. 1999a. Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo State, Brazil. *Rev. Bras. Biol.* 59(1): 23-31.
- MANTELATTO, F. L. M. & A. FRANSOZO. 1999b. Reproductive biology and moulting cycle of the crab *Callinectes ornatus* (Decapoda, Portunidae) from the Ubatuba Region, São Paulo, Brazil. *Crustaceana* 72(1): 63-76.
- MANTELATTO, F. L. M., R. ROBLES & D. L. FELDER. 2007. Molecular phylogeny of the Western Atlantic species of the genus *Portunus* (Crustacea, Brachyura, Portunidae). *Zool. J. Linn. Soc.* 150: 211-220.
- MANTELATTO, F. L. M., R. ROBLES, C. D. SCHUBART & D. L. FELDER. 2009. *Molecular phylogeny of the genus Cronius Stimpson, 1860, with reassignment of C. tumidulus and several American species of Portunus to the genus Achelous De Haan, 1833 (Brachyura: Portunidae)*. In: *Decapod Crustacean Phylogenetics*. Ed. J. W. Martin, K. A. Crandall & D. L. Felder. Crustacean Issues, New York, 18: 567-579.
- MANTELATTO, F. L. M, F. C. R. FARIA & R. B. GARCIA. 2003. Biological aspects of *Mithraculus forceps* (Brachyura: Mithracidae) from Anchieta Island, Ubatuba, Brazil. *J. Mar. Biol. Ass. U. K.* 83: 789-791.
- MELO, G. A. S. 1996. *Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro*. Plêiade/FAPESP, São Paulo, Brasil. 604pp.
- NG, P. K. L.; D. GUINO & P. J. F. DAVIE. 2008. Systema brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles B. Zool.* 17: 1-286.
- PARDAL-SOUZA, A. L. & M. A. A. PINHEIRO. 2013. Relative growth and reproduction in *Achelous spinicarpus* (Crustacea: Portunidae) on the south-eastern continental shelf of Brazil. *J. Mar. Biol. Assoc. U. K.* 93(3): 667-674.
- PINHEIRO, M. A. & A. FRANSOZO. 1999. Reproductive behavior of the swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Crustacea, Decapoda, Portunidae) in captivity. *Bull. Mar. Sci.* 64(2): 243-253.
- PIRES, A. M. S. 1992. Structure and dynamics of benthic megafauna on the continental shelf offshore of Ubatuba, Southeastern Brazil. *Mar. Ecol. Prog. Ser.* 86: 63-76.
- REIGADA, A. L. D. & M. L. NEGREIROS-FRANSOZO. 1999. Maturidade sexual em *Hepatus pudibundus* (Decapoda, Brachyura, Calappidae). *Iheringia Ser. Zool.* 86: 159-164.
- SEVERINO-RODRIGUES, E., D. S. F. GUERRA, R. GRAÇA-LOPES. 2002. Carcinofauna acompanhante da pesca dirigida ao camarão-sete-barbas (*Xiphopenaeus kroyeri*) desembarcada na praia do Perequê, Estado de São Paulo, Brasil. *Bol. Inst. Pesca* 28(1): 33-48.
- SILVA, T. E., P. B. FUMIS, A. C. ALMEIDA, G. BERTINI & V. FRANSOZO. 2014. Morphometric analysis of the mud crab *Hexapanopeus paulensis* Rathbun, 1930 (Decapoda, Xanthoidea) from the southeastern coast of Brazil. *Lat. Am. J. Aquat. Res.* 42(3): 588-597.
- VAZZOLER, A. E. A. M. 1966. *Biologia da reprodução de peixes teleóteo: teorias e prática*. EDUEM, Maringá. 169 pp.
- VEGA-PEREZ, L. A. 1993. Estudo do zooplâncton da região de Ubatuba, Estado de São Paulo. *Inst. Oceanogr. S. P.* 10: 65-84.
- WILLIAMS, A.B. 1984. *Shrimps, lobsters and crabs of the Atlantic coast of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, 550 pp.
- WILSON, K. & I. C. W. HARDY. 2002. *Statistical analysis of sex ratios: an introduction*. In: *Sex Ratios: Concepts and Research Methods*. Ed. I.C.W. Hardy, Cambridge University Press, Cambridge. 48-92 pp.

RECIBIDO: Marzo 2017.

ACEPTADO: Mayo 2017.