



## Nursery grounds of the commercially important shrimp *Farfantepenaeus brasiliensis* (Latreille, 1817) (Decapoda, Penaeoidea): comparison of the population structure between two periods

ALINE NONATO DE SOUSA<sup>1\*</sup>, VERONICA PEREIRA BERNARDES<sup>1</sup>, KÁTIA APARECIDA NUNES HIROKI<sup>1,2</sup>, ARIÁDINE CRISTINE DE ALMEIDA<sup>1,3</sup>, GUSTAVO MONTEIRO TEIXEIRA<sup>1,4</sup> & ADILSON FRANSOZO<sup>1</sup>

<sup>1</sup> Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos (NEBECC), Instituto de Biociências de Botucatu, Departamento de Zoologia, Universidade Estadual Paulista “Júlio de Mesquita Filho”. Rua Professor Doutor Antonio Celso Wagner Zanin, s/n, Distrito de Rubião Junior, Botucatu, São Paulo, Brasil.

<sup>2</sup> Universidade Federal do Triângulo Mineiro (UFMT), Campus Uberaba. Avenida Getúlio Guarita, 150, Uberaba, Minas Gerais, Brasil.

<sup>3</sup> Universidade Federal de Uberlândia (UFU), Campus Umuarama. Avenida Pará, 1720, Uberlândia, Minas Gerais, Brasil.

<sup>4</sup> Universidade Estadual de Londrina (UEL), Campus Universitário. Rodovia Celso Garcia Cid, Km 380, s/n Londrina, Paraná, Brasil.

\* Corresponding author: [alinensousa1@gmail.com](mailto:alinensousa1@gmail.com)

**Abstract.** This study compared the population structure of *Farfantepenaeus brasiliensis* in two distinct periods in Fortaleza Bay, southeastern Brazil. Individuals were monthly sampled in November 1988–October 1989 (period 1) and in November 2008–October 2009 (period 2). In period 1, 80 juveniles were found (36 males and 44 females), whereas in period 2 were found 226 juveniles (62 males and 164 females). The individuals from period 2 were smaller (males:  $17.0 \pm 3.0$  mm; females:  $16.4 \pm 3.3$  mm) than those from period 1 (males:  $22.1 \pm 6.4$  mm; females:  $21.7 \pm 6.3$  mm). This reduction in body size throughout the study period might have been a consequence of an improper conservation management in the area up to 2008. In both sampling periods, the recruitment occurred in summer; however, in period 2, there was a higher abundance of juveniles in autumn too. This might be related to a higher precipitation caused by the El Niño South Oscillation (ENSO) in 2009. The increased precipitation might have prolonged the reproductive period and, consequently, the recruitment.

**Key words:** Recruitment, fishing, pink shrimp, environmental protection area, Ubatuba.

**Resumo.** Um berçário para o camarão de importância econômica *Farfantepenaeus brasiliensis* (Latreille, 1817) (Decapoda, Penaeoidea): comparação da estrutura populacional em dois períodos distintos. Este estudo comparou a estrutura populacional de *Farfantepenaeus brasiliensis* em dois períodos distintos na Enseada de Fortaleza, Sudeste do Brasil. Os indivíduos foram coletados mensalmente em Novembro de 1988 a Outubro de 1989 (período 1) e Novembro de 2008 a Outubro de 2009 (período 2). No período 1 80 juvenis foram coletados (36 machos e 44 fêmeas), enquanto no período 2 foram amostrados 226 juvenis (62 machos and 164 fêmeas). Os indivíduos do período 2 apresentaram um tamanho médio menor (machos =  $17.0 \pm 3.0$  e fêmeas =  $16.4 \pm 3.3$  mm), quando comparado com os indivíduos do período 1 (machos =  $22.1 \pm 6.4$  e fêmeas =  $21.7 \pm 6.3$ ). Esta redução no tamanho corporal, provavelmente, é consequência da ausência de manejo consciente na área, até 2008. Em ambos os períodos, o recrutamento ocorreu no verão, entretanto, no período 2, também houve uma grande abundância de juvenis durante o outono. Esse resultado pode estar relacionado ao fato

de que, com a presença do El Niño-Oscilação Sul (ENOS) em 2009, houve uma maior pluviosidade e isso pode ter prolongado o período reprodutivo e, conseqüentemente, o de recrutamento.

**Palavras-chave:** Recrutamento, pesca, camarão - rosa, área de proteção ambiental, Ubatuba

## Introduction

Coastal regions and estuaries have high primary and secondary productivity rates caused by mixture and distribution of nutrients (Göltenboth *et al.* 2006). As a consequence, these areas are used as nursery grounds by many marine organisms, mainly fishes and crustaceans (Boesch & Turner, 1984, Robertson & Duke, 1987).

Species of *Farfantepenaeus* use estuaries and coastal areas to improve growth and survival rates of juveniles. These shrimps have a type II life cycle, in which reproduction and egg release take place offshore (Dall *et al.* 1990). Later, the post-larvae migrate to estuarine waters where they stay until the juvenile stage (Dall *et al.* 1990, Costa & Fransozo, 1999, Costa *et al.* 2008). After two to four months, juveniles return to the coast, moving towards oceanic waters where they complete their life cycles (Pérez-Castañeda & Defeo, 2001).

In Brazil, two species of *Farfantepenaeus* are targeted by shrimp fisheries: *F. brasiliensis* (Latreille, 1817) and *F. paulensis* (Pérez-Farfante, 1967) (D’Incao *et al.* 2002, Dias-Neto, 2011). Subadults/juveniles are targets in estuarine and coastal areas, and adults in oceanic waters (D’Incao *et al.* 2002). The decreasing shrimp stocks of the Brazilian coast, especially in the southeastern and southern regions, indicates that fishing might be a predatory activity to these organisms (Dias-Neto & Dornelles, 1996, Kaiser *et al.* 2002, Fransozo *et al.* 2016). During the 1970’s, the annual commercial shrimp biomass was in average 16,000 tons (D’Incao *et al.* 2002). In the 1980’s, it decreased to 500 tons  $y^{-1}$  despite the increased boat fleets (D’Incao *et al.* 2002). Therefore, comparative studies focusing on the reproductive biology, population structure, and growth of these species in different periods are imperative. Knowledge of the population features in different space-temporal scenarios will support the establishment of future management strategies aiming at the sustainable use of fishing resources.

Previous studies addressed the populational features of species of the genus *Farfantepenaeus* in Santos (Mello, 1973), Cananéia estuary (Chagas-Soares *et al.* 1995), Ubatuba Bay (Costa & Fransozo, 1999), and Lagoa da Conceição (Branco

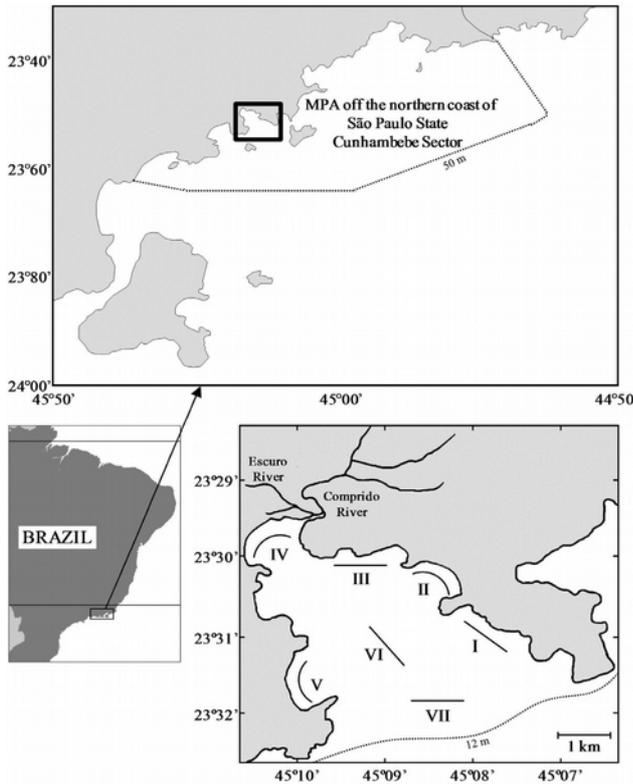
& Verani, 1998a,b). However, none of them compared the structure of the same population of *F. brasiliensis* in two different periods. Aiming to fill this gap, we compared the population structure and recruitment of *F. brasiliensis* in two periods over a 20-year gap, in Fortaleza Bay, Ubatuba, Brazil.

## Materials and Methods

**Study area:** Fortaleza Bay is located on the north coast of São Paulo state. This region has a topographic conformation marked by the terminal spurs of Serra do Mar (Ab’Sáber, 1955) which creates a jagged coastline suitable to the establishment and development of many organisms (Negreiros-Fransozo *et al.* 1991).

Since October 8, 2008, Fortaleza Bay is part of a Marine Protection Area (MPA) (APA Marinha do Litoral — Cunhambebe Sector) created by the Ministry of Environment (decree number 53.525). This MPA was established to ensure the conservation and sustainable use of marine resources. Fishing is only permitted for the subsistence of traditional communities, by amateurs, and as a sportive activity, thus, commercial fishing is not allowed. These restrictions aim to protect the area and drive the rational use of its natural resources, ensuring the region’s sustainable development.

**Sampling:** Sampling was performed in two periods: November 1988–October 1989 (period 1) and November 2008–October 2009 (period 2). Sampling was done monthly with an artisanal boat equipped with a double-rig net (7.5 m long, 2.0 m horizontal mouth opening, 15 and 10 mm mesh diameter along the body and cod-end of the net, respectively). A total of 7 permanent sampling stations were established within Fortaleza Bay (Fig. 1) and sampled monthly. One haul per transect and month was made throughout the sampling period. Each transect was trawled for 1 km (each haul lasted ~20 min with a mean speed of, approximately, 1.5 knots). The sampling stations depths ranging from 1 to 12 m (period 1: I =  $11.2 \pm 0.9$ , II =  $7.0 \pm 0.9$ , III =  $8.5 \pm 0.9$ , IV =  $4.4 \pm 0.6$ , V =  $7.1 \pm 0.8$ , VI =  $11.1 \pm 1.2$  and VII =  $13.3 \pm 1.6$ ; period 2: I =  $9.0 \pm 1.1$ , II =  $7.3 \pm 0.9$ , III =  $6.9 \pm 0.9$ , IV =  $5.7 \pm 1.0$ , V =  $7.6 \pm 1.6$ , VI =  $8.1 \pm 1.1$  and VII =  $10.7 \pm 1.6$ ). The same method was applied in both sample periods.



**Figure 1.** Marine protected area (MPA) and sampling stations in Fortaleza Bay (adapted from ALMEIDA *et al.*, 2012).

Individuals were identified according to Pérez Farfante 1969 and Costa *et al.* (2003), sexed (by checking the petasma in males and thelycum in females), and measured using a caliper to the nearest 0.1 mm. Carapace length (CL, mm), measured from the orbital angle to the posterior margin of the carapace, was recorded for each shrimp. All shrimp were classified as juveniles according to the macroscopic secondary sexual characteristics (petasma and thelycum). In males, the endopods of the first pleopods form the petasma and are completely separated in juveniles and fused in adults (Pérez Farfante 1969, Costa & Fransozo, 1999). In females, the thelycum corresponds to any external modification of the posterior thoracic sternites and/or coxae. This structure stores the spermatophores transferred by males during insemination. In adult females, the thelycum is a single smooth broad plate and bears an aperture flanked by a transverse ridge that runs from right to left. In immature (juvenile) females, the ridge has a space between the plates (Pérez Farfante 1969, Costa & Fransozo, 1999).

**Data Analyses:** Our data were not normally distributed (Shapiro-Wilk,  $p > 0.05$ ) or homoscedastic (Levene's test,  $p > 0.05$ ). A Mann-Whitney test for two independent samples of non-parametric data was used to compare the carapace length (CL) of shrimps between periods 1 and 2 and between sexes. Individuals were grouped into size classes determined according to Zenger & Agnes (1977) and Costa & Fransozo (1999). The size class frequency of *F. brasiliensis* individuals from periods 1 and 2 were compared with the Kolmogorov-Smirnov test. A binomial test (two sided) was performed to detect possible deviations from the 1:1 sex ratio (Wilson & Hardy, 2002). All tests were performed in statistical software R (R Development Core Team, 2013).

The recruitment period was identified based on the months with highest abundance of juveniles. Months were grouped as follows: spring = November–January; summer = February–April; autumn = May–July; and winter = August–October. All analyses were performed at a  $p \leq 0.05$  (Zar, 2010).

## Results

No adults were found during both periods. In period 1, 80 juveniles were found (36 males and 44 females), whereas in period 2 were found 226 juveniles (62 males and 164 females).

The mean CL, with standard deviation and range, of males and females, are shown in Table I. Shrimp from period 1 had significantly larger mean size ( $U = 4,072$ ;  $P < 0.01$ ) (Table I). Although not significant in both sampling periods, females reached the largest size classes (period 1  $U = 654$ ;  $P = 0.18$ ; period 2  $U = 4313$ ;  $P = 0.07$ ) (Fig. 2).

The frequency per size class was significantly different between the two periods ( $d_{max} = 0.395$ ;  $P < 0.001$ ). In period 1, most individuals were in the sixth size class (20.0–22.5 mm CL) whereas in period 2, most occurred in the fourth size class (15.0–17.5 mm CL) (Figure 2).

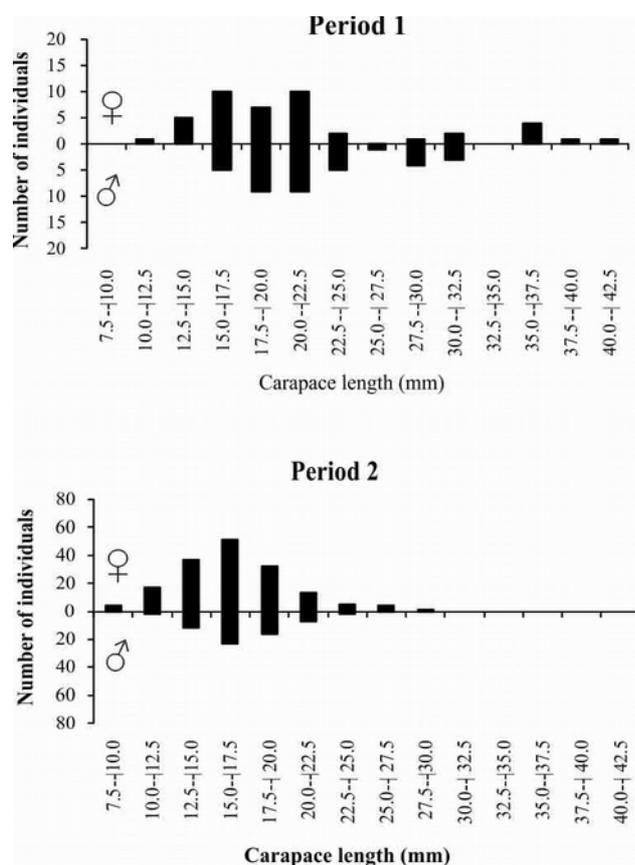
A female-biased sex ratio significant was observed only in period 2 (Binomial test = 76.5;  $P = 0.001$ ), mainly during summer (Table II-III). In both periods, there was a female-biased sex ratio in the smaller size classes (Figure 3).

The recruitment of *F. brasiliensis* occurred in summer in both periods (Figure 4). However, in period 2, there was a higher abundance of juveniles in autumn too.

**Table I.** *Farfantepenaeus brasiliensis* (Latreille, 1817). Size (mm) of the specimens based on carapace length (SD = standard deviation).

Demographic category	N		Size Range (mm)		Mean $\pm$ SD (mm)	
	P1	P2	P1	P2	P1	P2
Males	36	62	15.1 - 31.9	12.4 - 23.7	22.1 $\pm$ 6.4	17.0 $\pm$ 3.0
Females	44	164	11.3 - 41.2	8.7 - 28.3	21.7 $\pm$ 6.3	16.4 $\pm$ 3.3

N = number of individuals; Min = minimum; Max = maximum; P1 = study period from November 1988 to October 1989; P2 = study period from November 2008 to October 2009.



**Figure 2.** *Farfantepenaeus brasiliensis* (Latreille, 1817). Frequency distribution in size classes for males and females in the Fortaleza Bay, during the period 1 (November/1988 to October /1989) and period 2 (November/2008 to October/2009).

## Discussion

During the sampling periods, 80% (period 1) and 98% (period 2) of the *F. brasiliensis* population from Fortaleza Bay was composed of juveniles (CL  $\leq$  25 mm) and the remaining portion of the population can be considered as late subadults since during winter they did not migrate towards the open sea along with the adults (D'Incao, 1991). Based on this finding, it is evident that this bay has been used a nursery ground for juveniles of this species.

Studies performed in the Ubatuba region also recorded a higher occurrence of juvenile (7–37 mm CL) than adults of *F. brasiliensis* (Costa *et al.* 2008, Costa & Fransozo, 1999). However, in deeper areas along the southern and southeastern Brazilian coast, adult males and females of *F. brasiliensis* were found, which had mean CL of 40 and 60 mm, respectively (Zenger & Agnes, 1977). Therefore, we can infer that the recruitment of *F. brasiliensis* juveniles in a coastal area, such as Fortaleza Bay, might favor their development.

The smaller mean size of *F. brasiliensis* during period 2 is probably associated with the fishing activity in Ubatuba region. Throughout the 20-year gap between our samplings, several management regulations were implemented in the area. However, the management of fishing effort was only implemented from 2000 onwards, thus the lack of such regulation over the previous 12 years might have negatively impacted the population structure. In areas with high fishing pressure, a large portion of individuals is captured before reaching larger size classes (Kaiser *et al.* 2002). The consequence is a reduction in the size of the individuals which might decrease the size at the onset of the first maturation (Kaiser *et al.* 2002). This represents an additional damage to life history of the species. Reaching maturity at smaller sizes affects fecundity and leads to a lower reproductive effort.

In *F. brasiliensis*, females were larger than males, in both sampling periods. The size difference is known for several peneidean species such as *Rimapenaeus constrictus* (Stimpson, 1874), *Xiphopenaeus kroyeri* (Heller, 1862), and *Artemesia longinaris* Spence Bate, 1888 (Costa & Fransozo, 2004, Castro *et al.* 2005, Castilho *et al.*, 2007). According to those authors, the larger body size of females might be associated with an adaptation to maximize egg production.

The expected 1:1 sex ratio in populations is associated with the equal energetic cost needed to

**Table II.** *Farfantepenaeus brasiliensis* (Latreille, 1817). Sexual proportion for size class, relative to the period 1 (November 1988 to October 1989) and the period 2 (November 2008 to October 2009).

Size class (mm)	Period 1			Period 2		
	♀	♂	Binomial test/ <i>P</i>	♀	♂	Binomial test/ <i>P</i>
7.5 -- 10.0	0	0	-	4	0	0.9/0.0600
10.0 -- 12.5	1	0	0.9/0.5000	17	2	0.9/0.0001*
12.5 -- 15.0	5	0	0.9/0.0300*	37	12	0.7/0.0001*
15.0 -- 17.5	10	5	0.7/0.2000	51	23	0.7/0.0001*
17.5 --  20.0	7	9	0.5/0.6000	32	16	0.6/0.0200*
20.0 -- 22.5	10	9	0.5/0.8000	13	7	0.6/0.2000
22.5 --  25.0	2	5	0.4/0.2000	5	2	0.7/0.2000
25.0 --  27.5	0	1	0.9/0.5000	4	0	0.9/0.0600
27.5 -- 30.0	1	4	0.3/0.2000	1	0	0.9/0.5000
30.0 --  32.5	2	3	0.5/0.6000	0	0	-
32.5 -- 35.0	0	0	-	0	0	-
35.0 -- 37.5	4	0	0.9/0.0600	0	0	-
37.5 --  40.0	1	0	0.9/0.5000	0	0	-
40.0 --  42.5	1	0	0.9/0.5000	0	0	-
Total	44	36	0.5/0.3	164	62	0.7/0.0001

\*indicates statistical difference ( $P < 0.05$ )

**Table III.** *Farfantepenaeus brasiliensis* (Latreille, 1817). Sexual proportion for season, relative to the period 1 (November 1988 to October 1989) and the period 2 (November 2008 to October 2009).

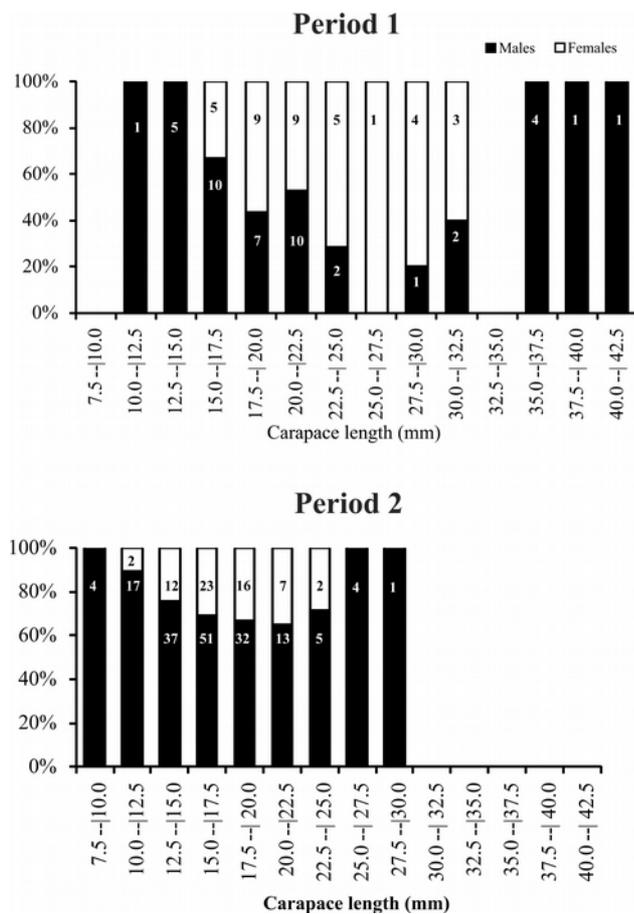
Seasons	Period 1		Binomial test/ <i>P</i>	Period 2		Binomial test / <i>P</i>
	♀	♂		♀	♂	
Spring	1	3	0.3/0.3000	3	0	0.9/0.1000
Summer	35	27	0.5/0.2000	116	25	0.8/0.0001*
Autumn	8	6	0.6/0.6000	44	37	0.5/0.4000
Winter	0	0	-	1	0	0.9/0.5000

\*indicates statistical difference ( $P < 0.05$ )

generate either sex (Fisher, 1930, Kolman, 1960). Deviations of this proportion are common in marine crustaceans since, after hatching, several factors can affect the sex ratio such as longevity, mortality, and differential growth (Wenner, 1972). In our study, the differential growth between sexes and, probably, the differential migration to open sea, might have favored the female-biased sex ratio. Since males are smaller than females, they tend to reach maturity earlier (Branco & Verani, 1998b). Therefore, once

reaching maturity adult males and females migrate to deeper regions to reproduce.

Females are more abundant than males in peneidean shrimp populations, such as *F. brasiliensis*, *X. kroyeri*, *Pleoticus muelleri* (Spence Bate, 1888), and *Artemesia longinaris* (Costa & Fransozo, 1999, Branco *et al.* 1999, Almeida *et al.* 2012, Castilho *et al.* 2008, Costa *et al.* 2010,



**Figure 3.** *Farfantepenaeus brasiliensis* (Latreille, 1817). Percentage of males and females by size classes in the period 1 (November/1988 to October /1989) and period 2 (November/2008 to October/2009).

Sancinetti *et al.* 2015). According to those authors, a combination of hypotheses might explain the female-biased sex ratio in shrimp populations: 1) a single male can inseminate several females in the same reproductive season (Pianka, 1983); 2) males have increased mortality levels due to behavioral aspects (Boschi, 1969); 3) the migration pattern of males and females differs because, after copulation in deep waters, the females migrate to coastal waters to release the eggs (Costa *et al.* 2010) or more males than females would have migrated at the times of samplings.

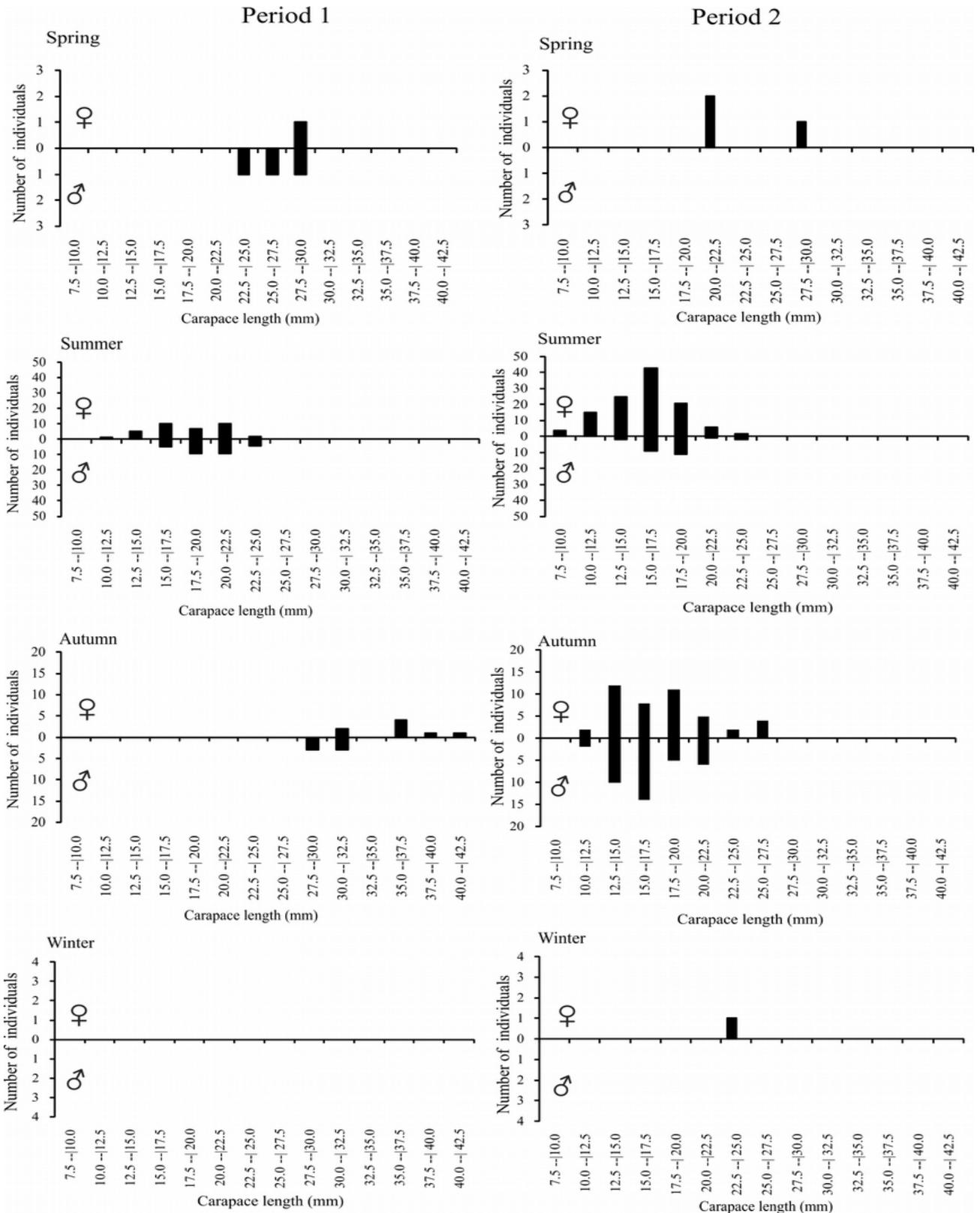
In both sampling periods, *F. brasiliensis* had a seasonal recruitment with a large variation in juvenile abundances throughout the study. In our surveys, besides the recruitment peaks, behavioral differences related to migration strategies could have produced the variation in juvenile abundance. Groups of individuals of distinct sizes, mainly adults, are spatially segregated and our sampling might not

have captured all representatives of the population, as suggested by authors studying the same species (Dall *et al.* 1990, Costa & Fransozo, 1999, Costa *et al.* 2008).

Recruitment was more pronounced in summer in periods 1 and 2, which can be related to the higher rainfall during this season. The osmoregulatory capacity of Type II life cycle individuals tends to decrease along the development, driving them to more suitable areas such as bays and inlets (Dall *et al.* 1990). Other authors observed that the lowest abundance of *F. paulensis* from two different estuaries occurred during high rainfall periods (Costa *et al.* 2008, Pereira & D'Incao, 2012). According to those authors, the reduced salinity in the estuaries during intense rainfall might have driven individuals to the coastal region.

The recruitment observed in autumn in period 2 might be associated with the El Niño-Southern Oscillation (ENSO) of 2009. During this phenomenon, there was a higher precipitation which could have prolonged the reproductive period, and therefore, the recruitment. In the South and Southeast of Brazil, ENSO increases the precipitation rates (Grimm *et al.* 2000). Since the 1960's, some authors have investigated the relationship between this phenomenon and climatic anomalies. According to Nicholls (1988), the annual precipitation variability in regions affected by ENSO is often high. The variation of precipitation is a key factor controlling the annual presence of *F. brasiliensis* in inlets (Costa *et al.* 2016). In years without ENSO influence, the shrimp fishing ban in March–May is adequate since it covers the recruitment period of both *F. brasiliensis* and *F. paulensis* (Costa *et al.* 2016). However, in years of intense ENSO, the recruitment period might occur earlier or be delayed, leading to the presence of juveniles when the fishing is allowed.

The migration of juveniles of *Farfantepenaeus paulensis* and *L. schmitti* from inlets to coastal regions is positively influenced by ENSO (Pereira & D'Incao, 2012, Bochini *et al.* 2014). However, Costa & Fransozo (1999) stated that the recruitment of *F. brasiliensis* during summer and autumn is mainly a result of the intense reproductive activity during spring. During spring, there is the influence of the South Atlantic Central Water intrusion (SACW; temperature  $\leq 18^{\circ}\text{C}$ ; salinity  $\leq 36$ ) in the southeastern Brazilian coast. The SACW has physical and chemical features that increase the nutrient input and primary production (Castro-Filho *et al.* 1987, Aidar *et al.* 1993), thus



**Figure 4.** *Farfantepenaeus brasiliensis* (Latreille, 1817). Frequency distribution in size classes for males and females during the seasons in the Fortaleza Bay in the period 1 (November/1988 to October /1989) and period 2 (November/2008 to October/2009).

contributing to the food supply to the larvae (Vega-Pérez, 1993).

Based on our results it seems that the overall lack of conservation actions between the two sampling periods might have disturbed the population structure of *F. brasiliensis* and might have been responsible for the reduction in body size during period 2. In our study region, conservation actions were implemented only in the 2000's. First, the region became part of the conservation unit Ilha Anchieta State Park (created upon guidelines of Decree n° 9629, 29 March 1977, and Federal Law n° 9985, 18 July 2000). In 2004, an ecological-economic coastal zone (ZEE) was implemented (Decree n° 5300, 07 December 2004). In 2008, two special management zones were created in Mar Virado Island and in the Litoral Norte APAM (Decree n° 53525), and the annual shrimp fishing ban between March 1<sup>st</sup> and May 31<sup>st</sup> was established in the South and Southeast of Brazil (Normative Instruction n° 189, 23 September 2008).

To conclude, this study indicates the importance of Fortaleza Bay for the early development of these shrimps. As this area can be considered as a nursery ground of *F. brasiliensis*, its conservation is very important to the continuity of the life cycle of this important fishing resource.

#### Acknowledgments

We are thankful to the NEBECC co-workers for their help during the fieldwork. Funding for this research was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Process n°401908/88 7ZO and Fundação para o Desenvolvimento da UNESP (Fundunesp), Process n° 287/88/DFP.

#### References

- Ab'Saber, A. N. 1955. Contribuição à geomorfologia do litoral paulista. **Revista Brasileira de Geografia**, 17(1): 3-48.
- Aidar, E., Gaeta, S. A., Giancesella-Galvão, S. M. F., Kutner, M. B. B. & Teixeira, C. 1993. Ecossistema costeiro subtropical: nutrientes dissolvidos, fitoplâncton e clorofila-*a* e suas relações com as condições oceanográficas na região de Ubatuba, SP. **Publicação especial do Instituto Oceanográfico**, 10: 9-43.
- Almeida, A. C., Baeza, J. A., Fransozo, V., Castilho, A. L. & Fransozo, A. 2012. Reproductive biology and recruitment of *Xiphopenaeus kroyeri* in a marine protected area in the Western Atlantic: implications for resource management. **Aquatic Biology**, 17(1): 57-69.
- Bochini, G. L., Fransozo, A., Castilho, A. L., Hirose, G. L. & Costa, R. C. 2014. Temporal and spatial distribution of the commercial shrimp *Litopenaeus schmitti* (Dendrobranchiata: Penaeidae) in the south-eastern Brazilian coast. **Journal of the Marine Biological Association of the United Kingdom**, 94(05): 1001-1008.
- Boesch, D. F. & Turner, R. E. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. **Estuaries**, 7(4): 460-468.
- Boschi, E. E. 1969. Crecimiento, migración y ecología del camarón comercial *Artemesia longinaris* Bate, 1888, de Mar del Plata. **FAO Fisheries Report**, 57(3): 833-846.
- Branco, J. O., Lunardon-Branco, M. J., Souto, F. X. E. & Guerra, C. R. 1999. Estrutura populacional do camarão sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862), na Foz do Rio Itajaí-Açú, Itajaí, SC, Brasil. **Brazilian of Archives Biology and Technology**, 42(1): 395-399.
- Branco, J.O. & Verani, J. R. 1998a. Aspectos bioecológicos do camarão-rosa *Penaeus brasiliensis* Latreille (Natantia, Penaeidae) da Lagoa da Conceição, Florianópolis, Santa Catarina, Brasil. **Revista Brasileira de Zoologia**, 15(1): 45-351.
- Branco, J.O. & Verani, J. R. 1998b. Estudo populacional do camarão-rosa *Penaeus paulensis* Pérez Farfante (Natantia, Penaeidae) na Lagoa da Conceição, Santa Catarina, Brasil. **Revista Brasileira de Zoologia**, 15(2): 353-364.
- Castilho, A. L., Costa, R. C., Fransozo, A. & Negreiros-Fransozo, M. L. 2008. Reproduction and recruitment of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. **Marine Biology Research**, 4(1): 361-368.
- Castilho, A. L., Gavio, M. A., Costa, R. C., Boschi, E. E., Bauer, R. T. & Fransozo, A. 2007. Latitudinal variation in structure and maturity size in the South American endemic shrimp *Artemesia longinaris* (Decapoda: Penaeoidea). **Journal of Crustacean Biology**, 27: 1-12.
- Castro, R. H., Costa, R. C., Fransozo, A. & Mantelatto, F. L. M. 2005. Population structure of seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Crustacea: Penaeoidea)

- in the littoral of São Paulo, Brazil. **Scientia Marina**, 69: 105-112.
- Castro-Filho, B. M., Miranda, L. B. & Myao, S. Y. 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. **Boletim do Instituto Oceanográfico**, 35(2): 135-151.
- Chagas-Soares, F., Pereira, O. M. & Santos, E. P. 1995. Contribuição ao ciclo biológico de *Penaeus schmitti* Burkenroad, 1936, *Penaeus brasiliensis* Latreille, 1817 e *Penaeus paulensis* Pérez-Farfante, 1967, na região Lagunar-Estuarina de Cananéia, São Paulo, Brasil. **Boletim do Instituto de Pesca**, 22: 49-59.
- Costa, R. C., Bochini, G. L., Simões, S. M., Lopes, M., Sancinetti, G. S., Castilho, A. L. & Fransozo, A. 2016. Distribution pattern of juveniles of the pink shrimps *Farfantepenaeus brasiliensis* (Latreille, 1817) and *F. paulensis* (Pérez-Farfante, 1967) on the southeastern Brazilian coast. **Nauplius**, 24: e2016024.
- Costa, R. C., Branco, J. O., Machado, I. F., Campos, B. R. & Avila, M. G. 2010. Population biology of shrimp *Artemesia longinaris* (Crustacea: Decapoda: Penaeidae) from the southern coast of Brazil. **Journal of the Marine Biological Association of the United Kingdom**, 90(4): 663-669.
- Costa, R. C. & Fransozo, A. 1999. A nursery ground for two tropical pink-shrimp *Penaeus* species: Ubatuba bay northern coast of São Paulo, Brazil. **Nauplius**, 7: 73-81.
- Costa, R. C. & Fransozo, A. 2004. Reproductive biology of the shrimp *Rimapenaeus constrictus* (Decapoda, Penaeidae) in the Ubatuba region of Brazil. **Journal of Crustacean Biology**, 24(2): 274-281.
- Costa, R. C., Lopes, M., Castilho, A. L., Fransozo, A. & Simões, S. M. 2008. Abundance and distribution of juveniles pink shrimps *Farfantepenaeus spp.* in a mangrove estuary and adjacent bay on the northern shore of São Paulo State, southeastern Brazil. **Invertebrate Reproduction & Development**, 52: 51-58.
- Costa, R. C., Fransozo, A., Schmidt, G. A. & Freire, F. A. M. 2003. Chave ilustrada para identificação dos camarões Dendrobranchiata do litoral norte do Estado de São Paulo. **Biota Neotropical**, 3(1): 1-12.
- Dall, W., Hill, B. J., Rothlisberg, P. C. & Sharples, D. J. 1990. **Advances marine biology: the biology of the Penaeidae**. Academic Press, London, 489 p.
- D’Incao, F. 1991. Pesca e biologia de *Penaeus paulensis* na Lagoa dos Patos, RS. **Atlântica**, 13: 159-169.
- D’Incao, F., Valentini, H. & Rodrigues, L. F. 2002. Avaliação da pesca de camarões nas regiões Sudeste e Sul do Brasil. **Atlântica**, 24: 103-116.
- Dias-Neto, J. 2011. **Proposta de plano nacional de gestão para o uso sustentável de camarões marinhos do Brasil**. IBAMA, Brasília, 242 p.
- Dias-Neto, J. & Dornelles, L. D. C. 1996. **Diagnóstico da pesca marítima do Brasil**. IBAMA, Brasília, 163 p.
- Fisher, R. A. 1930. **The genetical theory of natural selection**. The Clarendon Press, United Kingdom, 219 p.
- Fransozo, A., Sousa, A. N., Rodrigues, G. F. B., Telles, J. N., Fransozo, V. & Negreiros-Fransozo, M. L. 2016. Crustáceos decápodes capturados na pesca do camarão-sete-barbas no sublitoral não consolidado do litoral norte do Estado de São Paulo, Brasil. **Boletim do Instituto de Pesca**, 42(2): 369-386.
- Göltenboth, F., Timotius, K. H., Milan, P. P. & Margraf, J. 2006. **Ecology of insular Southeast Asia: the Indonesian archipelago**. Elsevier, Amsterdam, 547 p.
- Grimm, A. M., Bartros, V. R. & Doyle, M. E. 2000. Climate variability in southern South America associated with El Niño and La Niña events. **Journal of Climate**, 13: 35-58.
- Kaiser, M. J., Collie, J. S., Hall, S. J., Jennings, S. & Poiner, I. R. 2002. Modification of marine habitats by trawling activities: prognosis and solutions. **Fish and Fisheries**, 3: 114-136.
- Kolman, W. A. 1960. The mechanism of natural selection for the sex ratio. **The American Naturalist**, 94: 373-377.
- Mello, J. T. C. 1973. Estudo populacional do “camarão-rosa” *Penaeus brasiliensis* (Latreille, 1817) e *Penaeus paulensis* (Pérez-Farfante, 1967). **Boletim do Instituto de Pesca**, 2(2): 19-65.
- Negreiros-Fransozo, M. L., Fransozo, A., Pinheiro, M. A. A., Mantelatto, F. L. M. & Santos, S. 1991. Caracterização física e química da Enseada de Fortaleza, Ubatuba, SP. **Revista Brasileira de Geociência**, 21(2): 114-120.
- Nicholls, N. 1988. El Niño-Southern Oscillation and rainfall variability. **Journal of Climate**, 1: 418-421.

- Pereira, N. & D'Incao, F. 2012. Relationship between rainfall, pink shrimp harvest (*Farfantepenaeus paulensis*) and adult stock, associated with El Niño and La Niña phenomena in Patos Lagoon, southern Brazil. **Journal of the Marine Biological Association of the United Kingdom**, 92(7): 1451-1456.
- Pérez-Castañeda, R. & Defeo, O. 2001. Population variability of four sympatric penaeid shrimps (*Farfantepenaeus spp.*) in a tropical coastal Lagoon of Mexico. **Estuarine, Coastal and Shelf Science**, 52: 631–641.
- Pérez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. **Fishery Bulletin**, 67: 461-591.
- Pianka, E. R. 1983. **Evolutionary Ecology**. Harper and Row, New York, 416 p.
- Robertson, A. I. & Duke, N.C. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. **Marine Biology**, 96(2): 193-205.
- Sancinetti, G. S., Azevedo, A., Castilho, A. L., Fransozo, A. & Costa, R. C. 2015. Population biology of the commercially exploited shrimp *Artemesia longinaris* (Decapoda: Penaeidae) in an upwelling region in the Western Atlantic: comparisons at different latitudes. **Brazilian Journal of Biology**, 75(2): 305-313.
- Vega-Pérez, L. A. 1993. Estudo do zooplâncton da região de Ubatuba, Estado de São Paulo. **Boletim do Instituto Oceanográfico**, 10: 65–84.
- Wenner, A. M. 1972. Sex ratio as a function of size in marine Crustacea. **The American Naturalist**, 106(949): 321–350.
- Wilson, K. & Hardy, I. C. W. 2002. Sex ratios: concepts and research methods. Pp. 48-92. In: I. C. W. Hardy, (Ed). **Statistical analysis of sex ratio: an introduction**. Cambridge University Press, New York.
- Zar, J. H. 2010. **Biostatistical analysis**. Prentice-Hall, New Jersey, 718 p.
- Zenger, H. H. & Agnes, J. L. 1977. Distribuição do camarão-rosa (*Penaeus brasiliensis* e *Penaeus paulensis*) ao longo da costa sudeste-sul do Brasil. **SUDEPE/PDP Documentos Técnicos**, 21: 1–106.

Received: September 2018

Accepted: December 2018

Published: June 2019