LONG-TERM ASSESSMENT OF TEMPORAL VARIABILITY IN SPATIAL PATTERNS OF EARLY LIFE STAGES OF FISHES TO FACILITATE ESTUARINE CONSERVATION

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ABSTRACT

Estuaries are among the most productive coastal ecosystems, supporting a wide variety of marine fishes and their early stages. High spatial and temporal variability in estuaries implies that management strategies must incorporate dynamic features to be efficient. In our study, we analysed 13 years of data on ichthyoplankton from the Patos Lagoon estuary (Brazil) to assess whether temporal variability can show distinct spatial patterns of fish eggs and larval distribution and to discuss how these results can be helpful to conservation planning. Spatial patterns of fish egg and larval assemblages were evaluated using cluster analysis. Indicator taxa for each group were also calculated as a product of the relative frequency and relative average abundance in each group. In addition, we used generalized linear models to analyse fish egg and larval abundance in relation to environmental variables. Results showed that fish eggs and larvae exhibit high variability among months, years and sampling stations in the time series. Temporal occurrence and spatial distribution were mainly associated with salinity. We found distinct spatial patterns for fish eggs and larvae in the Patos Lagoon estuary. Groups identified were different among years and indicated by a distinct genus. Our results can be considered as a first exploratory step to help managers to decide which species and temporal scale should be studied in detail and incorporated in management plans. Spatial conservation planning incorporating fluctuations in abundance and assemblage structure over time may help to ensure conservation for biodiversity persistence in highly dynamic ecosystems such as the Patos Lagoon estuary.

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INTRODUCTION

Estuaries are among the most productive coastal environments and support a wide variety of species, especially fish and their early life stages. The main advantages for early life stages that depend on estuaries are related to nursery, breeding and refuge functions (Blaber 2000). In addition, estuaries are also important for many ecological processes such as preventing disturbance, sediment retention and nutrient regulation (Barbier et al. 2011). Due to their dynamic nature and interactions across the continent-ocean interface, ecological processes in estuaries are characterized by a complex pattern of biological, physical, chemical or socioeconomic components (Pittman et al. 2011), influencing species distribution and biological production. Distribution patterns of fish eggs and larvae are usually correlated with physical and chemical variables, with salinity and temperature being the most relevant environmental variables influencing their abundance and occurrence (Marques et al. 2005). Biotic factors, such as food availability, predation and competition can also influence mortality and recruitment processes in estuaries (Costa et al. 2002). Usually, estuaries exhibit extreme temporal and spatial variability in many ecological processes (McLusky & Elliott 2006). Salinity gradients, for example, are influenced by continental discharge that affects the geographical limits of the estuarine area, and consequently, the distribution of most species that depend on this ecosystem. Furthermore, natural variations can interact with human activities, such as urban development, overfishing and habitat degradation, and these collectively influence the structure of communities that depend on this ecosystem. The heterogeneity and variability in spatial and temporal scales in estuaries and their influence on living resources such as fishes implies that management...
strategies must incorporate these dynamic features in a spatial framework for conservation (Pittman et al. 2011).

Time and place of spawning are also important because the maintenance of the population depends on the successful recruitment of juveniles to nursery areas and their entry into the adult population (Hinckley et al. 2001). The strategies used by fish eggs and larvae to enter estuaries are often related to hydrodynamics, influenced by variation in precipitation, terrestrial run-off and changes in salinity gradients, which affect ichthyoplankton assemblages in most temperate estuaries (Marques et al. 2005; Primo et al. 2011). In the Patos Lagoon estuary (Brazil), for example, we can find approximately 110 species of fishes (Vieira & Castello 1997). However, only 29 species can be found in this estuary during early life stages (Sique & Muelbert 1997). The fish assemblage in this estuary is characterized by marine (e.g. Trichiurus lepturus Linnaeus, 1758), estuarine-dependent such as Brevoortia pectinata (Jenyns, 1842) and Micropogonias furnieri (Desmarest, 1823), true estuarine (e.g. Catathyridium garmani Jordan, 1889), marine/estuarine-resident (e.g. Lycengraulis grossidentis Spix & Agassiz, 1829) and freshwater species Parapimelodus nigrribarbis (Boulenger, 1889) (McLusky & Elliott 2006; Mai et al. 2014). In this sense, spawning can occur inside the estuary, in freshwater or in the adjacent ocean. Spawning of M. furnieri, for example, occurs in the adjacent ocean of the Patos Lagoon estuary and eggs and larvae are transported into the estuary by deep currents (Muelbert & Weiss 1991; Martins et al. 2007).

In Brazil, as in the rest of the world, estuaries such as the Patos Lagoon estuary are among the most heavily impacted coastal ecosystems, with human activities directly affecting the benefits provided by these ecosystems (McLusky & Elliott 2006). It is well known that to understand ecosystems and their responses to anthropic activities requires the ability to describe, interpret and predict temporal and spatial scales of variability (Elliott 2002). However, species distributions are usually treated as static in spatial prioritization analysis for conservation (Moilanen et al. 2009). Not accounting for dynamic distributions in space over time can lead to inadequate conservation actions (e.g. identifying priority sites for conservation) (Runge et al. 2015). This is particularly important when dealing with fish conservation in estuaries. Several, mainly marine, species depend on estuaries to complete their development and successfully recruit to the adult population (Elliott & Hemingway 2002; McLusky & Elliott 2006). Most of these species have a planktonic early life stage, which means that life stages that use estuarine ecosystems have different habitat requirements during their development, resulting in diverse spatial distributions for different ontogenetic stages (Costa et al. 2014). In this case, the designation of essential habitats can be misled when temporal dynamics or life stages are neglected. In this sense, protecting habitats used by early life stages is crucial for ensuring the recruitment process and maintenance of adult populations. Also, early life stages are of great importance when identifying essential habitats and/or designing protected areas (Costa et al. 2015a, 2015b). The identification of the main characteristics of habitats used by fishes throughout their life cycle and how environmental variables influence the connectivity within habitats is vital to the study of population dynamics, management of fish stocks, definition of key habitats and the design of protected areas (Benaka 1999).

Here, we outline a simple method to assess whether temporal variability can show distinct spatial patterns of fish eggs and larval distribution and discuss how these results can be helpful to conservation planning. We used 13 years of continuous data on fish egg and larval abundances from the Patos Lagoon estuary, southern Brazil, as a case study. This estuary was chosen as a case study because of the existence of a continuous long-term data set of ichthyoplankton, and several ecological variables have been monitored in the Patos Lagoon estuary since 1975. We explore the influence of environmental variables on fish egg and larval abundances, and spatial pattern variability in relation to a static (entire study period) and a dynamic (considering each year separately) situation. The framework we developed is transferable to other taxonomic groups and can be easily modified for a wide range of temporal scales.

**Material and methods**

**Study area**

Patos Lagoon (32°S, Figure 1), the largest choked lagoon in the world (Kjerfve 1986), is a warm temperate coastal lagoon located in southern Brazil. Its estuarine region at the southern limit encompasses approximately 1000 km² (around 10% of the lagoon total area) (Seeliger 2001). Most of the estuary is shallow (< 1.5 m), but it is also composed of intermediate (1.5–5.0 m) and deep (> 5 m) water channels. Bottom types in the Patos Lagoon include mud flats (300 km²), submerged aquatic vegetation (up to 120 km²) and fringe salt marshes (40 km²) (Seeliger 2001). All of these habitats contribute to the life cycle...
of many species to complete their development, including fishes and their early life stages (Costa et al. 2014). Studies of the early life stages of fishes in this estuary started in the 1970s to analyse the ecology, distribution and the influence of environmental variables on species occurrence and abundance. In this estuary, fish eggs and larvae reach the Patos Lagoon estuary through the channel transported by currents, and their retention depends mainly on the water exchange and prevailing winds (Muelbert & Weiss 1991; Martins et al. 2007).

Patos Lagoon can be divided into three regions: (1) the lower lagoon, which is the estuarine zone because salt water intrusion is generally restricted to this area; (2) the central lagoon; and (3) the upper lagoon (Castello 1985; Möller et al. 2001). The estuarine zone and the central lagoon are separated by a deltaic structure formed by sand banks (Möller et al. 2001) while the upper lagoon is delimited by the Lagoa do Casamento and the mouth region of the Guaiba River (Figure 1). However, the upper and lower geographic limits of the estuarine zone can also be influenced by climatic factors (Odebrecht et al. 2010). Unlike many estuaries where variability is determined by astronomic tides, Patos Lagoon estuary is located in a micro-tide region meaning that tide is not the main force influencing this ecosystem (Möller et al. 2001). In contrast, Patos Lagoon estuary is influenced primarily by meteorological forcing. Biological, chemical and physical alterations are determined mainly by winds and precipitation. Low-frequency events, such as the El Niño Southern Oscillation, also influence the structure and processes in the Patos Lagoon estuary and induce interannual fluctuations (Odebrecht et al. 2010). Besides its ecological importance, Patos Lagoon is of great relevance for many social and economic activities, being exposed to anthropic pressures, including untreated domestic effluents, rice and cattle farming, industrial pollution, mining, dredging, port activities and fishing (Barletta et al. 2010).

**Fish eggs and larvae: temporal and spatial analysis**

Analyses of the temporal and spatial abundance of fish eggs and larvae were based on continuous data obtained over a 13-year period (2000–2012) at the Patos Lagoon estuary (Figure 1). Samples were taken monthly with a conical plankton net (300 µm, 60 cm mouth diameter) equipped with a flow-meter, towed for about two minutes at the surface, at five sampling stations located in shallow waters (<1.5 m) in the estuary. All samples were taken during the daytime. Station 1 is the closest to the mouth of the estuary and Station 5 is the innermost in the estuary (Figure 1). All samples were preserved in a 4% formalin solution. Temperature (°C) and salinity were recorded with a YSI-30 thermosalinometer at each sampling station during all study periods. Fish eggs and larvae were sorted and identified under a stereo microscope following specialized literature. Egg and larval abundances were estimated as the number of individuals per 100 m³.

A common problem in ichthyoplankton studies is the lack of taxonomic information available to identity many fish eggs and larvae to the species level. For the Patos Lagoon estuary, as many other coastal ecosystems of the world (Hernandez Jr et al. 2013), many
fish eggs and larvae collected in the estuary can be identified only to the family or genus level. Considering this, we used the genus level as a proxy for species (Hernandez Jr et al. 2013) to examine ichthyoplankton assemblages in multivariate analysis. Spatial patterns of fish eggs and larvae assemblage were evaluated using cluster analysis of standardized fish egg and larval abundances as the number of individuals per 100 m$^3$ of water filtered. Assemblage structure was first obtained for the entire study period, and then compared to the assemblage structure obtained when considering each year separately. The data matrix was composed of the density of selected taxa according to the above and transformed by $\log(x + 1)$, using Bray–Curtis similarity as the distance coefficient and clustering method by Unweighted Pair Group Method with Arithmetic Mean (UPGMA). Indicator species for each group were calculated as a product of the relative frequency and relative average abundance in each group (Dufrêne & Legendre 1997).

We used a generalized linear model (GLM) to analyse the variability of fish egg and larval abundance in relation to environmental variables throughout the study period. In the model, we only included data from November to March, which is the period associated with fish reproduction and with the maximum abundance of ichthyoplankton at the Patos Lagoon estuary (Muelbert & Weiss 1991; Sinque & Muelbert 1997; Muelbert et al. 2010). We defined the response variable $y_{ij}$ as the number of fish eggs or larvae in each plankton tow. At first, we assumed our response variable $y_{ij}$ to follow a Poisson distribution. However, as our data showed overdispersion, we further assumed our response variable $y_{ij}$ to follow a Negative Binomial distribution with mean $\mu_i$ and parameter $k$. Explanatory variables were temperature, salinity, volume of water filtered by the tow, sampling station, month and year. The last three variables were categorical. The structure of the model was as follows:

$$y_{ij} \sim \text{NB}(\mu_i, k)$$

$$E(y_{ij}) = \mu_i \text{ and var}(y_{ij}) = \mu_i + \mu_i^2/k$$

$$\log(\mu_i) = \gamma(\mathbf{x}_{ij}, \ldots, \mathbf{x}_{iq})$$

Four alternative models are proposed:

Model 1: $\eta = \log(\text{volume}) + \text{sampling station} + \text{month} + \text{year} + \text{temperature} + \text{salinity}$

Model 2: $\eta = \log(\text{volume}) + \text{sampling station} + \text{month} + \text{year} + \text{temperature} \times \text{salinity}$

Model 3: $\eta = \log(\text{volume}) + \text{sampling station} \times \text{month} + \text{year} + \text{temperature} + \text{salinity}$

Model 4: $\eta = \log(\text{volume}) + \text{sampling station} + \text{month} + \text{temperature} + \text{salinity}$

The selection process to choose the best model for our data was based on the Akaike Information Criterion (AIC). All GLM analysis was performed using R 2.15.1 (R Development Core Team 2014).

**Results**

Fish eggs and larvae exhibited high variability among years and months (Figure 2), associated mainly with salinity fluctuations in the Patos Lagoon estuary. When analysing the interannual variability of fish eggs and larval abundance, we found a distinct recruitment pattern at different sites. Station 1 showed a continuous recruitment of eggs and larvae during almost the entire study period (Figure 2), while the other stations presented a variable pattern (Figure 2). For example, at station 2 a continuous recruitment of fish larvae was found but with a low income of fish eggs (Figure 2). Also, the year 2010 in general showed low abundance of ichthyoplankton, and the year 2003 no abundance of fish eggs (Figure 2). When analysing the monthly variation of ichthyoplankton abundance, eggs were present during the entire year only at two sites (stations 1 and 3), while larvae were found during the entire year at all sampling stations (Figure 2). Despite the fact that a high abundance of fish eggs and larvae was associated with warmer months, we observed a peak in July at all sampling stations (Figure 2). Across all samples, 13,478 eggs and 9192 larvae were collected from the Patos Lagoon estuary. Here, we describe the intra- and interannual variability in the abundance and spatial distribution patterns of the fish egg and larval assemblages.

**Variability in spatial patterns and structure of fish egg and larval assemblages**

When considering the entire study period, the cluster analysis resulted in a distinct spatial pattern for fish eggs and larvae with the discovery of two groups (Figure 3). For eggs (Figure 3A), the first group consisted of sampling stations 1, 3 and 5 and was indicated by the genera *Catathyridium* and *Lycengraulis*. The second group consisted of sampling stations 2 and 4, and was indicated by the genera *Brevoortia* and *Trichiurus* (Figure 3A). For larvae (Figure 3B), we also identified two groups. The first group was represented by sampling stations 2 and 5, indicated by the genera *Syngnathus* and *Lycengraulis*. The second group was indicated by the genera *Odontesthes* and...
**Micropogonias**, and consisted of sampling stations 1, 3 and 4 (Figure 3B).

When analysing fish egg and larval assemblages in a dynamic situation considering each year separately, we found that spatial patterns varied over time and space (Figures 4 and 5). For eggs, spatial patterns varied substantially over the year (Figure 4). In general, we found two main groups, except in 2002 when we identified three groups, which were indicated by distinct genera (Figure 4). For fish larvae, we also did not find a well-defined spatial pattern (Figure 5). In general, the fish larval assemblage was divided into two main groups defined by distinct stations and an indicator genus over time (Figure 5). Three exceptions to this spatial pattern occurred in 2002, 2005 and 2009, when three groups were formed. On these three occasions, sampling station 2 was alone (Figure 5). In 2002 and 2005 station 2 was defined by the marine genera *Macrodon* and *Menticirrhus*, while in 2009 it was defined by *Lycengraulis*.

### Assemblage composition and abundance variability of fish eggs and larvae in relation to environmental variables

Egg and larval identification resulted in 11 and 38 taxa, respectively, for the entire study period (Table I). Identification included distinct taxonomic levels, with 5 and 16 taxa identified to species level for fish eggs and larvae, respectively. Fish eggs and larvae were identified to different taxonomic levels: genus (1/10), family (4/9) and order (1/3). We found different ecological guilds, including marine (e.g. *Anchoa marinii* Hildebrand, 1943 and *Trichiurus lepturus*), estuarine-dependent (e.g. *Micropogonias furnieri*), estuarine residents (e.g. *Catathyridium garmani*) and freshwater

![Figure 2](image-url) Interannual and monthly variation of mean abundance (± standard error) of fish eggs (black bars) and larvae (grey bars) at each sampling station in the Patos Lagoon estuary (Brazil).
species (e.g. *Parapimelodus nigribarbis*). Considering the contribution (%) of each taxon to the total density of eggs and larvae, the most important were Sciaenidae (78.2%) and *Brevoortia pectinata* (10.65%) for eggs, and Atherinopsidae (57%) and *B. pectinata* (16.63%). Only 6.2% and 0.4% of eggs and larvae, respectively, remained unidentified (not included in any taxonomic group).

Based on the lowest AIC value, two models were selected as best describing fish egg and larval abundance: models 4 and 1, respectively. AIC values for all models are summarized in Table SI (supplementary

**Figure 3.** Spatial cluster analysis using Bray–Curtis similarity and the method of UPGMA with the transformed matrix of fish eggs (A) and larvae (B) total density and their respective indicator genera (black circle: group I; dark grey circle: group II).

**Figure 4.** Spatial cluster analysis for each year (2000–2012) using Bray–Curtis similarity and the method of UPGMA with the transformed matrix of fish eggs density and their respective indicator genera (black circle: group I; dark grey circle: group II; light grey circle: group III) (fish eggs were restricted to one or two sampling stations and/or registered only two genera on 2001, 2003, 2006, 2007, 2009, 2010, 2011, 2012. These years were excluded from this spatial analysis). Genera named in the figure represent indicator genus with highest values.
material). The following analysis refers to these models. Selected GLMs fitted to fish egg and larval abundances produced the estimated parameters listed in Table II (columns 2 and 5). The baseline estimate of the logarithm of the expected number of fish eggs $\eta = \log \mu$ at station 1 in November was given by the intercept. For fish larvae, the intercept represents the expected number of fish larvae $\eta = \log \mu$ at station 1 in November 2000. The expected number of fish eggs and larvae was adjusted by temperature, salinity, the volume of water filtered by the tow, and also increments for different stations, months and years (only for fish larvae).

For fish eggs, the months November, December and February and sampling stations 1, 2 and 4 showed statistically significant differences in $\eta$. Temperature and salinity had a positive and significant effect on the number of fish eggs estimated for the Patos Lagoon estuary. For fish larvae, the months November, February and March, sampling stations 1–5 and years 2000, 2002, 2004, 2005, 2007, 2008 and 2009 exhibited statistically significant increments in $\eta$. However, in this case, only salinity had a positive and significant difference (Table I).

Here, we used egg abundance of *B. pectinata* and Sciaenidae to evaluate the influence of environmental variables on egg abundance, and to analyse the spatial and temporal variability in the recruitment process. These taxa were chosen because they were the two most abundant during the study period at the Patos Lagoon estuary. *Brevoortia pectinata* eggs occurred at all sampling stations, with a strong variability among years and months (Figure 6). Eggs were found throughout the year except during April and May, and were strongly related to high salinity (Figure 6). When analysing the entire study period, we observed a failure in the recruitment process to shallow waters in 2003 and extremely low recruitment in the years 2007 and 2010 (Figure 6). Sciaenidae eggs also occurred at all sampling stations, with a high variability among years and months (Figure 6) and with...
higher values being more related to high salinity and warm months (Figure 6). We observed a failure in the recruitment of Sciaenidae eggs to shallow waters during 2003 and 2010, and low recruitment in 2007 (Figure 6). Spatially, sampling station 2 was identified as unsuitable for the occurrence of eggs of both taxa. We found a different pattern for Atherinopsidae and B. pectinata larvae, which were found in all sampling stations throughout the year and during the entire study period (Figure 7).

**Discussion**

We found that fish eggs and larvae in shallow waters at the Patos Lagoon estuary exhibit temporal variability in spatial patterns. Our case study considered data from 13 years of fish egg and larval collection to explore the influence of environmental variables on their abundance, and spatial pattern variability in relation to a static (entire study period) and a dynamic (considering each year separately) situation. We found changes in temporal variability in spatial patterns of early life stages of fishes in relation to sampling stations, months and years. Also, cluster analysis revealed that fish egg and larval assemblages have a distinct structure over space and time. In our GLM results, we observed an inverse relationship between temperature and the number of fish eggs. As we used data only from November to March in GLMs, this inverse relationship between temperature and the number of fish eggs...
indicates that the lowest temperatures registered during these months were associated with the highest abundance of eggs in the Patos Lagoon estuary.

In general, planktonic stages such as fish eggs and larvae have a wide distribution and depend on nursery (e.g. estuaries) and spawning areas. Because of that, understanding the spatial distribution of these early life stages is vital to increase the effectiveness of fish conservation (Allison et al. 1998; Warner et al. 2000). In addition, fish eggs and larvae are the most vulnerable stage of the fish life cycle, with mortality rates over 90% during this period (Fulman & Werner 2002). Mortality of early life stages can be associated with various processes such as predation, nutrition, diseases, unfavourable environmental conditions and human impacts such as habitat degradation and pollution. All of these factors can influence the recruitment process. Recruitment of fish eggs and larvae to the Patos Lagoon estuary is an extremely variable process and mainly influenced by estuarine circulation and salinity. Circulation within the Patos Lagoon estuary is mainly influenced by winds and precipitation in the region (Möller et al. 2001), and largely controls the occurrence and distribution of species in this estuarine system. Comparing previous ichthyoplankton studies in the Patos Lagoon estuary to our temporal plots (Figure 2), spring is the main reproductive season for many species in the Patos Lagoon estuary and adjacent ocean (Muelbert & Weiss 1991), which is reflected in the maximum abundance of ichthyoplankton that also occurs during these months. However, the peak found in July at all sampling stations (Figure 2) was related to the presence of species with continuous spawning during the year, such as Brevoortia pectinata and species of Atherinopsidae (Muelbert et al. 2010). The highest abundance was found at station 1, which is the station closest to the entrance of the estuary, due to the spawning of many marine species in the adjacent coastal area (Muelbert & Weiss 1991; Sinque & Muelbert 1997). Spatial patterns of fish eggs and larvae in the Patos Lagoon estuary are highly related to estuarine circulation, which explains the retention process and the indicator genus of our assemblages groups (Figures 3–5). In general, sampling stations 2 and 5 were related to estuarine and/or freshwater genera, while sampling stations 1, 3 and 4 were associated with marine and/or estuarine genera. This complex spatial pattern can help to elucidate which species should be investigated and incorporated into conservation planning for this estuary. For example, future studies at the Patos Lagoon estuary should focus on the spatial–temporal variation of the indicator genera found in this study.

Our spatial coverage is restricted to estuarine shallow waters (< 1.5 m). However, these habitats are extremely important for biodiversity in the Patos Lagoon estuary (Costa et al. 2015a). Our study reveals high spatial variability on habitat usage by early life stages of fishes and we suggest that conservation
Table II. Estimates, standard errors, and \( p \)-values of coefficients for selected GLMs fitted to the number of fish eggs and larvae at the Patos Lagoon estuary, Brazil (N/A, not applicable; significant \( p \)-values (< 0.05) in bold).

| Parameter                  | Fish eggs | Fish larvae |
|----------------------------|-----------|-------------|
|                            | Estimate  | Std. error  | \( p \)-value | Estimate  | Std. error  | \( p \)-value |
| Intercept                  | 7.01      | 1.89        | 0.00          | 4.34      | 1.03        | 2.58e-0 |
| Log(volume)                | -0.20     | 0.15        | 0.17          | 0.05      | 0.07        | 0.47    |
| Sampling station 2         | -2.57     | 0.77        | 0.00          | -1.85     | 0.32        | 1.73e-0 |
| Sampling station 3         | 0.63      | 0.57        | 0.27          | -0.98     | 0.29        | 0.00    |
| Sampling station 4         | -1.51     | 0.60        | 0.01          | -0.94     | 0.28        | 0.00    |
| Sampling station 5         | 0.90      | 0.58        | 0.12          | -0.92     | 0.30        | 0.00    |
| Month December             | 1.85      | 0.68        | 0.00          | 0.11      | 0.30        | 0.71    |
| Month January              | 1.41      | 0.73        | 0.05          | -0.63     | 0.34        | 0.06    |
| Month February             | 2.76      | 0.71        | 0.00          | -1.18     | 0.35        | 0.00    |
| Month March                | -0.38     | 0.81        | 0.63          | -1.90     | 0.38        | 7.38e-0 |
| Year 2001                  | N/A       | N/A         | N/A           | -0.11     | 0.48        | 0.80    |
| Year 2002                  | N/A       | N/A         | N/A           | 1.63      | 0.47        | 0.00    |
| Year 2003                  | N/A       | N/A         | N/A           | 0.41      | 0.49        | 0.40    |
| Year 2004                  | N/A       | N/A         | N/A           | -1.12     | 0.50        | 0.02    |
| Year 2005                  | N/A       | N/A         | N/A           | -1.14     | 0.49        | 0.02    |
| Year 2006                  | N/A       | N/A         | N/A           | -0.03     | 0.48        | 0.94    |
| Year 2007                  | N/A       | N/A         | N/A           | -0.98     | 0.49        | 0.04    |
| Year 2008                  | N/A       | N/A         | N/A           | -1.04     | 0.50        | 0.03    |
| Year 2009                  | N/A       | N/A         | N/A           | -0.99     | 0.50        | 0.04    |
| Year 2010                  | N/A       | N/A         | N/A           | -0.79     | 0.49        | 0.10    |
| Year 2011                  | N/A       | N/A         | N/A           | -0.41     | 0.52        | 0.43    |
| Year 2012                  | N/A       | N/A         | N/A           | -0.37     | 0.50        | 0.46    |
| Temperature                | -0.39     | 0.08        | 5.70e-0       | -0.05     | 0.04        | 0.19    |
| Salinity                   | 0.15      | 0.01        | 3.66e-1       | 0.02      | 0.01        | 0.04    |

practices need to account for this variability. Changes in circulation patterns induced by wind and freshwater run-off modify the habitat occupied by fish eggs and larvae, and consequently the importance of geographically localized conservation sites. This is in agreement with recent studies that considered a spatial conservation prioritization approach in the Patos Lagoon estuary, and showed that different habitats are selected as a reserve system when data on fish eggs and larvae are not considered (Costa et al. 2015a).

Apart from salinity and estuarine circulation, climatic events such as El Niño (high precipitation and low salinity) and La Niña (low precipitation and high salinity) can influence intra- and interannual distribution patterns. It has been shown that the El Niño Southern Oscillation phenomenon strongly influences the distribution of several species in the Patos Lagoon estuary and fisheries production (Möller et al. 2009; Muelbert et al. 2010; Odebrecht et al. 2010; Schroeder & Castello 2010). El Niño periods are usually associated with a low abundance of fish eggs and larvae in the estuary. In contrast, due to low precipitation and the increase of salt water in the estuary, we observed a higher recruitment of fish eggs and larvae into the estuary during La Niña years (Muelbert et al. 2010). For example, 2003 and 2010 were characterized by moderate El Niño events. During these years, the recruitment of eggs to the estuary was very low compared to the remaining years of this study (Figure 2). *Micropogonias furnieri* is a well-studied species for the Patos Lagoon estuary and a good example of how Southern Oscillation events can influence the occurrence and distribution of fish eggs and larvae in the estuary. Spring 1982 and summer 1993 were characterized by a low abundance of eggs and larvae of *M. furnieri* in the Patos Lagoon estuary, while summer 1992 showed an increase in the recruitment of fish eggs and larvae into the estuary. The first periods (spring 1982 and summer 1993) coincided with higher than average freshwater discharge. In contrast, the latter period (summer 1992) was characterized by lower than average freshwater discharge and high salt water intrusion (Odebrecht et al. 2010). Consequently, the recruitment process into the Patos Lagoon estuary is closely related to salt water intrusion and freshwater discharge.

Understanding the temporal variability of spatial distribution patterns of species is essential for biodiversity conservation. For example, neglecting the temporal variation of mobile species (e.g. fish) can misdirect and lead to inadequate conservation actions (Runge et al. 2015). However, a lack of long-term studies limits the applicability of temporal scale into conservation. In the case of fish conservation, the designation of essential habitats can be misled when temporal dynamics or life stages are neglected. This is particularly important when dealing with such dynamic ecosystems as estuaries. Our results, for example, can be helpful in deciding which species should be considered for detailed studies and
incorporated into management plans. Then, these data could be compiled and used for distribution modelling and spatial prioritization analysis. In our case, we used genus as a proxy for species due to our mixed taxonomic-level matrix and showed temporal variation in spatial patterns of the ichthyoplankton assemblage in the Patos Lagoon estuary. This framework can be easily adapted for species and/or temporal scales (e.g. monthly) regarding the study objective. Our case study also reinforces the importance of long-term studies for the conservation of coastal environments.

The goal of our study was to assess whether temporal variability can show distinct spatial patterns of fish eggs and larvae and discuss how these results can be helpful to conservation planning. In general, our results can be considered as a first exploratory step to help managers to decide which species and temporal scale should be incorporated into spatial planning. Our results showed that long-term studies are helpful in this respect, as they evaluate the variability of abundance and composition over time. Most of the variation found in our study is related to fluctuations in salinity being responsible for the structure

Figure 6. Interannual and monthly variation in the mean abundance (± standard error) of *Brevoortia pectinata* (Bp) and Sciaenidae (Scia) eggs from 2000 to 2012 at each sampling station in relation to temperature and salinity in the Patos Lagoon estuary (Brazil).
of fish egg and larval assemblages at different sites in the Patos Lagoon estuary. As the main variable controlling the estuarine system, salinity also influences the diversity of many planktonic organisms (Muelbert et al. 2010) and adult fishes in this ecosystem (Garcia et al. 2003). Estuaries show variability on monthly and yearly scales, suggesting that conservation planning should also consider time scales in determining appropriate policy. Spatial conservation planning combined with fluctuations in abundance and assemblage structure over time may be an adequate solution to ensure conservation for biodiversity persistence in highly dynamic ecosystems such as the Patos Lagoon estuary.

Figure 7. Interannual and monthly variation of the mean abundance (± standard error) of Brevoortia pectinata (Bp) and Atherinopsideae (Athe) larvae from 2000 to 2012 at each sampling station in relation to temperature and salinity in the Patos Lagoon estuary (Brazil).
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Disclosure statement

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