



## Reproductive and population traits of the swimming crab *Achelous spinimanus* (Crustacea: Decapoda) in an upwelling region in southeastern Brazil

Luciana Segura de Andrade<sup>1</sup>, Rogério Caetano da Costa<sup>2</sup>, Antônio Leão Castilho<sup>3</sup>, Israel Fernandes Frameschi<sup>3</sup>, Gustavo Sérgio Sancinetti<sup>3</sup> and Adilson Fransozo<sup>3</sup>

<sup>1</sup> Universidade Federal do Triângulo Mineiro, Campus Iturama. Avenida Rio Paranaíba, 1229, Centro. 38280-000 Iturama, Minas Gerais, Brazil.

<sup>2</sup> Departamento de Ciências Biológicas, Faculdade de Ciências, UNESP. Bauru, São Paulo, Brazil.

<sup>3</sup> NEBECC – Grupo de Estudos sobre Biologia, Ecologia e Cultivo de Crustáceos, Departamento de Zoologia, Instituto de Biociências, UNESP. Botucatu, São Paulo, Brazil.

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### ABSTRACT

This study investigated the temporal abundance, periods of reproduction and recruitment, gonad sexual maturity, and population structure of the swimming crab *Achelous spinimanus* (Latreille, 1819) in Macaé, a region of the Brazilian coast affected by upwelling events. The samples were collected monthly during one year. The crabs were counted, sexed and measured for maximum carapace width (MCW). Four developmental stages were described in males and females. Environmental variables as temperature, salinity, organic matter and Phi were measured. A Principal Components Analysis indicated that environmental variables were strongly correlated with seasons, affecting the abundance of this species, which was high during summer and autumn. The periods of reproduction and recruitment were also seasonal, with a peak of females with developed gonads and ovigerous females during autumn and immatures during summer and autumn. Males and females did not differ in size at gonad sexual maturity, estimated at 39.9

#### CORRESPONDING AUTHOR

Luciana Segura de Andrade  
[andradels.nebecc@gmail.com](mailto:andradels.nebecc@gmail.com)

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and Adilson Fransozo

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and 42.9 mm MCW, respectively. The environmental conditions in this upwelling region may have induced this population of *A. spinimanus* to show different characteristics and behaviors from other populations on the Brazilian coast, since alterations linked to the periods of reproduction and recruitment, as well as the population structure and distribution, may reveal different survival strategies of the species.

## KEY WORDS

Geographic variation, management, Portunidae, *Portunus*.

## INTRODUCTION

Regions with unusual features such as upwelling may provide substantial enrichment for the marine communities, which show distribution patterns closely related to the dynamics of the water masses (De Léo and Pires-Vanin, 2006). Species found in these regions may show different population characteristics (i.e., periods of reproduction and recruitment, size at which sexual maturity is reached, proportion of males and females, size of individuals, and others) in relation to other parts of the Brazilian coast (Andrade *et al.*, 2015a).

Portunid crabs are key elements of the trophic chain and strongly influence the dynamics and organization of marine shallow-water environments (Bertini and Fransozo, 2004). The blotched swimming crab *Achelous spinimanus* (Latreille, 1819) is widely distributed in the western Atlantic from the states of New Jersey (USA) to Rio Grande do Sul (Brazil), and is found at depths down to 90 m (Melo, 1996). Exploitation of the meat and byproducts of *A. spinimanus* for economic uses is increasing in Brazil, as also in other countries since 1999 (FAO-Globefish, 2007). Knowledge of the dynamics of populations that are captured by the fishing gear used in different regions is essential for the development of appropriate management plans to reach a balance between shrimp fishing and recovery of fish stocks.

Seasonal changes in water temperature and salinity, high sedimentation rate and increased primary productivity may be critical proximate factors that cause changes in population patterns, as abundance (Andrade *et al.*, 2015c; Lima *et al.*, 2014), reproductive and recruitment strategy (Andrade *et al.*, 2015a; 2015b; Frameschi *et al.*, 2015), spatio-temporal distribution (Bertini and Fransozo, 2004; Lima *et al.*, 2014; Andrade *et al.*, 2015a), longevity and others (Frameschi *et al.*, 2015). Our question was whether the

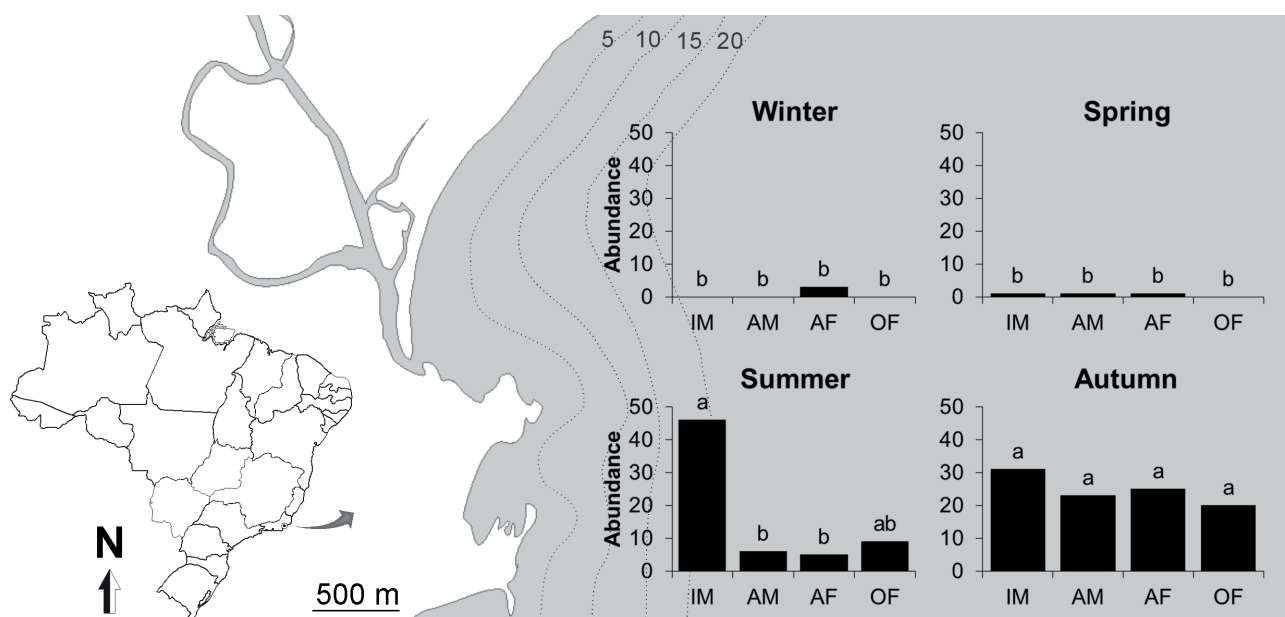
characteristics of a region near an upwelling zone would be reflected in the biology of *A. spinimanus*, compared to literature records from other regions. The present study investigated the population characteristics of *A. spinimanus* in Macaé, state of Rio de Janeiro, in order to assess (a) temporal abundance, (b) periods of reproduction and recruitment, (c) estimated gonad sexual maturity, and (d) the proportion of sexes and sizes of individuals.

## MATERIAL AND METHODS

The samples were collected systematically from July 2010 to June 2011 in Macaé, Rio de Janeiro state (22°47'S 41°45'W) on the southeastern Brazilian coast (Fig. 1). Macaé is near Cabo Frio, where coastal upwelling occurs due to atmospheric circulation associated with the center of the South Atlantic High Pressure. Three main water masses are present in the region. North of Macaé, the warm ( $T > 20^{\circ}\text{C}$ ) saline ( $S > 36$ ) Tropical Water (TW) covers the entire shelf, constituting the main stream of the Brazil Current (BC). To the south, a mixture of TW and the South Atlantic Central Water (SACW), a relatively cold ( $< 20^{\circ}\text{C}$ ) and less saline ( $< 36$ ) water mass, is predominant. The third water mass is the Coastal Water (CW), a mixture of continental runoff and the Shelf Water (SW) (Castro-Filho and Miranda, 1998; Silveira *et al.*, 2000; Valentin, 2001; Coelho-Souza *et al.*, 2012).

### Data collection

Each month, an area of 108,000 m<sup>2</sup> was sampled, covering depths ranging from 5–20 m. The crabs were collected from a shrimp-fishing boat equipped with double-rig nets, with the following net specifications: length 10 m, mouth 4.5 m, body mesh diameter 20 mm, cod-end mesh diameter 18 mm. At the end of each trawl, the material was screened on the boat, packed in labeled plastic bags, and kept in a freezer until



**Figure 1.** Upwelling region off Macaé in southeastern Brazil, showing the seasonal abundance of demographic groups of the swimming crab *Achelous spinimanus*. IM = immatures, AM = adult males, AF = adult females, OF = ovigerous females. Different letters over bars denote significant differences among seasons and demographic groups.

the specimens were examined. Part of the collected material is deposited in the zoological collection of NEBECC, IBB, UNESP, Botucatu, São Paulo.

#### Laboratory procedures

The specimens of *A. spinimanus* were identified according to Melo (1996). The crabs were counted, sexed, and measured for maximum carapace width (MCW), disregarding the lateral teeth, using a calliper (0.01 mm). All individuals obtained were grouped in the following demographic categories: adult males, adult females, ovigerous females, and juveniles (checked by the adherence of the abdomen to the thoracic sternites and the stage of the gonads, which are thin and translucent in juveniles). Four developmental stages were characterized in males and females based on size, shape and color of the gonads: immature – IM (no differentiated gonads), rudimentary – RU (gonads are recognized only by magnifying on males and look filamentous, thin and with pale yellow color on females), developing – ED (on males, the gonads are visible in the anterolateral region of the abdominal cavity and the vas deferent can be divided in two different regions, the front one being thinner; on females beginning of ovary maturation with yellow color and the connection between right and left trumpet are clear), and developed – DE (on

males, the gonad reaches its highest development, and the vasa deferentia can be clearly divided in front, median and back; females have bright orange ovary which fills almost the whole thoracic cavity) (adapted by Santos and Negreiros-Fransozo, 1999; illustrative photos available on Mantelatto, 1995).

#### Environmental variables

For each 1-h haul, the bottom- and surface-water temperatures were recorded using a thermometer attached to a Nansen bottle. Sediment samples were collected in each season with a Van Veen grab, sampling a bottom area of 0.06 m<sup>2</sup> in order to measure the organic-matter content (%) and grain size distribution of the sediments. In the laboratory, the sediment was dried at 70°C for 72 h in an oven. The sediment organic-matter content (%) was obtained by ash-weighing: 3 aliquots of 10 g each per station were placed in porcelain crucibles and incinerated for 3 h at 500°C. The samples were then re-weighed to calculate the organic-matter content. All these procedures followed those used by Mantelatto and Fransozo (1999b). Sediment grain-size composition was analyzed according to Bertini and Fransozo (2004). The sediment remaining after analysis of the organic matter was re-dried and passed through a series of sieves with graduated mesh sizes, following the Wentworth scale (Wentworth, 1922).

The concentration of chlorophyll a in the water ( $\mu\text{g}\cdot\text{L}^{-1}$ ) was determined according to Golterman *et al.* (1978).

#### Data analyses

Prerequisites of normality and homoscedasticity were tested and accepted by the routines of Kolmogorov-Smirnov ( $P < 0.2$ ) and Levene ( $P > 0.05$ ) tests. A Principal Components Analysis (PCA) was used to identify the relationship between environmental variables (bottom and surface temperature, bottom and surface salinity, organic matter, phi, and chlorophyll a) and seasons (Winter = July to September, Spring = October to December, Summer = January to March, Autumn = April to June). To determine which principal components would be performed, the hypothesis of randomness obtained from the Broken Stick model (Jackson, 1993) was used. Environmental variables with a component load  $\geq \pm 0.5$  were retained in the description of the principal components (McCune and Grace, 2002; Maliao *et al.*, 2008).

The values for abundance of each demographic group were log-transformed, and a one-way analysis of variance (One-Way ANOVA) was carried out to assess differences among seasons ( $\alpha = 0.05$ ) (Zar, 1996). To determine the relationships between environmental variables and abundance of demographic groups, a redundancy analysis (RDA), a constrained ordination method, was used. For this, the data were normalized ( $\log_{x+1}$ ), and the RDA constrained the ordination to a space defined by a linear combination of the measured environmental variables (Jongman *et al.*, 1995). RDA allowed the selection of the variables that best described the distribution of the selected species. Randomization tests (Monte Carlo test, 999 permutations), which provided p-values, were performed to check the validity axis of multivariate analysis (ter Braak, 1986). P-values from these randomization tests indicate the level of confidence in the predictions (Peck, 2010).

The Binomial test (Wilson and Hardy, 2002) was applied to evaluate the proportion between males (M) and females (F) in each season. To represent the size of the population structure, from the maximum and minimum size of the crabs, size classes were defined following the method suggested by Sturges (1926). To evaluate gonad sexual maturity dimorphism by size, the Mann-Whitney test was used to compare

sizes of adults. To estimate gonad sexual maturity, the relative frequency (%) of adult size classes was plotted on graphs, which were fitted by the method of least squares to a sigmoid curve resulting from the logarithmic equation:  $Y = 1/[1 + e^{r(MCW - MCW_{50})}]$ , where  $MCW_{50}$  is the carapace width at which 50% of individuals attain gonad sexual maturity, and  $r$  is the curve slope (Vazzoler, 1996). The matrices for frequency of immature and adult crabs by size classes, of males and females, were compared using the Mantel test (distance measure by Sørensen index). This test allows a comparison of the patterns of response redundancy in two structurally related matrices, and an evaluation of the similarity between them. In this test, a low p value indicated that the observed association between the matrices was statistically unusually high, leading us to reject the null hypothesis of no relationship between matrices (Legendre *et al.*, 2005), indicating that there is some association in the patterns of redundancy within these two datasets. The randomization was evaluated by Monte Carlo test (999 permutations) (Peck, 2010). All multivariate analyses were performed using PC-ORD (version 6, McCune and Mefford, 2011).

The reproductive period was determined by the presence of females with developed gonads or bearing eggs (Rasheed and Mustaqim, 2010). The presence of immatures in each season was used to estimate the recruitment period.

## RESULTS

The environmental factors analyzed varied widely. During the summer months, concentrations of chlorophyll a were high, and the difference between bottom and surface water temperatures was largest (Tab. 1).

The PCA indicated that the environmental variables were strongly correlated with the seasons (Monte Carlo test,  $P = 0.0001$ ). The seven environmental variables were reduced to four principal components (PC), which explained 80.07% of the total variation in the data set. Sediment organic matter was the only variable that was correlated with PC1, which explained 36.46% of the variation. The variable with the highest correlation with the axis 2 was bottom salinity (Spearman rank correlation = 0.69) (Tab. 2).

We analyzed a total of 171 specimens, including 30 adult males, 34 no ovigerous adult females, 29

**Table 1.** Values (mean  $\pm$  standard deviation) of the environmental variables recorded from July 2010 to June 2011 off Macaé, southeastern Brazilian coast. Winter = July to September; Spring = October to December; Summer = January to March; Autumn = April to June. OM = sediment organic matter; PHI = mean grain size; ST = surface temperature; BT = bottom temperature; SS = surface salinity; BS = bottom salinity; Clo = chlorophyll a.

Environmental variables	Winter	Spring	Summer	Autumn
OM (%)	4.51 $\pm$ 2.04	11.78 $\pm$ 1.05	9.33 $\pm$ 1.80	10.53 $\pm$ 2.90
PHI	3.47 $\pm$ 0.98	4.55 $\pm$ 0.60	4.18 $\pm$ 0.73	4.69 $\pm$ 0.14
ST ( $^{\circ}$ C)	20.50 $\pm$ 0.54	23.75 $\pm$ 1.06	22.25 $\pm$ 0.89	23.75 $\pm$ 0.35
BT ( $^{\circ}$ C)	19.58 $\pm$ 0.12	22.92 $\pm$ 0.47	19.50 $\pm$ 0.35	21.67 $\pm$ 0.12
SS	35.83 $\pm$ 0.23	36.33 $\pm$ 1.03	35.67 $\pm$ 1.54	36.92 $\pm$ 0.65
BS	37.00 $\pm$ 0.14	36.17 $\pm$ 0.85	36.50 $\pm$ 0.41	38.00 $\pm$ 0.41
Clo ( $\mu$ g.L $^{-1}$ )	2.22 $\pm$ 0.66	1.42 $\pm$ 0.25	6.84 $\pm$ 5.71	0.66 $\pm$ 0.42

**Table 2.** Summary statistics of the axes (PC) generated by the Principal Components Analysis for seven environmental variables measured during one year off Macaé, southeastern Brazilian coast. Coefficients  $\geq \pm 0.4$  are considered ecologically important and are indicated in bold.

Environmental variables	Component			
	PC1	PC2	PC3	PC4
Organic matter (OM)	<b>-0.53</b>	-0.09	-0.18	0.20
Bottom salinity (BS)	-0.02	<b>0.69</b>	-0.06	-0.33
Surface salinity (SS)	0.14	<b>0.54</b>	<b>-0.58</b>	0.36
Chlorophyll a (Clo)	0.33	-0.39	<b>-0.58</b>	-0.15
Mean grain size (PHI)	-0.44	-0.18	<b>-0.52</b>	-0.35
Surface temperature (ST)	-0.46	0.00	0.01	<b>0.57</b>
Bottom temperature (BT)	-0.42	0.15	0.10	<b>-0.50</b>
Percent variance explained (Total = 80.07)	36.46	20.19	12.96	10.46

ovigerous females and 78 immature individuals. The crabs were most abundant in summer and autumn, differing significantly from winter and spring (One-Way ANOVA:  $F = 52.07$ ,  $P = 0.003$ ) (Fig. 1). Among demographic groups, adult males ( $F = 9.97$ ,  $P = 0.004$ ) and females ( $F = 18.82$ ,  $P < 0.0006$ ) were most abundant in autumn. Ovigerous females ( $F = 53.96$ ,  $P = 0.00001$ ) and immatures ( $F = 32.61$ ,  $P = 0.00008$ ) were most abundant in summer and autumn (Fig. 1).

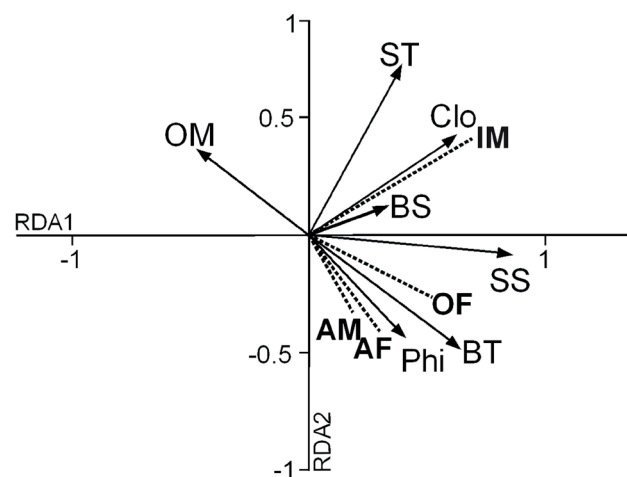
The permutation test of RDA showed that the eigenvalue calculated for the first axis (RDA1) was significant, indicating that the patterns of association were identified (Tab. 3). This permutation also revealed that the variation between the embedded scores and the scores for the dependent variable was significant, suggesting that the environmental variables explain part of the seasonal variation in the abundance of demographic groups (Tab. 2). The first two RDA axes represented 48% of the variation in the abundance

of the demographic groups of *A. spinimanus* (Fig. 2). The correlation between the environmental variables and the ordination axis showed that the surface and bottom temperature, surface salinity and chlorophyll a all showed positive relationships to the distribution of the demographic groups. According to the resulting correlation, these variables best explained the temporal distribution of the demographic groups. Immature individuals showed the best correlation with the variables (Tab. 2), and similarly to the ovigerous females, were positively associated with the variables that affected axis 1 (Fig. 2).

The reproductive period was clearly seasonal, with a peak of females with developed gonads (dark texture) and ovigerous females (black) during summer and autumn (Fig. 3a). Males with developed gonads were most abundant in autumn, and they were also present in summer (Fig. 3b). Seasonal recruitment occurred during summer and autumn, when immature

**Table 3.** Summary of Results of Redundancy Analysis (RDA) for demographic groups of *Achelous spinimanus* in an upwelling region off southeastern Brazil. Variables that were considered to be biologically meaningful for that RDA axis are indicated in bold (i.e.  $\geq 0.4$ ; Rakocinski et al., 1996).

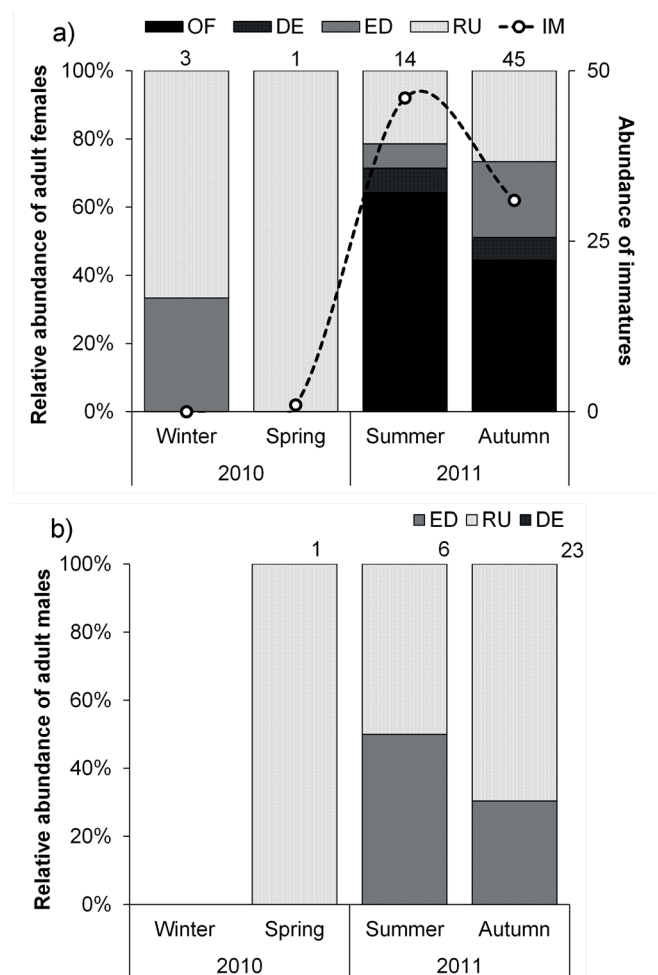
	Axis		Permutation test
	RDA1	RDA2	
Eigenvalue (total inertia = 0.26)	0.15	0.10	0.02
Cumulative % variation explained	28.6	48.0	
Species-predictor correlation	0.70	0.81	0.03
Immatures (IM)	<b>0.78</b>	<b>0.44</b>	
Adult Males (AM)	0.21	-0.39	
Adult Females (AF)	0.28	<b>-0.44</b>	
Ovigerous Females (OF)	<b>0.46</b>	-0.29	
Organic matter (OM)	-0.32	0.24	
Mean grain size (Phi)	0.27	-0.29	
Surface Temperature (ST)	0.28	<b>0.50</b>	
Bottom Temperature (BT)	<b>0.43</b>	-0.32	
Surface Salinity (SS)	<b>0.59</b>	-0.00	
Bottom Salinity (BS)	0.21	0.14	
Chlorophyll a (Clo)	<b>0.42</b>	0.28	



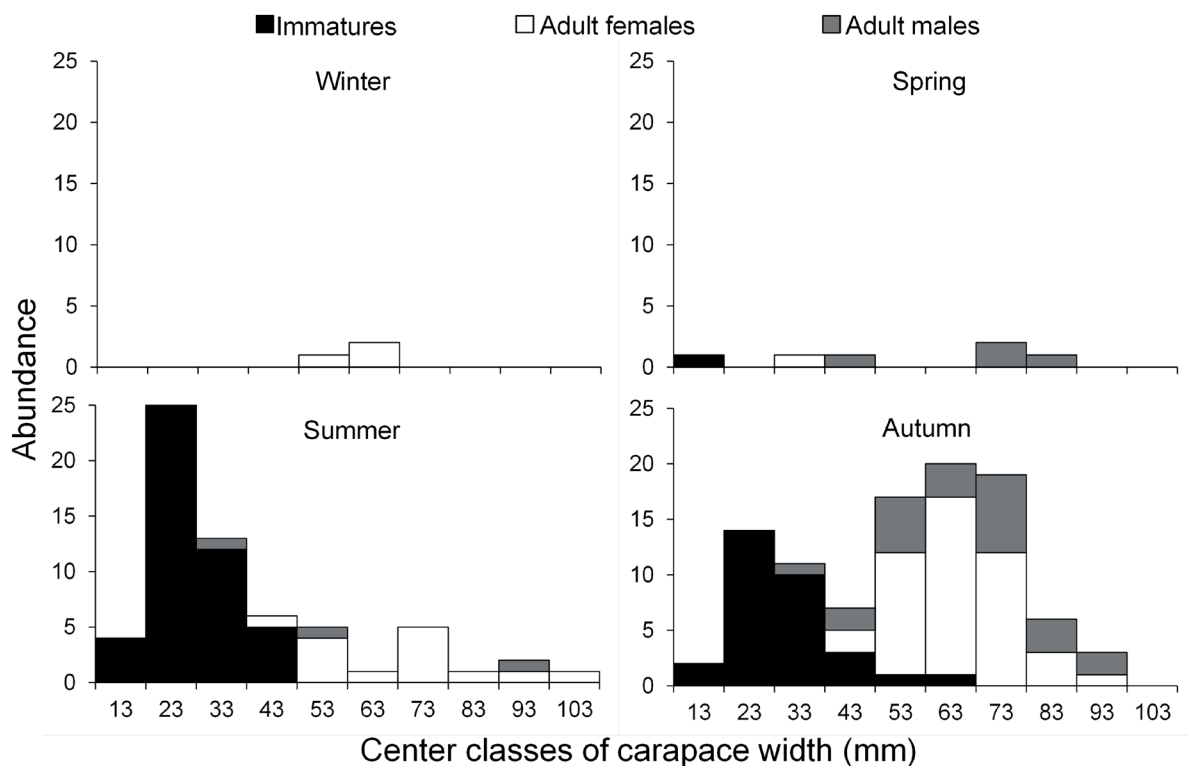
**Figure 2.** Biplot of the redundancy analysis (RDA) of variations in environmental variables (indicated by solid arrows) of demographic groups of the swimming crab *Achelous spinimanus* (indicated by dashed arrows). Refer to Tab. 2 for codes of each demographic group and environmental variable.

individuals were most abundant. Immatures were rarely found in spring and they were no captured during the winter (Fig. 4).

The sex ratio favored females during the period of study (0.7M:1.0F,  $P = 0.008$ ). This difference was apparent in each season, but it was significant only during summer (1M: 2.7F,  $P = 0.0002$ ). The swimming crabs were separated into 10 size classes with an interval of 10 mm. The smallest individual caught was a male, in autumn, measuring 16.4 mm MCW. The largest was an ovigerous female, in summer, measuring 98.6 mm MCW (Fig. 4). The MCW showed no sexual



**Figure 3.** Seasonal variation in the proportion of (a) adult females and (b) adult males of the swimming crab *Achelous spinimanus* in different gonadal stages from the upwelling region off Macaé in southeastern Brazil. OF = ovigerous females, DE = developed gonads, ED = developing gonads, RU = rudimentary gonads, and IM = immatures.



**Figure 4.** Size-frequency distribution for demographic groups and recruitment period of the swimming crab *Achelous spinimanus* collected off Macaé, an upwelling region on the southeastern Brazilian coast. Intervals of 10 mm size class were used, ranging from 8 |— 18 mm (class 1) to 98 |— 108 mm (class 10).

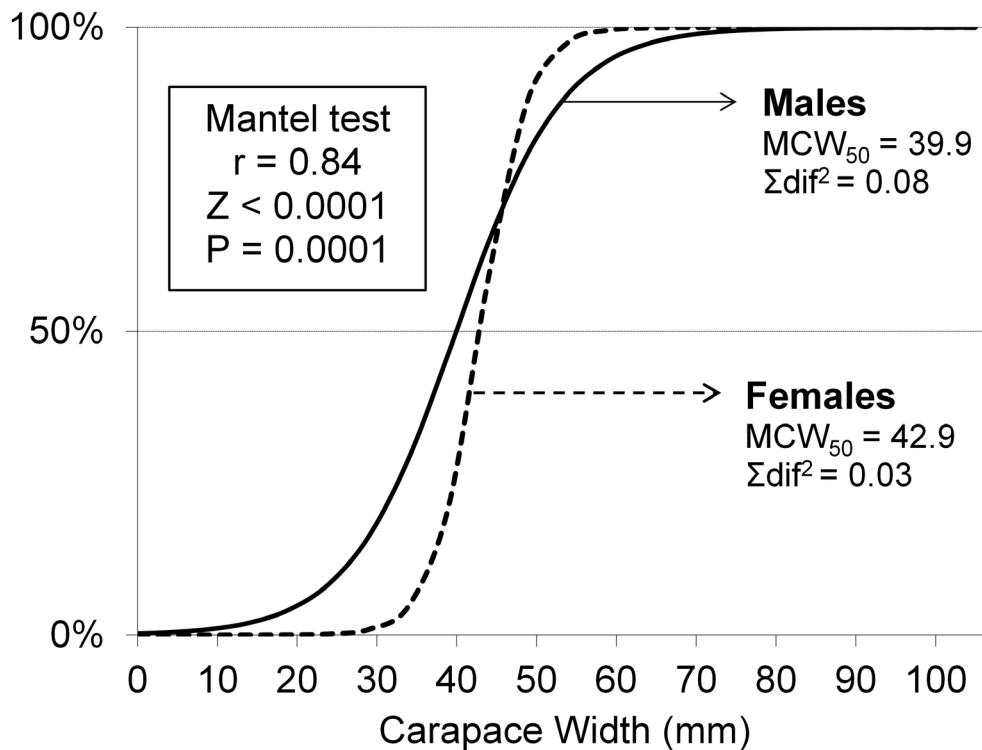
dimorphism in the carapace size, i.e., there was no significant difference between the sizes of males and females (Mann-Whitney:  $Z = 0.34$ ,  $P > 0.74$ ). The sizes at which males and females reached gonad sexual maturity (39.9 mm MCW and 42.9 mm MCW, respectively) also did not differ (Fig. 5); the matrices of males and females, with frequency of juveniles and adults by size class, were strongly associated (Mantel:  $r = 0.84$ ,  $P = 0.0001$ ). The smallest ovigerous female measured 52.8 mm MCW.

## DISCUSSION

The variations of temperature, salinity and chlorophyll a concentration are characteristic of the water masses off Macaé coast. According to Valentin *et al.* (1987) and Coelho-Souza *et al.* (2012), during winter, the SACW remains farther off the coast, while the Tropical Water (TW) remains at the subsurface, indicating subsidence. During summer, the SACW remains at the subsurface, resulting in a typical seasonal thermocline; the intrusion of this water mass with the temperature increase at the surface is a characteristic of coastal upwelling (Valentin *et al.*, 1987; Valentin,

2001). The exchange between the upwelling and the subsidence, and the inconstant entry of inorganic nutrients influence the structure of the local biological communities (De Léo and Pires-Vanin, 2006). The organic-matter content may also vary significantly among seasons; however, this factor is not necessarily a precursor of *A. spinimanus* abundance, as ordinated by RDA.

Our results revealed that the crabs showed a marked tendency to move out of the system at the beginning of winter and spring. Their return seems to coincide with the upwelling, when productivity and consequently the availability of food sources increase (De Léo and Pires Vanin, 2006) for juveniles of *A. spinimanus*. This suggestion is based on the correlation of the demographic groups with temperature, salinity and chlorophyll a; the latter was mainly associated with the abundance of juveniles. These variables are most influenced by the dynamics of the water masses (Valentin *et al.*, 1987; Gonzalez-Rodriguez *et al.*, 1992; Moser and Giancesella-Galvão, 1997; Carbonel and Valentin, 1999; Valentin, 2001; Sumida *et al.*, 2005; De Léo and Pires Vanin, 2006; Coelho-Souza *et al.*, 2012).



**Figure 5.** Adjustment of the logistic equation indicating the maximum carapace width (MCW) for males and females of the swimming crab *Achelous spinimanus*, in which 50% of the crabs are mature according to the analyses of gonadal development. The result of the Mantel test refers to the comparative matrices (frequency per size class of adult and immature females vs. adult and immature males) and the similarity between them (Legendre *et al.*, 2005).

The hydrological structure changes with the distance offshore and the depth (Valentin *et al.*, 1987). These authors stated that at a depth of 30 m, the hydrological changes continue but the amount of chlorophyll varies only slightly. According to Lima *et al.* (2014), off Ubatuba *A. spinimanus* was most abundant at 25 m; and De Léo and Pires Vanin (2006) did not find this species deeper than 40 m, in the upwelling zone. It seems reasonable that the seasonality of abundance of *A. spinimanus* may be related to a preference for areas deeper than 20 m (sampled in this study); the crabs may enter shallower areas only when, according to Valentin *et al.* (1987), the concentrations of chlorophyll are higher.

Together with the supposed preference for areas that oscillate slightly in primary production, the data from this study suggest a seasonal reproduction period during summer and autumn. Less than 500 km to the south, Santos and Negreiros-Fransozo (1999) reported the presence of ovigerous females of *A. spinimanus* in all months, during two years of collection. Branco *et al.* (2002), in southern Brazil, also reported that ovigerous females were continuously present. The

present results, however, are more similar to those in the northern hemisphere. In the southeastern United States, ovigerous females of this species were caught during the warmest months of the year (Dudley and Judy, 1971; Camp *et al.*, 1977; Olsen *et al.*, 1978).

The reproductive period of species with a broad geographic distribution may vary along a latitudinal gradient, and is affected by many environmental factors (Sastry, 1983). The reproductive pattern observed here represents a physiological adjustment of reproduction to the local upwelling conditions. The reproduction of marine invertebrates must be highly synchronized with the environmental conditions to assure success. Andrade *et al.* (2014) reported that the adult females of *Callinectes ornatus* (Ordway, 1863) migrate to areas farther from the coast to disperse their larvae, and few males with developed gonads follow them, remaining near the coast in order to ensure mating with primiparous females. For *Arenaeus cribrarius* (Lamarck, 1818), Andrade *et al.* (2015b) observed that the population adjusted to new environmental conditions by changing from continuous reproduction to seasonal reproduction, which assured a better food supply for the



larvae. Andrade *et al.* (2015a) also found that this same species showed continued recruitment in the upwelling region. Our results indicate that synchronization of reproduction occurs in the months of higher availability of food for the larvae, i.e., during summer and autumn. Therefore, the juvenile recruitment is also seasonal, in this same period.

The estimated size at which *A. spinimanus* reaches gonad sexual maturity was similar for males and females, in agreement with the findings of Santos and Negreiros-Fransozo (1996). In contrast to many other portunoid species, where females mature earlier than males (see Mantelatto and Fransozo, 1999a; Marochi *et al.*, 2013), carapace width showed no sexual dimorphism. Other portunid crabs also show a similar maturation size between sexes, with males maturing earlier than females, including *A. cribrarius* (see Andrade *et al.*, 2015b), *Portunus sanguinolentus* (Herbst, 1783) (Rasheed and Mustaqim, 2010) and *Achelous spinicarpus* Stimpson, 1871 (Pardal-Souza and Pinheiro, 2013). Assuming that the mortality rate tends to be higher among adults, and that the sooner an animal reaches sexual maturity the sooner it can produce descendants (Haefner, 1990), the elimination of a molt cycle must be another adaptive strategy of *A. spinimanus*. Andrade *et al.* (2015b) noted that estimates of the size at which gonad sexual maturity is reached, especially in the case of edible species, are among the most important sources of information for understanding the biology and conservation requirements of a population. These authors also noted that reproductive activity may be related not only to seasonal variations of temperature or other environmental factors, but also to adaptive synchrony between the most intense periods of larval release and greater food availability. Thus, the strategy in which females reach maturity at larger sizes may be ideal for maximizing their reproductive success, guaranteeing that more larvae will survive (Andrade *et al.*, 2015b).

The environmental conditions in this upwelling region may have induced the population of *A. spinimanus* to show different characteristics and behaviors from populations elsewhere off the Brazilian coast. This study revealed that the crabs moved out of the system at the beginning of winter and spring and they returned with the upwelling. Differences in the periods of reproduction and recruitment, as well

as in the population structure and distribution may reveal differentiated survival strategies of the species. The results of this study also raise the question of whether the patterns shown by other species with broad geographic distributions may also be altered by local geographic variations. Answers to these questions would improve understanding the effects of local environmental conditions on the dynamics and distribution of populations, which is essential for the development of appropriate management plans.

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