



Effects of biological and environmental factors on the variability of *Paralonchurus brasiliensis* (Sciaenidae) density: An GAMLSS application

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ABSTRACT

The hypothesis of this study was based on the premise that complex interactions between biological and environmental factors may explain variability in fish population dynamics. To test this, *Paralonchurus brasiliensis* (Sciaenidae), a keystone species associated with coastal waters, was used as a model fish species. Generalized Additive Models for Location, Scale and Shape were performed to evaluate relationships among biological and environmental variables. Fish biomass, repletion index (RI), hepatosomatic index (HSI), condition factor (K) and sex ratio was in models as biological factors whereas water temperature, salinity, organic matter, grain size and depth were included as environmental variables. The results revealed significant effects of biological and abiotic factors on population density of *P. brasiliensis*. The selected model explained 94% of the variability in the explanatory variables. Fish biomass, HSI and K were the most important biological factors, whereas temperature and organic matter were the most important abiotic factors. Variability in fish density suggests that HSI and K both could be used as an additional ecosystem indicator of environmental status (food availability) and fish population health. We also highlight the importance of using robust and flexible statistical methods to model fish population dynamics and the need to incorporate biological and environmental factors into fishery resource management.

1. Introduction

A central question in ecology is what causes fluctuations in population abundance and distribution (Heath, 2006; Shelton and Mangel, 2011). The relationships between environmental factors and the abundances of marine organisms have received considerable attention in fishery sciences (Cury et al., 2003; Orio et al., 2019; Alheit and Peck, 2019). In addition, information on fish biology and the environment in which individuals live is essential for identifying the appropriate management tools that are needed to maintain sustainably manage fish populations (King, 2007). Among the biological indices used in fishery science, fish density, biomass and condition indices (repletion index, hepatosomatic index-HSI and condition factor-K) have been identified as indicators of changes the level of the organism, population and ecosystem (Lloret et al., 2014; Izzo et al., 2016; Cantafaro et al., 2017;

Matthias et al., 2018; Rau et al., 2019).

HSI and K indices, for instance, have been used as a proxy for detecting feeding periods and fish habitats, assuming that they reflect the quality and amount of available food (Lloret and Planes, 2003; Cantafaro et al., 2017). Liver is an important organ for energy storage, and it is usually the first site for lipid (energy) storage in many demersal fish species (Lloret et al., 2014). For this reason, HSI has been used as a measure of body condition for indirectly evaluating energetic reserves and metabolic activity (Lloret and Planes, 2003; Lloret et al., 2014). On the other hand, K is a quantitative parameter of the well-being state of the fish, and it reflects recent feeding activities (Le Cren, 1951; Dutta, 1994). Changes in the K values indicate alterations in energy acquisition (Dutta, 1994). High values of the K indicate better condition of the fish due to abundance and/or high quality of preys in the ecosystem, showing that the fish are making good use of food resources in terms of

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energy acquisition (Weatherley, 1972; Nash et al., 2006). However, it should not be expected that a single factor will be solely responsible for generating fluctuations in populations; it is important to recognize the potential contributions of multiple factors and work toward understanding how these factors interact to affect the variability of natural populations (Wolf and Mangel, 2008; Shelton and Mangel, 2011; Mathias et al., 2018). Therefore, variability in fish density can be determined from the combined effects of biological and environmental factors that directly or indirectly affect general population dynamics (Cury et al., 2003; Orio et al., 2019; Perez et al., 2019).

The magnitude of impact of individual factors that cause variability in fish abundance and distribution is not simple to assess, mainly because environments are highly dimensional and nonlinear population-dynamic responses (Rothschild, 1991; Orio et al., 2019; Rau et al., 2019). Thus, new statistical approaches with more flexible modeling structures are needed for a better understand variability on wild fish populations. Generalized Additive Models for Location, Scale and Shape (GAMLSS) is a modern distribution-based approach to regression analysis that expands the classical Linear Regression Model (LM), Generalized Linear Models (GLM) and Generalized Additive Models (GAM),

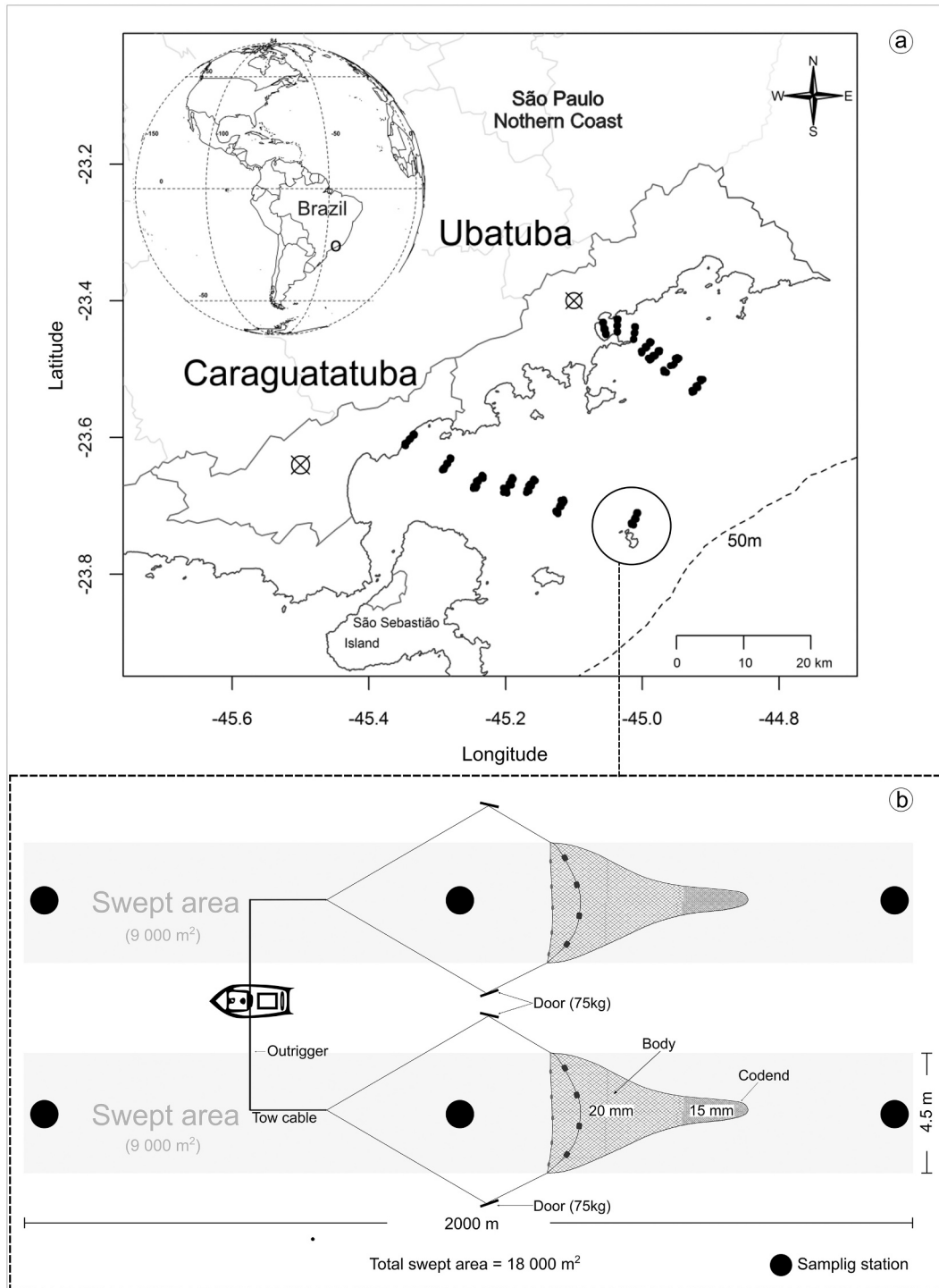


Fig. 1. Areas of study and sampling method; a- Caraguatatuba and Ubatuba regions, inner shelf of São Paulo State, Brazil, b- method used for sampling the demersal fish *Paralichthys brasiliensis*. Black circles indicate sample stations for abiotic factors.

which are focused on the mean, to accommodate distribution parameters that are modeled as additive functions of predictor variables (Rigby and Stasinopoulos, 2005; Stasinopoulos et al., 2017; Groll et al., 2019). The main features of GAMLSS are that the distribution of the response variable can be any parametric distribution, and all parameters of the distribution, not only the mean, can be modeled using linear, nonlinear or smooth functions, according to the explanatory variables (Rigby and Stasinopoulos, 2005; Stasinopoulos et al., 2017). In addition, the distribution of the response variable does not have to belong to the exponential family, as in conventional regression (Rigby and Stasinopoulos, 2005; Stasinopoulos and Rigby, 2007). Therefore, the response variable can assume from one to four parameter families of continuous distribution, according to the values of the explanatory variables, which also become GAMLSS highly flexible models (Stasinopoulos and Rigby, 2007; Groll et al., 2019).

The species *Paralanchurus brasiliensis* (Steindachner, 1996) (Actinopterygii, Sciaenidae) is a demersal fish that is widely distributed along the Atlantic coast from Central to south America (Menezes and Figueiredo, 1980). *P. brasiliensis* is a keystone species associated with shallow waters and is the most frequently and abundant sciaenid caught as by-catch by shrimp trawl fisheries in southeastern Brazil (Braga et al., 1985; Coelho et al., 1993; Soares et al., 2008; Souza et al., 2008; Costa et al., 2012). The entire life cycle of this species occurs in shallow coastal habitats in depths below 40 m (Paiva-Filho and Rossi, 1980; Braga et al., 1985; Coelho et al., 1993; Costa, 2010; Costa et al., 2012; Costa et al., 2018). *P. brasiliensis* seems to be ideally suited to evaluate how habitat conditions influence populations by using new statistical techniques. Thus, the objective of the present study was to apply GAMLSS models to investigate the complex interaction between biological and environmental factors on the variability of *P. brasiliensis* density in the southeastern Atlantic Ocean. To achieve this, biomass, repletion index, hepatosomatic index, condition factor and sex ratio were included in population models as biological factors whereas water temperature, salinity, organic matter, sediment size and depth were included as environmental variables.

2. Material and methods

2.1. Areas of study

The study areas were located on the inner shelf of the coastal system of Caraguatatuba and Ubatuba, northern coast of São Paulo State, Brazil. Caraguatatuba is considered a sheltered area compared to Ubatuba (Fig. 1a). Both ecosystems are strongly influenced by three water masses: Tropical Waters (TW; Temperature > 20 °C, salinity > 36), South Atlantic Central Waters (SACW; T < 20 °C, S < 36) and Coastal Waters (CW; T > 20 °C, S < 36) (Castro-Filho et al., 1987; Castro-Filho and Miranda, 1998). The intrusion of the cold, and nutrient rich SACW, during the spring and summer months (between November and March), is more intense in exposed areas, i.e., Ubatuba (Costa et al., 2012; Nogueira and Brandini, 2018). The spatial distribution of grain size (Phi) and organic matter content also differ between areas (Costa et al., 2012). The dynamics of the water masses and the spatial distribution of sediments affect nourishment condition and the reproduction of species inhabiting both ecosystems (Matsuura et al., 1992; Katsuragawa et al., 1993; Myashita et al., 2011; Costa et al., 2012). Therefore, temperature, salinity, type of sediment (grain size and organic matter content) and depth are important environmental factors influencing population dynamics of demersal fishes. These factors can affect life-history strategies and the distribution of individual species in different ways in different regions (Lowe-McConnell, 1987; Costa et al., 2012).

2.2. Biological data

Specimens of *P. brasiliensis* were captured as bycatch on a monthly basis from January to December 2002, during sea-bob (*Xiphopenaues*

kroyeri) shrimp fishing in the study areas. A shrimp fishing vessel with “double-rig” trawling nets was used for the samplings in Ubatuba (84 trawlings) and Caraguatatuba (84 trawlings). Each area was grouped into seven stations (depth), located at mean depths of 5, 10, 15, 20, 25, 30 and 35 m (Fig. 1a). Each depth was trawled over 30 min with the same speed (~2 knots), and at the same swept area (18,000 m²). The swept distance was measured by GPS from the position where the trawl settled onto the sea floor, to the position where the gear left the bottom (Fig. 1b). The sampling stations were based on the distribution of the sea-bob shrimps, which also coincide with the *P. brasiliensis* distribution, which ranges from 4.5 to 40 m (Souza et al., 2008; Costa et al., 2012). After trawling, the specimens of *P. brasiliensis* were separated from the others organism in the catches and the total number of individuals collected was registered.

In the laboratory, the fish collected were weighed (total weight of the sample by depth, i.e., the biomass), measured in standard length (SL, to the nearest mm) and sex was identified based on macroscopic description of the gonads (Vazzoler, 1996). To estimate fish density, the total number of fish collected by depth was divided by the swept area. Due to the values containing four decimal places, all density values were multiplied by 1000 for better visualization of the data (Costa et al., 2012).

Total weight (TW), somatic weight (SW- total weight minus gonads and stomach contents weights), digestive tract weight (DT) and live weight (LW) were estimated based on the equations proposed by Costa (2015) (Fig. A1). Sex ratio was estimated by dividing the number of females by the number of males. Condition indices (repletion index- RI, hepatosomatic index- HSI and condition factor- K) were calculated as follows: $RI = (DT/SW) \times 10^2$, $HSI = (LW/SW) \times 10^2$ and $K = (SW/aTL^b) \times 10^3$, where *a* and *b* are the intercept and slope parameters from the length-weight relationship equation, respectively (Fig. A1) (Lloret et al., 2014; Costa et al., 2018). Fish density was estimated based on the total number of fish captured (29,808 specimens), whereas biomass and the biological measurements were based on 5995 specimens sampled.

2.3. Environmental variables

All abiotic data were collected before trawling. Depth of each station was determined using a single beam echobathymeter. Temperature and salinity were measured with protected reversing thermometers attached to Nansen bottles and an optical salinometer, respectively. Sediment samples were collected at each station with a Van Veen grab (1/40 m²). In the laboratory, about 200 g of the sediment per station was dried at 70 °C for 24 h, divided into subsamples and submitted to organic matter and grain size analyses (Mantelatto and Fransozo, 1999). Organic matter (%) content was obtained by ash-weighing (Mantelatto and Fransozo, 1999; Costa et al., 2012). Sediment size was calculated in accordance with the Wentworth (1922) scale, in which the sediment is sieved in six sieves with different diameters to obtain gravel (2 mm), very coarse sand (2.0–1.0 mm), coarse sand (1.0–0.5 mm), medium sand (0.5–0.25 mm), fine sand (0.25–0.125 mm), very fine sand (0.125–0.063 mm) and silt-clay (smaller particles). Cumulative particle size curves were plotted using the ϕ scale with values corresponding to the 16th, 50th and 84th percentiles being used to determine the mean diameter (Md) of the sediment: $Md = (\phi_{16} + \phi_{50} + \phi_{84})/3$ (Folk and Ward, 1957). The ϕ values were calculated using the equation proposed by Tucker (1988), where $\phi = -\log_2 d$ (*d*, grain diameter in mm). Finally, the type of sediment was classified based on ϕ value ranges: $-1 = \phi < 0$ (very coarse sand); $0 = \phi < 1$ (coarse sand); $1 = \phi < 2$ (medium sand); $2 = \phi < 3$ (fine sand); $3 = \phi < 4$ (very fine sand) and $\phi \geq 4$ (silte-clay) (Fig. A6).

2.4. Statistical modeling approach

GAMLSS models were performed to evaluate the relationship between the response variable fish density (Dens) and the explanatory variables biomass, RI, HSI, K, Sex ratio (Sexrat), temperature (Temp),

salinity (Sal), organic matter (OM), mean grain size of the sediment (φ) and depth; region and month were included as factors. The variance inflation factor (VIF) was used to evaluate multicollinearity between explanatory variables; we select those variables that had VIF values less than four (Zuur et al., 2010).

A GAMLSS model assumes that y_i independent observations of a random variable Y (where $i = 1, 2, 3, \dots, n$) have the probability (density) function $f_Y(y_i|\theta^i)$ of four distribution parameters, i.e. $\theta^i = (\theta_{1i}, \theta_{2i}, \theta_{3i}, \theta_{4i}) = (\mu_i, \sigma_i, \nu_i, \tau_i)$, related to the explanatory variables and random effects, accounting for the location, scale and shape. The shape parameters (ν and τ) are often related to the skewness and kurtosis aspects of the distribution. Each distribution parameter θ_k is modeled by its own additive predictor (η_k):

$$g_k(\theta_k) = \eta_k = X_k\beta_k + \sum_{j=1}^m h_{jk}(x_{jk})$$

where $g_k()$ is the monotonic link function related to θ_k , X_k is the matrix of the explanatory variables, β_k is a coefficient vector, and $h_{jk}()$ is an unspecified smooth function of the explanatory variable x_{jk} for $k=1, 2, 3, 4$ and $j=1, \dots, J_k$. The functional dependence of $h_{jk}()$ on x_{jk} can be parametric (linear) or nonparametric (non-linear) via smoothing terms (Rigby and Stasinopoulos, 2005; Stasinopoulos and Rigby, 2007).

Statistical analyses were carried out in the R environment for statistical computing and visualization (version 3.6.1), using the packages ‘gamlss’ and ‘gamlss.dist’ (R Development Core Team, 2013; Stasinopoulos et al., 2017). Seven families of distributions, i.e., exponential, gamma, log normal, log normal (Box-Cox), normal, Weibull and Weibull (μ the mean), were tested using the command `gamlss(y~1, family = " ")` (Stasinopoulos et al., 2017; Rigby et al., 2019). The most adequate

probability distribution for y was selected by Generalized Akaike Information Criterion (GAIC). A cubic spline smoothing function (cs) was adopted in all models as an additive term function with varying degrees of freedom (Stasinopoulos and Rigby, 2007). The appropriate degrees of freedom in relation to each explanatory variable were estimated based on values of GAIC after application of the functions ‘quote()’ and ‘find.hyper()’. The latter function minimized GAIC with a penalty term $k = 2$ by default (Stasinopoulos et al., 2017). The worm plot function, ‘wp()’, was applied to detect inadequacies in the final model and within specific ranges of the explanatory variables, i.e., to analyze how well the final model fit the data and to find locations at which the fit could be improved (van Buuren and Fredriks, 2001; van Buuren, 2007; Stasinopoulos et al., 2017). A total of 13 possible model combinations were created and tested. The best fit model was also selected using the function ‘GAIC()’ (Stasinopoulos et al., 2017; Rigby et al., 2019). The ‘drop1()’ function revealed the significance of each smoothing term in the selected model. The relative importance of these terms was assessed based on the AIC, likelihood-ratio test (LRT) and the probability of the Chi-squared test criteria (PrChi) (Stasinopoulos and Rigby, 2007; Stasinopoulos et al., 2017). The Generalized R-squared (Nagelkerke’s R^2) for GAMLSS models was calculated to estimate the proportion of variance explained by each model as also a measure of success of predicting the dependent variable (Nagelkerke, 1991; Stasinopoulos et al., 2017).

3. Results

3.1. Variability of the biological traits and environmental predictors

A total of 29,809 specimens of *P. brasiliensis* was collected during the period of study. In general, the lowest and highest median values of the

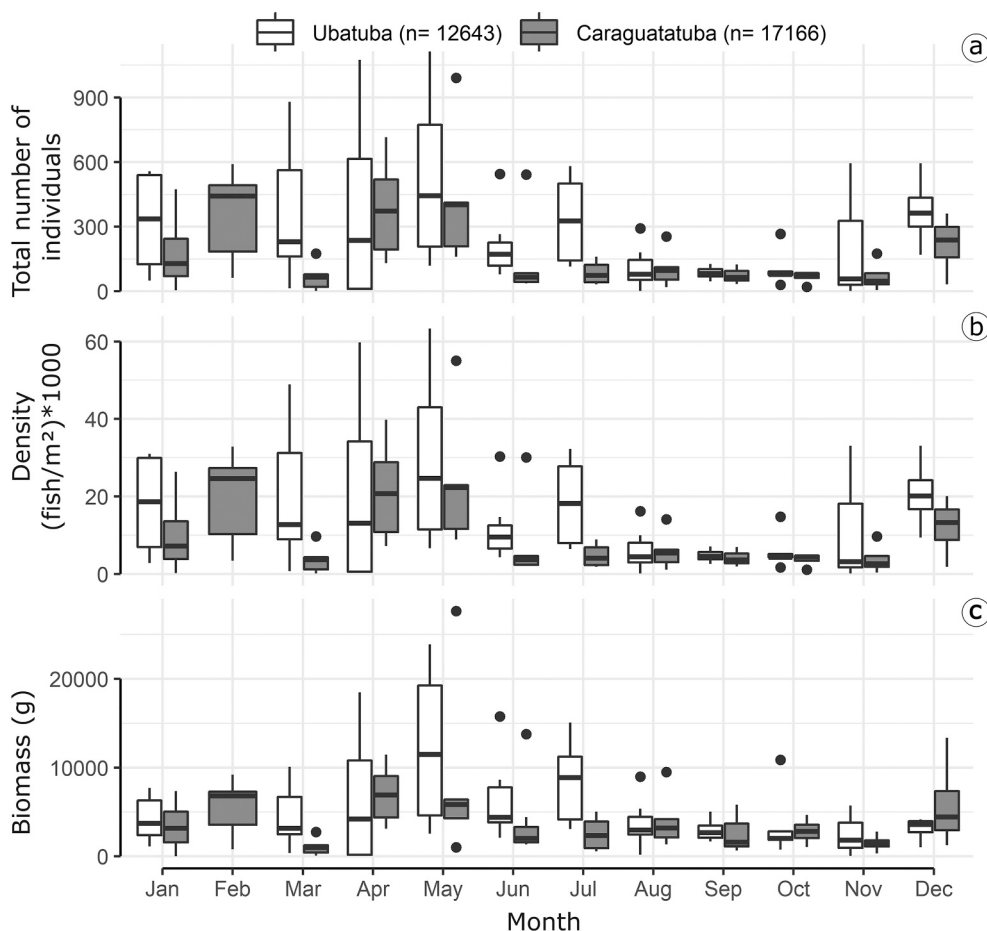


Fig. 2. Box plots of the total number of individuals (n), density and biomass of *Paralonchurus brasiliensis* sampled by month at Ubatuba and Caraguatatuba, northern coast of São Paulo State, Brazil. The central box represents the 25th to 75th percentile range; lines inside the box show the median and 95% confidence interval for median value; the whiskers extend from the minimum to the maximum value, excluding outliers, which are illustrated by the black circles. The sample size is given between brackets.

number of individuals, biomass and fish density in Ubatuba and Caraguatatuba were recorded between August and November and between December and July, respectively (Fig. 2a, b, c) (Appendices, Table A1, Fig. A3). A total subsample of 5993 specimens was taken to analyze the composition of the population in terms of adults and juveniles, and to estimate the standard length, total weight and condition indices. The proportion of juveniles and adults varied between areas with the highest percentages of juveniles from January to April in both regions, September in Ubatuba and December in Caraguatatuba (Fig. 3; Appendices, Fig. A4). The size of both adults and juveniles also varied among months (Appendices, Fig. A5). The largest and heavier group of individuals were captured from June to December (Fig. 4a-b) (Appendices, Fig. A4). The condition indices HSI and K showed the lowest median values from November to February and the highest from March to June (Fig. 4c, d). The RI did not show a clear pattern (Fig. 4e) (Appendices, Fig. A6).

The environmental factors varied between areas and among months. The highest and lowest temperature and the lowest salinity were recorded in Ubatuba, whereas the highest salinity in Caraguatatuba (Fig. 5a, b). Organic matter content and φ also varied between areas and among depth (station). In Ubatuba, both variables tended to decrease as the depth increase. However, in Caraguatatuba, the highest percentages of organic matter were observed in the mean depths of 15, 20 and 25 m, whereas the highest φ values in 15 and 20 m, showing a decrease as increase the depth from 20 m (Fig. 5c, d) (Appendices, Table A2).

3.2. Model selection and validation

GAMLSS models revealed significant effects of biological and abiotic factors on population density of *P. brasiliensis*. The VIF value showed that the variance estimated coefficient of RI was inflated by a factor of 5.34, indicating that this variable was correlated with at least one of the other explanatory variables in the model (Table 1, Fig. A7). For this reason, RI was removed from all models.

AIC indicated mod0 as the best model (Table 2). Mean and variance of the mod0 residuals were 4.39^{-13} and 1.02, respectively. Lognormal distribution with two parameters (μ and σ) was selected by AIC as the best distribution for modeling the response variable density (Table A3, Fig. A2). The mod0 residuals attended the normality and homoscedasticity assumptions (see diagnostic plots for residuals in Fig. A8). However, only the scale parameter μ was fitted for mod0 because σ was constant for all explanatory variables ($\sigma = 0.2347$) (Figs. A9; A10).

The selected model explained 94% of the variability in the explanatory variables around the mean of fish density. The model included all biological variables except RI, which was excluded from all the models (Table 2). Likelihood ratio tests revealed fish biomass, HSI and K were the most important biological factors, but temperature and organic matter were the most important abiotic factors. Both region and month were also statistically significant (Table 3). The relationship between density and biomass of *P. brasiliensis* displayed a dome shaped effect with a peak at 15000 g (Fig. 6a). Fish density was negatively associated with HSI (Fig. 6b). Specimens in higher density exhibited better condition (K over 0.180) than those in lower density (Fig. 6c). Temperature

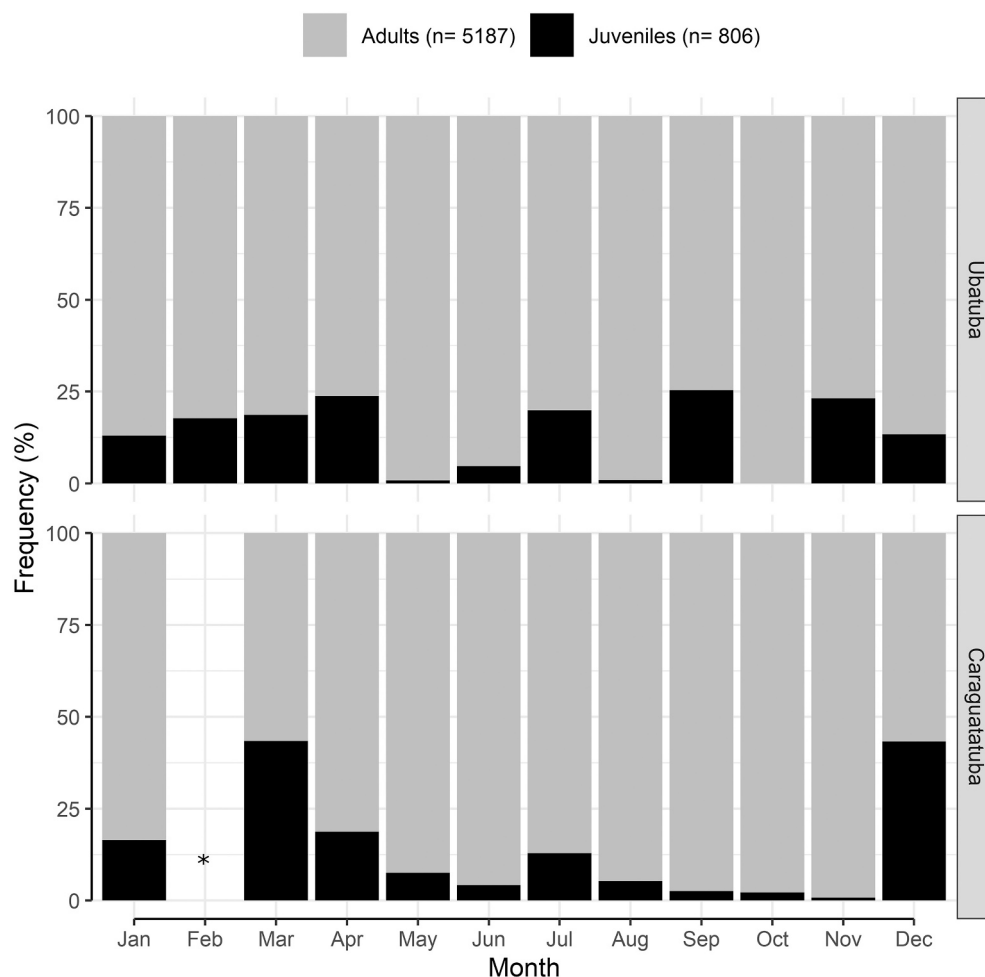


Fig. 3. Proportion of adults and juveniles of *Paralonchurus brasiliensis* sampled by month at Ubatuba and Caraguatatuba, northern coast of São Paulo State, Brazil. * No individuals were captured. The sample size is given between brackets.

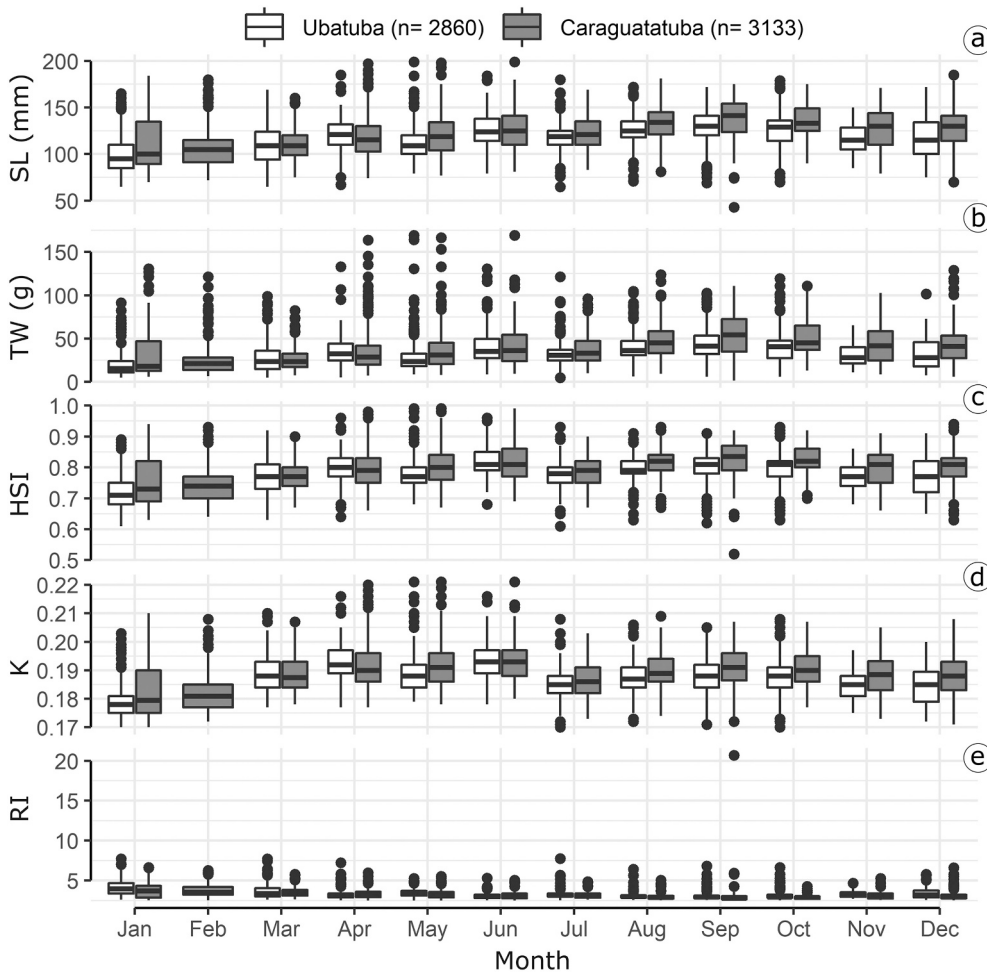


Fig. 4. Box plots of the standard length (TL), total weight (TW), hepatosomatic index (HSI), condition factor (K) and repletion index (RI) of *Paralochurus brasiliensis* sampled by month at Ubatuba and Caraguatatuba, northern coast of São Paulo State, Brazil. The central box represents the 25th to 75th percentile range; lines inside the box show the median and 95% confidence interval for median value; the whiskers extend from the minimum to the maximum value, excluding outliers, which are illustrated by the black circles. The sample size is given between brackets.

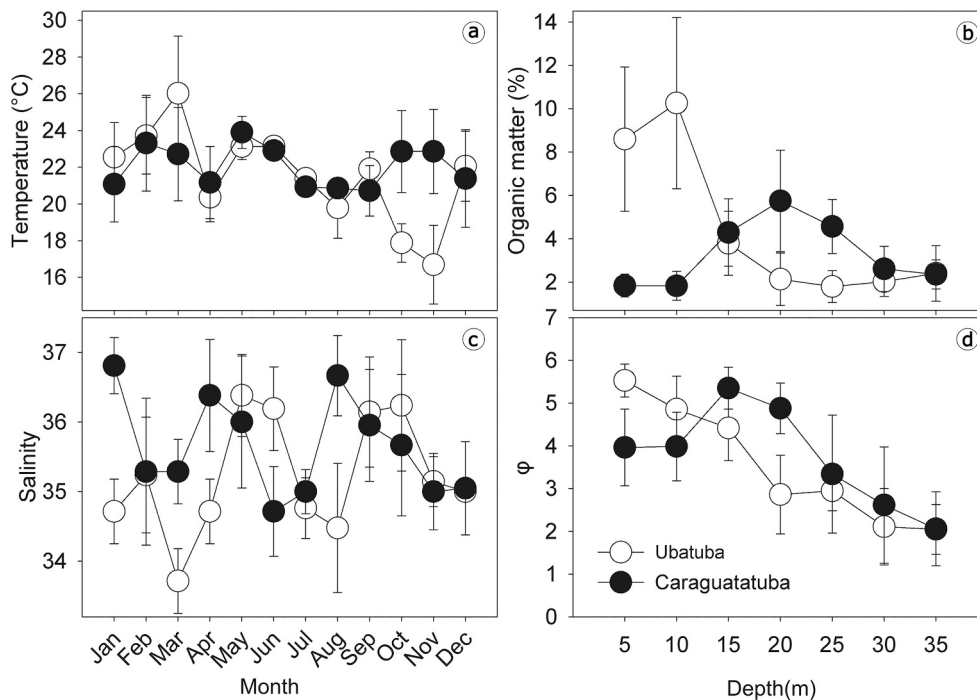


Fig. 5. Seasonal and spatial variation of the environmental variables temperature, salinity, organic matter and sediment grain size (ϕ - ϕ) measured in the regions of Ubatuba and Caraguatatuba, northern coast of São Paulo State, Brazil. Circles and bars represent the mean \pm standard deviation, respectively.

Table 1
Results of the variance inflation factor analysis (VIF).

Biological variables ^a					Abiotic variables ^a				
Biomass (g)	HSI	K	Sexrat	RI	Temp (°C)	Sal	OM	Phi	Depth (m)
1.50	3.76	3.39	1.22	5.34	1.35	1.32	1.74	2.26	2.17

^a HSI– hepatosomatic index, K– condition factor, sexrat– sex ratio (female/male), RI– repletion index, Temp– temperature, Sal– salinity, OM– organic matter, Phi– sediment grain size.

Table 2
Goodness of fit measures associated with the addition of each term to the GAMLSS model of fish density (Dens).

Models	AIC	R ²
<i>General model</i>		
mod0 Dens~ cs(Biomass) + cs(HSI) + cs(K) + cs(Sexrat) + cs(Temp) + cs(Sal) + cs(OM) + cs(Phi) + cs(Depth) + Region+Month	374.2	0.94
<i>Biological models</i>		
mod1 Dens~ cs(K) + cs(HSI) + cs(Sexrat) + cs(Biomass) + Region+Month	390.0	0.89
mod2 cs(K) + cs(HSI) + cs(Sexrat) + cs(Biomass) + Region	411.6	0.78
mod3 cs(K) + cs(HS) + cs(Sexrat) + cs(Biomass)	410.2	0.77
mod4 cs(K) + cs(HSI)	480.9	0.77
mod5 cs(Sexrat) + cs(Biomass)	408.0	0.72
<i>Abiotic models</i>		
mod6 Dens~ cs(Temp) + cs(Sal2) + cs(OM) + cs(Phi) + cs(Depth) + Region+Month	411.8	0.85
mod7 cs(Temp) + cs(Sal) + cs(OM) + cs(Phi) + cs(Depth) + Region	444.4	0.64
mod8 cs(Temp) + cs(Sal) + cs(OM) + cs(Phi) + cs(Depth)	443.9	0.63
mod9 cs(Temp) + cs(Sal) + cs(Depth) + Region	451.6	0.46
mod10 cs(Temp) + cs(Sal) + cs(Depth)	457.8	0.38
mod11 cs(OM) + cs(Phi) + cs(Depth) + Region	443.5	0.58
mod12 cs(OM) + cs(Phi) + cs(Depth)	444.2	0.56

HSI– hepatosomatic index, K– condition factor, Sexrat– sex ratio (female/male), Temp– temperature, Sal– salinity, OM– organic matter, Phi– sediment grain size, AIC– Akaike information criteria, R²– generalized R-squared, cs– additive cubic spline function. The selected model is indicated by bold type.

Table 3
Testing the significance of individual terms of the selected GAMLSS model (local parameter- μ).

Biological and abiotic variables	df	AIC	LRT	Pr(chi)	
Biomass	2.0	399.64	31.412	0.0000	***
Hepatosomatic index (HSI)	3.0	384.38	18.149	0.0011	**
Condition factor (K)	3.0	380.84	14.614	0.0056	**
Sex ratio (sexrat)	1.0	372.90	2.671	0.2630	
Temperature (Temp)	1.0	377.02	6.796	0.0334	*
Salinity (Sal)	2.0	368.82	0.593	0.8981	
Organic matter (OM)	3.0	379.65	13.422	0.0094	**
Sediment size (Phi)	4.0	372.47	8.238	0.1435	
Depth	2.5	369.76	2.530	0.5583	
Region	–	382.00	9.771	0.0018	**
Month	–	411.01	58.786	0.0000	***

AIC– Akaike information criteria, df– degrees of freedom, LRT– likelihood-ratio test, Pr(chi) – probability of chi-square, cs– additive cubic spline function.

*** 0.001.

** 0.01.

* 0.05.

negatively affected fish density (Fig. 6e). On the other hand, fish density was highest with sediments containing between 2% and 5% OM, then decreased with increasing OM (Fig. 6g). Specimens from Caraguatuba presented markedly higher density than those from Ubatuba (Fig. 6j). Temporal variability showed high densities of *P. brasiliensis* from January to May, as well as from November to December, and lower from

June to October (Fig. 6k).

Although sex ratio, salinity, Phi and depth were not found to be statistically significant effects, these variables contributed to explain fish density variability (Table 3). No effect of the sex ratio on fish density was observed up to the proportion of 4 females to 1 male; however, fish density declined as the sex ratio increased from 4 to 10 (Fig. 6d). Although salinity varied from 32 to 37, this variable did not significantly affect fish density (Fig. 6f). Phi exhibited two small peaks; at 3 and 5, decreasing from 5 to 6 (Fig. 6h). Finally, a slight variation in spatial distribution of the fish density was observed (Fig. 6i).

Worm plots of the residuals from the selected model also indicated lognormal was the most adequate distribution and mod0 was the best model for fitting the data, with more than 95% of the residual points falling within the acceptance region for variance, skewness and kurtosis (outside of the two elliptic curves) (Fig. 6l) (see also DTOP plot in Fig. A11).

4. Discussion

In the present study, GAMLSS models were applied to investigate the effects of both biological and environmental factors on the variability of *P. brasiliensis* density in the southeastern Atlantic Ocean. The dome-shaped relationship between fish density and biomass may indicate that the maximum density supported by the population and habitat has been reached. High abundances of *P. brasiliensis* usually occur during the summer and autumn (i.e., from late December to June) on the continental shelf of southeastern Brazil (Coelho et al., 1993; Rossi-Wongtenschowski et al., 2008; Costa et al., 2012). This species has a long recruitment period with the highest proportion of juveniles in the population recorded during the summer and autumn, coinciding with SACW intrusion (Costa, 2010). SACW movement is the most relevant mesoscale physical feature over the shelf of the Southeastern Brazilian Bight, impacting biological communities, causing considerable increases in primary production and subsequently zooplankton and benthic abundance, biomass and production (Léo and Pires-Vanin, 2006; Myashita et al., 2011; Nogueira and Brandini, 2018). On the other hand, at high abundances, fish populations approach the carrying capacity, resulting in reduced individual food intake in highest densities, promoting movement of individuals toward less suitable low-density habitats (Casini et al., 2014). Therefore, the period of high density and biomass of *P. brasiliensis* can be attributed to the recruitment period along with high food abundance in the area promoted by SACW intrusion. However, the decrease in fish density with increasing fish biomass can be explained by the migration of juveniles toward more suitable areas in terms of food availability and temperature.

Analyses of the HSI and K support the idea that food availability also plays an important role in regulating *P. brasiliensis* density in the study areas. The negative relationship between HSI and density can be attributed to food availability and/or a decline in consumption from June to October. The K analysis corroborates this idea. Thus, a positive relationship between the density of *P. brasiliensis* and K indicates feeding aggregation, during the period of food abundance with peaks of intense feeding activity (summer and autumn). Energy accumulated during this period is very important for growth of juveniles and the reproduction of those individuals in the onset of maturation and pre-spawning (Lloret et al., 2014; Cantafaro et al., 2017).

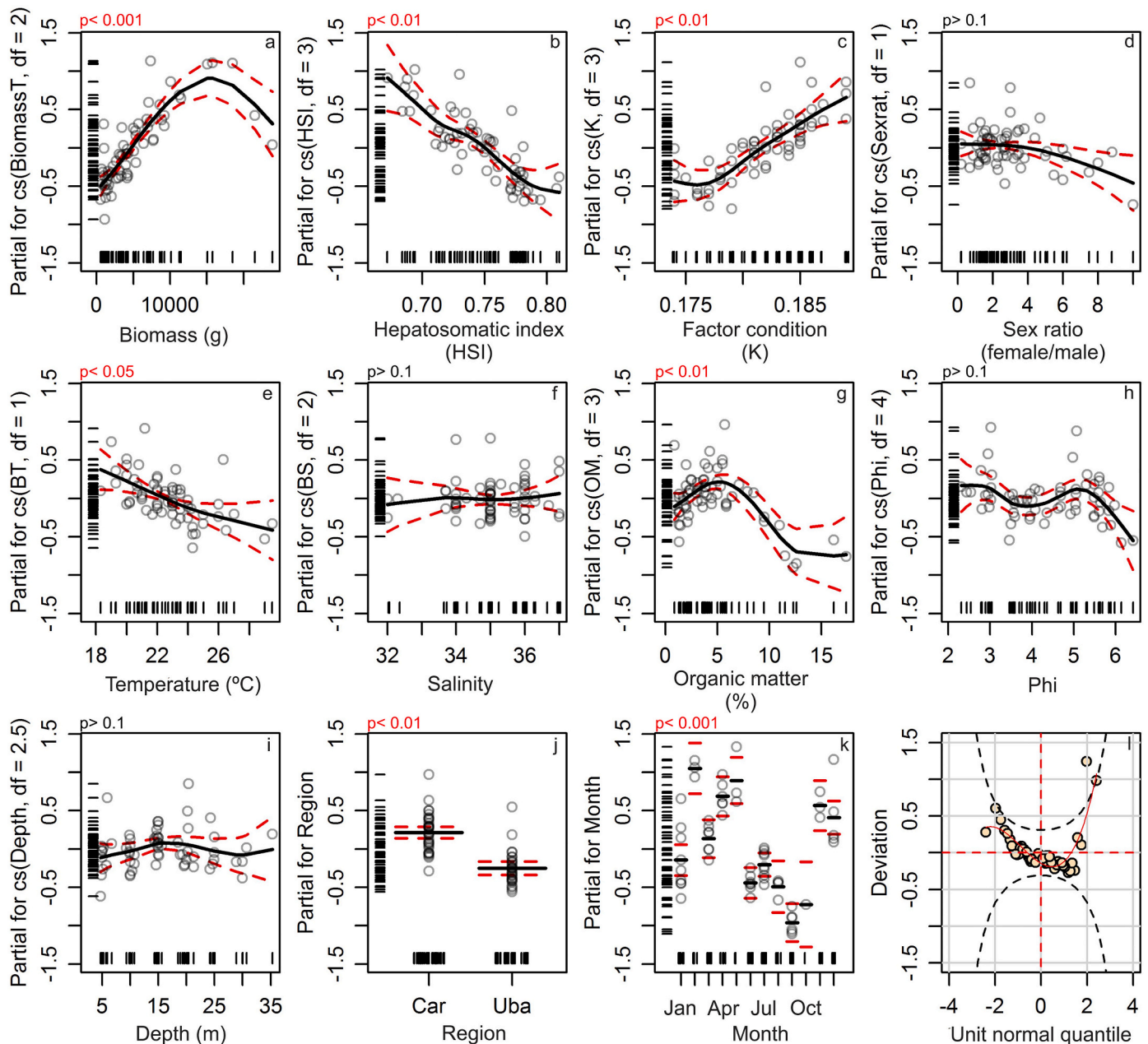


Fig. 6. Smoothed effects of the explanatory variables on the mean (local parameter- μ) of the population density of *Paralichthys brasiliensis*. Zero on the y axis indicates no effect of the predictor variable. Standard errors (dashed lines) and partial residual (points - y axis) have been added. Bands in worm plots (plot l- dashed lines) represent 95% confidence intervals. HSI- hepatosomatic index, K- condition factor, sexrat- sex ratio (female/male), Temp- temperature, Sal- salinity, OM- organic matter, Phi- sediment grain size, Car- Caraguatatuba, Uba- Ubatuba.

Fish in good condition are assumed to have larger energy reserves than poor-conditioned fish, with condition being strictly related to the recruitment and reproductive potential of the population (Lloret et al., 2014). Fish energetic status also influences the timing of sexual maturity and spawning in the year (Saborido-Rey and Kjesbu, 2005; Yoneda and Wright, 2005; Kjesbu, 2009). Morphophysiological (HSI) and morphometric (K) indicators are very important in fisheries and fish biology as indirect indices for assessing the period of reproduction and reproductive status (Nash et al., 2013; Lloret et al., 2014). Changes in HSI and K also indicate alterations in fish gonad maturation because the formation of sexual products in the gonads consumes the internal stores of energy (Dutta, 1994; McBride et al., 2015). This energy diminishes in the muscle, liver and other tissues during the spawning period (Lloret and Rätz, 2000; Alonso-Fernández and Saborido-Rey, 2012). Thus, decrease

in energetic condition of adults indicated by low values of HSI and K are expected during or just after spawning periods (Lloret and Rätz, 2000; Lloret et al., 2014; McBride et al., 2015). The period of lowest densities recorded in the present study, from June to October, as well as the lowest values of HSI and K, coincide with the reproductive period of the species. These results corroborate Paiva-Filho and Rossi (1980), Paiva-Filho and Zani-Teixeira (1980), Vazzoler et al. (1999) and Costa et al. (2015) who have reported the reproductive period of *P. brasiliensis* being from July to December (winter and spring), showing peaks of spawning from August to December in the inner shelf of São Paulo State, Brazil.

Temperature and organic matter content significantly affected the density of *P. brasiliensis*. Temperature directly influences fish metabolism at the individual level, increasing metabolic rate, which can accelerate starvation, reducing growth and slowing or stopping

maturation, besides it affects recruitment process through trophic transfer, egg development rate, survival and recruitment of young fish (Gillooly et al., 2001; Houde, 2009; Neuheimer and Grønkvær, 2012; Tu et al., 2018). Rossi-Wongtschowski et al. (2008) and Costa et al. (2012) reported an association between high abundances of *P. brasiliensis* and temperatures ranging from 21 to 24 °C in the northern coast of São Paulo State. The latter authors also observed the lowest densities in temperatures less than 20 °C and higher than 24 °C. In the present study, although the density of *P. brasiliensis* showed a tendency to decrease with increasing temperature, the highest density points in the Fig. 2e fall between 20 and 24 °C. This indicates higher aggregations of the species with the presence of the CW ($T > 20$ and $S < 36$), as was suggested by Rossi-Wongtschowski et al. (2008), Souza et al. (2008) and Costa et al. (2012). The influence of the SACW and CW on the spatial-temporal distribution of demersal fishes in the inner shelf of São Paulo State was also reported by Muto et al. (2000), Rocha et al. (2010) and Schmidt and Dias (2012).

Sediment type is also very important to the demersal fish community (Costa et al., 2012). Sand, mud and clay exhibit specific invertebrate communities that are important as food for demersal fishes (Lowe-McConnell, 1987; Soares et al., 2008). *P. brasiliensis* feeds mainly on polychaetes and crustaceans (Braga et al., 1985). These benthic invertebrates live above or burrow in the sediment and are more abundant in fine sediment due to high concentrations of organic matter (Furtado et al., 2008; Soares et al., 2008). Seasonal dynamics of the water masses also affect the distribution and abundance of polychaetes and crustaceans in the Brazilian South-eastern Bight (Pires, 1992; Léo and Pires-Vanin, 2006; Souza et al., 2008). The absence of a significant effect of Phi on fish density suggests that *P. brasiliensis* uses various types of sediments in the study areas, from very coarse sand to silt-clay. However, the strong relationship between the density of *P. brasiliensis* and sediments containing around 5% organic matter may be explained by food availability associated with the presence of the SACW and CW.

GAMLSS offers the user a wide range of options for model design and analysis, which can be very useful to investigate complex interactions between a response variable and biological and environmental factors in fisheries. The number of continuous distributions available, methods to analyze and select the best distribution for response variable, functions to estimate the degrees of freedom for each explanatory variable, model selection and diagnostics techniques are highlighted here as the most important options available within GAMLSS framework. For instance, GAIC analysis indicated three suitable families of distribution for modeling the response variable, i.e., lognormal, gamma and Weibull (Table A1). According to Rigby et al. (2019), lognormal and gamma are the most appropriate for positively skewed data. Thus, to make a better decision on which distribution fits better *P. brasiliensis* density, histograms and fitted distributions (GAMLSS family) were also plotted (Fig. A2). The results confirmed that the most parsimonious distribution with the lowest AIC (lognormal) was also the most appropriate for modeling the data, showing that the response variable was closer to a normal distribution than gamma and Weibull, providing constant variance of the error terms (residuals). In addition, it's also important to point out both worm and detrended transformed Owen's plots to detect inadequacies in the final model to improve the quality of the model predictions. Therefore, the flexibility provided by GAMLSS and the number of tools available to analyze the variables and measure the quality of the models are very helpful to understand the model results and validation in this type of study.

Classical regressions (e.g., Linear Models, Generalized Linear Models and Generalized Additive Models) are focused on the mean to accommodate the distributions parameters (Rigby and Stasinopoulos, 2005). In GAMLSS, lognormal distribution, μ and σ are the median and variance, respectively (Rigby et al., 2019). This distribution can give a good representation of a normal distribution that has small absolute value of σ (less than 0.25), as observed in present study ($\sigma = 0.2348$) (Johnson et al., 1994; Torrent, 1978; Ellassais-Schaap and Duisters, 2020). The μ

value with constant variance estimated for the final model indicates that the variance is not affected by changes in the values of the location parameter; in other words, changes in the value of the parameter μ affects only the location of the distribution (Johnson et al., 1994). According to Stasinopoulos et al. (2017), there are occasions that a constant σ is appropriate for the data, and the number and type of parameters to be modeled (μ , σ , ν , τ) vary according to the distribution family of the response variable. Therefore, it's also demonstrated here that GAMLSS can also use the median of a positively skewed response variable to predict variations in fish density.

5. Conclusion

The population dynamics of *P. brasiliensis* are regulated by complex interactions between environmental (temperature and organic matter content) and biological factors (biomass, HSI and K), with high densities occurring in areas where environmental conditions are more suitable in terms of temperature and food availability. Temporal changes in body condition of *P. brasiliensis* suggest that HSI and K can both be used as additional ecosystem indicators in terms of food availability and fish population health. In addition, seasonality in reproduction and recruitment may play important roles in temporal density-dependent regulation. Understanding and predicting the dynamics of populations has important implications for fisheries management and biological conservation. Better knowledge of these dynamics can improve our understanding of causal species–environment relationships and help prevent accidental bycatch of ecologically important species on shrimp fishery grounds such as the keystone species *P. brasiliensis*. The present study also highlights the importance of using robust statistical methods to model fish population dynamics and the need to incorporate biological and environmental factors into fishery resource management.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2022.102203>.

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