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Factoring scales of spatial and temporal variation in fish abundance in a subtropical estuary

A. M. Garcia[1,*,], J. P. Vieira[1], K. O. Winemiller[2], L. E. Moraes[1], E. T. Paes[3,**]**

[1]Instituto de Oceanografia, Laboratório de Ictiologia, Universidade Federal de Rio Grande (FURG), Caixa Postal 474, Rio Grande, RS 96201-900, Brazil

[2]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258, USA

[3]Instituto de Sócio Ambiental e dos Recursos Hídricos, Universidade Federal Rural da Amazônia (UFRA), Caixa Postal 917, Belém, PA 66077-530, Brazil

ABSTRACT: We employed a new approach linking multivariate and time series analyses to identify common versus unique spatiotemporal components of abundance variation of marine spawning fishes recruiting into a subtropical Western Atlantic estuary. Based on a 10 yr standardized monthly data set, we also investigated patterns of association for local and regional factors with annual and inter-annual variation in abundance of 5 dominant marine estuarine-dependent fishes. The total amount of variation in fish abundance explained by environmental variables was 22.4 %. After factoring out shared spatiotemporal variation (0.8 %), our analysis showed that temporal components had an almost 5-fold greater contribution (28.0 %) than spatial components (6.4 %) in explaining the variation in abundance of the 5 species. Most of the variation across the temporal scale (58.5 %) was associated with annual (from 0.5 to 1.3 yr) rather than multi-year oscillations (>2 yr). Such annual patterns were probably associated with adaptations of marine estuarine-dependent fishes for exploiting predictable pulses in seasonal productivity typically found in subtropical estuaries. In contrast, inter-annual variation in abundance occurring at a scale of 3 to 7 yr could be attributed to rainfall anomalies associated with El Niño Southern Oscillation (ENSO) events, whereas those occurring at a scale of 2 yr could be influenced by the Southern Annular Mode (SAM). Our findings corroborate the hypothesis that prevalent annual patterns of variation in the abundance of marine estuarine-dependent fishes are associated with predictable productivity pulses linked to the annual temperature regime, whereas inter-annual variations in fish abundance are associated with the influence of large-scale climatic phenomena.

KEY WORDS: Time-series analyses · Partitioning variation · Estuarine-dependent species · Mullet · Whitemouth croaker · Argentine menhaden · Patos Lagoon estuary · Brazilian-LTER

INTRODUCTION

Estuarine fish abundance shows high intra- and inter-annual variability across spatial and temporal scales (e.g. Power et al. 2000, Garcia et al. 2004a, James et al. 2008). Such modes of variation are especially strong in marine migrant fishes that spawn in the sea and use estuarine areas as nursery grounds (Vieira & Scalabrin 1991, Able 2005, Akin et al. 2005). Abundance of marine estuarine-dependent fishes often varies widely across coastal salinity gradients, with postlarvae entering deeper waters and juveniles dispersing within shallow waters (<1.5 m) along the estuarine margins (Martino & Able 2003, Greenwood 2007, Sosa-López et al. 2007, Upchurch & Wenner 2008, González-Castro et al. 2009). Juveniles and/or adults of certain marine migrant fishes move several kilometers up the salinity gradient into oligohaline waters near the boundaries with freshwater inflows, or even into the main channels of rivers (Martino &

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*Email: amgarcia@mikrus.com.br
**These authors contributed equally to this work

Able 2003). Abundance of marine migrant fishes within estuarine habitats may change greatly over time scales that range from days, months or years (Whitfield 1996). Most studies of abundance dynamics of estuarine fishes have focused on seasonal (e.g. Chao et al. 1985, Ambrose & Meffert 1999, Gordo & Cabral 2001, Upchurch & Wenner 2008, Herrell & Methven 2009, Love et al. 2009, Plavan et al. 2010) and, to a lesser extent, inter-annual scales of variation (e.g. Power et al. 2000, Garcia et al. 2004a, Martinho et al. 2009, Reum et al. 2011). For instance, dry and wet episodes associated with cold and warm El Niño Southern Oscillation (ENSO) events have been shown to play an important role in structuring fish assemblages on an inter-annual basis in subtropical estuaries of the Southwest Atlantic Ocean (Garcia et al. 2001, 2003a, 2004a).

However, prior studies of estuarine fish abundance across spatiotemporal scales have not clearly addressed the issue of multicolinearity between these scales of variation. There may be redundancy in the variation explained by temporal and spatial variables (Bertolo & Magnan 2006, Peres-Neto 2006) that has not been taken into account in previous studies on spatiotemporal patterns in the abundance of fishes occurring in estuaries (Martino & Able 2003, Pérez-Ruzafa et al. 2007, González-Castro et al. 2009). In this paper, we employed a 4-step analysis using Canonical Correspondence Analysis (CCA) and partial CCA to partition the variation in the abundance of 5 estuarine-dependent fishes (mullets *Mugil liza, M. gaimardianus* and *M. curema*, Argentine menhaden *Brevoortia pectinata*, and whitemouth croaker *Micropogonias furnieri*) explained by independent variables into different components (Borcard et al. 1992). This approach factors out common and unique contributions of spatial and temporal components when modeling variation in fish abundance (Borcard et al. 1992, Peres-Neto 2006), yielding a more accurate representation of patterns and insights into potential causal factors.

In addition, based on a 10 yr data set of monthly abundances, we employed a new analytical approach linking multivariate and time series analyses to investigate patterns of temporal variation of the 5 marine-spawning fishes recruiting into a subtropical estuary. This continuous and standardized time series of marine estuarine-dependent fishes, probably the largest available in the estuaries emptying into the southwestern Atlantic Ocean, allowed us to address 3 basic questions. What are the most prominent patterns of variation in abundance among marine estuarine-dependent fishes in subtropical estuaries? Are these patterns associated primarily with temporal or spatial dimensions? How do local (temperature, salinity) and regional (rainfall) physicochemical factors correlate with temporal patterns of variation observed at different scales? We evaluate the hypothesis that annual patterns of variation in abundance of new recruits are linked to temperature regime, whereas patterns of inter-annual variation are associated with occurrence of larger-scale climatic phenomena.

MATERIALS AND METHODS

Study area

Patos Lagoon (32° S, 52° W) is located along the coastal plain of Rio Grande do Sul in southern Brazil. It is the largest choked lagoon in the world, measuring 250 km long and 60 km wide and covering an area of 10 360 km^2 (Fig. 1). According to Kjerfve (1986), choked lagoons have a single entrance channel and small ratios of entrance-channel cross-sectional area to lagoon surface area. The brackish area is restricted to the southern portion of the Patos Lagoon (ca. 10.0 % of total area). This lagoon is connected to the ocean by a single inlet about 4 km long and 740 m wide at the mouth (Fig. 1). The lagoon's drainage basin covers 201 626 km^2 (Asmus 1997). Wind patterns and fluvial discharge control circulation, salinity distribution, and water levels. Seasonal freshwater discharge varies considerably (47 to 30 300 m^3 s^{-1}), and during El Niño years, runoff greatly exceeds average values. Tidal influence in the estuary is minimal (mean tidal amplitude of 0.47 m). Winds are predominantly NE to SW in the region (Möller et al. 2001). Sand is the dominant fraction in the shallower waters (<1.5 m) of the estuary, whereas the proportion of silt and clay increases with depth (Calliari et al. 1977). Vegetated habitats are commonly found within the estuary, especially saltmarsh plants such as *Spartina densiflora* and *S. alterniflora* and widgeon grass *Ruppia maritima*, which forms extensive meadows during spring and summer (Costa et al. 1997).

The ichthyofauna of the Patos Lagoon Estuary is composed of about 110 species, but only a few are frequent and abundant throughout the year (Chao et al. 1985, Vieira et al. 2010). A few species complete their entire life cycle within this estuary, such as the one-sided livebearer *Jenynsia multidentata* (Garcia et al. 2004b) and the silverside *Odontesthes argentinensis* (Bemvenuti 1987), whereas others spawn in the sea and their young-of-the-year (YOY) recruit into the estuary, where they remain until maturation

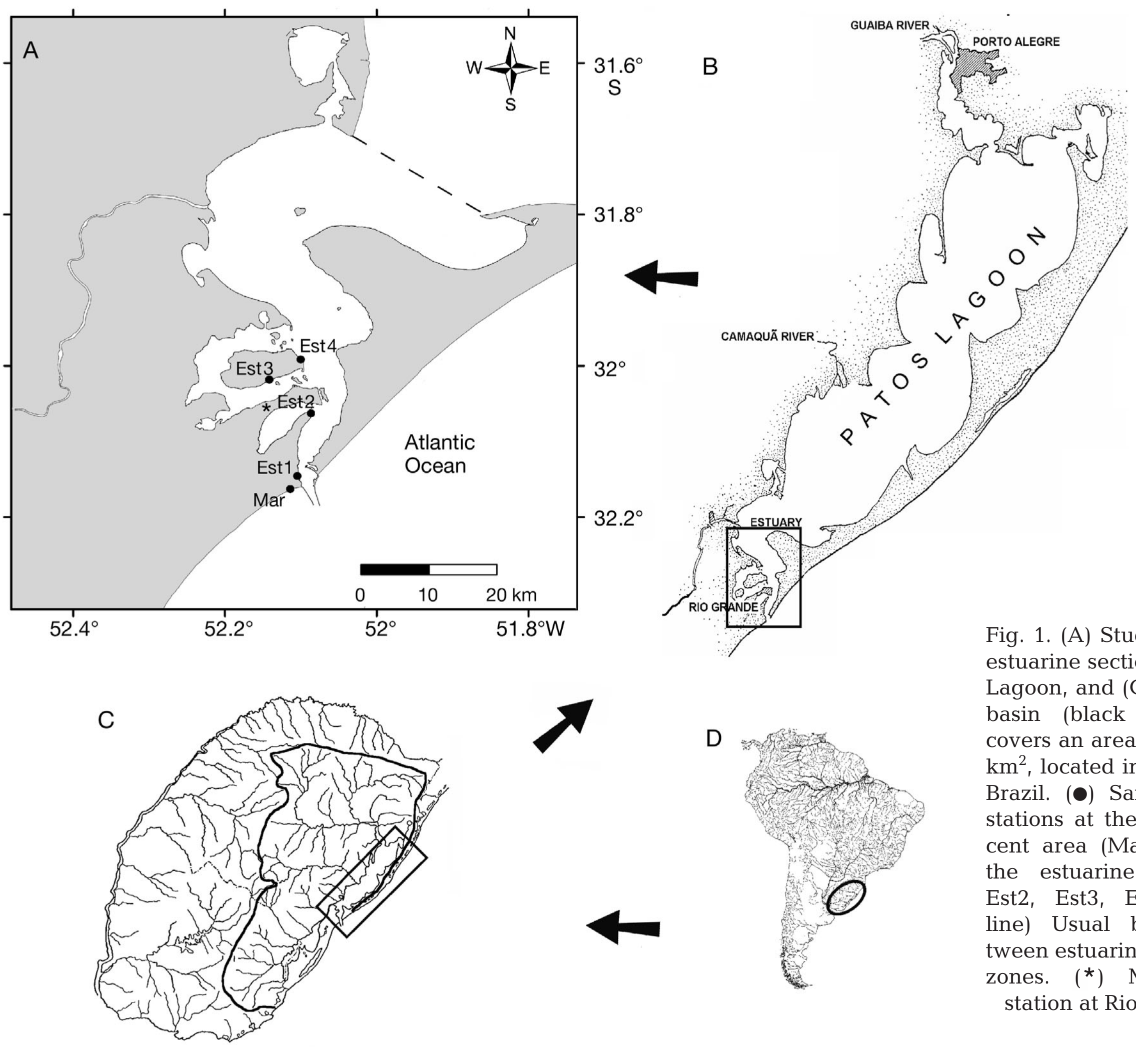

Fig. 1. (A) Study area in the estuarine section of (B) Patos Lagoon, and (C) its drainage basin (black line), which covers an area of ca. 201 626 km^2, located in (D) Southern Brazil. (●) Sampling beach stations at the marine adjacent area (Mar) and inside the estuarine zone (Est1, Est2, Est3, Est4). (dashed line) Usual boundary between estuarine and limnetic zones. (*) Meteorological station at Rio Grande city

and then return to the sea to spawn and complete their life cycles (Vieira & Castello 1997). Some of these marine estuarine-dependent species (e.g. mullets and whitemouth croaker) dominate the biomass of industrial and artisanal fisheries along the southern Brazilian coast (Haimovici et al. 1996, Reis & D'Incao 2000). For this study, we chose the most abundant marine estuarine-dependent fishes occurring in the Patos Lagoon Estuary and its adjacent marine area: the Argentine menhaden, whitemouth croaker, and the 3 species of mullets occurring in this estuary. These species account for 62.0 % of the total abundance of juvenile fishes recruiting annually in this estuary (Vieira et al. 2010).

Field collections and sample procedures

Sampling field stations were located in the shallow waters of the Patos Lagoon Estuary (mean depth < 1.5 m), where abundant marine estuarine-dependent fishes can be efficiently sampled with a seine net (Fig. 1). Fish were sampled using a 9 m beach seine (13 mm bar mesh in the wings and 0.5 mm mesh in the 3 m center section) that was pulled to cover an area of about 60 m^2 during each haul. Five hauls were made monthly (usually in the first week of each month) at each beach station from August 1996 to January 2007. Specimens were preserved in 10 % formalin and later identified, counted and measured for total length (TL) to the nearest mm. Concomitant with fish sampling, we measured the water temperature and salinity at each site. We obtained monthly rainfall data from 1996 to 2007 from the nearby meteorological station of the Federal University of Rio Grande (Fig. 1).

Statistical procedures

Relationships between fish species' abundance and spatiotemporal modes of variation were analyzed with

CCA using the software package CANOCO (ter Braak 1986, ter Braak & Šmilauer 2002). We used a Monte Carlo permutation test (no. of permutations = 9999) to assess the statistical significance of these relationships. When the length of first factorial axis obtained by Detrended Correspondence Analysis (DCA) is greater than 3 standard deviations, it is more appropriate to use a unimodal method (CCA) instead of linear models such as Redundancy Analysis (RDA, ter Braak & Šmilauer 2002). According to this criterion, CCA was chosen because it assumes unimodal relationships between dependent and independent variables (Lepš & Šmilauer 2003).

Because temporal variation can show multicolinearity across spatial scales, there can be a degree of redundancy in the variation explained by temporal and spatial variables (Bertolo & Magnan 2006, Peres-Neto 2006). To account for this potential redundancy, we used a 4-step analysis using CCA and partial CCA (i.e. CCA with covariables) to partition the variation in fish abundance explained by independent variables into different components (see Borcard et al. 1992 and Legendre 2008 for further details of computation). This method allows factoring of common and unique contributions of independent components when explaining variation in the dependent variable (Borcard et al. 1992), resulting in a better understanding of the influences of both groups of independent variables (Peres-Neto 2006).

Four adjusted fractions (Peres-Neto et al. 2006) were obtained using this method. First, we obtained the unique or 'pure' variation in species abundance explained by space (i.e. after controlling the variation related to temporal scale). According to Borcard et al. (1992), this spatial effect, in general terms, may reflect contagious biological processes (e.g. dispersal, habitat preference) that have no relation with the temporal variables per se. Second, we calculated the equivalent unique or 'pure' contribution of the temporal component (after controlling for spatial effect). Third, we obtained the variation in fish abundance that cannot be uniquely assigned to spatial or temporal scales (i.e. colinearity or shared variation). Finally, we estimated the undetermined variation in fish species abundance that is not explained by spatial coordinates or by temporal independent variables (Borcard et al. 1992, Peres-Neto 2006).

We applied this partition variation method to determine which scale (spatial or temporal) explains more variation in fish species abundance, followed by a detailed description of how fish abundance varied for the scale identified as being most important in structuring the data set. Fish species abundance in catch per unit effort (CPUE) populated the dependent-variable matrix, and spatial and temporal descriptor variables populated sets of independent-variable matrices.

There are different ways to represent space (or time) in multivariate analyses, including use of polynomials of geographic coordinates and dummy variables (binary scores for presence or absence) (Legendre & Legendre 1998). However, these methods are sufficient to represent only coarse scales of variation. To better represent spatial and temporal variation at finer scales, Borcard & Legendre (2002) proposed a new technique called principal coordinates of neighbor matrices (PCNM). Starting from a matrix of Euclidean distances among objects representing sample sites or time intervals, a truncated matrix of neighbor distance is produced. This matrix is used to compute principal coordinates in which positive eigenvectors represent Euclidean components of the neighborhood relationships of the truncated matrix. These principal coordinates represent spatial or temporal descriptors and can be used post hoc as explanatory (independent) variables in multivariate analyses (see Borcard & Legendre 2002 for further details). This method was originally proposed to depict spatial structure, but it also can be used to explore temporal structure (Peres-Neto 2006). Thus, PCNM analysis is analogous to a spectral decomposition of spatial and temporal relationships among sampling sites or temporal units (e.g. months), creating variables that correspond to all spatial and temporal scales that can be perceived in a given data set (Borcard et al. 2004, Peres-Neto 2006). PCNM eigenvectors (herein referred to as 'temporal descriptors') were computed using the SpaceMaker 2 software (Borcard & Legendre 2004). We used a value of 0.092 as the truncation point in the distance matrix of latitude and longitude coordinates corresponding to our 5 irregularly distributed sampling sites, and 3 spatial descriptors were generated. For the regularly distributed time scale, we used 1.0 mo as the truncation value in our 126 sample-months matrix, and 85 temporal descriptors were generated. Previously, we tested distinct forms of space and time representations (dummy, geographic coordinates, polynomial, PCNM) to determine which ones explained the greatest amount of variation in the dependent variables. Dummy variables performed best for sampling sites, and temporal descriptors were best for collection periods; these spatial (dummy) and temporal (PCNM) descriptors were used as 2 sets of independent variables in CCA.

We employed CCA bi-plot diagrams to depict the principal relationships between dependent (fish species abundance) and independent (spatial, temporal) variables (ter Braak & Šmilauer 2002). In this ordination diagram, the relative importance of independent variables in explaining variability in species abundance is indicated by the length and angle of vectors in bi-plots. The angle and length of the vector relative to a given canonical axis reveals the magnitude of the variable's correlation with that axis, effectively revealing its relative influence in producing the gradient modeled by the axis. The position of a species on a given canonical axis reveals its association with the gradient (i.e. increasing abundance in response to the gradient).

A forward selection procedure for CCA was employed in order to select, for inclusion in the ultimate model, only those independent variables that were statistically significant ($p < 0.05$; $p < 0.006$ following Bonferroni correction) in explaining variation in fish abundance. We used *t*-value bi-plots with Van Dobben circles to evaluate the relationship between individual explanatory variables and fish species abundance (ter Braak & Looman 1994). These ordination diagrams are built based on *t*-values of canonical coefficients from CCA and are useful to identify significant pair-wise positive and negative correlations between dependent and independent variables (Lepš & Šmilauer 2003). In the Van Dobben diagrams, those species with arrow-heads ending inside the circles have statistically significant pair-wise relationship with the assigned explanatory variable (*t*-values regression coefficient between −2 and +2), where gray and white circles denote positive and negative relationships, respectively. Those fishes with arrow-heads ending out of the circles lack statistically significant association with the explanatory variable analyzed (*t*-value < −2 or > +2).

Finally, relationships between fish species abundance and environmental variables (water temperature, salinity, rainfall) were analyzed with a CCA (ter Braak 1986). We used the same basic parameters (e.g. significance level) and the software used for the partial CCAs explained above.

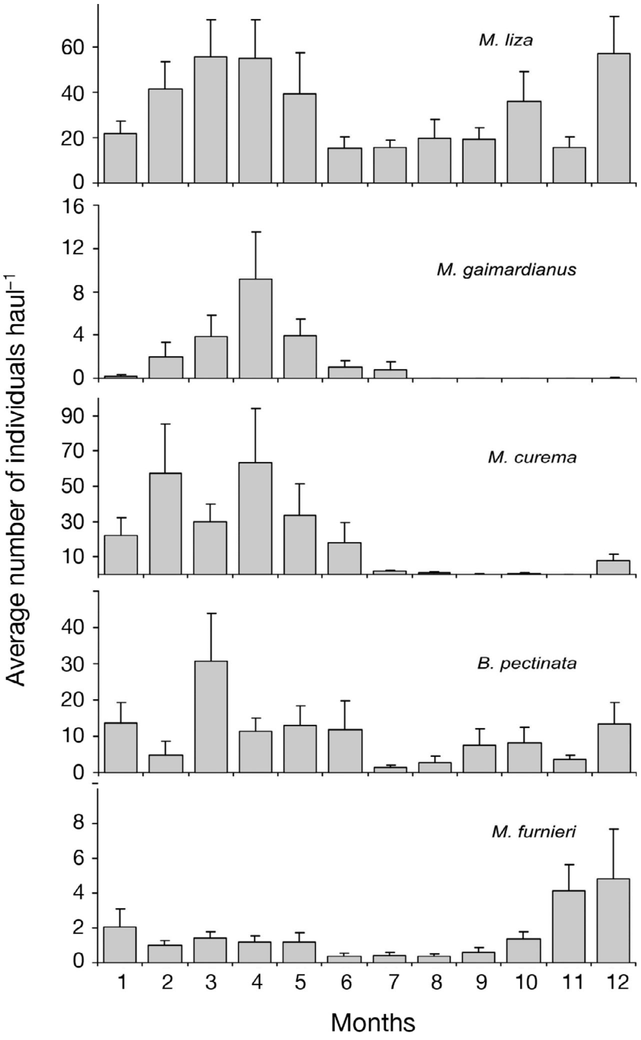

Fig. 2. *Mugil liza*, *M. gaimardianus*, *M. curema*, *Brevoortia pectinata* and *Micropogonias furnieri.* Intra-annual variation of the average (+SE) number of individuals per haul, determined from the natural logarithm of catch per unit effort (ln CPUE + 1) for the 5 fish species collected (3 mullet species, Argentine menhaden and whitemouth croaker). Months from January (1) to December (12) are shown on *x*-axis

RESULTS

Overall abundance patterns

A total of 206 801 individuals of the 5 studied fish species were caught throughout the 126 mo of standardized sampling. Most individuals (76.1%) were captured inside the estuary, especially in the 2 sites closest to the estuary's mouth (21.4% at Est1 and 30.4% at Est2, Fig. 1).

The 3 mullet species comprised 83.2% of the total catch; *Mugil liza* alone represented 54.6% of the overall catch. The Argentine menhaden and whitemouth croaker constituted 14.9 and 2.0% of the catch, respectively. All species revealed marked intra- and inter-annual variation in their relative abundance (Figs. 2 & 3, respectively) and, with the exception of mullets *M. gaimardianus* and *M. curema*, occurred year-round in the study area.

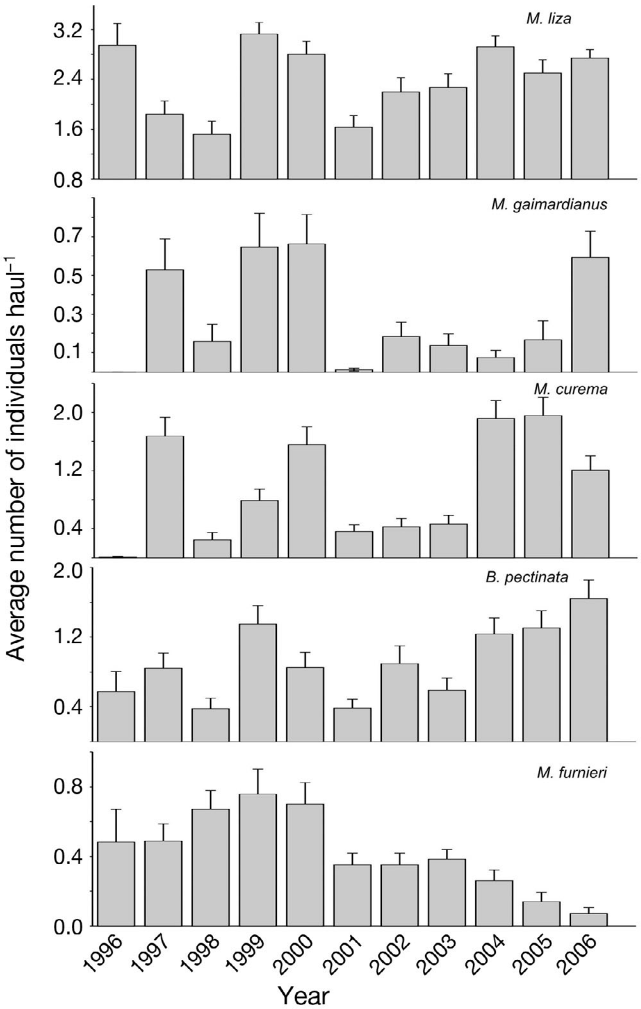

Fig. 3. *Mugil liza*, *M. gaimardianus*, *M. curema*, *Brevoortia pectinata* and *Micropogonias furnieri.* Inter-annual variation of the average (+SE) number of individuals per haul, determined from the natural logarithm of catch per unit effort (ln CPUE + 1) for the 5 fish species collected (3 mullet species, Argentine menhaden and whitemouth croaker)

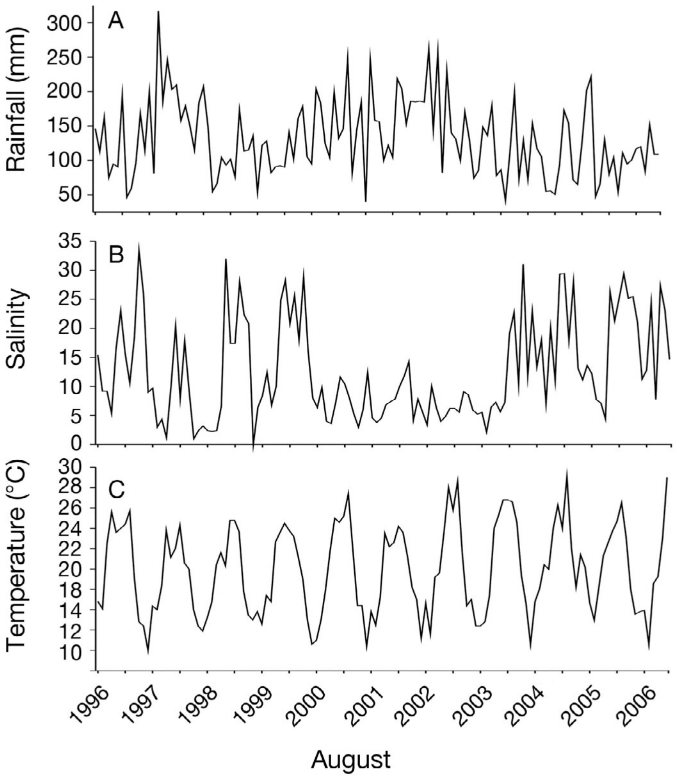

Fig. 4. (A) Total rainfall (mm), and average values of (B) salinity and (C) water temperature (°C) in the estuarine area of Patos Lagoon from August 1996 to January 2007. *X*-axis ticks correspond to August and January of each year

Species abundance correlations with environmental factors

Fig. 4 shows average monthly variation in rainfall, salinity and water temperature in the study site from 1996 to 2007. Water temperature revealed a seasonal pattern of fluctuation, with lowest values (11.5°C) occurring during austral winter months (July and August) and highest average values (26.5°C) during summer months (December to February). Salinity also showed a tendency towards lower values (~5) during colder months and higher values (~25) during warmer months. However, in contrast with the regular pattern observed for temperature, salinity showed strong intra- and inter-annual variation with different patterns observed in different years. For instance, in some years (e.g. 1997–1998 and 2000–2003) there was a predominance of near-zero salinity recordings, whereas in others (e.g. 1999–2000 and 2004–2006) salinity achieved higher values (>25) (Fig. 4).

CCA using rainfall, temperature and salinity as environmental variables explained 22.4 % of the variation in fish abundance during the 10 yr study period, with the first and second axes accounting for 96.1 % of total variation (Fig. 5). Relationships between species abundances and environmental variables influencing these axes were statistically significant ($p < 0.05$), with salinity and temperature accounting for a greater fraction of the explained variation (75.3 %) than rainfall.

According to the CCA results, the 5 fish species had distinct responses to temperature, salinity and rainfall gradients over the 10 yr period (Fig. 5). Salinity and rainfall gradients were inversely correlated and fish abundances showed opposite responses to these variables. Abundance of the mullets *Mugil gaimardianus* and *M. curema* and Argentine men-

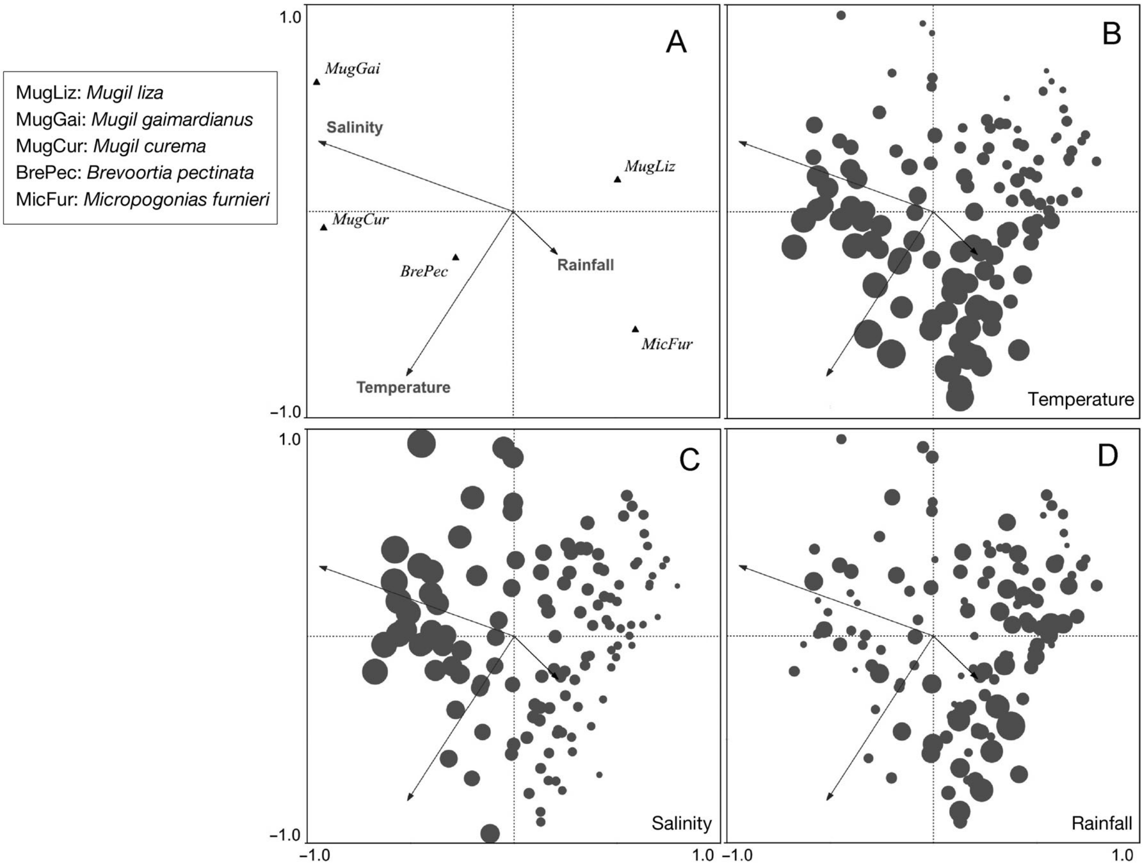

Fig. 5. Canonical Correspondence Analysis (CCA) ordination plots showing (A) association of fish species with temperature, salinity and rainfall gradients, where each axis is represented by its score (plotted) and correlation between environmental variables and axes is represented by the length and angle of arrows, and association of samples with (B) temperature, (C) salinity and (D) rainfall gradients. The diameter of each circle is proportional to the observed values of each parameter in each month in each sample site

haden were positively correlated with salinity and negatively correlated with rainfall. In contrast, the mullet *M. liza* and the whitemouth croaker were more abundant during intervals of low salinity and high rainfall. Abundances of mullet *M. curema* and Argentine menhaden were positively associated with temperature, whereas mullet *M. liza* was more abundant during cooler periods (Fig. 5).

Partitioning of the spatiotemporal components of variation in fish abundance

Analysis of fish abundance variation across spatiotemporal scales using CCA and partial CCA revealed that variation in species abundance was almost 5-fold higher across the temporal than the spatial scale (Table 1). Differences in species abundance across estuarine sites explained by the spatial descriptors (after controlling the variation related to temporal scale) were only 6.4 %. In contrast, the variation across the 10 yr period explained by the temporal descriptors (after controlling the variation related to spatial scale) was 28.0 %. Interaction, or colinearity, between spatial and temporal scales was minimal (0.8 %), but a large fraction of fish abundance variation (64.8 %) could not be explained by any spatial or temporal components estimated in this study (Table 1).

Spatial differences in fish species abundance occurred mainly between sites near the estuary mouth and those located in the estuary's interior (Est2, Est3) (Fig. 6). The location Est4 was not included in the CCA analysis because it did not make a significant contribution to the model according to the forward selection procedure. Abundance of mullets was strongly associated with sites near the channel that connects the estuary to the ocean, particularly *Mugil*

Table 1. Overall results of the 4 partial Canonical Correspondence Analyses (CCAs) performed to partition the variation in abundance of the 5 dominant marine estuarine-dependent fishes into (a) pure space (6.4%), (b) space and time combined (colinearity) (0.8%), (c) pure time (28.0%) and (d) undetermined variation ([100 − (a + b + c)] = 100 − 35.2 = 64.8%) (sensu Borcard et al. 1992). Total inertia in all CCA was 0.987. Significance based on Monte Carlo permutation (n = 9999) test for the first and all axes. *p < 0.001

Axes	Eigenvalues				Trace	% variance explained
	1	2	3	4		
Species vs. Space	0.040*	0.017	0.010	0.003	0.071*	7.2
Species vs. Time	0.162*	0.053	0.045	0.023	0.284*	28.8
Species vs. Space with Time as covariate	0.050*	0.018	0.009	0.002	0.063*	6.4
Species vs. Time with Space as covariate	0.165*	0.053	0.049	0.024	0.276*	28.0

Table 2. Thirteen (out of 85) eigenvectors obtained by the principal coordinates of neighbor matrices (PCNM) that were considered as significant (p < 0.006, after Bonferroni's correction and the Forward Selection procedure) for patterns in variation of fish abundance of 5 marine estuarine-dependent fish species based on (A) annual and (B) inter-annual time scales. LambdaA (conditional effect) accounts for the amount of variability explained by the variable (eigenvector), whereas LambdaA (%) is the percentage related to the total inertia (0.284) explained by all eigenvectors

Eigenvector	*F*-ratio	p-value	LambdaA	LambdaA (%)	Scale of variation (mo)	(yr)
(A) Annual variation patterns (0.5 to 1.3 yr)						
PC-41	6.71	0.004	0.009	3.2	6.0	0.5
PC-25	8.48	0.001	0.011	3.9	9.7	0.8
PC-21	30.82	0.001	0.047	16.5	11.4	0.9
PC-23	7.23	0.002	0.009	3.2	10.5	0.9
PC-20	37.09	0.001	0.059	20.8	12.0	1.0
PC-19	16.57	0.001	0.023	8.1	12.6	1.0
PC-15	6.22	0.001	0.008	2.8	15.7	1.3
(B) Inter-annual variation patterns (>2 yr)						
PC-8	9.03	0.001	0.012	4.2	28.0	2.3
PC-7	8.31	0.001	0.011	3.9	31.5	2.6
PC-5	13.84	0.001	0.019	6.7	42.0	3.5
PC-3	6.4	0.003	0.008	2.8	63.0	5.2
PC-2	18.92	0.001	0.026	9.2	84.0	7.0
PC-1	24.23	0.001	0.035	12.3	126.0	10.5

gaimardianus at Mar and *M. liza* and *M. curema* at Est1. In contrast, the Argentine menhaden and the whitemouth croaker tended to be more abundant at sites in the middle region of the estuary (Est2, Est3) (Fig. 6).

Forward selection procedure identified 13 (out of 85) variables as significant temporal descriptors (Table 2), and these were included in the partial CCA as independent variables. These temporal descriptors (PCNM) revealed variation at 2 main scales: annual (0.5 to 1.3 yr) and inter-annual (2.3 to 10.5 yr) (Table 2). Seven annual and 6 inter-annual temporal descriptors accounted for 58.5 and 39.1%, respectively, of total explained variation (fraction c = 28.8%) in fish species abundance. For example, the temporal descriptor PC-20, which depicted fluctuation occurring in a temporal scale of 1 yr, accounted for 20.8% of explained variation in fish abundance (Table 2, Fig. 7).

Correlations of individual species abundances with these annual and inter-annual descriptors varied considerably, and this can be observed in the *t*-value bi-plots with Van Dobben diagrams that show statistically significant pair-wise relationships between species and selected explanatory variables (Fig. 8). For instance, the mullets *Mugil gaimardianus* and *M. curema* were positively correlated with PC-20 (1 yr), whereas mullet *M. liza* and whitemouth croaker were negatively correlated with these same temporal descriptors (Fig. 8). These opposite correlation patterns were associated with distinct peaks of recruitment of these fishes into the estuary. Juveniles of mullets *M. gaimardianus* and *M. curema* were abundant in the estuary from January–February to March–April, whereas juveniles of mullet *M. liza* and whitemouth croaker occurred year-round in the estuary (Fig. 2). In contrast, the Argentine menhaden had no significant correlation with PC-20, as indicated by the vector representing this species not being circumscribed by either of the 2 Van Dobben circles (Fig. 8). Other temporal descriptors with similar annual cycles (PC-41, 25, 21, 23, 19, and 15, ranging from 0.5 to 1.3 yr) also made significant contributions to the model, and together accounted for an additional 37.7% of total explained variation (Table 2). These temporal de-

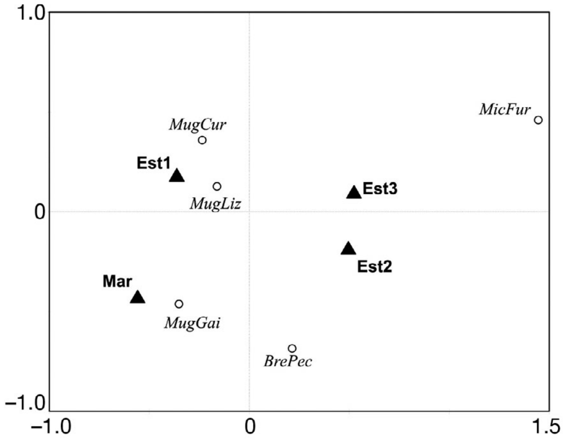

Fig. 6. Canonical Correspondence Analysis (CCA) ordination plot showing the association of fish species abundance across different sampling sites in the study area. Association of species with each axis is represented by its score (plotted) and correlation between sampling sites (nominal variables denoted by triangles) and axes are represented by their position relative to each canonical axis. (○) Fish species (abbreviations in Fig. 5). (▲) Sample sites: Mar: marine adjacent area; Est1, Est2, Est3: estuarine sites

scriptors operated at slightly shorter or longer scales than the annual cycle depicted by PC-20, but they were either out of phase or in opposition with each other.

Inter-annual variation (temporal scales from 2.3 to 10.5 yr), although accounting for less total variation in fish abundance (39.1 %), was significant, particularly the temporal descriptors PC-1 (10.5 yr period) that alone modeled 12.3 % of explained variation in fish abundance (Table 2). Correlations between abundance of individual fish species with these inter-annual temporal descriptors varied (Fig. 8). For instance, the Argentine menhaden and the mullet *Mugil curema* were positively correlated with the large fluctuation depicted by PC-1, showing significantly lower catches in the first half of the sampling period and a subsequent increase in the remaining years (Figs. 3 & 8). In contrast, the whitemouth croaker and the mullet *M. gaimardianus* were negatively correlated with PC-1 (Fig. 8), with higher abundances during the first half and lower abundances during the second half of the study period (Fig. 3). The mullet *M. liza* had no significant correlation with the ~10 yr period represented by PC-1.

Between the annual and decadal fluctuations, it was possible to identify other significant fluctuations of 3.5 (PC-5) and 7.0 (PC-2) yr, accounting for 6.7 and 9.2 %, respectively, of the explained variation in fish species abundance (Table 2). Mullets and the whitemouth croaker were the only species showing significant relationships with these fluctuations (Fig. 8). Mullets *Mugil curema* and *M. gaimardianus* were positively correlated (*t*-values > 0 and < +2) with the 7 yr temporal fluctuation, whereas abundances of the other mullet, *M. liza,* and the whitemouth croaker were negatively correlated with this trend (*t*-values < 0 and > −2). The only species showing a correlation with the 3.5 yr fluctuation was the mullet *M. curema* (Fig. 8).

DISCUSSION

Spatial versus temporal dimensions

Our results showed that rainfall, temperature and salinity explained 22.4 % of the variation in abundance of marine estuarine-dependent fishes occurring in Patos Lagoon Estuary. Prior studies in this estuary have already discussed the relevance of these environmental variables in explaining fish

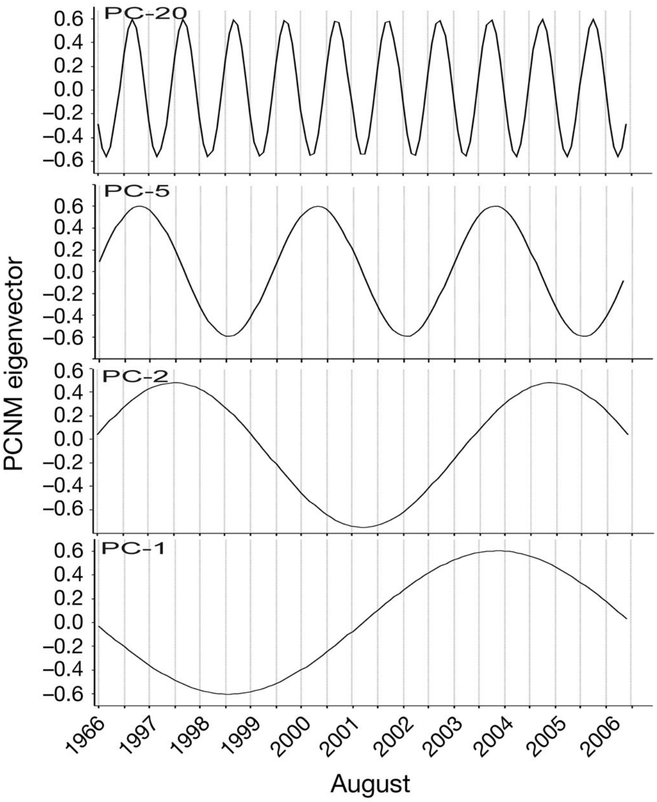

Fig. 7. Temporal fluctuation patterns of selected principal coordinates of neighbor matrix (PCNM) eigenvectors associated with annual (PC-20) and inter-annual variation (PC-5, PC-2, PC-1) of the abundance of the studied marine estuarine-dependent fishes species in Patos Lagoon Estuary from August 1996 to January 2007

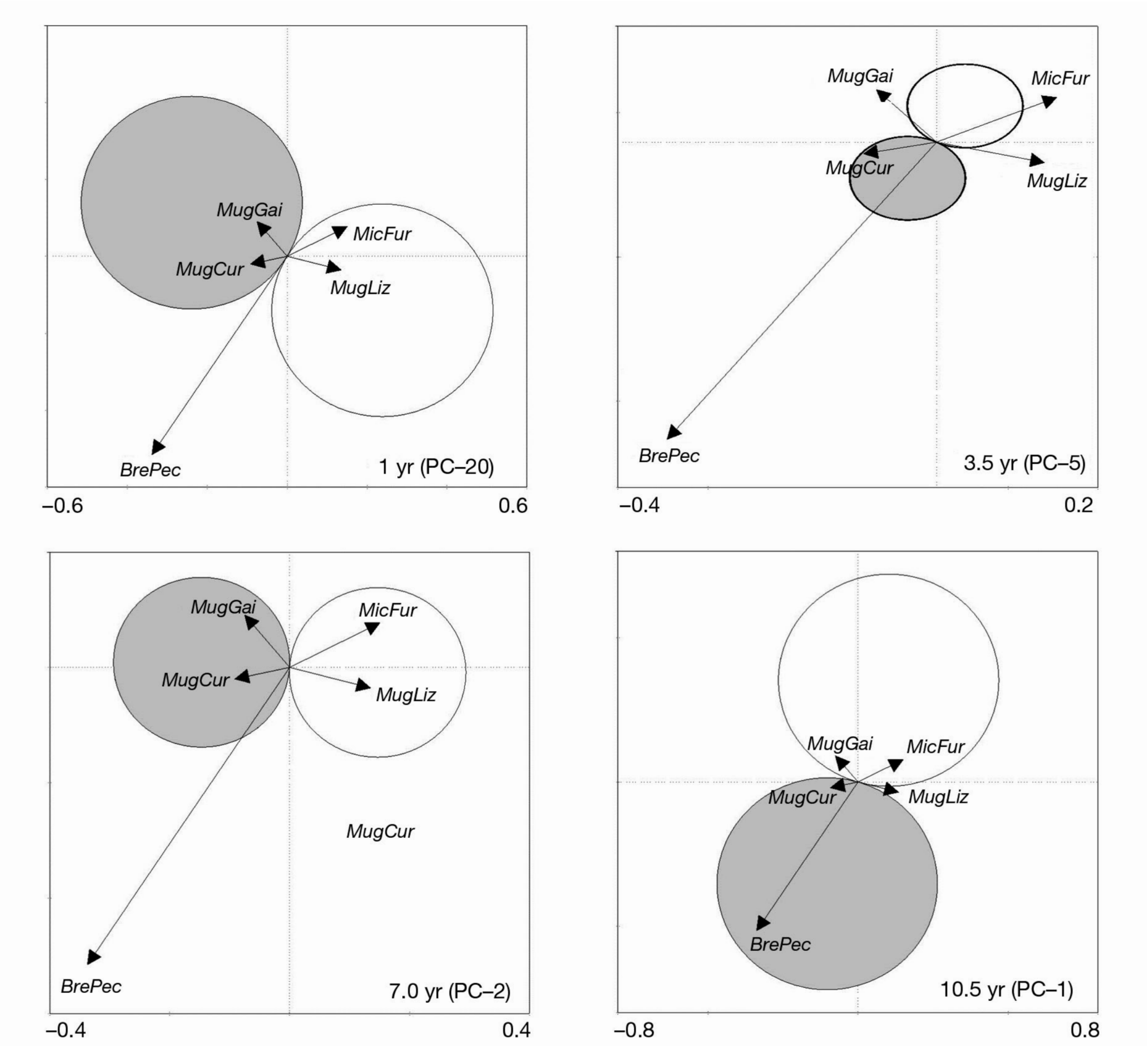

Fig. 8. Bi-plots of *t*-values with Van Dobben circles showing pair-wise relationships between each fish species and temporal descriptors: PC-20 (1 yr fluctuation period), PC-5 (3.5 yr), PC-2 (7 yr) and PC-1 (10.5 yr). Those vectors with arrowheads ending inside the circles have statistically significant pair-wise relationships with the assigned explanatory variables (*t*-value regression coefficients between −2 and +2). Gray and white circles denote positive and negative relationships, respectively. See Fig. 5 for abbreviations

abundance (Garcia et al. 2001, 2003a, 2004a). However, the predominant modes of variation in fish abundance in this system were unknown and our analytical approach, combining partition variation associated with a multivariate time series analysis, substantially contributed to advance our understanding in this area. After factoring out common spatiotemporal variation (0.8%), our partitioning analysis showed that the temporal dimension (after controlling the variation related to spatial scale) had an almost 5-fold greater contribution (28.0%) than the spatial scale (6.4%) in explaining variation in abundance of marine estuarine-dependent fishes recruiting to a subtropical Western Atlantic estuary. Moreover, we found that most of the temporal variation (58.5%) was associated with annual (0.5 to 1.3 yr) rather than multi-year (>2 yr) patterns of fluctuation.

Relatively low spatial variation in the abundance of marine estuarine-dependent fishes in Patos Lagoon Estuary could be explained by the species' tolerance of a broad range of salinities (Chao et al. 1985). These euryhaline species are widespread along the marine–estuarine gradient of this region (Chao et al. 1985, Vieira et al. 2010), with most spawning in the sea and their juveniles particularly abundant in shallow waters (<1.5 m) of the estuary (Chao et al. 1985, Vieira et al. 2010, Becker et al. 2011), where food is abundant (Figueiredo & Vieira 2005, Rosa & Bemvenuti 2006, Mendoza-Carranza & Vieira 2008, Vieira et al. 2010). The marine estuarine-dependent species studied are commonly found between the Patos Lagoon Estuary and adjacent marine areas probably because salinity differences between these systems does not constitute a physiological barrier to these euryhaline species. This may partially explain why the spatial scale had a lower contribution to the explanation of variation in abundance of marine estuarine-dependent fishes recruiting into this estuary.

The annual patterns of variation that dominated our analysis of fish abundance are probably associated with evolutionary adaptations of these marine estuarine-dependent fishes to exploit predictable seasonal pulses of aquatic primary and secondary production that commonly occur in temperate and subtropical estuaries. Seasonality in solar irradiance and temperature in these mid-latitudes drive peaks of productivity during spring and summer and lower production during late fall and winter (Day et al. 1989, Murrell & Lores 2004, Strydom & d'Hotman 2005, Jeong et al. 2009). Long-term ecological studies carried out in Patos Lagoon Estuary clearly show such seasonal pulses in both primary and secondary production (Seeliger et al. 1997, Abreu et al. 2010, Seeliger & Odebrecht 2010). Water temperature variation in this region is typical of warm temperate systems, with lowest values (10 to 15°C) during the austral winter (July) and highest temperatures from January to March (22 to 30°C) (Odebrecht et al. 2010). Accordingly, chlorophyll *a* concentrations increase in spring (10 to 70 µg l^{-1}) and high values are common in the estuary throughout the summer, especially due to growth of diatoms (Fujita & Odebrecht 2007). Seagrass beds (dominated by the widgeon grass *Ruppia maritima*) and macroalgae (e.g. *Ulva* spp., *Cladophora* spp., *Rhizoclonium riparium*) also make significant contributions to seasonal production in this system, with biomass production ranging from 50 to 300 g dry wt m^{-2} (seagrass) and 0.5 to 1.2 C m^{-2} yr^{-1} (macroalgae) (Coutinho & Seeliger 1986, da Silva & Asmus 2001). This seasonal production sustains an array of micro- and macro-consumers, especially decapod crustaceans and fishes (Rosa & Bemvenuti 2006, Odebrecht et al. 2010, Vieira et al. 2010). Consequently, patterns of abundance of primary producers and estuarine fishes in Patos Lagoon covary on an intra-annual scale.

Coupling of producer and consumer biomass has been recognized in estuaries and pelagic oceanic waters of temperate latitudes of the Atlantic Ocean (Strydom & d'Hotman 2005, Haynes et al. 2010, Kristiansen et al. 2011). Our temporal analysis based on PCNM, however, suggests that such annual cycles in abundance of marine estuarine-dependent fishes are more complex than relationships portrayed in previous studies (Chao et al. 1985, Vieira 1991, Garcia & Vieira 1997, Vieira et al. 1998). Instead of a regular intra-annual seasonal cycle, annual abundance of marine estuarine-dependent fishes at Patos Lagoon reveals cycles with distinct peaks that occur every 0.5 to 1.3 yr. Differences in amplitude among these annual peaks are probably modulated by conspicuous short-term (from hours to months) variability in physicochemical parameters (e.g. salinity, turbidity) and their effects on primary and secondary production. Other abiotic factors that strongly influence movements of juvenile marine migrant fishes between the sea and estuary, such as wind patterns and freshwater discharge, could reduce or increase the periodicity of abundance peaks. For instance, the mullet *Mugil liza* spawns in the sea and postlarvae (<50 mm) are transported into the estuary by a net upstream circulation near the bottom of the water column at the estuary mouth. Recruits remain in shallow waters of the estuary until maturation and then migrate, usually during April and May, towards offshore spawning grounds (Vieira 1991). A sudden drop in water temperature (<19°C) and intrusion of marine waters into the estuary seem to trigger spawning migrations (Vieira & Scalabrin 1991). Therefore, differences in the onset of these environmental cues (e.g. delay in the intrusion of salinity waters into the estuary during El Niño events; Vieira et al. 2008) could delay or hinder migration towards the sea, thereby altering their residence time within the estuary and, consequently, temporal abundance patterns.

Multi-year variation

Although to a lesser extent than the annual scale, inter-annual scales from 2.3 to 10.5 yr were also significant in modeling fish abundance in Patos Lagoon. Previous long-term studies in this estuarine system have shown that such multi-year variation in fish abundance is strongly linked to climatological and hydrological effects trigged by the ENSO phenomenon (Garcia et al. 2001, 2003a,b, 2004a, Vieira et al. 2008). Positive and negative rainfall anomalies in the drainage basin of Patos Lagoon (~200 000 km^2) are associated with El Niño and La Niña episodes, respectively (Grimm et al. 1998, 2000). Such anomalies seem to modulate the diversity and abundance patterns of several taxa in Patos Lagoon Estuary and the adjacent marine area (Odebrecht et al. 2010). For instance, the high rainfall associated with strong El Niño events produces freshwater outflow anomalies (from 2400 $m^3 s^{-1}$ to 12 000 $m^3 s^{-1}$) that flush freshwater species into the lower portion of the estuarine zone (Garcia et al. 2003b). At the same time, such high freshwater outflow acts as a physical barrier for larvae and juveniles of marine-spawning species, such as pink shrimp *Farfantepenaeus paulensis* (Möller et al. 2009) and mullets (Garcia et al. 2004a), that seek to enter the estuary to complete their life cycles. The opposite pattern is found during La Niña events, when negative rainfall anomalies cause lower freshwater outflow and greater intrusion of seawater into the estuary. This condition favors the entrance of larvae and post-larvae of marine-spawning species into the estuary and, consequently, potential for enhanced recruitment of marine migrant fishes (Grimm et al. 1998, Martins et al. 2007, Vieira et al. 2008, Möller et al. 2009, Muelbert et al. 2010). Thus, the observed inter-annual patterns of variation in marine estuarine-dependent fish abundance occurring from 3.5 to 7.0 yr are probably related to ENSO events reported to occur with a similar periodicity (Rodbell et al. 1999, Glantz 2001). Therefore, a large fraction (18.7 %) of the explained variation in the inter-annual abundance of marine estuarine-dependent fishes in Patos Lagoon could be attributed to the influence of the ENSO.

Our analysis also revealed that a significant fraction of inter-annual variation in the abundance of marine estuarine-dependent fishes occurred at approximately 2 yr (e.g. PC-8: 2.3 yr and PC-7: 2.6 yr) and 10 yr (e.g. PC-1) time scales, which accounted for 8.1 % (considering both PC-8 and PC-7) and 12.3 % of the explained variance, respectively. Variation in the larger scale (~10 yr) was most apparent in the Argentine menhaden. According to Legendre & Legendre (1998), an event or pattern needs to be observed at least twice in order to draw inferences about temporal dynamics. Therefore, a larger data set would be needed in order to determine the real importance of this ~10 yr cycle in fish abundance. The shorter 2 yr scale could not be attributed to the ENSO, which is reported to occur with a distinct frequency in the Equatorial Pacific Ocean (Rodbell et al. 1999, Glantz 2001). Rather, we speculated that 2 yr fluctuations in estuarine-dependent fish abundance could be linked to other temperate-zone meteorological phenomena. For example, a climatic phenomenon known as the Southern Annular Mode (SAM) oscillates with a period of about 2 yr. Spectral analysis using SAM index time-series (1996 to 2010) shows significant periodic cycles of 2.21 yr, and SAM has been associated with large-scale climatic variability in middle and higher latitudes of the Southern Hemisphere (Hendon et al. 2007). This climatic phenomenon conventionally refers to oscillations of sea level pressure in the Southern Hemisphere, especially between polar regions and middle latitudes (Limpasuvan & Hartmann 1999, Oke & England 2004). The SAM phenomenon seems to influence rainfall patterns and the occurrence of storms and cyclones in South America, Africa and Australia through its connection with atmospheric components, such as latitudinal migration shifts of the subtropical upper-level jet, variations in the intensity of the polar jet, and fluctuations in the subpolar westerly winds (Rao et al. 2003, Carvalho et al. 2005, Harry et al. 2006, Hendon et al. 2007, Nicholls 2010, Sun et al. 2010). SAM has been also linked with ocean circulation around the South Pole (Rintoul & England 2002, Oke & England 2004), with potential effects on water circulation and biological production in the Subtropical Convergence Zone. Patos Lagoon is located under the influence of this important convergence zone (Seeliger et al. 1997), and, as noted previously, wind and rainfall regimes influence the abundance of aquatic organisms in Patos Lagoon (Garcia et al. 2001, 2003a, 2004a, Martins et al. 2007, Möller et al. 2009, Odebrecht et al. 2010). It seems plausible, therefore, that such large-scale phenomenon affecting atmospheric and oceanographic conditions in the South Atlantic with approximately a 2 yr frequency would play a role in the post-spawning success of marine migrant species that use the Patos Lagoon Estuary as a nursery. The current study supports findings from several prior studies that demonstrated the influence of large-scale coupled ocean–atmosphere phenomena in the Pacific Ocean (ENSO) on the estuarine fish assemblage inhabiting the Southwestern Atlantic Coast of Brazil (Garcia et al. 2001, 2003a, Vieira et al. 2008, Dumont & D'Incao 2011). The influence of similar coupled ocean–atmosphere phenomena, such as the SAM, on inter-annual variation of estuarine-dependent fishes and other marine taxa in this region and elsewhere deserves further investigation.

In summary, our 10 yr data set of continuous and standardized monthly time series revealed that 5 marine-spawning fishes (3 species of mullets, Argentine menhaden, and whitemouth croaker) recruiting into a subtropical Western Atlantic estuary showed marked annual and inter-annual variation in their relative abundance. Temperature had a regular seasonal pattern in this system, with lowest values (11.5°C) during winter and highest values (26.5°C) during summer, which contrasted with the strong intra- and inter-annual variation observed in salinity and rainfall. These environmental variables explained 22.4% of the variation in fish abundance. More importantly, our partition variance analysis revealed that variation in species abundance was almost 5-fold higher across the temporal (28%) than the spatial scale (6.4%). The colinearity between these scales was minimal (0.8%) and there was a considerable amount of fish abundance variation (64.8%) that could not be explained by these spatial or temporal components. The temporal variation occurred mainly at annual (0.5 to 1.3 yr) and inter-annual (2.3 to 10.5 yr) scales, which accounted for 58.5 and 39.1% of the explained temporal variation in fish species abundance, respectively. We hypothesized that the prevalence of annual modes of variation in these marine estuarine-dependent fishes are probably associated with adaptations for exploiting predictable seasonal productivity pulses typically found in this subtropical estuary. In contrast, inter-annual variation in abundance could be attributed to the influence of large-scale climatic phenomena. For instance, positive and negative anomalies of rainfall and salinity triggered by strong ENSO events have marked influence in the ichthyofauna of this estuary (Garcia et al. 2004a) and could explain fish abundance variations at the 3 to 7 yr scale. We also speculated that another large-scale climatic phenomenon, the Southern Annular Mode (SAM), could be associated with variations in fish abundance at intermediate (2 yr) temporal scales.

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