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Bio ecology of the white shrimp *Litopenaeus schmitti* in Babitonga Bay. Do the current regulation of closed seasons is suitable to the lifecycle of this species?



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ABSTRACT

The white shrimp Litopenaeus schimitti is the main way of living for artisanal fishermen who use the gerival for their capture in one of the main estuaries off south Brazil: Babitonga Bay. The abundance of the species is regulated by closed fishing seasons to protect spawning and recruitment, which may not in accordance with species' life cycle. The present study evaluated the size structure, maturation, and abundance of white shrimp, to verify the effectiveness of these measures for the region. The highest abundances of the L. schmitti occurred between February and May, both in the inner bay and the adjacent marine area. Spawning occurred in the marine environment around 15 m depth, mainly in October and November, with the subsequent entry of post-larvae into the estuary around December, being available for artisanal fishing in January in the inner bay area. In February and March, juveniles migrated to the adjacent marine area, defining the main recruitment peak. Some lagging shrimp remained within the bay until September and October, with a complete disappearance in December. The first size of maturation for the white shrimp females was estimated at 15.16 cm. The results hereby obtained showed that the current closed season partially protects white shrimp spawning and recruitment in Babitonga Bay and the adjacent marine area suggesting that fishing restrictions during the months of February and March may benefit juvenile specimen's migration from the estuary, however, the protection of the spawning females in October/November could also be taken into account as a way of maintaining stocks of white shrimp in the region.

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1. Introduction

Penaeid shrimp are important fishing resources in coastal regions worldwide (Garcia and Le Reste, 1986; Pérez-Castañeda and Defeo, 2005; Suradi et al., 2017), as well as on the Brazilian coast (D'Incao, 1991; Albertoni et al., 2003; Leite and Petrere, 2006a,b; Robert et al., 2007). Among the commercial species of this family, the white shrimp *Litopenaeus schimitti* (Burkenroad, 1936) occurs in the Western Atlantic from the Antilles, Virgin Islands, and Cuba (23°30'N), passing through Honduras, West Caribbean coast, Venezuela, and along the Atlantic coast of South America, until south Brazil (29°25'S) (Perez-Farfante, 1970). Near the southern end of its distribution, the species represents the most profitable

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https://doi.org/10.1016/j.rsma.2021.101859 2352-4855/© 2021 Elsevier B.V. All rights reserved. resource to Babitonga's Bay artisanal fishermen who use the "gerival", a type of drifting-tow net. In this fishery, juveniles of the pink shrimp *Farfantepenaeus brasiliensis* (Latreille, 1817) and *Farfantepenaeus paulensis* (Pérez Farfante, 1967) are also caught as a seasonal target (IBAMA, 1998; Pacheco and Wahrlich, 2003).

Babitonga Bay is one of the largest estuarine systems in southern Brazil, encompassing a series of sub-environments along its area (Knie, 2002). The high primary productivity, which creates favorable conditions for a highly diverse fauna to develop, contributes to local biodiversity which directly influence the adjacent marine region (Cremer et al., 2006; Marafon-Almeida et al., 2008; Souza-Conceição et al., 2013). In addition to the environmental relevance, the surrounding region of this estuary concentrates diversified socio-economic activities such ports, fishing, tourism, and industry (mainly steel), which are of relevant importance on a regional and national scale (Knie, 2002). Fishing in Babitonga was one of the main ways of living for local residents, involving 2998 registered fishermen distributed in 33 fishing communities (IBAMA, 1998). However, recent census shows that only 1600 are actually active artisanal fishermen in the bay area (PMAP-SC, 2018).

Adult individuals of the white shrimp are commonly found in marine regions from shallow waters to depths around 30 m, with occurrence records up to 50 m, while juveniles occur in inlets, bays, and estuaries (Perez-Farfante, 1970; Iwai, 1973). Reproduction occurs year-round in the sea, at between 15 to 20 m depth. After spawning, the post-larvae are carried to estuaries where they find favorable conditions for growth, and later the pre-adults return from the breeding sites to the spawning areas at sea (Neiva et al., 1971; D'Incao, 1991; Coelho and Santos, 1993, 1994; Chagas-Soares et al., 1995; Branco and Verani, 1998a,b). Thus, the recruitment period is likely determined assuming that reductions in size-frequency distributions would show the entry of juveniles into the adult stock (Chagas-Soares et al., 1995; Miazaki et al., 2018). Despite its importance, knowledge about the recruitment for *L. schmitti* is limited.

Throughout its lifecycle, the white shrimp juveniles are captured by artisanal fishers inside the Bay, most of them using the "gerival" (IBAMA, 1998), while adults are caught at sea by shrimp trawlers (Santos et al., 1988; Chaves and Robert, 2003; Santos et al., 2008).

According to IBAMA (2011), the increasing levels of fishing effort and the downward trend in the white shrimp production in the Southeast and Southern regions between 1976 and 1999, suggested an overexploitation of the stocks. In contrast, closed seasons in these regions were implemented to recover the pink shrimp stocks, by protecting the juvenile recruitment to the adult stock and reducing the fishing effort. Thus, the no-catch periods in the estuarine environments of Santa Catarina and Paraná would be mainly protecting the recruitment of the pink shrimp *F. paulensis* (IBAMA, 2011).

In Babitonga Bay, the closed season takes place from November 1st to January 31st, and is applied indistinctly for white shrimp and pink shrimp (IBAMA Ordinance N° 70, October 30, 2003). On the other hand, trawl fishing directed at these species in the adjacent marine region is prohibited from March 1st to May 31st (Normative Instruction IBAMA N° 189, September 23rd, 2008). However, according to local fishermen claims, these periods would not be protecting well the white shrimp.

The present study describes the biological attributes and the population structure of the white shrimp in the Babitonga bay and the adjacent marine area. In addition, the effectiveness of the closed seasons is evaluated in light of the lifecycle of the white shrimp in the Bay, aiming to contribute to fisheries management by providing updated information to government agencies.

2. Material and methods

Biological samples of the white shrimp were collected on a monthly basis between March 2016 and February 2018 in ten sampling stations. Six of the sampling stations were located in the inner area of Babitonga Bay (I to VI), one at the mouth of the bay (VII), and in three bathymetry bands in the adjacent marine region 7–10, 15, and 20 m depth (VIII, IX, and X, respectively) (Fig. 1). In the inner area, the biological samples were collected with the aid of a gerival of 15 mm stretched mesh size. In the adjacent marine area, a double-rig trawling boat equipped with nets of 4.5 m wide and 11 m long was used. Each net had a 30 mm mesh on the wings and body and a 20 mm mesh on the codend. The trawling time was standardized in 30 min in all marine areas. Each sample was kept in plastic bags, labeled and stored in ice for further processing in the laboratory.

In addition to the numerical abundance obtained at the sampling sites, climatic variables such as temperature, humidity, dew point, and pressure were obtained in instantaneous, minimum and maximum values from the meteorological station of Itapoá within the vicinity of the study area (INMET, 2020). Additional variables like wind (intensity, direction and blasts), radiation and the amount of rain were also obtained.

In the laboratory, white and pink shrimps were sort from the rest of the catch, being identified in accord to Perez-Farfante (1978). Shrimp sex was assigned based on the macroscopic observation of the telic in females and the petasma in males. The total length was measured in centimeters with a caliper (0.01 mm precision) between the tip of the rostrum to the end of the telson, and the total weight taken in grams.

The degree of gonad maturation for females considered the color and the relative size of the ovary, following a maturity scale adapted from Neiva et al. (1971), which distinguish four stages: [0] Immature, [1] Maturing, [2] Mature, and [3] Spawned. Males were classified into two stages based on the lateral projections of petasma: immature (separate) or mature (joined).

The total number of shrimp collected at each sampling station was compared through an analysis of variance (ANOVA), after verifying the assumptions of homogeneity of variance (Bartlett test) and normality (Kolmogorov–Smirnov) (Zar, 1999). When significant differences were found, a Tukey–Kramer test identified which means were different (Sokal and Rohlf, 1981).

The population structure was evaluated based on the monthly variations of the size classes and sex ratio among sampling stations.

A generalized additive model for location scale and shape (GAMLSS) (Stasinopoulos et al., 2017; Rigby et al., 2019) verified the temporal variability between sexual proportion and size classes. The proportion of individuals from both sex in each month (response variable) was compared between month and sex under a beta inflated distribution. The recruitment period was determined from the analysis of the temporal variability of the average total length of the shrimp in the adjacent marine region of the bay, assuming that reductions in size-frequency distributions would show the entry of juveniles into the adult stock (Chagas-Soares et al., 1995; Miazaki et al., 2018).

The size of the first gonad maturation which corresponds to the length was estimated for males and females using the method proposed by Vazzoler (1981). In this method cumulative percentages of mature shrimps of both sexes per size class are reconstructed until reaching 50%, where 50% of the specimens of both sex have the same chance of achieving sexual maturation. This size was interpolated over the length distributions and used to verify the performance of fishing on juveniles and adult shrimp in different areas (Branco, 2005) and was compared to other studies along Brazilian coast (Table 1).

The laying time was determined by the percentage of spawned females (stages 3) (Neiva et al., 1971; Chagas-Soares et al., 1995; Santos et al., 2008; Barioto et al., 2017), as females of penaeid shrimp do not keep eggs in their pleopods (Perez-Farfante, 1969; Dall et al., 1990).

Based on the numerical abundance of white shrimps found in each sample station a Bray-Curtis dissimilarity matrix was calculated. Bray-Curtis distance measures the similarity between every pair of samples and is recommended to handle with large proportion of zeros. The numerical abundance of white shrimps among sampling stations was tested in a non-metric multidimensional scaling analysis (NMDS) with 1000 permutations (Oksanen et al., 2020). This analysis allowed the identification of spatialtemporal patterns of abundance and to find directions in the ordination space towards which the environmental variables vectors changed most rapidly and to which they have maximal correlations with the ordination configuration (Oksanen et al., 2020). The significance of each environmental variable was determined from the calculated distance (p < 0.05). Non-significant variables were excluded. All analyses were performed in R 4.0.3 (R Core Team, 2020) using packages vegan, gamlss and ggplot2.



Fig. 1. (A) Location of the study area (red square) of *Litopenaeus schmitti* in Babitonga Bay, South Brazil, and related studies with the species throughout Brazilian coast. (B) Location of sampling stations of *L. schmitti* in the inner bay area (I, II, III, IV, V and VI), at the mouth of the bay area (VII) and on the adjacent marine area (VIII, IX and X) between March 2016 and February 2018.

3. Results

3.1. Abundance

The abundance of the white shrimp showed a similar pattern of temporal fluctuation inside the bay and in the adjacent marine area (Fig. 2A and B). In 2016 catches in the inner bay area were significantly higher than in the adjacent marine area in March, April, and May, and February 2017 ($F_{11-60} = 6896$; p <

0.0001). High numbers of white shrimps were also observed in January 2018 ($F_{11-60} = 9.805$; p < 0.0001) (Fig. 2A). No significant differences between months were observed in the catches of white shrimp at the mouth of the estuary and the adjacent marine region ($F_{11-36} = 1.854$; p = 0.08 and $F_{11-36} = 1.384$; p = 0.22, respectively). However, like in the inner bay area the highest yields also occurred in March, April, and May 2016 and 2017 and in January and February 2018 (Fig. 2B), but high abundances were also observed between June and July 2017 (Fig. 2B).



Fig. 2. Average monthly variation in the number of individuals of *Litopenaeus schmitti* captured in the inner bay area sampling stations (A) and the adjacent marine area (B) and (C) the number of individuals of *Farfantepenaeus brasiliensis* captured in the sampling stations located in the inner bay area between March 2016 and February 2018.

Table 1

Number of males and females, sex ratio, and length at first maturation for *Litopenaeus schmitti* in Babitonga Bay in the hereby study, and related studies with the species throughout Brazilian coast. S, related studies that analyzed sex ratio of *L. schmitti* throughout Brazilian coast (Fig. 1). M, males. F, females. SR, sex ratio. L50, length at first maturation of females distinguished for carapace length (CL) in millimeters and total length (TL) in centimeters for *L. schmitti*. *Source*: Related studies with the species throughout Brazilian coast were adapted from Freire et al. (2019).

S	Location	State	Initials	М	F	SR	L ₅₀	Reference
1	Lagoa do Papari	Rio Grande do Norte	RN	805	2795	0.3:1 ^a	CL 17.0 - TL 9.04	Santos and Freitas (2004)
2	Sirinhaém River	Pernambuco	PE	491	678	0.7:1 ^a	TL 14.2	Peixoto et al. (2018)
3	Coruripe	Alagoas	AL	851	792	1.1:1	CL 34.8 - TL 16.2	Santos (2010)
4	Sergipe	Sergipe	SE	208	296	0.7:1	CL 12.5 - TL 7.22	Silva (2016)
5	Sergipe	Sergipe	SE	81	110	0.7:1 ^a	-	Freire et al. (2019)
6	Rio de Janeiro	Rio de Janeiro	RJ	437	355	1.2:1	-	Carvalho (2013)
7	Baixada Santista (Estuary)	São Paulo	SP	334	1008	0.3:1ª	CL 15.8 - TL 8.55	Santos et al. (2008)
8	Ubatuba	São Paulo	SP	567	78	-	-	Bochini et al. (2014)
9	São Vicente (Estuary)	São Paulo	SP	800	1041	0.8:1 ^a	-	Lopes (2012)
9	São Vicente (Marine Region)	São Paulo	SP	1502	1772	0.9:1 ^a	-	Lopes (2012)
10	Cananéia	São Paulo	SP	504	598	0.8:1 ^a	CL 26.7 - TL 12.9	Barioto (2017)
11	São Francisco do Sul (Estuary)	Santa Catarina	SC	-	-	-	TL 15.2	Machado et al. (2009)
12	São Francisco do Sul (Estuary)	Santa Catarina	SC	1493	1626	0.9:1	TL 15.16	Hereby Study
12	São Francisco do Sul (Marine Region)	Santa Catarina	SC	573	612	0.9:1		Hereby Study

^aIndicates sex ratio statistically different from 1:1.

In general, both adjacent marine and inner areas presented smaller catches of the white shrimp from August to December (Fig. 2A and B). However, when analyzing the catch data for the pink shrimp *F. brasiliensis*, the greatest abundance was found in the inner bay area precisely in the periods of the low abundance of the white shrimp, especially in October to December 2016 and 2017, as well as in January 2017 (Fig. 2C).

Regarding the spatial variability of the white shrimp, no significant differences were found for the inner bay area ($F_{5-138} = 0.442$; p = 0.82) (Fig. 3A), whereas in the adjacent marine area the catches were significantly higher ($F_{3-92} = 8.121$; p < 0.0001), between 7 and 10 m depth (Station VIII), showing a decreasing trend in numbers of shrimps with increasing depth (Fig. 3B).



Fig. 3. Average spatial variation in the number of individuals of *Litopenaeus schmitti*, along the inner bay area sampling stations (A) and on the adjacent marine area (B) of Babitonga bay between March 2016 and February 2018.

3.2. Sex ratio

In the period from March 2016 to February 2018, 3119 white shrimps were caught inside the bay, of these 1493 males (47.87%) and 1626 females (52.13%) (Fig. 4A, Table 1). Specimens of the white shrimp caught at the mouth of the bay, as well as in the adjacent marine area revealed a distribution pattern between sexes like that observed in the inner region, with a balanced sex ratio, 573 males (48.35%) and 612 females (51.65%) (Fig. 4B). The gamlss test revealed no significant differences in sex ratio for the inner bay area (GAMLSS, *t.value* = -0.261, p = 0.795, (Fig. 4A) or the adjacent marine area (GAMLSS, *t.value* = -0.549, p = 0.589, (Fig. 4B).

3.3. Size structure

The total length of the white shrimp captured in the inner bay area varied from 6.8 to 16.5 cm for males, and between 4.3 and 19.0 cm for females (Fig. 4A). Males were dominant only in the class of 6 cm, while females dominated the larger (Fig. 4A). In the adjacent marine area, the specimens were larger, with males varying between 9.0 and 18.0 cm, and females from 9.0 to 21.6 cm (Fig. 4B). Males showed higher numerical abundance between 9.0 and 12.0 cm, while females predominated in 10.0 cm and mainly in the higher size classes, between 16.0 and 21.0 cm (Fig. 4B). The other lengths classes analyzed were more equally distributed between sexes (Fig. 4B). In the inner bay area, the highest frequencies of juveniles occurred between 9.0 and 11.0 cm of total length, especially for females (Fig. 4B). In the sampling stations I and II, the modes were more frequent concentrated between 9.0 and 10.0 cm, while in the other locations a displacement to larger classes occurred in 10.0 and 11.0 cm (Fig. 4B).

A gradual increase in the size of the white shrimp was observed towards the mouth of the bay (Fig. 5).

3.4. Recruitment

A single-mode belonging to a homogeneous group was found in the inner bay area. This group was present in the catches during the first months of the year (January 2018, February 2017/2018; March 2016/2017 and April 2017) when the highest frequencies of juveniles (size class < 10 cm for males and < 15 cm for females) were observed. Monthly modes have progressively moved to the right until the end of the year. A great reduction in the number of immature individuals of the white shrimp captured occurred in September, but a few stragglers stay inside the estuary until December (Fig. 6). The cycle repeats at the beginning of the next year with the entry of a new class that followed the same trend.

In the adjacent marine region, the highest percentages of juveniles were observed in February (2017 and 2018), March (2016 and 2017), and in January 2018, thus constituting the main periods of recruitment when juveniles leave Babitonga Bay to incorporate the adult stock at sea. In addition to these months, in May 2017 a small entry of juveniles was observed in the adjacent marine area (Fig. 6), probably originated from an extended reproductive period of the species until December and January.



Fig. 4. Monthly frequency distributions and percentage of occurrence of males and females of *Litopenaeus schmitti* per total length class in the inner bay area (A) and the adjacent marine area (B) between March 2016 and February 2018. In Fig. 4B, number above the y axis indicate the number of males and females used, respectively.



Fig. 5. Size distribution of *Litopenaeus schmitti* by total length separated by sex in Babitonga Bay between March 2016 and February 2018. Sampling stations were represented by numbers I to X.

3.5. Reproductive aspects

The great majority of the females captured in the inner area of Babitonga Bay (1596; 98.15%) were placed in the first stage of gonad development, while 25 of them (1.54%) were in the maturation process and only five females (0.31%) presented mature gonads. No female with empty gonads was found inside the bay, indicating that spawning does not occur in the estuarine environment. In the adjacent marine area, 182 (29.74%) had gonads at some stage of development, with 111 (18.14%) through maturing, 49 (8.01%) were mature and 22 (3.59%) presented empty gonads (Fig. 7A). The highest occurrences of females with empty gonads (12 specimens) concentrate on the sampling stations IX at 15 m



Fig. 6. Monthly frequency distribution of total length class of males (dashed line) and females (solid line) of *Litopenaeus schmitti* for the inner bay area (IBA) and in the adjacent marine area (AMA) of Babitonga Bay between March 2016 and February 2018.

(Fig. 7B), and recorded at depths of 7–10 and 20 m (stations VIII and X, respectively).

Female gonad development was observed in all months except in August and September 2016 and July 2017. Despite the

presence of females with empty ovaries in November, January, and March 2016 to 2017 and in October, December, and February 2017 to 2018, the highest percentages occurred in November 2016 and October 2017 (Fig. 7A). This result allowed us to infer



Fig. 7. Frequency distributions of gonadal stages for females of *Litopenaeus schmitti* in the adjacent marine area of Babitonga Bay accumulated by month (A) and sampling stations (B) between March 2016 and February 2018.

that the spawning of the white shrimp extends from spring to the end of summer.

The length of the first sexual maturity of the white shrimp caught in the inner bay and in the adjacent marine areas was 10.4 cm for males and at 15.16 cm for females. Males and females reached 100% of sexual maturation at 12.5 cm and 15.5 cm in total length, respectively (Fig. 8).

3.6. Spatial-temporal patterns in abundance

The NMDS showed a clear separation between the sampling stations placed in the inner bay area and adjacent marine zone off Babitonga Bay (Fig. 9). The high records of *L. schmitii* numerical abundance were associated with inner bay area between January and September and at the adjacent area during the spring time (October to December). A significant inter-annual variation in the internal stations was associated with higher values of humidity (Fig. 9). In the adjacent coastal region, on the other hand, a significant influence of radiation and windblasts was detected. The amount of rain, expressed by contour lines (Fig. 9), in spite of the absence of significant importance (p > 0.05), showed that the highest abundance values recorded in sampling stations II and III in the inner bay area and VIII in the adjacent marine area were associated with a similar level of rainfall (Fig. 9).

4. Discussion

Several factors had been pointed out as responsible for variations in penaeid shrimp abundance, especially those linked to fluctuations in abiotic limits, with emphasis on temperature, salinity (Castilho et al., 2008; Santos et al., 2008; Bochini et al., 2014), the texture and the organic matter content of the sediment (Dall et al., 1990; Nakagaki et al., 1995; Bochini et al., 2014). Biotic variables such as community composition, intra and interspecific relationships and the species' life cycle interrelated may shape the distribution of penaeid shrimp (Mello, 1973; Chagas-Soares et al., 1995; Nakagaki et al., 1995; Pérez-Castañeda and Defeo, 2005; Castilho et al., 2008).

Two different sampling strategies were used due to the environmental conditions of the study area, due to the low depths in the inner areas, which did not allow typical shrimp trawling to be performed, besides the fact that this method is prohibited in these locations. Thus, it was only possible to use the gerival, which is the main method of capturing shrimp by artisanal fishermen in the Babitonga Bay. In the adjacent marine areas, the use of gerival is not possible due to the increasing depths (limitation of the gear).

In general, the white shrimp have shown high abundance in the warmest months of the year, in areas closer to the coast, with a preference for muddy bottoms, with medium to high levels of organic matter, which favor their food, in addition to facilitating the burial activity to avoid predation (Coelho and Santos, 1993; Chagas-Soares et al., 1995; Santos et al., 2008; Santos, 2010; Bochini et al., 2014). According to Santos and Freitas (2004) and Bochini et al. (2014) rainfall also plays an important role to govern the white shrimp distribution, with the best yields being obtained after the rainy seasons.

In the inner Babitonga Bay area, the greatest abundance of white shrimp also occurred during the warmest months and after the period of greatest precipitation (spring and early summer) (Camacho and Souza-Conceição, 2007). The highest yields occurred just after in February, March, April, and May 2017, while in the second year (2018), the highest catches of the white shrimp occurred both in the inner sampling stations, and at the bay mouth and in the adjacent marine area during January.

These results align with those observed for the São Paulo coast in the estuarine and marine region of the Baixada Santista (Santos et al., 2008), in Cananéia (Chagas-Soares et al., 1995), and in Ubatuba (Bochini et al., 2014) (Fig. 1). On the other hand, they differ from the pattern observed by Santos and Freitas (2004), in the Papari lagoon, in Rio Grande do Norte, where the highest catches of the white shrimp occurred from August to September, as well as in Alagoas (AL), showing the greatest abundances in August (Santos, 2010) (Fig. 1). The reproductive asynchrony between northeastern and southern Brazil fishing areas of the white shrimp was demonstrated by Santos et al. (2008) and Peixoto et al. (2018). This difference is probably associated with the rainfall regime in these two regions, which intensify in southern Brazil during the spring months (October to December) in contrast to the dry season in the northeast region (CPTEC/INPE, 2020).

Regarding the spatial variability of the white shrimp, in the present study, no significant differences were found inside the bay, although the nominal abundance observed was slightly higher in sampling stations II and III. Such stations seemed to be characterized as the preferred fishing areas of the artisanal white shrimp as observed in this study, possibly associated with the high supply of food derived from the continental contribution which increases biological production (Camacho and Souza-Conceição, 2007), and configure themselves as adequate depth for the species (Iwai, 1973).

On the other hand, the intense silting inside the Linguado Channel (sampling station I) resulted from a weak water flow at this site after the closure of this channel in 1935 (Cristofolini et al., 2011) could explain the smallest nominal abundance observed at this site. However, this region (Linguado Channel) can be considered a nursery ground for the white shrimp, given the smaller length classes found in this site.

In the sampling station at the mouth of Babitonga Bay (VII) and in the adjacent marine region (VIII–X), the distribution pattern of the white shrimp corroborated those observed along the Brazilian coast (Chagas-Soares et al., 1995; Santos and Freitas, 2004; Santos et al., 2008; Santos, 2010; Bochini et al., 2014; Santos et al., 2017). The greatest abundance was observed in the shallowest



Fig. 8. Size of first gonadal maturation for males (a) and females (b) of Litopenaeus schmitti, in the Babitonga Bay region between March 2016 and February 2018.



Fig. 9. Graphical representation of the non-metric multidimensional scaling analysis (NMDS) for the environmental variables collected from the Itapoá meteorological station and the numerical abundance of *L. schmitti* at the sampling stations. The NMDS aimed to identify spatio-temporal patterns between the environmental variables and the numerical abundance of *L. schmitti* in the inner bay area (I to VI), mouth of the estuary (VII) and in the adjacent marine region (VIII–X) between March 2016 and February 2018. The black dots represent each sampling campaign (MAR 2016–FEB 2018). In red, the sampling stations (I–X), and the numbered boxes months of the year. The green lines show the rainfall modeled according to the ordering scores of the NMDS. The arrows represent the significant environmental variables. R, solar radiation. WB, wind blasts. H_ins, H_min and H_ max, represents the instantaneous, minimum and maximum humidity.

areas close to the estuarine region (between 7 to 10 m depth), with a significant decrease in the number of specimens to 20 m depth, most likely linked to the sedimentary composition (Dall et al., 1990; Nakagaki et al., 1995; Bochini et al., 2014). The lower nominal values of shrimp abundance at station VII could be associated to an intense hydrodynamic in that region (Subrahmanyam, 1971).

The sex ratio between males and females approached the expected 1:1 ratio in the population, with slightly higher values in favor of females in total catches, both in the inner bay area and the adjacent marine region, as observed in Rio de Janeiro, Alagoas, and Sergipe (Carvalho, 2013; Santos, 2010; Silva, 2016 respectively) as recently reviewed by Freire et al. (2019) (Table 1). Conversely, in the littoral of São Paulo (Santos et al., 2008), Alagoas (Santos and Freitas, 2004; Santos et al., 2004, 2005), and Pernambuco (Peixoto et al., 2018) a significant dominance of females had been observed. Coelho and Santos (1993) suggest

that these differences in the proportions between males and females are related to the reproductive cycle, with approximation of the percentages between the sexes (\sim 50%) in mating areas, since in the spawning areas the frequency of females would be higher. In addition to the reproductive pattern, such disparities between the sexes would be attributed to the rates of growth, mortality, longevity, different migration between the sexes and selectivity of the fishing gear (D'Incao, 1990; Albertoni et al., 2003; Santos and Freitas, 2004; Santos et al., 2004; Pérez-Castañeda and Defeo, 2005; Leite and Petrere, 2006a,b; Santos et al., 2008, 2017; Freire et al., 2019).

Sexual dimorphism related to size is common among crustaceans, especially in penaeid shrimps, where the large volume of cephalothorax in females allows a large production of oocytes, resulting in high fertility rates (Boschi, 1969; Perez-Farfante, 1970; Heckler et al., 2013). In general, females achieved larger sizes than males (Santos et al., 2006; Santos and Freitas, 2004; Miazaki et al., 2018), corroborating the observations in the present study. Coelho and Santos (1994) found that females become larger than males after the fourth month of life.

The life cycle of the white shrimp begins with reproduction in the marine environment followed by the entry of post-larvae into the estuaries, where they grow, given the high food supply and natural refuges against predators, culminating in the later migration of these juvenile specimens to the sea from 3 to 4 months after reproduction (Perez-Farfante, 1970; D'Incao, 1991; Chagas-Soares et al., 1995; Santos, 2000; Santos and Freitas, 2004)). The spawning period in the adjacent marine area occurs during spring and summer around 15 m depth concentrated in October and November corroborate other studies along the São Paulo coast (Chagas-Soares et al., 1995; Santos et al., 2008; Barioto et al., 2017; Miazaki et al., 2018).

The spawning ground at 15 m depth may favor penaeid larvae to be transported within inshore waters, namely the inner bay area (Subrahmanyam, 1971). Tidal currents are particularly effective in the transport of penaeid larvae into coastal bays until 10 m depth. In the coast of Florida, Idyll et al. (1962) have shown that tidal and wind driven currents were responsible for penaeid larvae transport from 15 to 33 m depth. Moreover, during the spring season, moderate to strong winds are also common, arising from convective systems that originate wind blasts, blowing from the high seas to the land (CPTEC/INPE, 2020). Thus, the combination of the preferable spawning ground (15 m) during the spring time evidenced the timing of the white shrimp life cycle with the environment of Babitonga Bay, as observed in other penaeid species (Subrahmanyam, 1971).

Shrimp species tend to adjust their reproductive periods with the most favorable food supply conditions for larvae development after hatching (Thorson, 1950; Costa and Fransozo, 2004; Castilho et al., 2008; Barioto et al., 2017). The increase in temperatures joined to the intense volume of rainfall during the spring and early summer increase the primary production in the bay (Camacho and Souza-Conceição, 2007; Marafon-Almeida et al., 2008), providing an ideal environment for the larvae to grow, passing through the ontogenetic stages (nauplius, protozoa and mysids) in the plankton in four weeks (Perez-Farfante, 1970; Dall et al., 1990)). Considering the analysis of the length distributions in the inner bay area, and the main spawning peak in November 2017, larvae settlement is likely to occur in December, experiencing intense growth conditions (Viosca, 1920; Gunter, 1950; Williams, 1955) being available to the fishing inside the bay in January and the further migration to fishing on the adjacent marine region in February. In this way, the fishing in the inner area of Babitonga Bay would be acting mainly on the juvenile stock, with white shrimp from 3 to 4 months old.

Considering the entire sampling period, two reproductive cycles of the species had been covered. Therefore, it was possible to infer that the main periods of recruitment to the marine environment occurred in February and March, according with previous research (Neiva et al., 1971; Chagas-Soares et al., 1995; Santos et al., 2008; Barioto et al., 2017; Miazaki et al., 2018). However, some laggard specimens remained in the estuarine environment until the months of September and October, where females with mature gonads were common, with complete disappearance in December.

According to Kutkuhn (1966), penaeid shrimp's residence in estuarine environments tends to vary according to the behavioral requirements of each species, and for *F. paulensis* it can extend up to 10 months in the estuary from Lagoa dos Patos in Rio Grande do Sul (RS) (D'Incao, 1991). For the white shrimp, this period varied from 6 to 9 months (Ewald, 1965; Neiva et al., 1971), and from 1 to 5 months (Coelho and Santos, 1994). Barioto

et al. (2017) stated that this migration of maturing individuals to the marine region would be related to a decrease in the species' physiological tolerance, mainly related to salinity.

Pacheco and Wahrlich (2003) had previously reported that shrimp fishing is the main way of living for artisanal fishermen that use the gerival in the Babitonga Bay, with the white shrimp being responsible for the largest productions, although the pink shrimp *F. brasiliensis* and *F. paulensis* were also present. These authors highlighted a marked alternation in abundance between the species *L. schmitti* and *Farfantepenaeus* spp., so that in December the catches were entirely composed of the pink shrimp, reaching around 50% in January and only 2.6% in March, while the white shrimp showed an increase in catches from January, being dominant in February and March.

The results obtained in the present study confirm this alternation between the white and pink shrimp populations, clearly demonstrating the presence of two important fishing seasons for artisanal fishermen in the inner bay area: one between February and May for white shrimp and another from October to December (possibly extending to January), for the pink shrimp.

The length of first sexual maturation is an important biological indicator in the study of exploited populations, providing subsidies on how the exploratory activity is acting on the reproductive individuals (Vazzoler, 1996; Campbell and Fielder, 1986). The overlap of this size with the carapace width curves also allowed to estimate the stratum of the population is most subjected to the directed fishery (Branco and Verani, 1998a,b; Branco, 2005).

In Babitonga Bay, the estimated length at first maturation for the white shrimp (15.16 cm) was very close to that found for Machado et al. (2009) (15.2 cm) in the same area. In this way, artisanal fishing in the inner bay area should predominantly act upon the juvenile stock of white shrimp, as well as that observed in other Brazilian estuaries. Such information corroborates Babitonga's bay importance in the life cycle of several commercial species of regional interest, which could be considered as a nursery for white shrimp, with emphasis on the regions of the Linguado Channel (station I) and the mouth of the Morretes River (station III), where the smallest lengths had been registered.

Studies conducted on the reproductive biology and recruitment dynamics of penaeid species ((Staples and Rothlisberg, 1990; Dall et al., 1990; Coelho and Santos, 1994; Santos et al., 2017)) suggested spatial patterns in reproductive dynamics may exist, associated with environmental variations due to their wide distribution. In this way, one could expect that fisheries regulations, especially the closed seasons, should be adapted to the biological, social and economic specificities of each region. However, this is not what has been observed in practice, as reported by artisanal fishermen during the field activities. Indeed, the present data demonstrated that the white shrimp recruited predominantly in February and March, showing that the defense instrument in the region seems to be better adjusted to the pink shrimp lifecycle rather than to the white shrimp's. On the other hand, the open sea shrimp closure period partially contemplates juvenile recruitment of the white shrimp, allowing recruits to integrate the fishing stock and complete the life cycle, with the reproduction occurring mainly during the spring fishing season (October and November).

5. Conclusions

The results hereby obtained showed that the current closed season partially protects white shrimp spawning and recruitment in Babitonga Bay and the adjacent marine area. Methods applied demonstrated that biological and reproductive attributes of *L*.

schmitti are synchronized with regional environmental variables of Babitonga Bay, thus providing significant information for revision in the current ordinance efficiency for this region. It is noteworthy that in addition to ensuring juvenile specimens migration from the Babitonga Bay estuary, with fishing restrictions during the months of February and March could also be taken into account the protection of the spawning females in October/November as a way of maintaining stocks of white shrimp in the region.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Felipe Freitas Junior: Conceptualization, Investigation, Formal analysis, Methodology, Writing - original draft. Rafael Schroeder: Investigation, Formal analysis, Methodology, Writing - review & editing. Juliano César Hillesheim: Investigation. Roberto Wahrlich: Writing - review & editing. Fernando Luiz Diehl: Resources, Writing - review & editing. Joaquim Olinto Branco: Conceptualization, Investigation, Methodology, Supervision, Writing - review & editing.

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