Medium- and long-term temporal trends in the fish assemblage inhabiting a surf zone, analyzed by Bayesian generalized additive models

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Abstract The present study characterizes the fish assemblage in the surf zone of Cassino Beach, Rio Grande, Brazil, and analyzes temporal fluctuations in richness and abundance of these species in medium (months) and long terms (years), associating them also with abiotic covariates. Data were collected monthly between 1996 and 2012 at two locations. Bayesian generalized additive models (GAMs) were used as statistical tool, placing this study among few that have used Bayesian GAMs in Ecology. Our results show a decrease in both species richness and abundance of the most representative species, over the last 16 years, but no significant distinction between locations. Water temperature and salinity along with seasonality were the statistically most influential explanatory covariates to describe fluctuations in richness and abundance. Higher discharge rates of the three main rivers that flow into Patos Lagoon (Jacuí, Taquari, Camaquã) were associated with increased richness and abundance of some species in the assemblage. Hence, our findings show that medium- and long-term fluctuations in richness and species abundance are controlled by abiotic factors related to seasonal cycles (temperature) and productivity of the ecosystem. Long-term changes seem to be also related to man-induced factors and climate change; but further research is needed.

Keywords Species richness · Abundance · Covariates · Bayesian GAM

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Introduction

Species richness, defined as the total number of species in a unit of area (Brown et al. 2007), is a parameter of some concern in conservation biology, biogeography and community ecology (Royle and Dorazio 2008). It is the simplest way to describe community and regional diversity (Magurran 2004). A vast amount of ecological research has been undertaken using species richness as a measure to understand what affects, and is affected by, biodiversity. At the small spatial scale, species richness is generally

used as a measure of diversity within a single ecological community, habitat or microhabitat (Brown et al. 2007). These authors cite as main factors of small-scale variation in species richness: (1) geographic factors; (2) biotic factors such as competition or predation; and (3) abiotic factors, such as temperature and salinity. Since probability of detection differs among species, all measures of species richness have a positive correlation with sample size (Silvy 2012); therefore, it is important to also take the effects of abundance into account (Magurran 2004).

Among the main ways to analyze species richness are diversity indices (Hubálek 2000) and numerical modeling (Royle and Dorazio 2008). The trouble with diversity indices is that there are several to choose from (Margalef 1958; Menhinick 1964; McIntosh 1967; etc.). Alternatively, in numerical modeling, species richness can be characterized by a Poisson distribution and the variation in the latent ecological process described statistically by covariates (Royle and Dorazio 2008; Kinas and Andrade 2010). This is the approach used here.

Much of contemporary ecological theory, conservation biology and natural resource management are further concerned with variation in the abundance of species (Royle and Dorazio 2008). While richness shows *which* individual species are present in space and time (Brown et al. 2007), the abundance of individuals associated with other parameters governs the *dynamics* of this process (Royle and Dorazio 2008). The typical distribution assumed for modeling abundance is also Poisson. Other widely used discrete distributions are Binomial and Negative Binomial. Among continuous distributions, the Normal, log-Normal and Gamma can be cited (Kéry 2010).

Statistical analysis of ecological data with generalized additive models (GAMs) has been recognized as a powerful statistical tool for exploratory data analysis (Schoeman and Richardson 2002; Venables and Dichmont 2004; Guisan and Thuiller 2005; Dalla Rosa et al. 2012). Despite the versatility of linear models (LMs) and generalized linear models (GLMs) for data analysis and prediction, the restriction to a linear structure in the covariates is, however, a limitation, circumvented by GAMs. This is so because GAMs go a step further and use smoothed functions (splines) to model nonlinear relationships for some or all the explanatory variables (Hastie and Tibshirani 1990; Wood 2006a).

The statistical analyses of LMs, GLMs and GAMs can be made by conventional maximum likelihood inference (Edwards 1972) or, alternatively, by Bayesian methods (Gelman et al. 2013). For LMs and GLMs, both approaches (classical and Bayesian) are already widely used in ecology and environmental science (Faraway 2006; Royle and Dorazio 2008). Comparatively, Bayesian GAMs are still rare and are, therefore, a methodological highlight in the present work.

The growing interest in Bayesian statistics in many fields of applied sciences, particularly ecology, is partially explained by (the Bayesian) definition of probability as a coherent metric for uncertainty, combined with the conceptually rigorous structure of statistical inference defined plainly as decision-making in the presence of uncertainty—in contrast to the largely *ad hoc* procedures of conventional frequentist statistics (Lindley 2000). The popularization of specialized software to perform complex mathematical operations required in some Bayesian numerical calculations further helps explain this expansion in ecology (McCarthy 2007; Kinas and Andrade 2010).

Sandy beaches constitute most of the coastal areas of the word, with surf zones characterized as the area between the outer limit of the breaking waves and the beach shoreline (Brown and McLachlan 1990). Studies of the ichthyofauna in marine surf zones have reported that these fish assemblages are highly variable and dominated by a small number of species made up largely of juveniles (Ayvazian and Hyndes 1995; Gibson et al.1996; Vasconcellos et al. 2007). Similar to estuarine beaches, marine surf zones are recognized as important nursery areas for several species (Bell et al. 2001; Strydom and d'Hotman 2005), and the recruitment variability in these habitats is related to a wide range of biotic and abiotic factors (e.g., food supply, predation risk, temperature and salinity) (Taylor et al. 2007; Haynes et al. 2010; Able et al. 2011).

Systematic long-term sampling programs contain valuable information to characterize most assuredly the community structure and simultaneously monitor changes in medium term (months) and long term (years). Rare or irregular events that affect fish populations, but are spread over large time intervals, can only be evaluated by long-term studies. This study uses a 16-year long database of the ichthyofauna inhabiting the surf zone of a sandy beach in southern

Brazil. Our working hypothesis is that variations in the surf-zone fish assemblage richness as well as changes in abundance of selected groups of species show associations, not necessarily linear, with environmental factors and that these features can be captured by GAMs.

Materials and methods

Study area

This study focuses on Cassino Beach, located in southern Brazil (32°10′S, 52°20′W) (Fig. 1). Cassino is a subtropical sandy beach strongly influenced by seasonal variation in physico-chemical parameters. In general, observed temperatures and salinities are significantly higher in summer than in winter (Lima and Vieira 2009). Along this beach, the morphodynamic stages vary between dissipative and reflective and are seasonally influenced by the action of winds and waves, which affect the dynamics of the surf zone (Calliari et al. 2001); additionally, freshwater flow from the Patos Lagoon into the adjacent coastal marine area that may increase during periods of rain (Moresco and Bemvenuti 2006) and *El Niño* (Garcia and Vieira 2001).
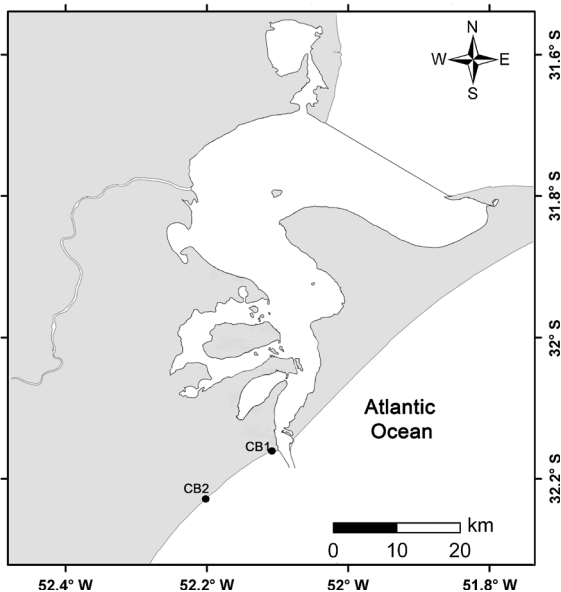

Fig. 1 Location of the two sites (CB1, CB2) where samplings from the surf zone of Cassino Beach, Rio Grande, RS, were performed, during the study period (1996–2012)

Data description

Samples were collected monthly in shallow waters (depth <20 m) from January 1997 to August 2012 at two fixed stations (1) CB1 (near Molhe Oeste) and (2) CB2 (near Estação Marinha de Aquacultura—EMA/FURG) (Fig. 1). From August to December of 1996, samples were collected only at station CB1. The sampling procedure is part of a long-term ecological research project (ICTIO/PELD CNPq-MCT, 1996–2012). The beach morphologies at both stations are the same; but CB1 is situated close to the outlet of the Patos Lagoon, being more sheltered in comparison with CB2 situated about 10 km south of this outlet.

Biological samplings ($n = 5$ hauls(site)$^{-1}$ (month)$^{-1}$) were performed at each site using a 9-m beach seine (13-mm bar mesh in the wings and 5 mm in the center). All applicable institutional and national guidelines for the care and use of animals were followed. Samplings had the "authorization for scientific purpose activities" n° 17762-1 of IBAMA-SIS-BIO. Specimens were fixed in formalin in the field, due to long time gap between sampling and the identification process to the lowest possible taxonomic level conducted in the laboratory. Along with biological sampling, measurements on water conditions (temperature, salinity and transparency) were made in situ. Data on flow of the three main rivers of the Patos–Mirim system (Jacuí, Taquari, Camaquã) for the study period (1996-2012) were obtained with the National Water Agency (ANA—hidroweb.ana.gov.br). The monthly discharges of these three rivers combined correspond to 70 % of flow throughout the watershed (Vaz et al. 2006). Therefore, it was used as an indicator of the flow of the Patos Lagoon Estuary into the surf zone of Cassino Beach. Monthly values of zonal (east–west) and meridional (north–south) wind components at the sea surface (32°S; 52°W) were obtained from the Division of Environmental Sciences Research Centre for Fisheries of NOAA ("National Oceanic and Atmospheric Administration"—http://las.pfeg.noaa.gov/las6_5/servlets/dataset).

Data analysis

Fluctuations in total abundance and species richness of fish in the surf zone of Cassino Beach over the past 16 years were associated with the covariates *month*, *year*, *location*, surface water temperature in °C

(*temperature*), water salinity (*salinity*), water transparency in cm (*transparency*) (Secchi), zonal wind component in $m(s)^{-1}$ (*zonal*), meridional wind component in $m(s)^{-1}$ (*meridional*) and flow of the three main rivers of the Patos-Mirim system in $m^3(s)^{-1}$: Jacuí (*jacui*), Taquari (*taquari*), Camaquã (*camaqua*); totaling 11 covariates. The model for species richness had additionally added the covariate *abundance* (monthly total number of collected specimens).

GAMs with a linear predictor composed of q linear components and k smooth functions are defined as.

$$g(\mu_i) = \beta_0 + \beta_1 z_{1i} + \cdots \beta_q z_{qi} + f_1(x_{1i}) + \cdots f_k(x_{ki})$$

where $\mu_i = E(Y_i)$ and Y_i has some distribution from the exponential family with associated known link function g. While Y_i denotes some response variable (in our context species richness and abundance), $z_{1i}, \ldots, z_{qi}$ and $x_{1i}, \ldots, x_{qi}$ are $q + k$ covariates, the former (z) being modeled with a strictly parametric model and the latter (x) with smooth functions.

The Bayesian fits of the GAMs were conducted in the free software BayesX, version 2.0.1 (Belitz et al. 2009), which uses penalized regression splines (P-splines) as smooth functions (Eilers and Marx 1996). In this approach, it is assumed that the unknown smooth functions f_j can be approximated by a spline of degree l with equally spaced knots $X_{j,\min} = \zeta_{j0} < \zeta_{j1} < = < \zeta_{j,r-1} < \zeta_{jr} = X_{j,\max}$ This spline can be written in terms of a linear combination of $m = r + l$ B-spline basis functions B_{jp}, which in turn are known and calculable functions for each value in the domain x_j, that is,

$$f_j(x_j) = \sum_{p=1}^{m} \beta_{jp} B_{jp}(x_j)$$

Following the Bayesian approach, second-order random walks were used as priors for the coefficients, i.e., for $p > 2$, β_{jp} are given by: $\beta_{jp} = 2\beta_{jp-1} - \beta_{jp-2} + u_{jp}$ with Gaussians errors $u_{jp} \sim N(0, \tau_j^2)$ and diffuse priors $p(\beta_1) \propto$ const, $p(\beta_2) \propto$ const and $p(\tau_j) \sim IG(0.001, 0.001)$ with $IG(a, b)$ denoting an inverse-gamma distribution. The degree of smoothness is controlled by the variances τ_j^2, which correspond to the inverse of the parameter λ_2 that is used in the cross-validation technique of the classical approach (Lang and Brezger 2004). The joint posterior distribution for the set of parameters $(\alpha_*, \beta_{**}, \tau_*)$ was obtained with Markov Chain Monte Carlo (MCMC) stochastic simulation by the Metropolis–Hastings algorithm. For a chain of 12,000 values, the first 2,000 were discarded to eliminate the dependence of the initial value (*burn-in period*) after which each tenth value was retained (*thinning*) to achieve independence between sampled values (Kinas and Andrade 2010). Standard diagnostic tools were applied in preliminary analyses to check for MCMC convergence (Gelman et al. 2013).

For model comparison, the Deviance information criterion (DIC) was used (Spiegehalter et al. 2002). By this criterion, regarding predictive power, models with smaller value of DIC are better. A difference in DIC of at least two units can be considered indication of superior fit for the model with the lowest DIC (Spiegehalter et al. 2002).

Species richness

Species richness was analyzed by a Poisson model for the count data of number of species per area (Y_i), with the natural logarithm as link function.

$$Y_i \sim Poi(\mu_i)$$

$$\begin{aligned} g(\mu_i) = \log(\mu_i) &= \eta_i \\ &= \beta_0 + f_1(x_{1i}) + f_2(x_{2i}) + f_3(x_{3i}) + \cdots f_k(x_{ki}) \end{aligned}$$

Models with different combinations of covariates were fitted. The adequacy of each variable to a spline function or a linear structure was evaluated visually at first. When for some covariate x_j a linear structure was suspected, another fit after replacing $f_j(x_{ji})$ by $\alpha_j x_{ji}$ was performed and both alternatives compared by DIC.

Species abundance

For the analysis of abundance with all species combined, there is a chance that abundance remains nearly constant, while species composition keeps changing. Therefore, to analyze abundance fluctuations more carefully, we adopted the following strategy: (1) work only with species that had at least 10 % frequency of occurrence in the total database; (2) calculate some matrix of dissimilarity among the species; (3) identify subsets of species characterized by a low dissimilarity; and (4) perform abundance modeling for each identified subset of species.

The aim was to create groups of species that have a tendency to have occurred together over time during

the period of data collection. We then hypothesized that, because of their persistent co-occurrence, they should display similar responses to factors that may influence their abundance.

Cluster analysis of species

Cluster analysis was performed using the multivariate ordination method of metric multidimensional scaling (MDS) and the Jaccard similarity index based on a presence (1) and absence (0) matrix (i.e., the similarity between two species increases with growing numbers of co-occurrences) (Hardle and Simar 2007). The Jaccard similarity index has been widely used in studies of presence–absence (Romesburg 1984). The metric MDS finds the spatial configuration of points by algebraic reconstruction, taking into account the dissimilarities between these points, where the dissimilarities are Euclidean distances (Chatfield and Collins 1980). Calculations were performed with the free software Past (Hammer et al. 2001), version 2.17b.

Models for abundance

For each group of species identified by MDS, abundance was modeled by GAMs. A Gaussian distribution with identity link function was used to model the total number of individuals (Y_i). Because the number of individuals is sometimes very large, the Gaussian distribution combined with the identity link serves here as an approximation to the Poisson and showed a numerically more stable performance at fitting.

$$Y_i \sim N(\mu_i, \sigma_i)$$

$$\begin{aligned} g(\mu_i) &= \eta_i \\ &= \beta_0 + f_1(x_{1i}) + f_2(x_{2i}) + f_3(x_{3i}) + \cdots f_k(x_{ki}) \end{aligned}$$

Models with different combinations of variables were tested. The adequacy of each covariate to either a spline function or a linear structure was evaluated as previously described.

Results

List of species

During the study period, 171,737 individuals were collected at 343 sampling occasions. Sixty-four taxa were found, nine identified only to the family level, and 55 identified to the species level. The eight most abundant species, *Mugil liza*, *Trachinotus marginatus*, *Mugil curema*, *Brevoortia pectinata*, *Mugil sp*, *Odontesthes argentinensis*, *Menticirrhus littoralis* and *Atherinella brasiliensis*, comprise 97.1 % of all individuals captured. Regarding the frequency of occurrence, 13 species were present in at least 10 % of the samples (Table 1).

Species richness

The best GAM for species richness models richness as a function of *month, year, transparency, temperature, salinity, jacui, taquari, camaqua* and *abundance* (Model 1—Table 2). The results show that, on a monthly scale, the number of species displays seasonal variation, being higher especially in the austral summer months, with a decrease starting in April and increasing again from October onwards. In the long term (annual scale), species richness shows a decreasing trend (Fig. 2).

Among the abiotic covariates, only *temperature* affects variations in species richness, with peak of species richness occurring between 20 and 25 °C (Fig. 2). Flows *jacui* and *camaqua* display a positive linear association with the number of species. Variables *salinity*, *transparency* and *taquari* also have a linear relationship but with slope close to zero, indicating that individually their influence is nonsignificant. Nevertheless, they were maintained in the model because, in combination with other covariates, they improved the predictive power of the model decreasing the DIC (Table 2). Species richness was positively associated with *abundance* until about 1,000 individuals after which in flattens out (Fig. 2).

The sampling site (*location*), as well as the *zonal* and *meridional* wind components, was not included in the model, because they increased the DICs. This indicates that sampling stations as well as values of wind components do not help explain variations in species richness.

Species abundance

Cluster analysis

Two distinct groups were formed by MDS (Fig. 3), with the first two axes synthesizing about 40 % of the

Table 1 Abundances and relative frequencies of the species that occurred in at least 10 % of the samples collected in the surf zone of Cassino Beach (1996–2012)

Family	Species	Years																
		96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12
Mugilidae	*Mugil liza*	3444	5702	4484	3048	5747	2516	5170	4696	4793	6734	1193	741	2458	2350	2576	2574	1186
	Mugil curema		1308	140	152	3290	224	172	658	6060	3855	580	1646	1828	5483	364	1131	322
	Mugil sp		1010	277	413	3576	4	242	61	120	73	150	1005	808	823	10	8	35
Carangidae	*Trachinotus marginatus*	17	2830	28	2189	4023	10067	1966	4943	2375	2293	993	2128	3840	3901	711	2016	730
Clupeidae	*Brevoortia pectinata*	23	770	91	450	1526	589	1862	2953	1329	569	1978	280	1107	245	791	519	327
	Platanichthys platana	82	104	18	8	3	15	7	62	11			43	21				
Atherinopsidae	*Odontesthes argentinensis*	157	207	34	156	509	113	71	77	103	1270	105	127	479	824	201	102	14
	Atherinella brasiliensis	16	1117	193	72	106	68	783	6	8	111	33	71	75	118	5	13	17
Sciaenidae	*Menticirrhus littoralis*	227	293	497	511	238	615	841	89	211	44	97	27	103	66	83	21	19
	Menticirrhus americanus		15		2	2	9	431	60	50	19	60	13	29		17	25	2
	Micropogonias furnieri		11	62	118	9	6	4		59	20		55	4	7		2	2
Engraulidae	*Lycengraulis grossidens*	20	15	4	2	2	5	5	20	2	1	24	7	15	12	587	3	16
Pleuronectidae	*Oncopterus darwinii*	111	47	11	25	48	88	178	8	63	8	29	2		18	28	2	7

Legend:

1	not abundant and infrequent	**3**	*abundant* and infrequent
2	not abundant and *frequent*	**4**	*abundant* and *frequent*

If the species had a frequency of occurrence above the total average occurrence in that year, it was considered *frequent*; if had its abundance above the total average abundance in that year, it was considered *abundant*. The numbers inside the table are the total number of caught individuals of that species in the corresponding year

data variation. Group A is composed of species *Lycengraulis grossidens*, *Menticirrhus americanus*, *Micropogonias furnieri*, *Oncopterus darwinii* and *Platanichthys platana*, and Group B of *A. brasiliensis*, *B. pectinata*, *M. littoralis*, *M. curema*, *M. liza, M. sp*, *O. argentinensis* and *T. marginatus*.

Group A On a monthly scale, the abundance of species that composes Group A is higher in warmer months and lower during colder autumn–winter months, with the decrease starting in April, remaining stable with low abundance until August, when abundance increases again (Fig. 4). The covariate *year* enters the best model as a linear component, but with slope close to zero (Model 2—Table 2), indicating that the abundance of this group of species has remained stable over the years (1996–2012).

Regarding *temperature*, a slight oscillation around an optimum of 20 °C was found, with abundances

decreasing toward the extremes. Abundance decreases with increasing *salinity* (Fig. 4), which is associated negatively with *transparency* and positively with the *jacui* river discharge (Model 2—Table 2).

Group B For species of group B, the covariate *month* has a negative linear relationship with negative slope, indicating that in the first months of the year abundance is higher (Model 3—Table 2). In the long term (*year*), Group B shows a decreasing trend in abundance (Fig. 5).

This group further displays an increase in mean abundance at *salinities* from 25 upwards (Fig. 5). However, we point out that the variances in both tails are large; this is due to the fact that there were few sampled points with extreme salinities (≤5; 35≥). Group B also has a positive association with *temperature*. The variables *transparency*, *taquari* and *camaqua* were included in the best fitted model because they impacted reduction of DIC, although individually

Table 2 Composition of covariates for the best models for species richness (Model 1) and abundance (Model 2—Group A, Model 3—Group B)

	Models		
Covariates	1	2	3
Months (Jan–Dec)	S	S	L (−)
Years (1996–2012)	S	L	S
Site (1–2)	–	–	–
Water temperature	S	L(+)	L (+)
Water salinity	L	S	S
Water transparency	L	L (−)	L
Zonal component of wind	–	–	–
Meridional component of wind	–	–	–
Jacuí river flow	L (+)	L (+)	L
Taquari river flow	L	L	L
Camaquã river flow	L (+)	L	L
Abundance	S	–	–
DIC	191.5	277.2	279.3

The table indicates whether the covariate was entered as a spline function (S) or linear function (L). It is indicated in parenthesis when the variable with linear function had a statistically significant positive (+) or negative (−) influence on the response (Note: We consider "statistically significant" whenever the posterior 95 % credibility interval does not cover zero)
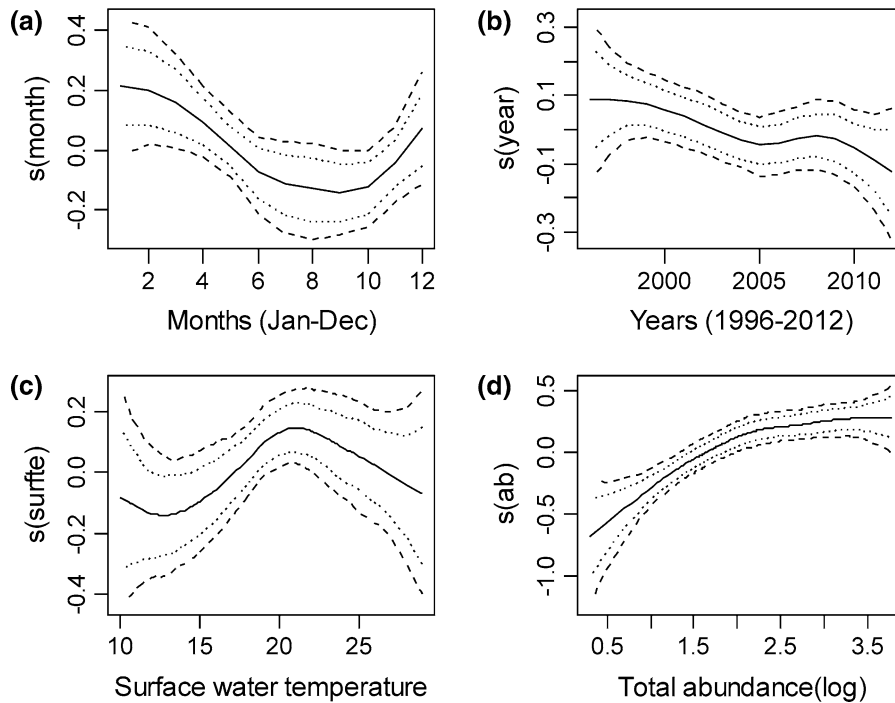

Fig. 2 Posterior means (central line) and credibility intervals of 80 % (dotted) and 95 % (outer lines) of P-splines related to the variables **a** month, **b** year, **c** surface water temperature and **d** logarithm of the total abundance, of the model that describes species richness
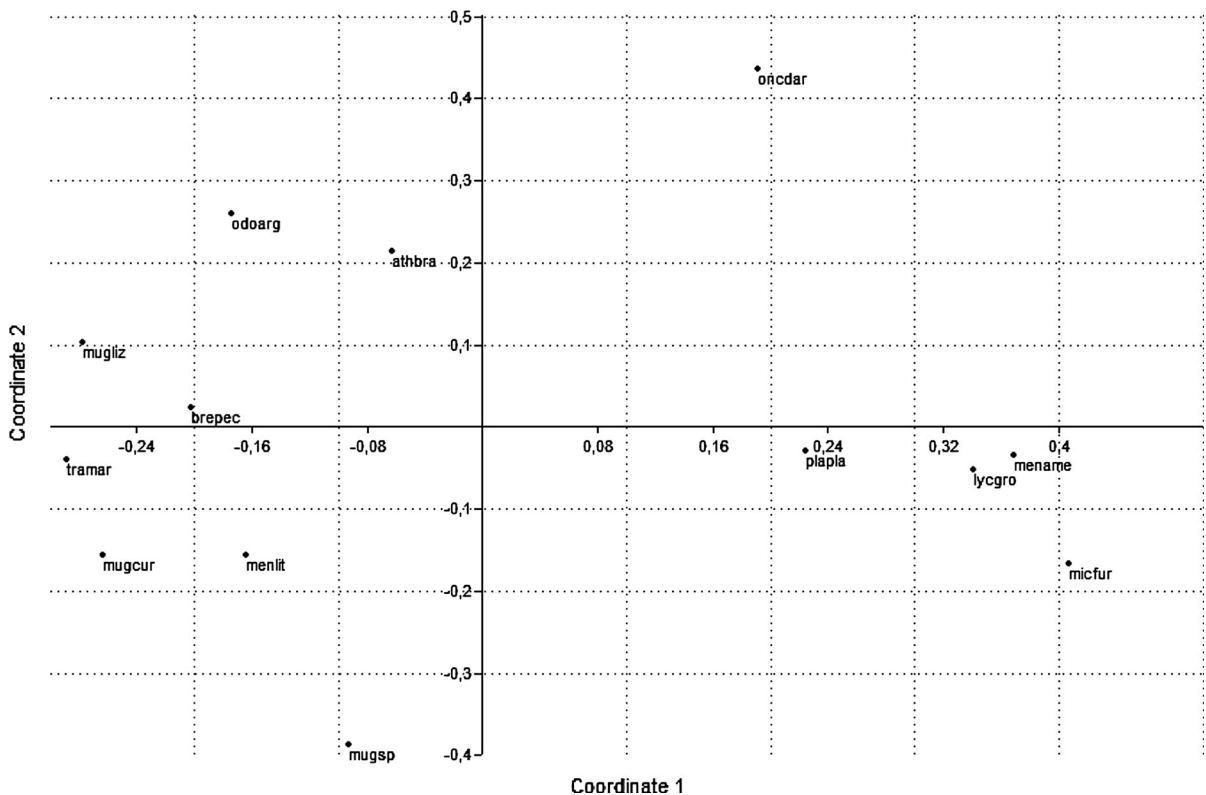
Fig. 3 Results of MDS cluster analysis for the 13 mostly occurring species in the database (those which occurred in at least 10 % of samples). The species to the *right* of coordinate 1 (*y axis*) were denoted as "Group A" and species to the *left* as "Group B"

Fig. 4 Posterior means (*central line*) and credibility intervals of 80 (*dotted*) and 95 % (*outer lines*) of P-splines related to the variables **a** month and **b** water salinity, for the model which describes the abundance of species of Group A
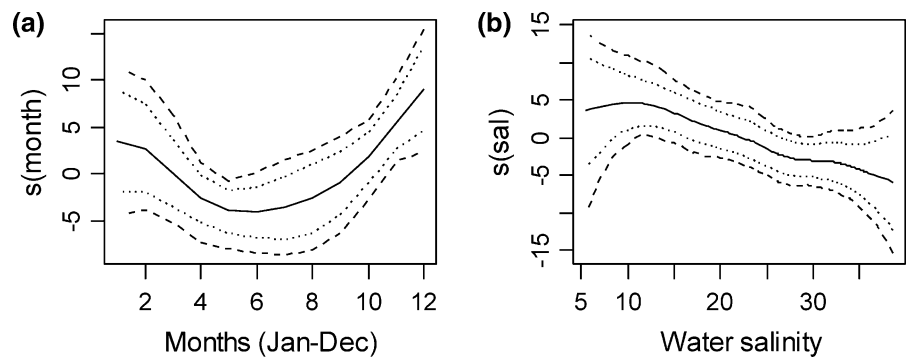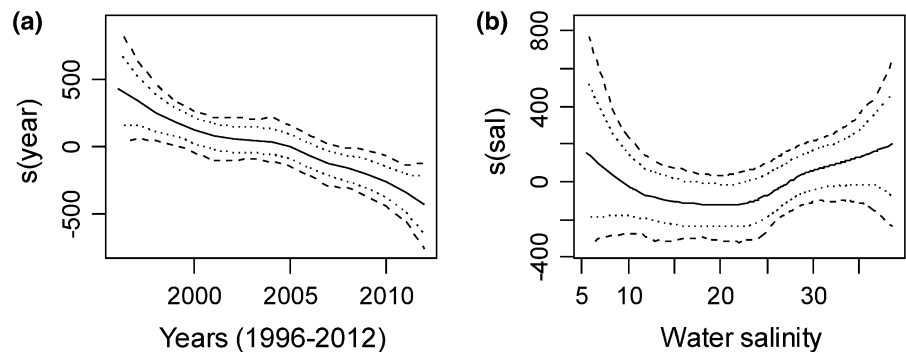

Fig. 5 Posterior means (*central line*) and credibility intervals of 80 (*dotted*) and 95 % (*outer lines*) of P-splines related to the variables **a** year and **b** water salinity, for the model which describes the abundance of species of Group B

their influence on changes in mean abundance is unclear (Model 3—Table 2).

Discussion

To understand which factors drive the spatial and temporal patterns in communities is a central goal of ecology. This study emerges as one of few to investigate this phenomenon with the use of Bayesian generalized additive models. To our knowledge, this is the first such approach to be published with data from Brazil. While there are several papers describing the formal development of these models (Denison et al. 1998; Lin and Zhang 1999; Fahrmeir and Lang 2001; Spiegehalter et al. 2002; Lang and Brezger 2004; Wood 2006b), there are still only a few with applications. Examples are Guisan and Zimmermann (2000) and Phillips et al. (2006), who applied these models to describe geographic distribution of species.

The models, fitted here with P-splines (Eilers and Marx 1996; Lang and Brezger 2004), proved very amenable to the study of species richness and abundance because direct visual inspection of nonlinear relationships and predictive power of covariates can be evaluated simultaneously. The nontrivial influence of sample size up to about 1,000 specimens on the observed species richness was handled easily by simply including *abundance* as a covariate into the model. The rarefaction technique is the most consecrated method in the comparison of the number of taxa in samples of different size (Krebs 1989). However, only the sampling effort (usually expressed as the total abundance of species) is considered as a covariate by this technique. Until recently, the comparison of the richness-to-sampling effort ratio considering environmental variables was only performed for linear models. However, since this relationship is clearly nonlinear, GAMs are an excellent replacement for the rarefaction technique when comparing species richness between different sampling units.

One fundamental pattern concerning life on Earth is the decrease of biological diversity from the equator toward the poles (Willig et al. 2003). This helps to explain why tropical oceans are in general biologically diverse, while coastal regions of temperate and polar zones are highly productive but less diverse (Caddy and Sharp 1986). In Brazil, there are higher numbers of species recorded in the surf zones on tropical beaches (Itamaracá (PE)—95 species (Santana and Severi 2009); Cabuçu (BA)—63 species (Silva et al. 2008); São Francisco do Itabapoana (RJ)—68 species (Gomes et al. 2003)) than on the subtropical beach of the present study (55 species). However, all share the same striking feature of only a few dominant species. This peculiarity had already been recognized by Modde and Ross (1981), when they say that "surf-zones are dominated by a small group of species, and this organization remains constant over wide geographic areas."

Surf zones, especially for sandy beaches, are uniform habitats characterized by low primary productivity (Knox 2001; McLachlan and Brown 2006). Thus, the abiotic factors seem to be the main components that drive the structure and composition of the communities in these habitats. This similarity in abiotic conditions explains the absence of sampling station effect in our study, corroborating Rodrigues and Vieira (2012), who also reported insignificant differences in the abundance and diversity of fish between these two locations, using another analytic approach.

Groups A and B of species were characterized on their co-occurrence. The pattern that emerged seems to be associated mainly with salinity and seasonality. While species in group A were shown to be more abundant in less salty waters, those in Group B had their abundance increased with increasing salinity. Species of Group A can be further described as occasional, only appearing in specific seasons of the year (*M. furnieri* and *L. grossidens* in Summer and Autumn, and *M. americanus* and *O. darwinii,* in Spring and Summer (Lima and Vieira 2009)); in contrast, species in Group B (*A. brasiliensis*, *B. pectinata*, *M. littoralis*, *M. curema*, *M. liza*, *M. sp*, *O. argentinensis*, *T. marginatus*) are usually present in the surf zone all year long (Lima and Vieira 2009).

Monteiro-Neto et al. (2003) for samples conducted from March 1980 to February 1982 found seven groups (A to G) in this surf zone using inverse cluster analysis and taking into account 24 species. Group C of their study has resemblance to our Group A, and their groups F and G together resemble our Group B. The time lag between both studies suggests that these associations tend to occur with some consistency in the surf zone of Cassino Beach, even in the long term.

The results obtained here show the strong influence of seasonality on the ichthyofauna structure in the surf

zone of Cassino Beach. The increase of marine productivity driven by the seasonality of temperatures and sunlight in subtropical habitats favors the survival of larvae and juveniles during warmer months, especially due to increase of food supply (Castillo-Rivera et al. 2010; Martino and Houde 2010; Kristiansen et al. 2011). Thus, the seasonal dynamics of the spawning activity and recruitment in subtropical areas is closely associated with the temperature regime. According to Moraes et al. (2012), the time required for the fish larvae produced in the spring reproductive period to grow and reach the shallow areas of the surf zone explains the lag of 1 month observed in the response of the species abundance to water temperature in Cassino beach. Similar to what happens in other subtropical environments, biological cycles of reproduction and recruitment of fishes associated with the increased productivity of the system during spring and summer also occur in this study site (Monteiro-Neto et al. 2003; Lima and Vieira 2009; Moraes et al. 2012; Rodrigues and Vieira 2012). Monteiro-Neto et al. (2003) emphasized that the occurrence and seasonal abundance of fish species in the surf zone reflect patterns of recruitment of juveniles determined by both the seasonality of reproduction and the seasonal variations in circulation patterns. These ecological mechanisms explain the strong positive relationships of temperature and seasonality with abundance and species richness that were detected by our models.

Salinity and surface water temperature appeared as important factors in the variation of abundance and in defining distinct groups A and B for the ichthyofauna. The river discharges were important components in all proposed models contributing with increased predictive power for both richness and abundance of the species that compose Group A. A hypothesis to help explain this result is the fertilization of the continental shelf promoted by the estuarine plume (Miranda et al. 2002). With more nutrients on the coast, there is an increase in marine productivity, which could attract more species into the assemblage and increase the abundance of at least some of them.

The unique possibility of the present study to glimpse at the fish assemblage over the long period of 16 years allows the identification of a decreasing trend in both species richness and in the overall abundance in Group B. Other studies in the region, covering shorter periods, had been unable to identify these concerning trends.

Over the past decades, natural and anthropogenic factors, and their conjunction, have been modifying the dynamics of the Patos Lagoon Estuary and adjacent coastal waters, which includes the Cassino Beach (Odebrecht et al. 2010a). For instance, positive anomalies of estuarine freshwater outflow associated with choked morphology of the Patos Lagoon Estuary can generate seaward currents that block the entrance of fish and crustaceans recruits of marine origin into the estuary. Additionally, the input of the strong freshwater outflow into the adjacent coastal zone, especially those observed during El Niño events, forces the drop in salinity and changes the structure and composition of the communities at Cassino Beach (e.g., Garcia et al. 2004, Odebrecht et al. 2010b). The estuarine plume of the Patos Lagoon also plays an important role with the input of fine sediments (silt and clay) into the coastal zone. These sediments form natural mud deposits that can reach the Cassino Beach during climatic events, changing the surf-zone hydrodynamics, especially in the attenuation of waves (Calliari et al. 2007), altering the concentrations of the dissolved inorganic nutrient (Odebrecht et al. 2010b) and causing significant changes in biotic components (e.g., phytoplankton species—Odebrecht et al. 2003; benthic invertebrates—Silva et al. 2008; and ichthyofauna—Mont'Alverne et al. 2012). Although it is a natural phenomenon, dredging operations on poorly sited dumpsites seems to amplify the production of fluid mud (Calliari et al. 2001) and this activity has become more frequent during the last century (Calliari et al. 2009).

Commercially important species, such as *O. argentinensis*, *T. marginatus* and, especially, *M. liza* (Fischer et al. 2011), are present in Group B. This fact allows us to restate the hypothesis that the increase in fishing effort has led to a decrease in the reproductive stock and consequent decrease in the recruitment of those species that are directly related to the surf zone. The long-term changes that have been observed in Cassino Beach, as well as in the Patos Lagoon Estuary, still need further investigation. Causes appear to be complex and are the fruit of an intricate network of natural and anthropogenic factors.

Species richness as response variable showed a positive association with the covariate *abundance*. Such relation between number of species and number of collected individuals had already been reported in other studies (Gotelli and Colwell 2001; Silvy 2012).

But, because our fitted GAM curve showed an asymptote, the number of collected specimens seems to have been sufficient to characterize the assemblies' richness. While abundance has been decreasing over the last years, its effect over species richness has become part of the explanation for the observed reduction in richness. However, *year* remains an important covariate in the model, showing that species richness is declining in time, irrespective of the effect induced by changes in abundance.

Finally, we emphasize the importance of continued monitoring of this fish assemblage in order to deepen the investigation of the long-term causes for changes in the abundance of individuals and species richness, perhaps associating these changes also with data from fisheries landing and proxies that serve as evidence of climate change. This is especially attractive due to the location of our study site near the boundary between tropical and temperate regimes.

Conclusions

The Bayesian generalized additive models (GAMs) proved to be an appropriate exploratory tool in ecological studies of species richness and abundance. No significant difference was found between the sampled sites (1) near Molhe Oeste and (2) near Marine Aquaculture Station—EMA/FURG. Seasonality, influenced by changes in water temperature and salinity, is the most influential in the oscillations of richness and abundance of the ichthyofauna in the surf zone of Cassino Beach, RS. Higher discharges of the three main rivers that flow into the Lagoa dos Patos (Jacuí, Taquari, Camaquã) were associated with an increase in species richness and in abundance of some occasional species of the assemblage (Group A). There has been a decrease in the total species richness and abundance of the most representative species in the surf zone of Cassino Beach over the past 16 years.

References

Able KW, Grothues TM, Rowe PM, Wuenschel MJ, Vasslides JM (2011) Near-surface larval and juvenile fish in coastal habitats: comparisons between the inner shelf and an estuary in the New York Bight during summer and fall. Estuar Coasts 34:726–738

Ayvazian SG, Hyndes GA (1995) Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? Mar Biol 122:527–536

Belitz C, Brezger A, Kneib T, Lang S (2009) BayesX—Bayesian inference in structured additive regression models. http://www.stat.uni-muenchen.de/~bayesx. Accessed March 2012

Bell KNI, Cowley PD, Whitfield AK (2001) Seasonality in frequency of marine access to an intermittently open estuary: implications for recruitment strategies. Estuar Coast Shelf Sci 52:327–337

Brown AC, McLachlan A (1990) Ecology of Sandy shores. Elsevier, New York

Brown RL, Jacobs LA, Peet RK (2007) Species richness: small scale, encyclopedia of life sciences, vol 26. Wiley, New Jersey

Caddy JF, Sharp GD (1986) An ecological framework for marine fishery investigations. FAO fisheries technical paper, Rome

Calliari LJ, Speranski N, Torronteguy M, Oliveira MB (2001) The mud banks of Cassino Beach, southern Brazil: characteristics, processes and effects. J Coast Res 34:318–325

Calliari LJ, Holland KT, Pereira PS, Guedes RMC, Santo RE (2007) the influence of mud on the Inner Shelf, Shoreface, Beach and Surf Zone Morphodynamics—Cassino, Southern Brazil. Coast Sedim 07:1–11

Calliari LJ, Winterwerp JC, Fernandes E, Cuchiara D, Vinzon SB, Sperle M, Holland KT (2009) Fine grain sediment transport and deposition in the Patos Lagoon—Cassino Beach sedimentary system. Cont Shelf Res 29:515–529

Castillo-Rivera M, Zárate-Hernandez R, Ortiz-Burgos S, Zavala-Hurtado J (2010) Diel and seasonal variability in the fish community structure of a mud-bottom estuarine habitat in the Gulf of Mexico. Mar Ecol 31:633–642

Chatfield C, Collins AJ (1980) Introduction to multivariate analysis. CRC Press, London

Dalla Rosa L, Ford JKB, Trites AW (2012) Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters. Cont Shelf Res 36:89–104

Denison DGT, Mallick BK, Smith AFM (1998) Automatic Bayesian curve fitting. J R Stat Soc B 60:333–350

Edwards AWF (1972) Likelihood. Cambridge Academic Press, Cambridge

Eilers P, Marx B (1996) Flexible smoothing using B-splines and penalizes likelihood. Stat Sci 11:89–121

Fahrmeir L, Lang S (2001) Bayesian inference for generalized additive mixed models based on Markov random field priors. Appl Stat 50:201–220

Faraway JJ (2006) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. CRC Press, Boca Raton

Fischer LG, Pereira LED, Vieira JP (2011) Peixes estuarinos e costeiros. Consciencia, Rio Grande

Garcia AM, Vieira JP (2001) O aumento da diversidade de peixes no estuário da Lagoa dos Patos durante o episódio El Niño 1997–1998. Atlantica 23:85–96

Garcia AM, Vieira JP, Winemiller KO, Grimm AM (2004) Comparison of 1982–1983 and 1997–1998 El Niño effects on the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). Estuar Coasts 27:905–914

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin D (2013) Bayesian data analysis. CRC Press, Boca Raton

Gibson RN, Robb L, Burrows MT, Ansell AD (1996) Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. Mar Ecol Prog Ser 130:1–17

Gomes MP, Cunha MS, Zalmon IR (2003) Spatial and Temporal Variations of Diurnal Ichthyofauna on Surf-Zone of São Francisco do Itabapoana Beaches, Rio de Janeiro State, Brazil. Braz Arch Biol Technol 46:653–664

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. http://folk.uio.no/ohammer/past/. Accessed March 2012

Hardle W, Simar L (2007) Applied multivariate statistical analysis. Springer, Berlin

Hastie TG, Tibshirani RJ (1990) Generalized additive models. CRC Press, Boca Raton

Haynes PS, Brophy D, McGrath D, O'Callaghan R, Comerford S, Casburn P (2010) Annual and spatial variation in the abundance length and condition of juvenile turbot (*Psetta maxima* L.) on nursery grounds on the west coast of Ireland: 2000–2007. J Sea Res 64:494–504

Hubálek Z (2000) Measures of species diversity in ecology: an evaluation. Folia Zool 49:241–260

Kéry M (2010) Introduction to WinBUGS for ecologists. Elsevier, London

Kinas PG, Andrade HA (2010) Introdução à Análise Bayesiana (com R). Mais Que Nada, Porto Alegre

Knox GA (2001) The Ecology of Sea Shores. CRC Press, Boca Raton

Krebs CJ (1989) Ecological methodology. Harper and Row, New York

Kristiansen T, Drinkwater KF, Lough RG, Sundby S (2011) Recruitment variability in North Atlantic cod and match-mismatch dynamics. PLoS One 6:e17456

Lang S, Brezger A (2004) Bayesian P-splines. J Comput Gr Stat 13:183–212

Lima MSP, Vieira JP (2009) Variação espaço-temporal da ictiofauna da zona de arrebentação da Praia do Cassino, Rio Grande do Sul, Brasil. Zoologia 26:499–510

Lin X, Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. J R Stat Soc B 61:381–400

Lindley D (2000) The philosophy of statistics. Statistician 49:233–337

Magurran AE (2004) Measuring biological diversity. Blackwell, Malden

Margalef DR (1958) Information theory in ecology. Gen Syst 3:36–71

Martino EJ, Houde ED (2010) Recruitment of striped bass in Chesapeake Bay: spatial and temporal environmental variability and availability of zooplankton prey. Mar Ecol Prog Ser 409:213–228

McCarthy MA (2007) Bayesian methods for ecology. Cambridge University Press, New York

McIntosh RP (1967) An index of diversity and the relation of certain concepts to diversity. Ecology 48:392–404

McLachlan A, Brown AC (2006) The ecology of sandy shores. Academic Press, Burlington

Menhinick EF (1964) A comparison of some species-individuals diversity indices applied to samples of field insects. Ecology 45:859–861

Miranda LB, Castro BM, Kjerfve B (2002) Princípios de Oceanografia Física de Estuários. Editora Universidade de São Paulo, São Paulo

Modde T, Ross ST (1981) Seasonality of fishes occupying a surf zone habitat in the Northern Gulf of Mexico. Fish Bull 78:911–922

Mont'Alverne R, Moraes LE, Rodrigues FL, Vieira JP (2012) Do mud deposition events on sandy beaches affect surf zone ichthyofauna? A southern Brazilian case study. Estuar Coast Shelf Sci 102–103:116–125

Monteiro-Neto C, Cunha LPR, Musick JA (2003) Community structure of surf-zone fishes at Cassino Beach, Rio Grande do Sul, Brazil. J Coast Res 35:492–501

Moraes LE, Paes E, Garcia A, Moller JRO, Vieira J (2012) Delayed response of fish abundance to environmental changes: a novel multivariate time-lag approach. Mar Ecol Prog Ser 456:159–168

Moresco A, Bemvenuti MA (2006) Biologia reprodutiva do peixe-rei Odontesthes argentinensis (Valenciennes) (Atherinopsidae) da região marinha costeira do sul do Brasil. Revista Brasileira de Zoologia 23:1168–1174

Odebrecht C, Abreu PC, Fujita CCY, Bergesch M (2003) The impact of mud deposition on the long term variability of the surf-zone diatom *Asterionellopsis glacialis* (Castracane) round. J Coastal Res 35:493–498

Odebrecht C, Abreu PC, Bemvenuti CE, Coppertino M, Muelbert JH, Vieira JP, Seeliger U (2010a) Coastal lagoons: critical habitats of environmental change. CRC Press, Boca Raton

Odebrecht C, Bergesch M, Rorig LR, Abreu PC (2010b) Phytoplankton interannual variability at Cassino Beach, Southern Brazil (1992–2007), with emphasis on the surf zone diatom *Asterionellopsis glacialis*. Estuar Coasts 33:570–583

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Rodrigues FL, Vieira JP (2012) Surf zone fish abundance and diversity at two sandy beaches separated by long rocky jetties. J Mar Biol Assoc U. K. 93:867–875

Romesburg HC (1984) Cluster analysis for researchers. Lifetime Learning Publications, California

Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology. Academic Press, San Diego

Santana FMS, Severi W (2009) Composition and structure of fish assemblage of the surf zone at Jaguaribe beach, Itamaracá (PE), Brazil. Bioikos 23:3–17

Schoeman DS, Richardson AJ (2002) Investigating biotic and abiotic factors affecting the recruitment of an intertidal clam on an exposed sandy beach using a generalized additive model. J Exp Mar Biol Ecol 276:67–81

Silva JTO, Aguiar MCP, Lopes PRD (2008) Ictiofauna das praias de Cabuçu e Berlinque: uma contribuição ao conhecimento das comunidades de peixes na Baía de Todos os Santos, Bahia, Brasil. Biotemas 21:105–115

Silvy NJ (2012) The wildlife techniques manual: volume 1: research, volume 2: management. Johns Hopkins University Press, Maryland

Spiegehalter DJ, Best NJ, Carlin BP, Van der Linde A (2002) Bayesian measure of model complexity and fit. J R Stat Soc B 64:583–639

Strydom NA, d'Hotman BD (2005) Estuary-dependence of larval fishes in a non-estuary associated South African surf zone: evidence for continuity of surf assemblages. Estuar Coast Shelf Sci 63:101–108

Taylor DA, Nichols RS, Able KW (2007) Habitat selection and quality for multiple cohorts of young-of-the-year bluefish (*Pomatomus saltatrix*): comparisons between estuarine and ocean beaches in southern New Jersey. Estuar Coast Shelf Sci 73:667–679

Vasconcellos RM, Santos JMS, Silva MA, Araujo FG (2007) Efeito do grau de exposição às ondas sobre a comunidade de peixes juvenis em praias arenosas do Município do Rio de Janeiro, Brasil. Biota Neotropica 7:93–100

Vaz AC, Möller OO, Almeida TL (2006) Análise Quantitativa da Descarga dos Rios Afluentes da Lagoa dos Patos. Atlântica 28:13–23

Venables WN, Dichmont CM (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fish Res 70:319–337

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal Gradients of Biodiversity: pattern, Processes, Scale and Synthesis. Annu Rev Ecol Evol Syst 34:273–309

Wood SN (2006a) On confidence intervals for Generalized additive models based on Penalized regression splines. Aust N. Z. J Stat 48:445–464

Wood SN (2006b) Generalized additive models: an introduction with r. CRC Press, Boca Raton