

Reproductive ecology of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) in a coastal area of Southern Brazil*

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Abstract The predictability of certain environmental factors that affect the life cycle of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) was evaluated in a study of its reproductive biology in an area adjacent to Babitonga Bay, State of Santa Catarina, Brazil. Monthly sampling was conducted from July 2010 through June 2011 at depths of 5, 8, 11, 14, and 17 m. 76 004 individuals were obtained, with a pronounced peak in absolute abundance in austral autumn (34 208), coinciding with the annual closed season from March to May. Grain size composition of the sediment showed the closest relationship to the distribution of individuals (multiple linear regression, $P < 0.05$), related to their burying habit. The observed correlations between the abundance of reproductive males (bearing spermatophores) and females with spent gonads (cross-correlation, $P < 0.05$), and between reproductive males and reproductive females (with a 1-month lag) suggest that the peak of reproductive males preceded the peak of female ones. This result agrees with the pattern expected for females, which copulate in post-ecdysis (spent gonads). Spawning seemed to take place at greater depths, as evidenced by the concentration of reproductive females in these areas. The reproductive activities observed here confirm that this species follows a tropical/subtropical reproductive pattern, spawning continuously throughout the year, with the highest peaks in spring and autumn. The data indicate that the juvenile recruitment period observed in August–September resulted from the reproductive output noted in April–May. Additionally, the reproductive period recorded in November led to the juvenile peak observed in March–May.

Keyword: crustacean fisheries; Dendrobranchiata; environmental effects; recruitment; spawning

1 INTRODUCTION

Popularly known as the “seabob shrimp”, *Xiphopenaeus kroyeri* (Heller, 1862) is widely distributed in the western Atlantic Ocean, from Virginia (United States) ($\approx 37^\circ\text{N}$) to Rio Grande do Sul (Brazil) ($\approx 30^\circ\text{S}$), and is commonly found at depths up to 25 m (Costa et al., 2000, 2003; D’Incao et al., 2002). The continuous exploitation of these commercially important crustaceans is causing a rapid decrease in shrimp stocks, overloading not only stocks of this species, but also stocks of the bycatch fauna (Castilho et al., 2008a). Trawling on soft bottoms has led into significant losses on spawning biomass and biodiversity. Moreover, the seabob shrimp is one of the most important species targeted by the artisanal fisherman in southern Brazil, besides being among the

top ten penaeid species caught worldwide (Pauly and Christensen, 1995; Pauly et al., 2002; Gillett, 2008; Silva et al., 2013). D’Incao et al. (2002) noted the need for improvements in the regulation of this fishery. According to some studies (Pires, 1992; Nakagaki and Negreiros-Fransozo, 1998; Costa et al., 2007; Grabowski et al., 2014), to achieve such improvements, it is essential to increase our knowledge of the biology of this species, which plays an important role in maintaining the stability of benthic communities.

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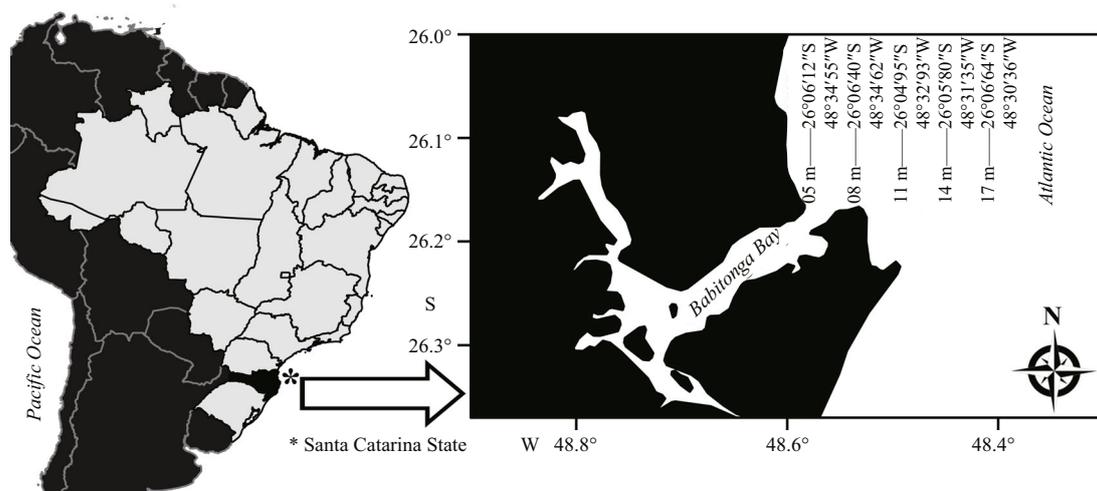


Fig.1 Map of the study area, highlighting the sampled stations in an area adjacent to Babitonga Bay, Southern Brazil

Modified from Grabowski et al., 2014.

Dall et al. (1990) found that the behavior of penaeid shrimps is affected by their physiological processes, which are closely related to environmental features. Fransozo et al. (2002), Costa et al. (2004) and Castilho et al. (2008b) found that salinity, temperature and sediment texture (i.e., grain-size composition and organic-matter content) are the most influential factors, and also tend to vary widely both spatially and temporally.

Two kinds of reproduction are known: A) continuously throughout the year (continuous pattern), or B) restricted to a period of the year (discontinuous), usually related to winter temperatures (Dall et al., 1990).

Closer to the Equator, crustaceans show a trend toward continuous spawning. In tropical regions, the spawning activity of penaeids is continuous, but usually presents a bimodal reproductive pattern, with a first minor peak in autumn and a massive investment in spring (Garcia, 1988). Finally, cold temperate penaeids tend to spawn seasonally, restrict to the spring-summer period (Dall et al., 1990).

The main breeding grounds for Penaeoidea are likely to be those areas with a higher abundance of females with developed gonads, because after the females reach gonadal maturation, they will spawn within a few hours (Yano, 1995). Although Dall et al. (1990) stated that the species of the genus *Xiphopenaeus* Smith, 1869 reproduce over the continental shelf and occupy estuarine environments in their post-larval stage, several studies conducted in coastal waters of the state of São Paulo, Brazil, have found that *X. kroyeri* does not follow this pattern (Castro et al., 2005; Costa et al., 2011; Heckler et al.,

2013, 2014). Castro et al. (2005) and Costa et al. (2011) assumed that *X. kroyeri* cannot tolerate the wide variations in salinity that are common in estuaries. Similarly, Kutkuhn (1966) found that these shrimp rarely (or never) penetrate estuaries, either as adults or as juveniles.

This study describes the reproductive ecology of the seabob shrimp in an area adjacent to Babitonga Bay on the northern coast of the state of Santa Catarina, Brazil, investigating the relationship of environmental factors to the distribution of individuals, reproductive periodicity, juvenile recruitment and sex ratio.

2 MATERIAL AND METHOD

2.1 Study area

Shrimp and environmental factors were sampled monthly from July 2010 through June 2011 at five sites parallel to the shoreline and at different depths (5, 8, 11, 14 and 17 m) near Babitonga Bay (Fig.1). This bay is located on the northern coast of the state of Santa Catarina, near the towns of Joinville, Itapoá and São Francisco do Sul. The area has a rich fauna, although studies have been limited to crustaceans, fishes, birds and aquatic mammals (Rodrigues et al., 1998).

2.2 Sampling

Sediment was obtained monthly, using a Petersen grab. The samples were packed individually and frozen to minimize loss of organic matter. At the laboratory, the sediment was dried in an oven 70°C

for 72 h. From each sample, a 10-g subsample was ash-weighed to determine the organic-matter content and 100 g was used to determine the grain-size distribution, according to Mantelatto and Fransozo (1999) and Castilho et al. (2012).

Bottom water samples were taken monthly, with a Van Dorn bottle, to measure salinity and temperature, for which an optical refractometer and a mercury thermometer were used.

Biological sampling was conducted in 30-min trawls using a shrimp boat outfitted with double-rig nets (mesh size: 3 cm; total mesh gap: 11.5 m; boat velocity during trawls: 1.6 knots; total distance traveled during trawls: approximately 0.5 miles) (Grabowski et al., 2014). Specimens were packed in a box containing crushed ice for later analyses. When biomass exceeded 500 g, a subsample was taken for morphometric analysis, i.e., measurements of shrimp carapace length (CL) (distance from the posterior margin of the carapace to the post-orbital angle) using a caliper (to the nearest 0.1 mm). During the shrimp-fishing closed season, sampling were performed in accordance to the federal laws, as to the requirements given by the responsible management agencies.

2.3 Temporal and spatial distribution

Homoscedasticity was tested by means of the Levene Test. Data with unequal variances were log-transformed ($x+1$) prior to further analyses. The abundance of individuals was compared to their spatial and temporal distribution using a variance analysis (ANOVA factorial), followed by the Tukey test, by depth and austral seasons (winter: July through September, and so on). The relationship of environmental factors to the abundance of individuals was tested with a multiple linear regression (MLR) for all the statistical analyses used, we adopted a significance level of 5% (Zar, 1999).

2.4 Reproductive biology

The presence of the petasma in males and the thelycum in females indicated each sex. The gonadal development stage in females was determined by macroscopic examination of ovaries, based on color and the volume of this organ. Ovaries of females categorized as immature (=juveniles - IM) varied from thin, transparent strands to thicker strands; classified as spent (SP; adult females not in a reproductive period) if they were white and much

larger and thicker than those of immature females; as developed if they were light green; or mature if they were green to dark green, occupying the entire dorsal part of the abdomen as well as part of the cephalothorax (more details in Almeida et al., 2012; Castilho et al., 2015). The spawning intensity of this population was estimated by the percentage of the combining females with developed or mature gonads, which were considered reproductive females (RE), in relation to the total number of adult ones (SP+RE) (Castilho et al., 2008a). The adult condition in males was determined by macroscopic observation of the petasma. In juveniles, the endopods of the first pleopods are completely separated, while in adults these structures are linked (Boschi and Scelzo, 1977; Bauer, 1986, 1991). The maturity of adult males was classified according to the development of spermatophores in the terminal ampoule (ejaculatory duct). This was convenient because spermatophores were visible through the exoskeleton (Chu, 1995). When the spermatophores were not visible by macroscopic observation, the adult male was classified as lacking spermatophores (SP). If spermatophores were visible and occupied part (developing) or all (developed) of the terminal ampoule, males were classified as spermatophore-bearing males (RE) (Castilho et al., 2012, 2015). Thus, the reproductive activity of the population was estimated by the abundance of reproductive females with developing and fully developed (mature) gonads and spermatophore-bearing males.

To determinate temporal oscillation in the effects of specific factors on reproduction, cross-correlation analyses were performed. In cross-correlations, two series of data are compared as a function of time lag (n), using the Pearson correlation coefficient to measure relationships between values of the first data series and values of the second series from months earlier (in negative lags) or later (in positive lags). Correlation coefficient values at lag 0 are equivalent to the standard Pearson correlation (STATSOFT, 2011). However, we considered lag coefficient values higher than 0.5 (positive or negative) as biologically significant when the analysis was statistically significant ($P < 0.05$). According to Dancey and Reidy's (2011) categorization, the correlation with coefficient 1 is perfect, 0.99–0.7 strong, 0.69–0.4 moderate, and 0.39–0.1 weak.

The periods and locations of juvenile recruitment were estimated from the proportion of immature individuals in the population.

Table 1 Temporal variation for environmental factors collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

Month	Temperature (°C)			Salinity			Phi			O.M. (%)		
	Mean±SD	Min	Max	Mean±SD	Min	Max	Mean±SD	Min	Max	Mean ±SD	Min	Max
Jul. 10	19.4±0.42	19.0	20.0	34.5±0.42	34.0	35.0	3.8±0.68	2.7	4.4	1.4±0.80	0.6	2.6
Aug.	18.2±0.57	17.5	19.0	34.0±0.89	32.0	34.0	3.8±0.68	2.7	4.4	1.6±0.73	0.8	2.8
Sep.	19.5±0.50	19.0	20.0	31.0±0.89	31.0	33.0	4.4±0.55	3.7	5.3	6.7±4.29	2.2	12.2
Oct.	20.1±0.25	19.9	20.5	32.0±0.45	32.0	33.0	4.5±0.58	3.7	5.3	8.0±6.70	1.2	16.7
Nov.	22.4±0.82	21.0	23.0	33.0±0.82	31.5	33.0	4.2±0.84	2.8	5.1	4.6±4.90	0.6	12.7
Dec.	24.6±0.42	24.0	25.0	32.0±0.67	31.5	33.0	4.2±0.88	2.8	5.1	5.0±5.34	0.6	13.9
Jan. 11	25.6±0.82	25.0	27.0	34.0±1.64	31.0	35.0	3.7±0.99	1.9	4.4	2.4±1.30	1.6	4.6
Feb.	26.1±0.22	26.0	26.5	32.0±0.84	31.0	33.0	3.7±0.96	2.0	4.3	1.8±0.91	1.1	3.2
Mar.	24.7±0.27	24.5	25.0	33.0±0.45	32.0	33.0	3.8±0.96	2.1	4.4	2.0±1.44	0.6	4.3
Apr.	23.2±0.57	22.5	24.0	35.0±0.45	34.0	35.0	3.8±0.98	2.1	4.4	2.0±1.35	0.6	3.8
May	22.3±0.27	22.0	22.5	35.5±0.45	34.5	35.5	4.3±0.26	4.1	4.7	2.4±1.61	1.3	5.2
Jun.	21.0±0.00	21.0	21.0	35.5±0.42	35.0	36.0	4.3±0.32	4.0	4.8	2.2±1.36	0.8	4.3

O.M.: organic matter content; Min: minimum values; Max: maximum values; SD: standard deviation.

Table 2 Spatial variation for environmental factors collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

Depth (m)	Temperature (°C)			Salinity			Phi			O.M. (%)		
	Mean±SD	Min	Max	Mean±SD	Min	Max	Mean±SD	Min	Max	Mean±SD	Min	Max
5	22.8±2.72	19.0	27.0	32.6±1.56	31.0	35.5	4.2±0.50	3.7	5.1	4.0±4.53	1.1	13.9
8	22.5±2.61	18.5	26.0	33.3±1.68	31.0	36.0	4.5±0.15	4.3	4.8	2.0±0.56	1.2	3.0
11	22.2±2.62	18.0	26.0	33.3±1.45	31.0	35.5	4.4±0.43	4.2	5.3	4.4±4.88	1.4	16.7
14	22.0±2.65	18.0	26.0	33.8±1.39	31.0	35.5	3.7±0.71	2.7	4.5	2.1±2.19	0.6	6.8
17	21.8±2.71	17.5	26.0	34.0±1.29	32.0	36.0	3.5±1.10	1.9	4.4	4.2±3.90	0.6	12.9

O.M.: organic matter content; Min: minimum values; Max: maximum values; SD: standard deviation.

3 RESULT

3.1 Environmental factors

Mean monthly salinities ranged from 31.0 (September) to 35.5 (May/June) (Table 1). Mean salinities increased with depth, from 32.6 (5 m) to 34 (17 m) (Table 2).

The mean monthly bottom temperature ranged from 18.2°C (August) to 26.1°C (February) (Table 1). The overall mean bottom temperature varied spatially from 21.8°C at 17 m to 22.8°C at 5 m (Table 2).

Organic-matter content (%) was higher at depths of 5, 11 and 17 m and lower at 8 and 14 m deep (Table 2). Phi decreased with depth, since the deeper sites consisted mainly of finer grains and silt+clay (Table 2).

3.2 Spatial and temporal distribution

We estimated a total abundance on 76 004 individuals. The highest peak was observed in May (19 320), and the lowest number in December (719). Abundance was highest in autumn (34 208) and lowest in spring (5 468). Spatially, a peak was observed at 5 m (36 057), and the lowest abundance at 17 m (3 674). The distribution of individuals differed significantly among both seasons and depths (ANOVA, $P<0.05$), and the numbers found in spring and at 14 and 17 m differed from the other seasons and depths (Tukey, $P<0.05$) (Figs.2, 3). Environmental factors significantly affected the distribution of the abundance of this species (MLR, $R^2=0.23$; $P=0.006$ 1; $F=4.04$). Seabob shrimp showed a positive association with phi values and a negative association with the organic-matter

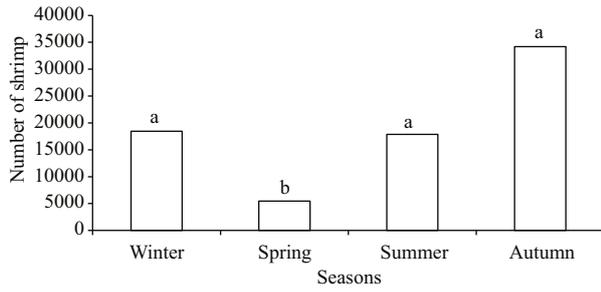


Fig.2 Abundance of shrimp collected in each season, from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

Bars with at least one similar letter did not show statistically significant difference (Tukey, $P < 0.05$).

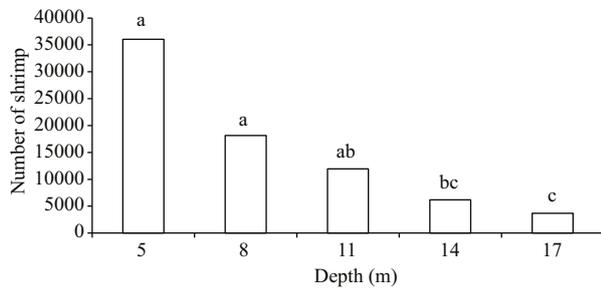


Fig.3 Abundance of shrimp collected in each depth, from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

Bars with at least one similar letter did not show statistically significant difference (Tukey, $P < 0.05$).

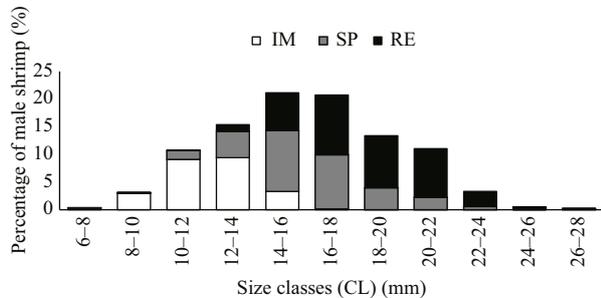


Fig.4 Distribution of gonadal stages in size classes for males collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

IM: immature; SP: adult males with spermatophores developing in the terminal ampoule; and RE: males bearing developed spermatophores.

content. No associations between bottom salinity/temperature and the abundance of shrimp were found.

During the whole sampling period, we collected a total of 226.78 kg of *X. kroyeri*. Nevertheless, we observed a both wide spatial and temporal variation in the total weight obtained, with the highest value recorded in May (30-min trawl: 53.75 kg), and a mean weight of 3.78 kg for each 30-min trawl performed along the study period.

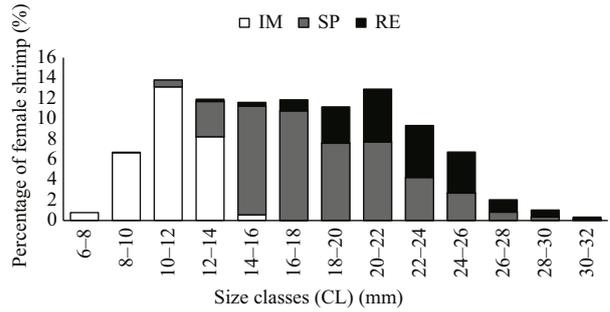


Fig.5 Distribution of gonadal stages in size classes for females collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

IM: immature gonad; SP: spent gonad; and RE: developed gonad.

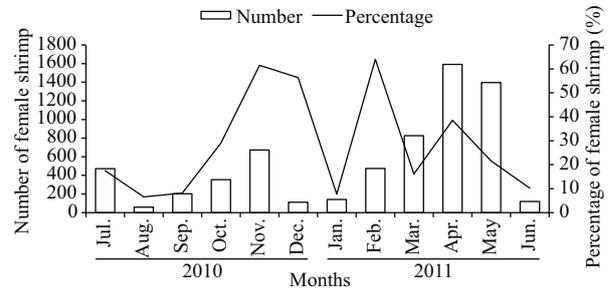


Fig.6 Number and percentage of reproductive females collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

3.3 Reproductive biology

A total of 4 007 individuals of *X. kroyeri*, including 2 285 (57%) females and 1 722 (43%) males, was analyzed to evaluate their reproductive biology.

Males were present from the first size classes, in which the majority of them were juveniles. Reproductive individuals first appeared in the size class of 12–14 mm, indicating the likely size at onset of sexual maturity. All males above 16–18 mm were adult (Fig.4).

The percentage of females was highest in the size class of 10–12 mm, the majority of them immature. An increase in the percentage of reproductive females was observed only above 16–18 mm, size class in which all of the females were in its reproductive stage (Fig.5). In size classes from 12 to 16 mm contained increasing proportions of adult females.

Reproductive females were collected throughout the study period, with percentage peaks in November, February, and April (Fig.6). The abundance of reproductive females was correlated with the monthly values of bottom salinity, with a 1-month lag (cross-correlation, $P < 0.05$; $R = 0.764$). The highest percentages of spent-females occurred in shallow waters (<11 m), while the reproductive females one

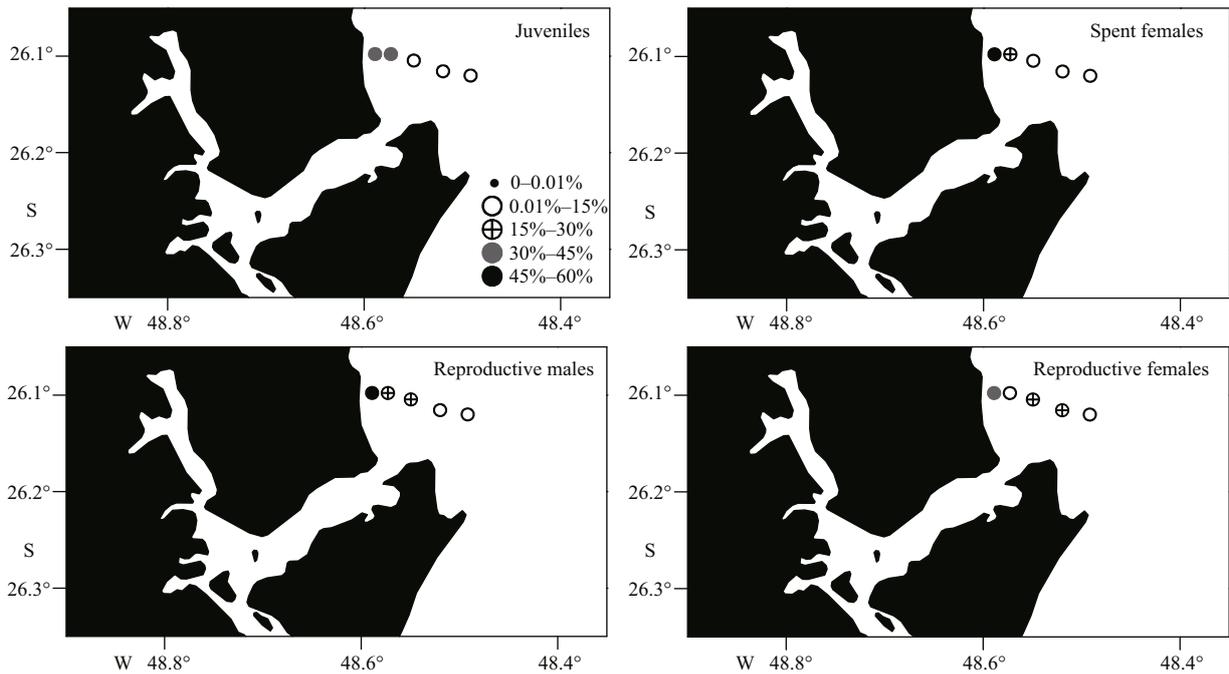


Fig.7 Spatial distribution of the percentage of individuals in each demographic group (juveniles, reproductive males, spent females and reproductive females) collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

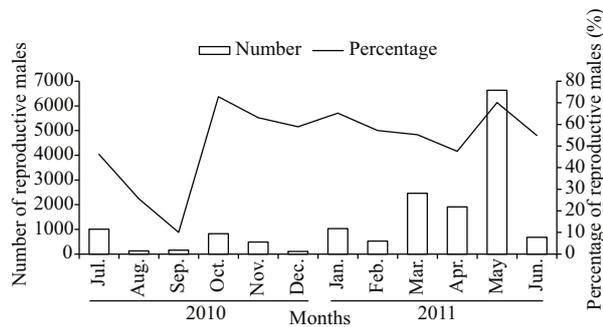


Fig.8 Number and percentage of reproductive males collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

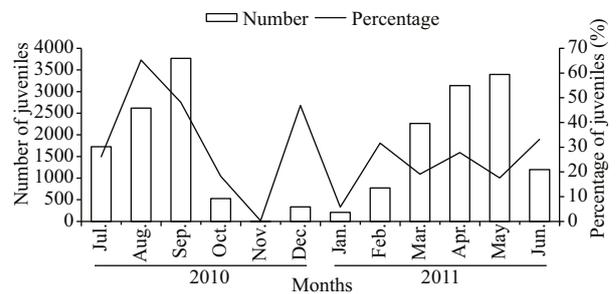


Fig.9 Number and percentage of juveniles collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, Southern Brazil

was higher at 5 m, 11 m and 14 m depth (Fig.7).

The highest percentages of reproductive males occurred mainly in shallow waters (Fig.7), and were present throughout the study period, with higher percentages in October, January, and May (Fig.8). These males were more abundant in months preceding the reproductive periods for females, with a 1-month lag, as October and January percentage peaks preceded the reproductive females of November and February, respectively (cross-correlation, $P < 0.05$; $R = -0.627$) (Figs.6, 8). Reproductive males showed a correlation with the monthly mean bottom salinity, with a 1-month lag (cross-correlation, $P < 0.05$; $R = 0.720$). Abundance of reproductive individuals

(males and females) did not show correlations with the monthly means of temperature, phi and organic-matter content (cross-correlation, $P > 0.05$).

The recruitment period showed two peaks of number of juveniles in September and May (Fig.9). The highest proportions of juveniles were recorded in August, September, December, and June (Fig.9). Juveniles were more abundant at lower depths (around 80% of all juveniles obtained) (Fig.7), and the number of immature individuals showed no correlation with the number of reproductive males and/or females (cross-correlation, $P > 0.05$). Juvenile individuals also did not show significant relation to any of the environmental factors sampled in this study (cross-correlation, $P > 0.05$).

4 DISCUSSION

This study showed that the seabob shrimp completes its life cycle in the area adjacent to Babitonga Bay. This area contained juveniles and adults of both sexes, with a wide size range, suggesting that this species does not depend on estuarine environments to complete its life cycle. The environmental factors most closely related to the abundance of *X. kroyeri* were grain size and bottom temperature; these crustaceans were more abundant in shallower, warmer water.

4.1 Ecological distribution

Shrimp were collected throughout the sampling period, although with an increase in abundance during autumn. Nakagaki and Negreiros-Fransozo (1998) and Costa et al. (2007, 2011) reported similar observations in coastal waters of the State of São Paulo, as did Branco et al. (1999) and Branco (2005) off Santa Catarina. This increase in abundance may be related to the three-month closed season (March to May) adopted by the national environmental resources managing agency (IBAMA, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) to protect shrimp stocks. The reproduction and recruitment periods (peaking in autumn in this study) are probably the cause of the increase in abundance.

The seabob shrimp was found at all the sampling sites used for this study, with the highest abundance recorded at the 5-m depth. Similar results were obtained by Costa et al. (2007) and Castilho et al. (2008b) for this species in coastal waters of São Paulo. The present results are within the distributional limits proposed by Costa et al. (2003), who found this species preferentially in coastal waters. The fine-textured sediment at these depths turn the burying activity much easier, once it is easier for the shrimp to move finer grain, what makes them prefer this kind of substrate. When buried, shrimp are protected against predators, and also their metabolic demand decreases (Ruello, 1973; Dall et al., 1990; Simões et al., 2010). According to Penn (1984), the preference of penaeoids for specific kinds of substrate is related to the capacity of each species to perform gas exchange in each kind of substrate. Costa et al. (2007) assumed that this relationship could act as a limiting factor or allow the expansion of the bathymetric distribution of species in certain locations. Costa et al. (2005) and Castilho et al. (2008a), studying respectively *Sicyonia dorsalis* Kingsley, 1878 and *Artemesia longinaris* Bate, 1888,

stated that penaeid shrimps show a preference for fine-grained substrates.

The abundance of *X. kroyeri* could also be associated with the higher temperatures in shallower waters, because very low temperatures could limit the occurrence of these shrimp (Costa et al., 2007; Castilho et al., 2008b). The Babitonga Bay is located in a subtropical region which belongs to the Atlantic upwelling zone, comprehended from 23°S to 29°S. The opposing flow of the Brazil (subtropical) and the Malvinas (subantarctic) currents dominates the open ocean circulation in Western Atlantic Ocean, and both meets on average 36°S. During winter, the water temperature is vertically homogenous, while during summer the South Atlantic Central Water (SACW) influences the region (Acha et al., 2004; Marafon-Almeida et al., 2008). Near Babitonga Bay the shrimp were most abundant in intermediate temperatures (21 to 25°C), although the relationship between temperature and abundance of individuals was not statistically significant, as also observed by Castro et al. (2005), Costa et al. (2007, 2011) and Lopes et al. (2010). In contrast, Castilho et al. (2008b) reported that bottom temperature affected the spatial abundance of *X. kroyeri* and *Pleoticus muelleri* (Bate, 1888). This can be noted when observing the difference in reproductive peaks among these two species, once *P. muelleri* shows its reproductive peak a few months before than *X. kroyeri*'s one (Nov.–Jan. and Feb.–Apr.) (Castilho et al., 2012, 2015). In the study carried out by Castilho et al. (2015) in southeastern Brazil, such negative influence of SACW over the reproductive cycle of *X. kroyeri* became even clearer when observing a later reproductive peak from April to May 2002, as a possible consequence of a stronger influence of SACW during Oct.–Nov. 2001. Additionally, Castilho et al. (2008b) assumed that the intrusion of SACW, with temperatures as low as 15°C is, a temporal limiting factor to tropical species and opportune to cold temperate regions species. Thus, temperature is an important factor limiting the distribution of *X. kroyeri*, although different species of penaeids may respond differently, depending on the locations where the specimens are collected.

Castilho et al. (2008b), Lopes et al. (2010), and Heckler et al. (2014) also found that the abundance of *X. kroyeri* was not related to mean salinity. In contrast, some studies have highlighted salinity as a key factor affecting this species' abundance (Costa et al., 2007, 2011). As suggested by Castilho et al. (2008b) and Heckler et al. (2014), the range of salinity and

temperature values in the study region may not have been wide enough to cause changes in the shrimp distribution. Gunter et al. (1964) showed that salinity affected shrimp abundance patterns in an area where salinity levels ranged from 5 to 35. In the present study, samples were taken only in the marine environment, with salinities from 31 to 36. This influence would probably be more apparent in environments with salinities below 30 (Costa et al., 2011).

The correlation between the organic-matter content and the abundance of shrimp was negative, in accordance with observations by Castilho et al. (2008b) and Costa et al. (2011). However, these results differ from those of Castro et al. (2005), who found no relationship between organic matter and the abundance of juveniles of *X. kroyeri*. Costa et al. (2007) found a positive relationship between the organic-matter content and the abundance of *X. kroyeri*. The spatial variation in the organic-matter content also did not seem to follow a clear pattern among the sampling sites.

The negative correlation between the distribution of the shrimp and the organic-matter content may be related to other environmental factors or ecological interactions that exert greater influence on this species' life cycle, leading them to seek more favorable environmental conditions. According to Krebs (2001), habitat selection considers a balance of chemical, physical and biological environmental factors. The ideal habitat must provide a variety of factors that together allow a species to establish itself in a certain location. For instance, the substrate texture, or factors other than those examined here may be operating, since the organic-matter content was measured only in the substrate, without considering decomposing organic matter or the availability of food on the substrate surface.

4.2 Reproductive biology

The higher abundance of females observed here is in accordance with the results obtained by Castro et al. (2005), De Campos et al. (2011) and Heckler et al. (2013). Nakagaki and Negreiros-Fransozo (1998) and Lopes et al. (2010) also found a male-biased sex ratio, which, according to Heckler et al. (2013) could be attributed to the segregated distribution of sexes observed in some months. Variations in a 0.5 sex ratio could be justified by distinct sex-responses to natural mortality or migration, beside the different occupation in the habitat (Nakagaki and Negreiros-Fransozo,

1998; Castilho et al., 2008a). On the other hand, Castilho et al. (2008a) also observed a higher abundance of females of *S. dorsalis*, suggesting that in this case the sex ratio was in fact female-biased. According to Lopes et al. (2010), a higher abundance of males is less common for this species and might occur, for instance, when females migrate to deeper areas during spawning periods. It is also important to note that for this species, as for other species of Penaeoidea, females reach larger sizes when compared to males of equal age. Such pattern was confirmed by Grabowski et al. (2014), when analyzing growth and longevity of *X. kroyeri* in this region.

Branco (2005) showed that this species has a long spawning period, with reproductive females present throughout the year. In this study, *X. kroyeri* followed a tropical/subtropical pattern (Garcia, 1988), with the presence of reproductive females throughout the year, suggesting a continuous reproductive pattern, with a peak of individuals in spring (November) and another in autumn (April). This pattern is similar to findings by Nakagaki and Negreiros-Fransozo (1998), Castro et al. (2005) and Heckler et al. (2013), in studies on the coast of São Paulo, as well as by Branco (2005) on the coast of Santa Catarina and by Santos et al. (2003) in coastal waters of Bahia. According to Dall et al. (1990), several penaeid shrimp species have two main reproductive periods each year, typically in September–November and March–May, with peculiar responses from each species to different local environmental features. In general, penaeid species located near the Equator tend to show continuity in spawning, although not fully homogeneous from month to month. The present study showed that the seabob shrimp follows this pattern, even in coastal waters of subtropical Southern Brazil.

Species with a closed thelycum mate just after ecdysis, when the female is in the spent gonadal stage (Dall et al., 1990). Accordingly, this study showed a correlation between the number of reproductive males and females, with a 1-month lag, i.e., higher percentage of males produce spermatophores one month before the females mature their gonads, proving that mating occurs in the shallower depths with reproductive males and spent females. Heckler et al. (2014) reported a similar pattern of congruency in the distribution of reproductive males and non-reproductive females in coastal waters of São Paulo. In accordance with Dall et al. (1990), just after mating, females apparently migrate to greater depths (in this case to 14 m), where spawning would occur, since

this demographic class was more concentrated in these locations. These features were also noted by Juneau (1977) in coastal waters of Louisiana, Gulf of Mexico, who considered that this species mates and spawns in offshore regions (deep waters), or else that this species migrates to other states along the Gulf to reproduce.

Bimodal spawning and recruitment patterns similar to those observed in this study are common at low latitudes (tropical/subtropical regions) (Dall et al., 1990). Similarly, Nakagaki and Negreiros-Franozo (1998) reported the presence of immature individuals from February to May, attributed to spring spawning events. This indicates that the period of most intense reproduction in April and May will originate the juveniles recruited in August and September, while the November reproductive period will originate the juveniles that appear from March to May. Such statement grows stronger observing the obtained cohorts used for the growth analyses conducted by Grabowski et al. (2014) in the same region that the present investigation. In such study, it is possible to note peaks in the number of smaller individuals recruiting in the population in the August–September and the March–June periods.

The higher abundance of juveniles in shallow waters (8 and 11 m deep) suggests where the juvenile recruitment is taking place. According to Stoner (1988), the preference for a certain type of substrate changes throughout the life cycle in penaeids, and juveniles tend to show a preference for finer sand. Ruello (1973) also noted that juveniles prefer fine sand. Because they have limited excavating ability, juveniles would expend more time and energy when moving through larger and/or heavier sediment particles, as suggested for *X. kroyeri* by Heckler et al. (2014), in coastal waters of São Paulo.

4 CONCLUSION

This study complements current knowledge of *X. kroyeri*, one of the most heavily exploited species by the trawling fishery. The results presented here can be useful in establishing efficient fishery management policies or improving existing policies. In view of the high economic value of *X. kroyeri*, the information from this study can also be used to detect possible decreases in these stocks and prevent their collapse.

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