

Delayed response of fish abundance to environmental changes: a novel multivariate time-lag approach

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ABSTRACT: We used long-term juvenile abundance data (2000 to 2010) of dominant fish species in 2 coastal habitats of Southern Brazil to test a novel adaptation of traditional multivariate analyses, as an alternative for evaluating the lag in species response relative to the changes in environmental variables. We investigated the hypothesis that the recruitment response to changes in environmental variables is not immediate. This new approach consisted of traditional multivariate analysis (e.g. canonical redundancy analysis) using an explanatory matrix composed of original and lagged environmental variables, and the performance of this analysis was assessed by comparison with traditional univariate time-lag analysis. Both the univariate and multivariate time-lag analyses showed similar results, but the multivariate approach had advantages and is presented as a useful and uncomplicated alternative to conduct time-lag analysis using a multivariate ecological dataset. Marine and estuarine recruitment processes were better explained by lagged temperature (predominant lags of 1 and 2 mo, respectively) than by in-phase (i.e. time lag = 0) temperature. In contrast, other environmental variables (transparency, salinity and freshwater outflow) did not show significant delays. Hence, our findings show that the species response to environmental variables is not immediate, especially for temperature. Rather, the time lag elapsed between the changes in abiotic factors and juvenile abundance is mediated by ecological and hydrological processes. Our study reaffirms the importance of time-lag analyses as a tool for better understanding of the temporal dynamics of estuarine and marine recruitment.

KEY WORDS: Time-series analyses · Delays · Young of the year · Fish · Estuary · Surf zone

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INTRODUCTION

Two of the main objectives of time-series analysis in ecology are to understand how large- and small-scale environmental variables drive ecosystem occupation patterns and to determine the structure and composition of communities on several temporal scales (e.g. inter-annual, annual and sub-annual) (Pascual & Ellner 2000, Cazelles 2004). However, the

response of the target variables to the explanatory variables is frequently not immediate but instead is delayed (Legendre & Legendre 1998, Olden & Neff 2001). The scale of this delay is variable and is related to the frequency of occurrence of the event (e.g. daily, monthly or inter-annually) in relation to the lifecycle of the different taxonomic groups being examined. For instance, variations in phytoplankton species response can be observed in relatively short

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time periods (e.g. hours or days) (Li et al. 2009, Chen et al. 2010, Vidal et al. 2010), whereas fishes usually respond over longer time scales (e.g. months or years) (Parraga et al. 2010, Qiu et al. 2010, von Biela et al. 2011).

The relationships and delay between species abundance and environmental variables are relevant to ecology (Legendre & Legendre 1998, Pascual & Ellner 2000, Delhez & Deleersnijder 2008). However, the identification of a time lag between changes in environmental variables and species abundance and the ecological significance of these time lags are still rare topics in coastal ecology studies. For instance, from a Web of Science® database search using keywords related to time-lag methods, we found <100 papers (5% of the total) employed these methods in studies of marine and estuarine ecology during the last 2 decades (1990 to the present). The majority of these studies refer to the oceanic pelagic ecosystem, and only a few studies have been conducted in estuarine systems (e.g. Lesen 2006, Guadayol et al. 2009, Gutierrez-Estrada et al. 2009, Yanez et al. 2010, Pan et al. 2011). Nevertheless, the increase in the availability of free software, the mathematical solutions related to time-series analysis and the increasing number of long-term datasets are making time-lag analyses more common.

Estuaries and marine surf zones are recognized as important nursery areas for several species (Bell et al. 2001, Strydom & d'Hotman 2005, Ramos et al. 2010), 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). Similar to other habitats, the complexity of ecological relationships in estuaries and marine surf zones requires the use of multivariate analysis, but there are only a few methods available to investigate the time lag of species response to environmental variables based on a multivariate approach. Thus, the present study presents a novel adaptation of a traditional multivariate analysis as an alternative for evaluating time lags. We analyzed a long-term record (from 2000 to 2010) of juvenile fish and crustacean abundance in 2 subtropical coastal habitats (Patos Lagoon Estuary and Cassino Beach in southern Brazil) to illustrate the potential use of the method. Additionally, we evaluated the hypothesis that the recruitment response of the dominant species of the Patos Lagoon Estuary and Cassino Beach to environmental variables (namely, temperature, salinity, transparency and freshwater outflow) is not immediate.

MATERIALS AND METHODS

Study area

The study was conducted in 2 subtropical coastal habitats in southern Brazil: Patos Lagoon Estuary and Cassino Beach. The Patos Lagoon Estuary is a river-dominated system where water exchange and estuarine circulation are controlled by the freshwater runoff from the Patos and Mirim drainage basin (201 626 km²) and by prevailing winds (northeasterly winds throughout the year, with a higher frequency of southwesterly winds during autumn and winter) (Möller et al. 2001, Möller & Fernandes 2010). The exchange of water with the Atlantic Ocean is restricted to an inlet 0.6 km wide and 16 m deep, fixed by a pair of 4 km long jetties that were constructed at the beginning of the 20th century near the city of Rio Grande (Odebrecht et al. 2010) (Fig. 1). Cassino

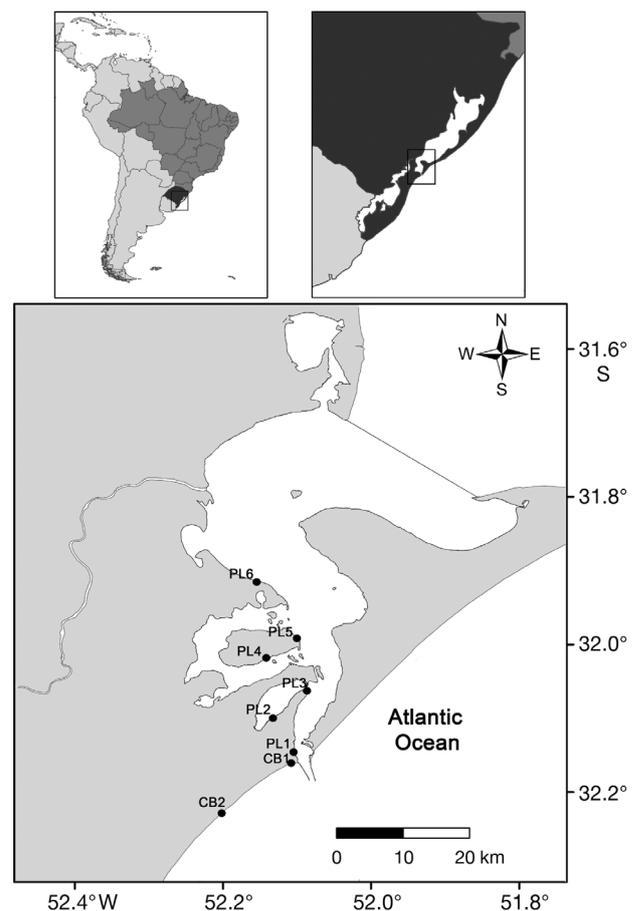


Fig. 1. Sampling sites in the Patos Lagoon Estuary (PL1, PL2, PL3, PL4, PL5 and PL6) and at Cassino Beach (CB1 and CB2). Upper panels: South America (left), with Brazil (dark grey); and the location of the Patos-Mirim Lagoon System (box, right)

Beach, which is located south of the Patos Lagoon inlet (Fig. 1), is an exposed sandy beach with a smooth profile that is characteristically dissipative and presents waves of average energy levels (Calliari et al. 2001). The Patos Lagoon plume generally behaves as a small-to-averaged size plume, covering the first few meters of the water column. The spread of the plume alongshore is mainly controlled by the wind regime and coastal currents. The dominant NE winds spread the plume towards the south, forming a pocket (pool) of brackish waters along the Cassino Beach coastal area (Marques et al. 2010).

Sampling strategy

Fishes and crustaceans were sampled monthly during a 10 yr period (January 2000 to July 2010) using a 9 m beach seine (13 mm bar mesh in the wings and 5 mm in the center 3 m section). Biological sampling ($n = 5$ hauls at each site per month, a total of $\sim 60 \text{ m}^2$) was performed at 8 sites (6 estuarine sites and 2 marine sites) located in shallow waters (mean depth $< 1.5 \text{ m}$) (Fig. 1). The selection of sites was arbitrary but designed to cover the largest possible spatial variability of the 2 studied habitats (estuary and surf zone). Therefore, only 2 sites were required for Cassino Beach due to its high spatial homogeneity, in contrast to the estuary, which has areas with different features (e.g. type of soil: sandy or muddy; presence of vegetation).

Before the sampling of the biological material, the water temperature ($^{\circ}\text{C}$), water transparency (Secchi depth, m) and salinity were measured at each of the sampling sites. The river discharge data from January 2000 to July 2010 for 3 rivers (the Jacuí, Taquarí and Camaquã) located north of the Patos Lagoon were acquired from the Brazilian National Agency of Water (Agência Nacional de Águas, 2010; hidroweb.ana.gov.br), and the sum of the monthly discharge ($\text{m}^3 \text{ s}^{-1}$) of these 3 rivers was used as a proxy for the freshwater outflow of the drainage basin of the Patos-Mirim Lagoon system (Vaz et al. 2006).

We chose 8 dominant species as the response variables from among the available long-term dataset. We considered dominant species as those accounting for 90% of the total fishes and crustaceans caught in shallow water ($< 1.5 \text{ m}$) of the Patos Lagoon Estuary and at Cassino Beach. These species can be classified into the following life history categories (sensu Garcia et al. 2001): estuarine-resident (RESI), typically occurring and breeding in estuaries and represented in the present study by *Atherinella brasiliensis* (Quoy & Gaimard, 1825), *Jenyntia multidentata* (Jenyns,

1842) and *Odontesthes argentinensis* (Valenciennes, 1835) (fishes); estuarine-dependent (DEPE), marine or freshwater spawning species found predictably in large numbers in estuaries during part of their life-cycle and represented in this study by *Brevoortia pectinata* (Jenyns, 1842), *Mugil cf. hospes*, *M. curema* Valenciennes, 1836, *M. liza* Valenciennes, 1836 (fishes) and *Farfantepenaeus paulensis* (Pérez-Farfante, 1967) (crustacean); and marine-resident (MARI = marine vagrant; Garcia et al. 2001), typically inhabiting marine environments while rarely occurring in estuaries and represented by the species *Trachinotus marginatus* Cuvier, 1832 (fish). The majority of the mullet (87%) caught in the study area were recruits of small size ($< 40.0 \text{ mm}$), increasing the difficulty in separating *Mugil cf. hospes* from *M. curema*. These 2 species are more often associated with higher temperatures and salinities and have similar patterns of seasonal occupation of the shallow areas of the Patos Lagoon Estuary and Cassino Beach (Vieira 1991). For these reasons, we considered *Mugil cf. hospes* and *M. curema* as a single species (*Mugil* spp., MUGSPP) in the present study.

Time-lag analyses

Species abundance data were expressed as the number of individuals per haul (catch per unit effort, CPUE). The monthly CPUE at the estuarine and coastal (surf zone) sites was calculated as the average of 5 hauls obtained at each sampling site per month. We transformed the data prior to analysis using Hellinger (Legendre & Gallagher 2001) and log transformations for the biological and environmental variables, respectively. Subsequently, the linear trend was removed from the data series by the subtraction of a linear regression line (detrending) (Legendre & Legendre 1998).

Initially, we were interested in identifying the main delays of the generalized species response relative to the environmental variables for each studied habitat from a univariate analysis. Thus, we used principal component analysis (PCA) to extract a major axis summarizing the variation in species abundance for both estuarine and marine habitats, reducing the dimensionality of highly correlated factors (Legendre & Legendre 1998, Azeria et al. 2009). We retained only the first axis PCA (PC1), which was extracted using a correlation matrix. The contribution of the different species (original variables) to the PC1 was observed from the PCA loadings (coefficients), and the significance of these loadings was evaluated using a row-wise boot-

strapping test ($n = 5000$) (Peres-Neto et al. 2003). The correlations of the response variables (now the PC1) related to the explanatory variables and their lags for each studied habitat were evaluated using the cross-correlation method, and the significance of each lag was evaluated using a t -test with $n - 2$ degrees of freedom, where n is the number of samples that overlap (Legendre & Legendre 1998). The PCAs and cross-correlation analyses were performed using PAST, which is a free statistics package (Hammer et al. 2001).

Our second step was to assess the time lag elapsed between the changes in the environmental variables and the species abundances for each studied habitat from a novel multivariate approach using canonical redundancy analysis (RDA) with CANOCO software. In this procedure, we identified the delay that maximized the percentage of the variation of the response matrix explained by the explanatory matrix (R^2), rather than analyzing the correlation values as performed using the cross-correlation method. Additionally, we contrasted these results with those obtained from the univariate analysis. For this multivariate approach, we generated new explanatory variables for each studied habitat that represented the original variable at different time lags. This was carried out by lagging the original explanatory variables relative to the response variables, with time lags of ' k ' units, where k represents the number of time-lag months. The new explanatory variable matrix was composed of both the original and lagged variables for the multivariate analysis (RDA), with each column corresponding to a variable. The rows containing empty cells generated in this procedure were removed from the matrix to make the number of cases uniform in all of the explanatory variables. Thus, the original matrix was reduced, and the number of deleted rows was equal to the total number of time-lag units (k). The same approach was repeated with the species matrix to ensure that the explanatory and response matrices were equivalent in size (i.e. conformable). This procedure resulted in the loss of cases from the dataset, which should be avoided, especially when the data matrix is small. Thus, the maximum number of time-lag units used in this analysis corresponded to a higher delay than that identified by the cross-correlation analysis.

For the step-by-step selection of the explanatory variables from the RDA, we assessed the statistical significance of the relationships using a Monte Carlo permutation test ($n = 5000$) (Lepš & Šmilauer 2003). The significance level of 0.05 was considered to include/exclude environmental variables in the model. The multicollinearity among environmental variables was inspected from the comparison between the val-

ues of the marginal and conditional effects of each variable. When 2 or more explanatory variables are closely correlated, the conditional effect of these variables decreases dramatically in relation to marginal effects after one of them is included in the model (Lepš & Šmilauer 2003). Environmental variables that play an important role in ecosystems may not be included in predictive models when multicollinearity is detected to avoid invalid results generated by these models containing highly correlated variables. Therefore, the RDA was redone using the non-significant collinear variable as a passive variable when multicollinearity was found for important environmental factors. In this procedure, the passive variable is not used during the calculations performed by RDA, but it is passively projected into the ordination space (Lepš & Šmilauer 2003). Therefore, this procedure allowed us to avoid the undesired effects of multicollinearity without giving up some environmental variables that are important for understanding the dynamics of the studied habitats.

RESULTS

The 2 extracted PC1s accounted for 32.7 and 39.2% of the variation in species abundance in the estuarine and marine habitats, respectively. These PC1s represented the monthly variation in the dominant species (response variables) and allowed us to distinguish between those months with relatively high species abundances (high temperatures and salinities; positive PCA scores) and those with lower abundances (low temperatures and/or salinities; negative PCA scores). Only the menhaden *Brevoortia pectinata* did not show a significant contribution to the composition of the PC1 that represented the Patos Lagoon Estuary (Fig. 2A). The mullet *Mugil liza* and the silverside *Odontesthes argentinensis* were negatively related to both of the PC1s (Fig. 2). The same relationship was observed between the silverside *Atherinella brasiliensis* and the PC1 that represented Cassino Beach (Fig. 2B). The other species analyzed were positively correlated with the PC1s (Fig. 2).

Using the cross-correlation method, we observed the highest correlations of the PC1s with explanatory variables when the variables were in-phase (i.e. time lag = 0) (Table 1). The exceptions were temperature-PC1s correlations, which were higher, with time lags equal to 1 and 2 mo for the marine and estuarine habitats, respectively, and transparency-PC1s correlations, which showed a significantly higher correlation with a 1 mo delay (Table 1).

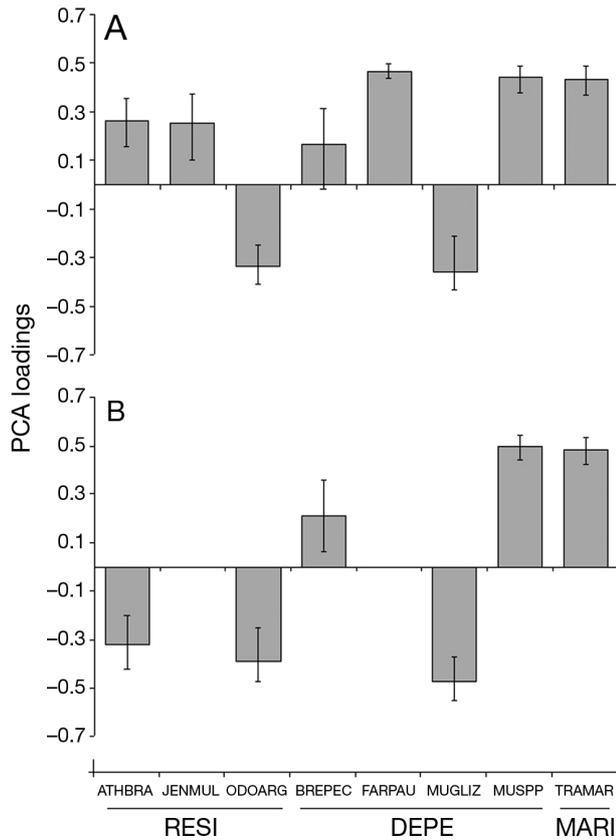


Fig. 2. Individual contribution (principal component analysis [PCA] loadings) relating the 8 dominant species (original variables) into the PC1 that represents (A) the Patos Lagoon Estuary and (B) Cassino Beach. Vertical error bars represent the 95% confidence intervals of the PCA loadings generated by bootstrapping ($n = 5000$). Estuarine-resident species (RESI): *Atherinella brasiliensis* (ATHBRA), *Jenynsia multidentata* (JENMUL) and *Odontesthes argentinensis* (ODOARG); estuarine-dependent species (DEPE): *Brevoortia pectinata* (BREPEC), *Farfantepenaeus paulensis* (FARPAU), *M. liza* (MUGLIZ) and *Mugil* spp. (MUGSPP); marine-resident species (MARI): *Trachinotus marginatus* (TRAMAR)

The models generated using RDA supported the patterns observed from the univariate analysis. These models revealed that the variations in the numerical abundance of the dominant species at Cassino Beach and the Patos Lagoon Estuary were better explained by temperature, with lags of 1 and 2 mo, respectively (TEMP-1 and TEMP-2), rather than by in-phase temperature (TEMP-0) (Table 2). The R^2 -values are presented in the total variance scale rather than in the explained variance scale (Table 2). Thus, the R^2 -values for each environmental variable are low because of high unexplained variance ($\sim 70\%$), but the first RDA ordination axes accounted for 71.7 and 77.4% of the total explained variance for the Patos Lagoon Estuary and Cassino Beach, respectively, and they also showed a high

Table 1. Cross-correlations of environmental variables (water transparency: TRAN, water temperature: TEMP, salinity: SAL and freshwater outflow: FLOW) with the first 2 principal component axes (summarizing species abundance) in 2 subtropical habitats (the Patos Lagoon Estuary and Cassino Beach surf zone). Values are Pearson's correlation coefficients. Bold values show maximal correlation between the response and explanatory variables. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Time lag (mo)	TRAN (m)	TEMP ($^{\circ}\text{C}$)	SAL	FLOW ($\text{m}^3 \text{s}^{-1}$)
Patos Lagoon estuary				
0	0.46***	0.45***	0.55***	-0.63***
1	0.39***	0.61***	0.49***	-0.54***
2	0.20*	0.63***	0.32***	-0.37***
3	0.04	0.49***	0.07	-0.15
4	-0.42**	0.19*	0.02	0.02
5	-0.33***	-0.14	-0.07	0.13
6	-0.27**	-0.45***	-0.13	0.26**
Cassino Beach				
0	0.15	0.64***	0.38***	-0.54***
1	0.26**	0.71***	0.36***	-0.37***
2	0.08	0.58***	0.25**	-0.15
3	0.04	0.43***	0.13	0.05
4	0.03	0.07	-0.01	0.22*
5	0.01	-0.28**	-0.02	0.32***
6	-0.07	-0.53***	-0.22*	0.38***

Table 2. Relative influence of significant environmental variables ($p < 0.05$, $n = 5000$, except for SAL-0) with different lags (R^2 , %) on species abundance. The R^2 values are presented in the total variance scale. Marginal and conditional effects represent the prior and posterior R^2 to the start of the forward selection process, respectively. Original and lagged variables are represented by the following codes: -0 (original), -1 (1 mo delay) and -2 (2 mo delay). F is the pseudo- F statistic. TEMP: water temperature; SAL: salinity; FLOW: freshwater outflow; TRAN: transparency

Variables	R^2 (%)		F	p
	Marginal effects	Conditional effects		
Patos Lagoon estuary				
TEMP-2	14.84	14.84	22.1	0.005
FLOW-0	14.37	6.80	10.9	0.009
TEMP-0	10.35	5.61	9.63	0.007
SAL-2	4.39	2.69	4.75	0.016
SAL-0	10.18	0.74	1.31	0.306
Casino Beach				
TEMP-1	20.39	20.39	32.5	0.001
TEMP-0	17.05	3.78	8.25	0.003
FLOW-0	12.25	3.04	6.02	0.004
TRAN-2	2.70	2.21	4.96	0.003

species-environment correlation (0.819 and 0.768, respectively) (Table 3).

In the estuarine system, the non-lagged freshwater outflow (FLOW-0) and salinity (SAL-0) and the 2 mo lagged temperature (TEMP-2) were strongly

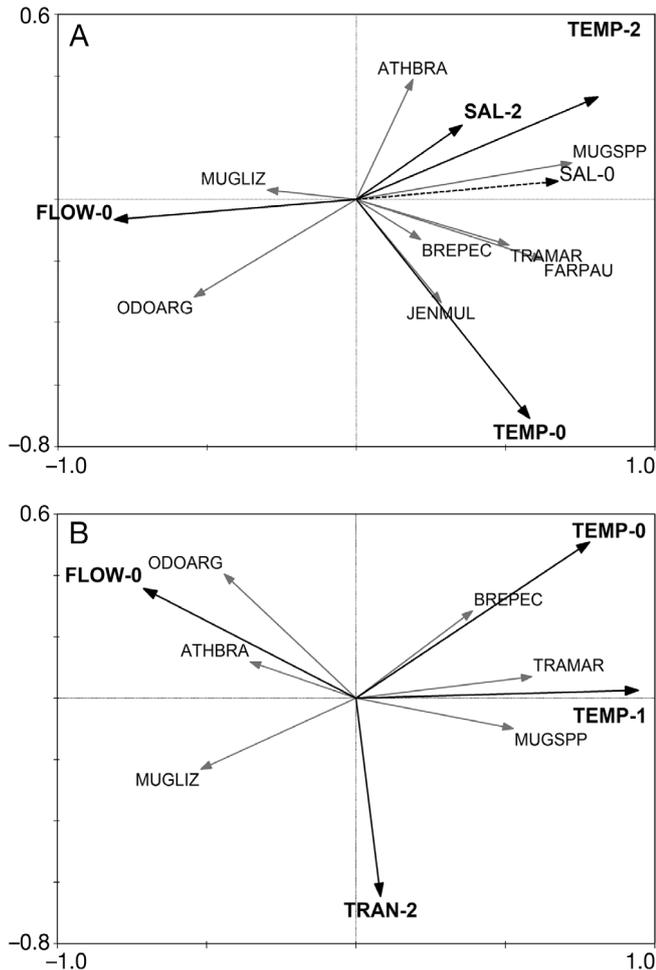


Fig. 3. Canonical redundancy analysis (RDA) ordination diagram based on the relative abundance (CPUE) of the dominant species and the distribution of the environmental variables (A) in the Patos Lagoon Estuary and (B) at Cassino Beach. Correlations of the fish species and environmental variables with each of the axes are represented by the length and angle of the arrows. Dashed arrows represent passive environmental variables. Original and lagged variables are represented by the following codes: -0 (original), -1 (1 mo delay) and -2 (2 mo delay). TEMP: water temperature; SAL: salinity; FLOW: freshwater outflow; TRAN: water transparency. Species abbreviations as in Fig. 2

correlated with the first axis, whereas the non-lagged temperature (TEMP-0) was correlated with the second axis (Table 3, Fig. 3A). The variation in the species abundance in Patos Lagoon Estuary explained by SAL-0 was not significant ($p > 0.05$) when the TEMP-2 and FLOW-0 variables were included in the model (Table 2). This lack of statistical significance probably occurred due to the high collinearity between these variables (Table 2, Fig. 3A). Nevertheless, SAL-0 was included in the ordination space as a passive variable due to its

importance for explaining the physiological mechanisms that influence species distributions in estuaries (Fig. 3A). Indeed, part of the influence of the freshwater outflow on species abundance occurs indirectly from the regulation of salinity.

In the marine system, the non-lagged (TEMP-0) and 1 mo lagged temperature (TEMP-1) were negatively correlated with the first axis, and FLOW-0 was positively correlated with the first axis (Table 3, Fig. 3B). The TEMP-0 and 2 mo lagged water transparency (TRAN-2) were also correlated with the second axis (Table 3, Fig. 3B). From the ordination diagrams, we can infer that the first axis represents a flow-generated thermohaline gradient for the Patos Lagoon Estuary, with the majority of species positively correlated with this gradient (Fig. 3A). In contrast, the first axis in the Cassino Beach diagram represents a temperature gradient, with which species of marine-origin (*Brevoortia pectinata*, *Mugil* spp. and *Trachinotus marginatus*) were positively correlated, whereas the estuarine-resident species (*Atherinella brasiliensis* and *Odontesthes argentinensis*) and the estuarine-associated species, such as *M. liza*, were negatively correlated (Fig. 3B). From the ordination diagrams, we also observed that the abundance of *B. pectinata*, *Mugil* spp. and *M. liza* (DEPE) were better explained by temperature, with a smaller lag for Cassino Beach than for the Patos Lagoon Estuary, whereas the opposite lag pattern was observed for the relationship between temperature and *A. brasiliensis* (RESI) (Fig. 3). These differences were not observed for *O. argentinensis* (RESI) or *T. marginatus* (MARI) (Fig. 3).

DISCUSSION

Multivariate analyses have several advantages compared with univariate analyses, which should be considered before choosing a method for ecological studies. Among the advantages, we highlight the following: (1) the simultaneous analysis of response variables, which allows the identification of common patterns among them (i.e. the redundant structure of data); (2) the ability to identify the commonly found multicollinearity among explanatory variables; (3) the possibility of obtaining a model that summarizes the relationship between the response and explanatory variables; and (4) the reduction of the probability of incurring a Type I error in statistical tests (i.e. finding a significant result by chance) due to the lower number of tests needed to assess the significance of the relationships between the variables (Gauch 1982,

Table 3. Canonical redundancy analysis (RDA) performed on the relative abundance (CPUE) of dominant species in the Patos Lagoon Estuary and at Cassino Beach using an environmental matrix composed for non-lagged (TEMP-0 = temperature, FLOW-0 = freshwater outflow, SAL-0 salinity, and lagged variables (-1 indicates a 1 mo delay, -2 indicates a 2 mo delay, TRAN = water transparency). Dashes in the table represent the environmental variables that did not show in the biplot diagram. Forward selection was performed with a cutoff level of $\alpha = 0.05$

	Patos Lagoon estuary		Cassino Beach	
Axes:	1	2	1	2
Summary statistics for ordination axes				
Eigenvalues	0.215	0.058	0.228	0.055
Species-environment correlations	0.819	0.659	0.768	0.519
Cumulative percentage variance				
of species data	21.5	27.3	22.8	28.2
of species-environment relation	71.7	91.2	77.4	95.9
Biplot scores of environmental variables				
TEMP-0	0.5801	-0.7211	-0.7821	-0.5099
TEMP-1	-	-	-0.9451	-0.0256
TEMP-2	0.8094	0.3359	-	-
FLOW-0	-0.8108	-0.0673	0.7104	-0.3574
SAL-0	-	-	-	-
SAL-2	0.3547	0.2440	-	-
TRAN-2	-	-	-0.0825	0.6464

Legendre & Legendre 1998, Gotelli & Ellison 2004, Manly 2005).

The uni- and multivariate approaches used in the present study generated similar results, in part, because of the pretreatment of the response variables by PCA, which concentrated the main variability of the response matrix into a single variable (PC1). The difficulty of relating the principal component scores back to the original measurements is a disadvantage of this ordination method (Gotelli & Ellison 2004). For instance, each score summarizes the linear combination of several measurements into only one value. Therefore, the use of PC1 or another variable that summarizes a multivariate matrix (e.g. total abundance) as the response variable makes it difficult to relate the results obtained by time-lag univariate analysis with the original variables and limits the extrapolation of these results. The use of a traditional multivariate analysis (i.e. RDA) based on an environmental matrix composed of original and previously lagged variables allowed us to identify the response of each species (or group of species/guilds) in relation to the environmental variables at different time-lags and to find the lag that maximized the species variability explained by each environmental variable. Therefore, this novel multivariate approach seemed to be a useful and direct alternative method for conducting a time-lag analysis using a multivariate ecological dataset.

Temperature appeared to be the primary factor regulating species recruitment at Cassino Beach and

Patos Lagoon Estuary, whereas salinity and freshwater outflow also play an important role in estuarine recruitment. Species abundance patterns at Cassino Beach are predominantly cyclical, following the seasonal trend of temperature (Lima & Vieira 2009). In the Patos Lagoon, recruitment also shows a seasonal pattern linked to temperature-driven biological processes typical of temperate systems (e.g. primary and secondary production), and it is regulated by the annual and inter-annual variability of salinity (Garcia et al. 2003, Vieira et al. 2008, Odebrecht et al. 2010), which is controlled by the dynamic between freshwater outflow from the Patos-Mirim Lagoon drainage and prevailing winds (Martins et al. 2007, Möller et al. 2009). Freshwater outflow also plays a crucial role in the

temporal dynamics of species recruitment at Patos Lagoon Estuary because it controls the entrance and retention of eggs, larvae and juveniles of marine-origin species into the estuary (Garcia et al. 2003, Martins et al. 2007, Möller et al. 2009, Odebrecht et al. 2010). Among the 4 environmental variables examined, only the time lags between the temperature and species abundance were statistically significant. Three hypotheses, which are not mutually exclusive, are presented to explain these results.

The first hypothesis concerns the synchronism of favorable conditions for the growth and survival of juveniles (e.g. an increase in the temperature and the food supply), which has been observed in coastal habitats during the spring and is typical of subtropical ecosystems (Day et al. 1989, Nezhlin & Li 2003, Taylor et al. 2007, Jeong et al. 2009, Li et al. 2009, Ramos et al. 2009, Able et al. 2011, Kristiansen et al. 2011). For instance, the peak ichthyoplankton abundance in the Southern Bay of Biscay was from late winter to the boreal spring, and the 3 mo delay between the peaks of egg and larval abundance was related to the timing of egg spawning and larval recruitment to the pelagic environment (d'Elbee et al. 2009). The shallow areas of the subtropical Patos Lagoon Estuary and the adjacent coastal zone (e.g. Cassino Beach) are used annually as nursery grounds by marine and estuarine-related species, which initially occupy the surrounding areas of the Patos Lagoon Estuary from early spring to summer to

reproduce, taking advantage of the warmer temperatures (Haimovici & Umpierre 1996, Garcia et al. 2004, Lima & Vieira 2009, Vieira et al. 2010, Lemos et al. 2011). Thus, it is plausible that the time lags observed in this study between the water temperature and juvenile abundance (1 and 2 mo at Cassino Beach and the Patos Lagoon Estuary, respectively) could be explained by the time required for the larvae from the spring reproductive period to take advantage of the spring food supply and to reach the size range captured by our fishing gear (beach seine). The negative relationship between the temperature and recruitment of the mullet *Mugil liza* and the silverside *Odontesthes argentinensis* was consistent with the reproductive activity of these species that occurs during the cold season, namely, between late fall and winter (Vieira 1991, Moresco & Bemvenuti 2006), and the time lags observed in this relationship. Especially for *O. argentinensis*, the 2 to 3 mo delay seems to be related to species' preferences for lower temperature and higher freshwater discharge, which are commonly found during colder months (Moresco & Bemvenuti 2006). Temperature, river discharge and food preference regulate the interspecific differences in the reproduction and recruitment patterns on both temporal and spatial scales (Peterson et al. 2004, Snickars et al. 2009, Trape et al. 2009, Primo et al. 2011). Therefore, the hypothesis that the observed time lags could be explained by the time required for the larvae to reach the size range captured by our fishing gear could also be applied to the species that reproduce during the cold season.

The second hypothesis takes into consideration the transport of marine recruits, especially estuarine-dependent species, into the Patos Lagoon Estuary. In general, the young-of-the-year (YOY) of those species enter the shallow waters (<1.5 m) of the estuary from late spring to summer. The lower river discharges at this time favor the intrusion of saline water into the estuary (Möller & Fernandes 2010) and thus facilitate the passive transport of the juveniles of marine-origin species into the estuary (Sinque & Muelbert 1997, Vieira et al. 2010). Therefore, this recruitment into the estuarine shallow waters between late spring and early summer occurs after the warming of the water during the early spring and could explain the lag of 2 mo in the species response to the estuarine water temperature, especially for those species of marine origin. The colonization of the Cassino Beach surf zone is not dependent on this complex transport system and instead favors species that occupy the surf zone rather than the estuary. This could explain the

differences in the time lags between species and water temperature observed in the Patos Lagoon Estuary (up to 1 mo) and the Cassino Beach surf zone (0 to 1 mo). There are no differences in the monthly temperatures between these 2 habitats. Thus, these spatial differences in the lag of the species response to temperature also seem to show a sequential movement of the recruits between the estuary and marine surf zone, suggesting a connection between these 2 habitats. For instance, an earlier appearance of marine-origin recruits in the Cassino Beach, followed by displacement of these recruits into Patos Lagoon Estuary, could explain the lower time lags between the temperature and marine-origin species in the marine surf zone than in the estuarine area.

The third hypothesis refers to the negative correlation between the species abundance and the freshwater outflow, which also had a lag of 2 mo with the temperature. Physical barriers generated by estuarine hydrodynamics (e.g. high freshwater outflow or sand bars) reduce the ability of juveniles to enter into the estuary, therefore, blocking or delaying the recruitment of marine species (Bell et al. 2001, Garcia et al. 2003, Vorwerk et al. 2003, Ramos et al. 2009). The shallow areas of the Patos Lagoon respond quickly to changes in atmospheric temperature (Chao et al. 1985), but the main tributary rivers of the Patos Lagoon have high discharges in late winter and early spring (Vaz et al. 2006, Möller et al. 2001). Thus, when the water temperature begins to rise in early spring, the estuary waters remain oligohaline due to the high river flows, discouraging recruits of marine origin from entering the lagoon. Therefore, the delay could also be explained as a response to the relationship between temperature and the interaction of freshwater outflow with the salinity in the estuary.

In summary, the use of time-lag methods to identify delays in relationships among variables highlights the importance of explanatory variables that would otherwise be masked by low correlations when the response and explanatory variables are only examined in-phase. In the present study, we observed that an important fraction of the temporal variability in the abundance of the dominant species in the Patos Lagoon Estuary and Cassino Beach was explained by a delayed response of these species to environmental variables, particularly the water temperature. Moreover, we showed that the findings are not simply a mathematical device but appeared to result from the biological and ecological features of the studied species. Therefore, the identification of time lags allowed a better characterization of the processes

that regulate the recruitment of species in the shallow areas of the examined habitats. An evaluated phenomenon must be observed at least twice to have minimal certainty that the observed phenomenon is real (Legendre & Legendre 1998). In this sense, it is not necessary to obtain long data series to evaluate small-scale cycles. For example, data series with a time-span of at least 2 yr will permit the assessment of phenomena with annual cycles. Thus, the use of time-lag analyses should be encouraged, even with short-term time series (<5 yr).

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