Environmental Biology of Fishes **68:** 215–228, 2003.

Spatiotemporal variation in shallow-water freshwater fish distribution and abundance in a large subtropical coastal lagoon

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Received 26 July 2003 Accepted 20 April 2003

Key words: assemblage structure, Brazil, drainage basin, El Niño, estuary, freshwater discharge, neotropical fishes, Patos Lagoon

Synopsis

Patos Lagoon is located off the southern Brazilian coast and represents one of the largest coastal lagoons in the world. We estimated hydrological and physicochemical conditions associated with spatial variation in the abundance and diversity of freshwater fishes along the lagoon, and inter-annual variability in abundances of freshwater fishes occurring in its estuarine zone. During our study, the region experienced two periods of average rainfall and two periods with above-average rainfall. The characids *Astyanax eigenmaniorum* and *Oligosarcus jenynsii* and the siluriform *Parapimelodus nigribarbis* were the most abundant freshwater fishes in the estuary during wet periods when water levels were higher and salinity was lower. Increases in abundance of these species in the estuarine area, all of which members of primary-division freshwater families, apparently were associated with pulses of reproduction and passive transport from freshwater habitats located near middle and upper lagoon reaches. Abundance of species from secondary freshwater families, such as poeciliids and cichlids, were less correlated with hydrological conditions, and their patterns of occurrence in the estuary suggest active migration from nearby freshwater habitats draining into this area. Findings indicate that freshwater discharge in the basin and expansion/retraction of freshwaters in the middle-upper lagoon determined patterns of freshwater fish abundance and species richness in the estuarine zone.

Introduction

Freshwater fishes are a distinct ecological group in estuaries (Day et al. 1989, Blaber 1997) that have been characterized as migratory (Rebelo 1992), adventitious (Elliott & Dewailly 1995), stragglers (Whitfield 1999), or vagrants (Garcia et al. 2001). Although some freshwater fishes inhabit and reproduce in brackish waters (e.g., Mayan cichlids in the coastal zone of Mexico's Yucatan Peninsula; Martinez-Palacios & Ross 1992), most are vagrants that intermittently enter estuaries in relatively low numbers (Garcia et al. 2001). These fishes usually complete their entire life cycle in freshwater upper reaches of estuaries and coastal lagoons, and invade lower mixohaline zones during periods of reduced salinity (Day et al. 1989).

The number of freshwater species found in estuarine fish assemblages appears to vary among regions. Potter et al. (1990) showed that freshwater fishes comprised a minor part of fish diversity in temperate estuaries of southern Africa and western Australia. In contrast, freshwater species can be diverse in warm temperate and tropical estuaries of the western Atlantic (Vieira & Musick 1994). In Patos Lagoon estuary of southern Brazil, inter-annual variation in estuarine fish diversity is strongly influenced by abundance and richness of freshwater species (Garcia et al. 2003).

Non-indigenous freshwater fishes frequently invade estuaries, especially after major hydrological disturbance (Moyle & Light 1996). Many studies (Lobón-Cerviá 1996, Livingston et al. 1997, Swales et al. 1999, Mol et al. 2000, Garcia & Vieira 2001) have shown that extreme climatic events (e.g., storms, flash floods, droughts, El Niño) can affect fish community dynamics. For instance, resident estuarine organisms in the Sacramento–San Joaquin estuary, California, declined rapidly after a flash flood. Simultaneously, non-indigenous invasive species of invertebrates and fishes increased, and, in some cases, exotics became the dominant species (Nichols et al. 1990, Moyle & Light 1996).

Our study examines relationships between freshwater fish abundance, rainfall, and abiotic environmental parameters in Patos Lagoon, particularly inter-annual variation in its estuarine zone. This system represents one of the largest coastal lagoons in the world, receiving freshwater discharge from a large drainage basin (Kjerfve 1986). Based on standardized surveys, we analyzed species abundance and species richness of freshwater fishes across large spatial (ca. 200 km) and temporal (5-yr) scales. In addition, we evaluated the potential influence of prolonged periods or high freshwater discharge trigged by a global atmospheric phenomenon (El Niño Southern Oscillation – ENSO) on the occurrence of primary- and secondary-division freshwater fishes (*sensu* Myers 1938) in the lower reaches (estuarine zone) of the Patos Lagoon. Finally, we discuss implications of our findings for the management of freshwater fish resources in this region.

Methods

Study site

Patos Lagoon (32°S 49°W) is ca. 250 km long and 60 km wide, covering an area of 10 360 km^2 along the coastal plain of Rio Grande do Sul in southern Brazil (Figure 1c). The estuarine zone is restricted to the southern portion of the lagoon (ca. 10% of total area) and is connected to the ocean via a channel bordered by jetties (4 km long and 740 m wide) constructed to stabilize the mouth of the estuary and allow navigation along the entrance channel (Figure 1d). Apart from a navigation channel, about 80% of this area is less than 2 m. Tidal influence on hydrodynamic characteristics is minimal (mean tidal amplitude is 0.47 m) (Seeliger 2001). Rather, wind patterns and seasonal pulses of freshwater inflow influence patterns of water circulation and salinity (longitudinal and vertical). Dominant northeasterly winds (mean 5 $m\,s^{-1}$) promote flushing of the estuary, but southerly winds (mean 8 $m\,s^{-1}$) tend to move seawater into the lower lagoon reach. The lagoon's drainage basin (201 626 km^2) is one of the largest in Latin America (Figure 1a). Freshwater discharge varies seasonally, with high discharge in late winter and early spring followed by moderate discharge through summer and autumn. The mean annual discharge is ca. 2 000 $m^3\,s^{-1}$, although large year-to-year variation can occur (700–3 000 $m^3\,s^{-1}$) (Moller et al. 2001). During El Niño episodes, runoff greatly exceeds average values and lagoon waters can remain fresh for several months (Moller et al. 2001, Garcia et al. 2003).

The lagoon and adjacent coastal area support one of the most important fisheries in the warm-temperate southwestern Atlantic, with about 3 500 artisanal (Reis & D'incao 2000) and 3 000 industrial fishermen (Haimovici et al. 1996) temporarily or permanently involved in fishing activities in this region. The estuary is an important nursery for several of the most important species in these fisheries (Chao et al. 1985, Vieira & Castello 1996). Estuarine resident and marine dependent species are the most abundant and frequently collected fishes in the estuarine area, whereas vagrant species are less frequently captured throughout the year. The occurrence and relative abundance of marine vagrants are strongly correlated with summer intrusion of salt water, whereas freshwater vagrants are associated with high rainfall and low salinity induced by high freshwater discharge (Garcia & Vieira 2001, Garcia et al. 2001).

Field sampling

Based on a standardized sampling protocol, we collected shallow-water freshwater fishes focusing both the spatial and temporal scales. During 1 year (Mar. 2000–Apr. 2001), we conducted monthly seine hauls (five hauls at each station each month) at 11 beach stations along the Patos Lagoon's main longitudinal axis extending over 200 km (Figure 1c). During a 5-yr period (Aug. 1996–Jun. 2001) we conducted monthly seine hauls (five hauls at each station at each month) at four beach stations located at its lower estuarine zone (Figure 1d). All stations were located in shallow waters, a habitat representative of about 80% of Patos Lagoon (Moller et al. 2001).

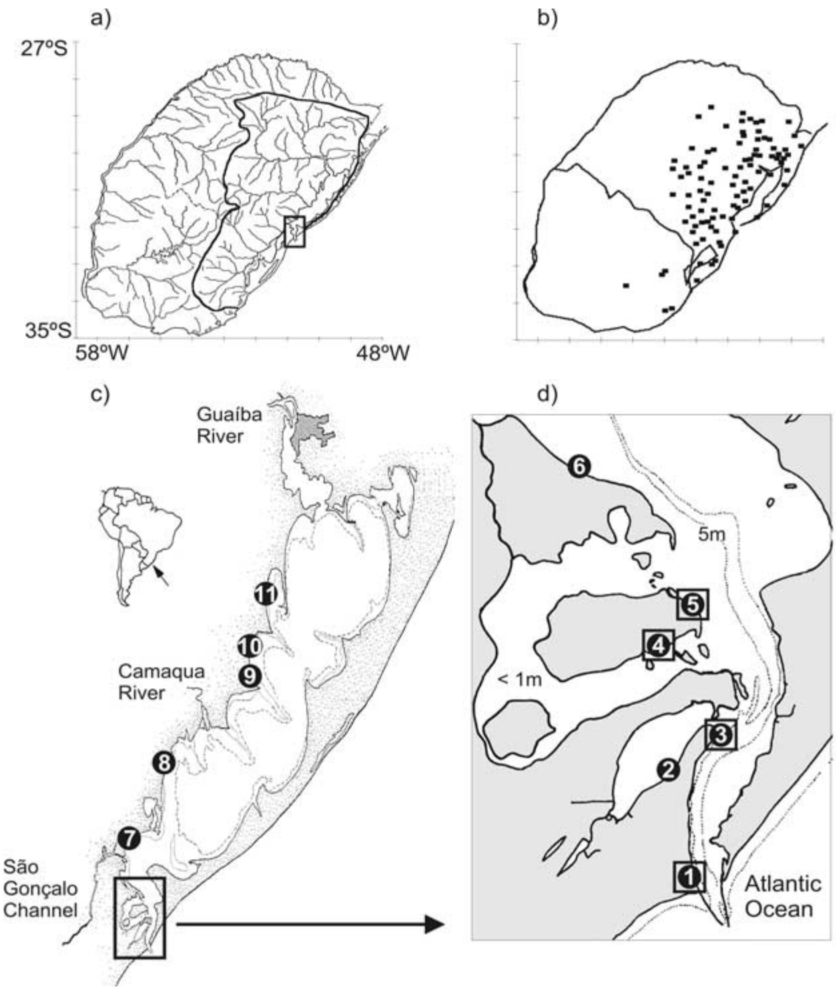

Figure 1. (a) Rio Grande do Sul state (Brazil) showing the drainage basin of the Patos Lagoon Basin (solid line); (b) Rainfall meteorological stations (n = 95) distributed throughout the drainage basin; (c) Patos Lagoon; and (d) its lower estuarine zone located at the lower reaches of the lagoon. Eleven beach seine stations were located in shallow waters (<1 m) along the lagoon's main longitudinal axis, from the estuary's mouth (1) to the upper lagoon (11). Beach stations 1–11 were sampled during a 1-yr (Mar. 2000–Apr. 2001), whereas estuarine stations 1,3,4,5 (square symbols) were sampled during a 5-yr (Aug. 1996–Jun. 2001). GPS location for each station: 1 (32° 09.047′ S, 52° 06.133′ W), 2 (32° 05.763′ S, 52° 07.662′ W), 3 (32° 03.649′ S, 52° 05.272′ W), 4 (32° 00.967′ S, 52° 08.089′ W), 5 (31° 59.553′ S, 52° 05.970′ W), 6 (31° 54.865′ S, 52° 09.138′ W), 7 (31° 45.092′ S, 52° 13.320′ W), 8 (31° 21.367′ S, 51° 57.236′ W), 9 (31° 00.061′ S, 51° 29.337′ W), 10 (30° 55.411′ S, 51° 29.589′ W), and 11 (30° 39.084′ S, 51° 23.113′ W).

Beach seine hauls were obtained using a 9 × 1.5 m seine (13 mm bar mesh in the wings and 5 mm in the center 3-m section) that was pulled to cover an area of $\sim$60 m^2. Specimens were preserved in 10% formalin and later identified, counted, and measured for total length (TL) to the nearest mm. Water temperature, transparency (Secchi depth), and salinity were measured at each station each month. Water level in the lower estuarine zone was estimated from daily depth records at station 4, which were averaged as monthly values. Precipitation was recorded daily at 95 meteorological stations scattered around the drainage basin of Patos Lagoon (Figure 1b).

The main rivers that contribute freshwater discharge into the Patos Lagoon are illustrated in Figure 1c. The mouth of the São Gonçalo Channel, which contributes an average of 700 $m^3 s^{-1}$, is located between stations 6 and 7, whereas the Camaquã River (mean = 307.6 $m^3 s^{-1}$) is located between stations 8 and 9. Station 11 was located at the northern limit of Patos Lagoon in an area that receives, via Guaíba Bay, freshwater outflow from large rivers of the northern drainage basin (Jacuí–Vacacaí and Taquari–Antas Complex). Guaíba Bay receives 84.6% of the freshwater discharge into the Patos Lagoon, with an average discharge of 1 182.95 $m^3 s^{-1}$ and records flow of 13 000 $m^3 s^{-1}$ (O.O. Moller Jr., pers. commun.).

Data analysis

Inter-annual precipitation variability in the drainage basin was determined by comparing monthly average rainfall in mm collected during our study (Aug. 1996–Jun. 2001) with a long-term (1988–2001) dataset composed from the precipitation data of 95 meteorological stations (Figure 1b). Monthly rainfall average ($\times$) from the short-term data set were contrasted with long-term averages (μ) using x-μ. Environmental parameters collected at the estuarine area were compared with a 14-yr database (water transparency and salinity: 1979–1984 and 1994–2001), and 10 yrs (water level: 1992–2001) of monthly samples from Patos Lagoon estuary.

Prolonged dry and wet periods were distinguished based on consecutive months with below- and above-average rainfall. The 'dry' period included 30 months (Aug. 1996–Jul. 1997; Oct. 1998–Mar. 2000), and the 'wet' period covered 29 months (Aug. 1997–Sep. 1998; Apr. 2000–Jun. 2001). Also, samples were grouped by seasons as follows: summer (Jan.–Mar.), autumn (Apr.–Jun.), winter (Jul.–Sep.), and spring (Oct.–Dec.).

Fish survey data did not meet the assumptions of homogeneity of variance and normality (Underwood 1997), therefore we used the non-parametric Kruskal–Wallis test to compare response variables (relative abundance, species richness, TL) between sample stations. To examine annual recruitment patterns and size structure, absolute and relative abundance of individuals per haul (CPUE) data for the dominant species were plotted by TL intervals for each season (Garcia et al. 2001).

We analyzed temporal patterns of variation in abundance after fish species were pooled according to Myers' (1938) model of primary- and secondary-division freshwater fishes. Primary freshwater families are strictly confined to freshwater, whereas secondary freshwater families are generally restricted to freshwater but may occasionally enter salt water. Based on information in the literature (Berra 1981 *in* Helfman et al. 1997, p. 282), we classified as primary freshwater fishes those species belonging to the Characidae, Curimatidae, Erythrinidae, Pimelodidae, and Loricariidae, and secondary freshwater fishes those specimens from the Poeciliidae and Cichlidae (Table 1). To assess whether frequency of occurrence of primary and secondary fish families were equal between dry and wet periods, z approximation for the binomial test was performed (Green et al. 2000). In addition, Spearman rank correlation was performed on environmental parameters (rainfall and salinity) and fish abundance data for primary- and secondary-division freshwater families. Captured euryhaline fishes (*Jenynsia multidentata*, *Lycengraulis grossidens*, and *Platanichthys platana*) were not included in our analysis, because they are not considered freshwater vagrants in the Patos Lagoon estuary (Vieira & Castello 1996, Garcia et al. 2001).

Results

Environmental parameters

Salinity had a steep gradient between the estuary and upper lagoon (Figure 2a). Estuarine stations (1–6) had higher mean salinity (7.4) and range of salinities (0–32) than upper lagoon (9–11) stations (mean = 0.05; range = 0–2). Stations at intermediate longitudinal positions (6 and 8) had intermediate mean salinities (3.0) but ranges (0–28) similar to estuarine sites. Water transparency and temperature did not display strong longitudinal trends (Figure 2b,c). Water transparency was low across all samples stations (mean values 0.3–0.5 m), particularly sites located in the estuary (6) or upper lagoon (10 and 11) that had lower means (0.1–0.3 m). Temperature had a strong seasonal pattern with values ranging from 10°C to 32°C and mean values between 20.1°C and 22.6°C. The exception was the sample station nearest the estuary mouth that had a mean temperature of 18.9°C.

Inter-annual variation in water depth, transparency, and salinity in the estuary revealed strong patterns that apparently were influenced by rainfall in the drainage basin of the Patos Lagoon (Figure 3). From Aug. 1997 to Sep. 1998 and Apr. 2000 to Jun. 2001, precipitation was above the historic average during nearly all months and was especially high during the 1997–1998 period. In contrast, there was less rainfall from Aug. 1996 to Jul. 1997 and from Oct. 1998 to Mar. 2000 (Figure 3a). These intervals of above- and below-average rainfall were classified as 'wet' and 'dry' periods, respectively. Water level at the lower estuarine zone seemed to be directly affected by rainfall fluctuation within the

Table 1. Number total (N), weight (W, g), maximum and minimum of TL in (mm) for each fish species captured along the sampling period in the Patos Lagoon and its lower estuarine zone.

Species	N	W	TL (max–min)	
Characiformes				
CHARACIDAE*				
Astyanax bimaculatus (Linnaeus, 1758)	1 372	6 306.0	22	105
Astyanax eigenmanniorum (Cope, 1894)	340	798.6	30	115
Astyanax fasciatus (Cuvier, 1819)	235	2 426.5	36	150
Oligosarcus jenynsii (Günther, 1864)	144	910.7	36	212
Oligosarcus robustus Menezes, 1969	27	298.7	45	185
Astyanax spp.	26	8.0	20	42
Astyanax alburnus (Hensel, 1870)	24	74.8	51	74
Cheirodon interruptus (Jenyns, 1842)	17	47.0	35	83
Hyphessobrycon anisitsi (Eigenmann)	10	63.2	62	132
Hyphessobrycon bifasciatus Ellis, 1911	3	2.5	37	44
Macropsobrycon uruguayanae Eigenmann, 1915	2	2.0	34	40
Hyphessobrycon luetkenii (Boulenger, 1887)	1	0.8	38	38
Hyphessobrycon meridionalis Ringuelet, Miquelarena & Menni, 1978	1	0.1	23	23
CURIMATIDAE*				
Cyphocharax voga (Hensel, 1870)	23	127.9	37	98
ERYTHRINIDAE*				
Hoplias malabaricus (Bloch, 1794)	8	191.5	96	182
Siluriformes				
PIMELODIDAE*				
Parapimelodus nigribarbis (Boulenger, 1889)	787	5 828.0	16	148
Pimelodus maculatus Lacepède, 1803	133	3 481.9	77	228
Rhamdia sp.	5	922.9	112	377
Pimelodella laticeps australis Eigenmann, 1917	5	11.5	44	86
LORICARIIDAE*				
Hypostomus commersoni Valenciennes, 1836	4	2 652.6	335	478
Rineloricaria strigilata (Hensel, 1868)	4	23.8	55	147
Loricariichthys anus (Valenciennes, 1840)	2	19.0	111	160
Cyprinodontiformes				
POECILIIDAE**				
Phalloceros caudimaculatus (Hensel, 1868)	40	21.4	18	52
Poecilia vivipara Schneider, 1801	5	8.2	42	56
Phalloptychus januarius (Hensel 1868)	3	1.6	30	37
Cnesterodon decemmaculatus (Jenyns, 1842)	2	1.6	38	41
Perciformes				
CICHLIDAE**				
Geophagus brasiliensis (Quoy & Gaimard, 1824)	25	231.7	30	152
Crenicichla lepidota Heckel, 1840	3	85.8	92	146

Primary (*) and secondary (**) freshwater fish families.

drainage basin, with highest values observed during wet periods (Figure 3b). Water transparency (Secchi depth) and salinity in the estuary (Figure 3c,d) were inversely related to rainfall in the drainage basin. Transparency and salinity tended to fall below their respective historic averages during wet periods and were above historic averages during dry periods.

Spatiotemporal trends in species composition and abundance

A total of 3 251 freshwater fishes, representing 4 orders, 7 families and 28 species, were captured during the study (Table 1). Characiformes and Siluriformes were the most abundant orders, with

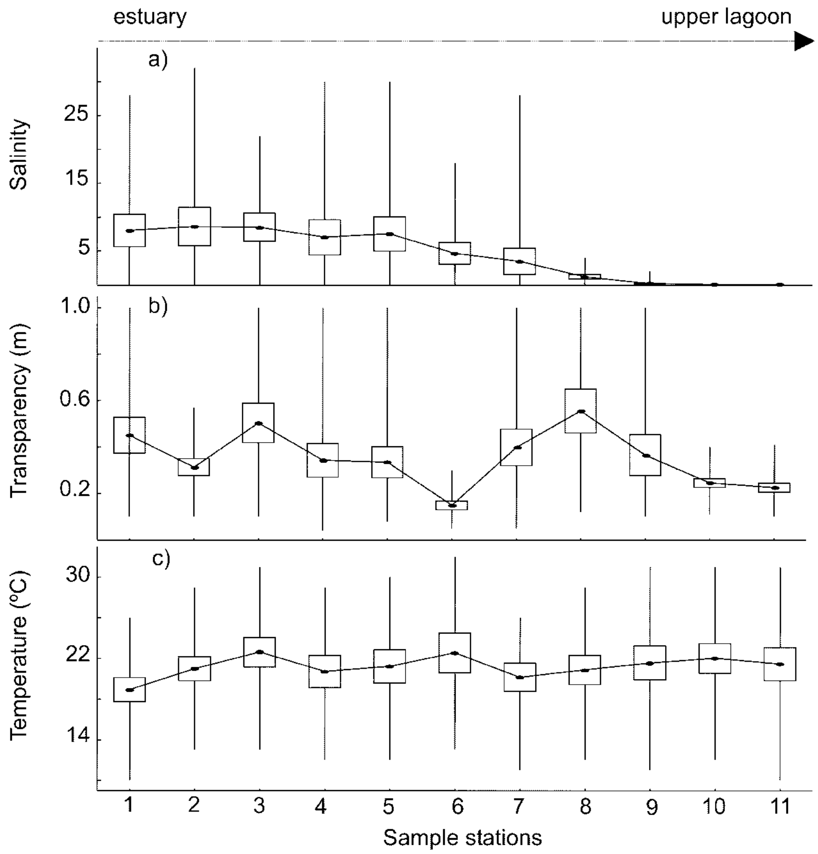

Figure 2. Average values (dot), standard error (box), and min–max (line) for (a) salinity, (b) water transparency (Secchi depth), and (c) water temperature (°C) in the beach stations (1–6 estuary; 7–11 middle-upper lagoon) sampled during 1-yr (Mar. 2000–Apr. 2001).

Cyprinodontiformes and Perciformes being frequently sampled but generally in low numbers. The dominant species in terms of numerical abundance were the characids *Astyanax bimaculatus*, *Astyanax eigenmanniorum*, *Astyanax fasciatus, Oligosarcus jenynsii* and the siluriforms *Parapimelodus nigribarbis* and *Pimelodus maculatus*, which together represented 92.6% of total fish abundance. With the exceptions of the piscivorous *O. jenynsii* and *Hoplias malabaricus*, which achieved sizes from 36 to 212 mm TL, most characiforms were small (20–150 mm TL). Siluriforms and perciforms tended to be larger, ranging from 16 to 478 mm TL (Table 1).

Species composition and abundance had strong trends along the longitudinal axis of the lagoon. Numerical abundance (N) and number of freshwater species (S) were significantly higher at upper lagoon stations than estuarine stations (N : H = 209.1, d.f. = 10, $p < 0.0001$, S : H = 30.9, d.f. = 10, $p < 0.0001$) (Figure 4a,b). TL varied considerably among stations, but was significantly greater in the upper lagoon (H = 690.76, d.f. = 10, $p < 0.0001$) (Figure 4c). These patterns, particularly in abundance, were strongly determined by the spatial distribution of the dominant characiforms and siluriforms that were common at the upper lagoon stations (9–11). The less abundant taxa were either restricted to a single estuarine site (cyprinodontiforms) or occurred in both the estuary and upper lagoon (perciforms) (Figure 5).

Inter-annual variation in relative abundances of dominant freshwater groups (characiforms and siluriforms) in the estuarine zone was associated with wet and dry periods (Figure 6). For example, characiforms and siluriforms were most abundant during wet periods. This pattern was strongest for siluriforms during the extreme wet conditions of 1997–1998. In contrast, cyprinodontiforms were abundant during the dry summer of 1999 and to a lesser extent during the wet fall of 2000, and perciforms were present in low abundance throughout the sampling period.

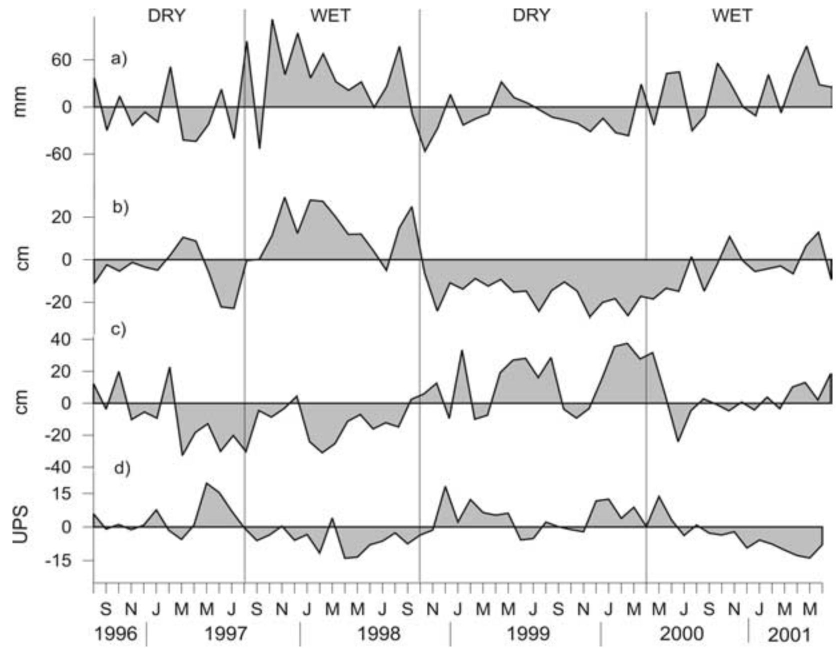

Figure 3. Monthly values for (a) rainfall in the drainage basin of Patos Lagoon, (b) water level, (c) water transparency, and (d) salinity in the lower estuarine zone. Shaded areas represent differences between each monthly value from 1996–2001 and each monthly long-term average (rainfall: 14-yr from 1988 to 2001; water level: 10-yr from 1992 to 2001; transparency and salinity: 14-yr from 1979 to 1984 and 1994 to 2001). Consecutive months (>3) with below- and above-average rainfall are designated as 'dry' (Aug. 1996–Jul. 1997; Oct. 1998–Mar. 2000) and 'wet' (Aug. 1997–Sep. 1998; Apr. 2000–Jun. 2001) periods, respectively.

Fishes grouped together as either primary or secondary freshwater families also showed patterns of abundance in the estuarine zone associated with wet and dry periods. A binomial test indicated a proportion of primary-divisions fishes during wet periods that was greater than the random expectation (observed proportion = 0.93; null proportion = 0.50; $p < 0.01$), and a significantly higher proportion of secondary-division fishes during dry periods (observed proportion = 0.84; null proportion = 0.50; $p < 0.01$).

This differential occurrence of primary and secondary freshwater fishes in the estuarine zone during wet and dry periods also can be observed from correlation analysis with environmental parameters (rainfall and salinity). Abundance of primary fishes was significantly positively correlated with rainfall ($R_s = 0.62$; $p < 0.01$) and significantly negatively correlated with salinity ($R_s = -0.71$; $p < 0.01$). Secondary-division fish abundance was not significantly correlated with rainfall ($R_s = -0.29$; $p > 0.21$) and was significantly positively correlated with salinity ($R_s = 0.56$; $p < 0.01$). Thus, these freshwater fish groups had opposite patterns of correlation with environmental factors associated with wet *versus* dry periods.

Seasonal patterns and size structure during wet periods

Numerical abundance of freshwater fishes in the estuary during wet periods was greatest during warm seasons (Oct.–Mar.) (Figure 7a,b). During spring, the size distribution was unimodal and dominated by juveniles (30–60 mm) of *A. eigenmaniorum* and *O. jenynsii*. During summer, the size distribution was weakly bimodal and dominated by small *A. eigenmaniorum* (15–65 mm TL) and larger juveniles (95–145 TL) of *O. jenynsii* and *P. nigribarbis*. Although fishes captured in seine samples ranged from 15 to 205 mm, larger individuals (>145) tended to be absent from the shallow waters of the estuary during cold seasons (Figure 7c,d).

Discussion

Environmental parameters showed strong spatial and temporal trends in Patos Lagoon, including a salinity gradient from the estuarine zone to the upper lagoon and large inter-annual variation in rainfall within the drainage basin. Prolonged periods of excessive rainfall

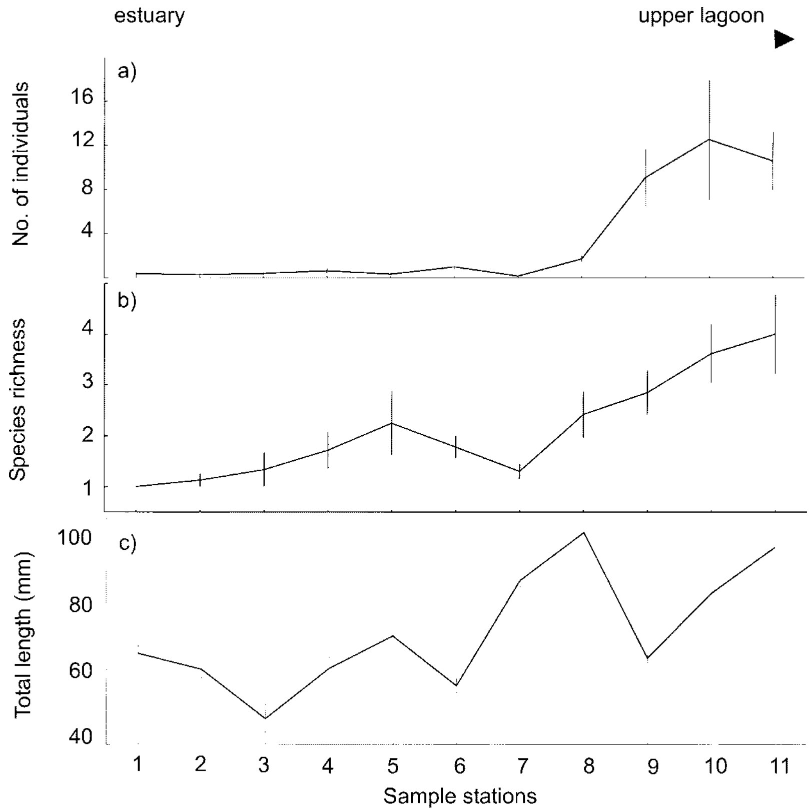

Figure 4. Average values (+SE) for (a) number of individuals, (b) species richness, and (c) TL (mm) in the beach stations (1–6 estuary stations; 7–11 middle-upper lagoon) sampled during 1-yr (Mar. 2000–Apr. 2001) period.

and drought had cascading effects on water level, salinity, and, to a lesser extent, water transparency. For instance, high rainfall, especially during 1997–1998, was associated with high water level and low salinity in the estuary in the lower reaches of the lagoon. Dry periods, particularly during 1999–2000, were associated with low water levels and high salinity. We suggest that variation, both spatial and inter-annual, in these gradients is a principal factor controlling patterns of species composition and abundance of shallow-water freshwater fishes within the lagoon, with their residence in the estuarine zone being particularly affected.

The dynamic interactions between abiotic environmental factors at different scales were strongly influenced by variation in rainfall over the drainage basin of the Patos Lagoon. Rainfall in this area is associated with local (e.g., topography), regional (e.g., cold fronts), and global (e.g., ENSO) factors. The annual cycle of rainfall in the drainage basin of Patos Lagoon is characterized by a well-defined wet season (Jul. through Sep.), whereas dry conditions reveal more spatial heterogeneity and generally extend from Mar. to Jun. (Rao & Hada 1990). Rainfall patterns are even more distinct during extreme ENSO episodes. Warm ENSO episodes (El Niño) cause higher than average rainfall in southern Brazil, and during cold ENSO period (La Niña), the dry season tends to be stronger (Grimm et al. 2000). However, unpredictable cold fronts unrelated to ENSO and sea surface temperatures off the coast of southern Brazil also influence rainfall in this region (Diaz et al. 1998, Kane 1999a,b).

During our study, extended dry and wet periods seemed to reflect an interaction among several forces driving rainfall patterns. The dry periods observed in 1995–1996 and 1999–2000 coincide with La Niña conditions in the equatorial Pacific Ocean (Leigh 1996, Bennett et al. 2000, Watkins 2000). Similarly, the first wet period (Aug. 1997–Sep. 1998) was clearly associated with the 1997–1998 El Niño (Kane 1999b, Glantz 2001), one of the strongest on record (Mcphaden 1999). Yet there was no El Niño episode between the wet

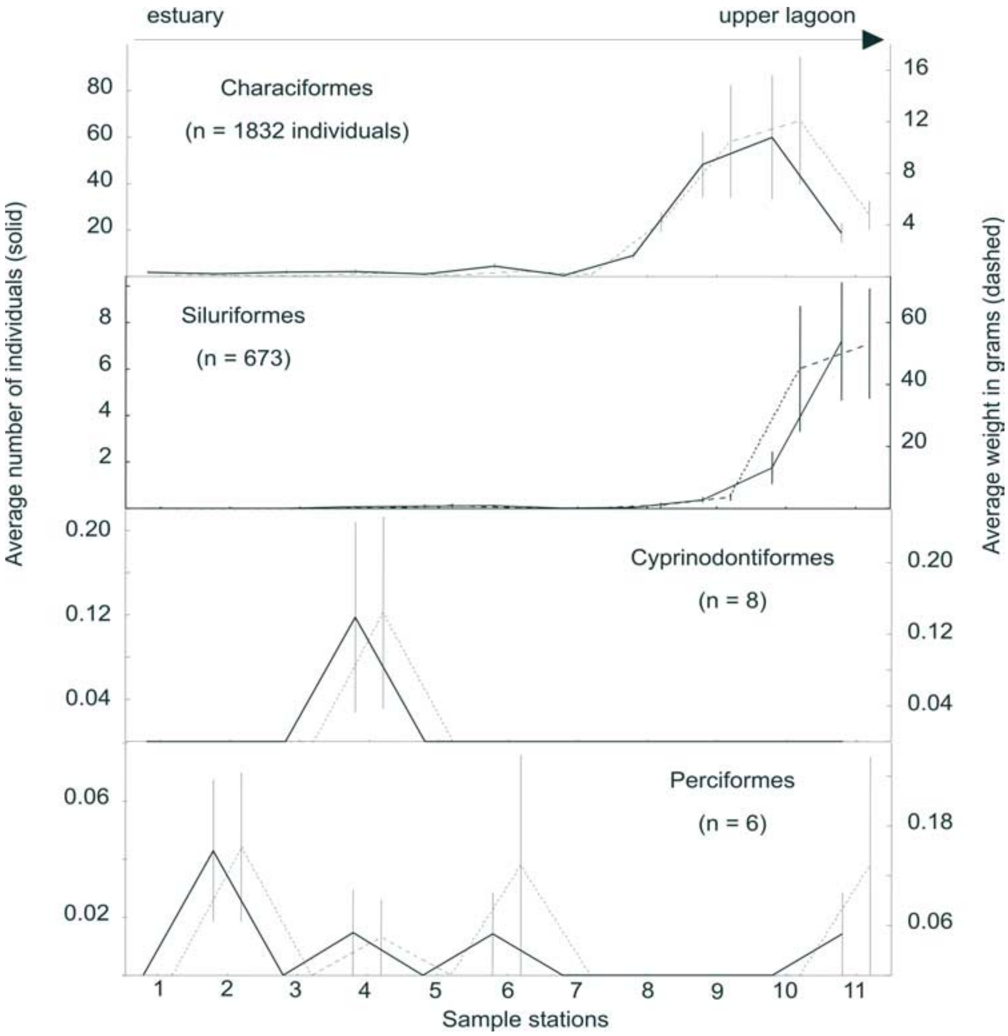

Figure 5. Average (+SE) number of individuals (solid line) and weight (dashed lines) of the four taxonomic groups (Characiformes, Siluriformes, Cyprinodontiformes, and Perciformes) sampled at beach stations (1–6 estuary stations; 7–11 middle-upper lagoon) during 1-yr (Mar. 2000–Apr. 2001) period. Values in parenthesis represent total number of individuals.

period of Apr. 2000–Jun. 2001. The high rainfall in the Patos Lagoon region during this period may have been influenced more by local and regional factors.

Myers' (1938) model of primary- and secondary-division freshwater fishes largely explains spatio-temporal patterns of abundance of the shallow-water freshwater fishes in Patos Lagoon. Estuarine captures of primary-division fishes (characiforms, siluriforms) were virtually restricted (93% of cases) to periods of high precipitation and low salinity, when the upper freshwater portion of the Patos Lagoon, which has an abundant and diverse freshwater fish fauna, expanded into the estuarine zone. During dry periods, these species rapidly declined in abundance in the estuarine zone, probably either by following receding freshwater back to upper lagoon reaches, or via mortality induced by physiological stress from intrusion of saline waters. In contrast, the less abundant secondary-division fishes (poeciliids, cichlids), which did not show a significant spatial gradient in abundance, were more common (84% of cases) in the estuary during periods with low precipitation and high and intermediate salinity, particularly during months that followed the extremely wet period of 1997–1998.

The two most abundant freshwater fishes in the estuarine area during wet periods were the characids

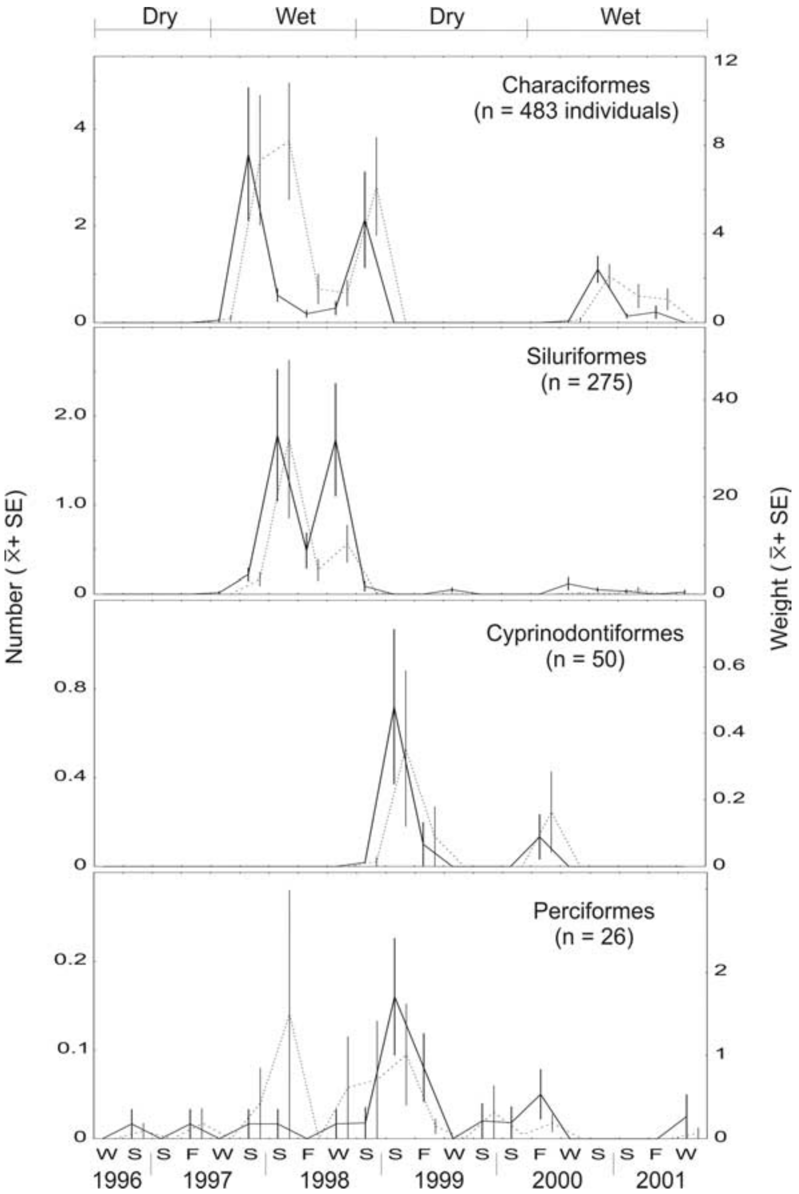

Figure 6. Seasonal fluctuations in average (+SE) for number of individuals (solid line) and weight (dashed lines) of the four taxonomic groups (Characiformes, Siluriformes, Cyprinodontiformes, and Perciformes) captured in the estuarine zone of Patos Lagoon during 5-yr (winter 1996–winter 2001) period.

A. eigenmaniorum and *O. jenynsii*. These species can be found throughout southern South America (Brazil, Paraguay, Uruguay and Argentina) (de Yuan & de Hassan 1985, Menezes 1987, Fernandez et al. 1998). Other studies have found characins across gradients of coastal habitats. Winemiller & Leslie (1992) found that *A. fasciatus* was a dominant species across a series of coastal habitats and ecotones on the Caribbean coast of Costa Rica, ranging from headwater streams to rivers to coastal lagoons. Yet, unlike *A. eigenmaniorum* and *O. jenynsii* in the Patos Lagoon system, *A. fasciatus* was not collected from the mixohaline estuarine zone of a deep coastal lagoon in Costa Rica.

Astyanax and *Oligosarcus* have distinct trophic niches and reproductive seasons. *A. eigenmaniorum* feeds on cladocera, copepoda, benthic microcrustacea,

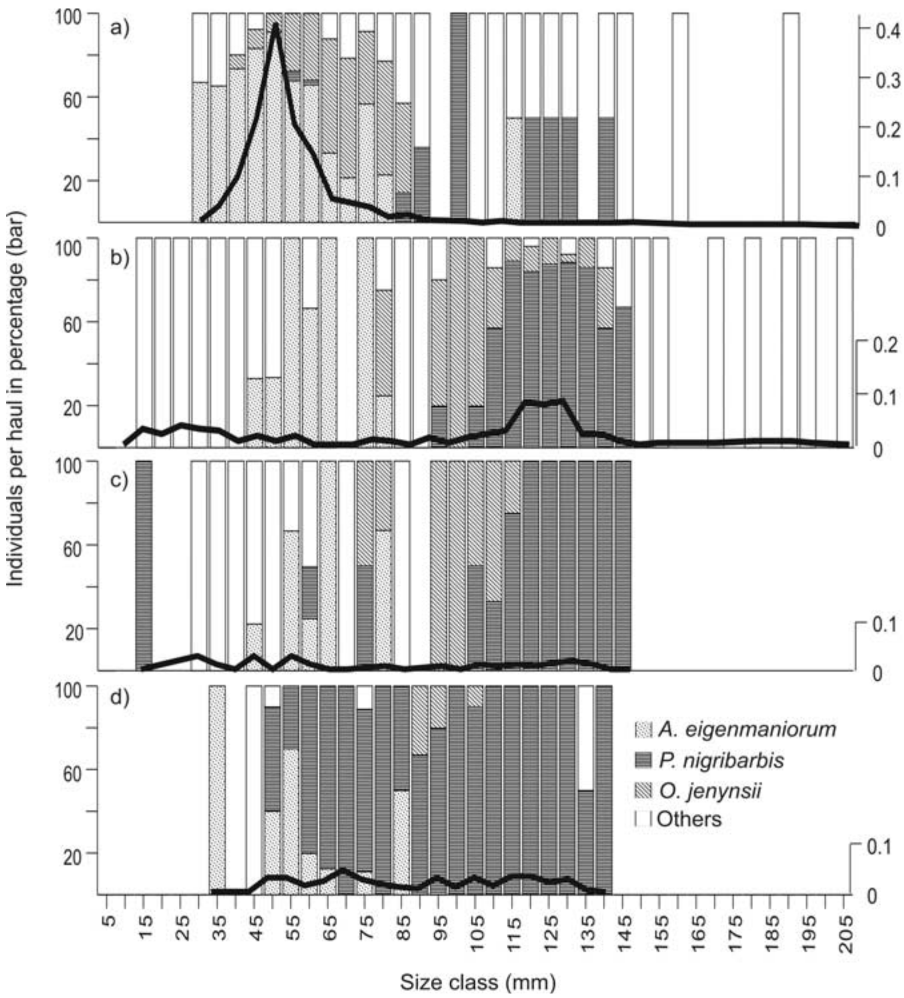

Figure 7. Relative (in percentage – bars) and absolute (line) average number of individuals per seine haul by size class (mm) for the most three abundant freshwater fishes (*A. eigenmaniorum*, *P. nigribarbis*, *O. jenynsii*, and others) captured in the estuarine zone of Patos Lagoon during (a) spring (Oct.–Dec.), (b) summer (Jan.–Mar.), (c) autumn (Apr.–Jun.), and (d) winter (Jul.–Sep.).

seeds, insects, and fragments of macrophytes (Grosman et al. 1996). There is no information published concerning its reproduction, but patterns of juvenile recruitment in congeneric species (*A. fasciatus* and *A. bimaculatus*) in the upper portion of the Patos Lagoon Basin suggest reproduction occurs during warm seasons (spring–summer) (Bertaco et al. 1998). In contrast, *O. jenynsii* spawns multiple clutches from early winter (Jul.) until late spring (Dec.). Winter spawning coincides with the wet season and highest water levels and lowest evaporation (Hartz et al. 1997). This breeding pattern probably contributes to the species' high abundance, especially for juvenile size classes, in the estuarine zone during wet periods.

Oligosarcus jenynsii is carnivorous with a tendency toward piscivory (Hartz et al. 1996). Piscivores are rare among the resident fishes inhabiting shallow waters of Patos Lagoon estuary (Vieira & Castello 1996), being restricted by marine species that move into the estuary with saltwater intrusions during summer (Chao et al. 1985). Our study indicates that during wet periods piscivores can also enter the estuary from freshwater habitats.

Strongly influenced by abundance patterns of *P. nigribarbis*, siluriforms (catfishes) ranked second among freshwater orders in relative abundance. Restricted to the Patos Lagoon Basin, *P. nigribarbis*, unlike most benthic catfishes, seems to be planktivorous

(Lucena et al. 1992). In shallow waters of Guaiba Bay, *P. nigribarbis* had higher relative abundance in spring and summer, and indirect evidence suggests the species moves toward deeper waters (channel) during winter (Bertaco & Becker 2000). Consequently, the species' planktivorous feeding behavior together with its occurrence in deep waters of the upper lagoon during winter (coinciding with wet season) would facilitate passive transport to the lower reaches of the lagoon during episodes of high freshwater discharge.

The two main sources of freshwater fishes in the estuarine zone of the Patos Lagoon are the small tributary creeks located around the estuary and the middle-upper reaches of the lagoon. The small creeks draining into the southern portion of the estuary have common characteristics such as low gradients, low depth (usually <1 m), slow flow, and abundant floating and submerged vegetation. Although these small tributaries have diverse fish faunas and are directly connected to the estuary (Tagliani 1994), there is a low percentage of fish species occurring in both habitats. Even secondary freshwater families (such as Cichlidae and Poecillidae) that are very common in these creeks (Tagliani 1994) were poorly represented in the estuary during wet periods. For instance, the cichlid *Geophagus brasiliensis* was weakly correlated with wet periods, and the poecilid *Phalloceros caudimaculatis* occurred in the estuary only during the dry period (spring and summer) that followed the strong wet period of 1997–1998. Low velocity, lateral flooding is the rule along the coastal plain, which probably yields low rates of passive displacement of fishes. In addition, these aquatic systems have high habitat heterogeneity derived from floating and submerged aquatic vegetation as well as submerged riparian. Several authors (Meffe 1984, Scrimgeour & Winterbourn 1987, Matheney & Rabeni 1995, Lobón-Cerviá 1996, Webb et al. 1996) have shown that fishes, especially juveniles inhabiting creeks and streams, can maximize station-holding performance and minimize displacement through behavioral response or due to habitat heterogeneity. Such evidence suggests that creeks draining into the Patos Lagoon estuary are not a major source of freshwater vagrant fishes in the estuarine zone. In fact, the role of tidal creeks as population sources of freshwater fishes seemed to be limited to occasional active migration by secondary freshwater fishes into the estuarine area.

Given that small tributaries apparently contributed few fishes to the lower estuary during wet periods, the upper reaches of the Patos Lagoon has to be the major source of freshwater fishes that appear in the estuarine zone during and after prolonged periods of high freshwater discharge. Expansion and retraction of freshwater in the middle-upper lagoon towards the estuarine zone appears to be the main factor influencing movement of freshwater fishes. In other words, fishes could be actively or passively tracking the freshwater intrusion into the estuarine zone. This hypothesis is partially supported by the high abundance and species richness of freshwater fishes found in the upper reaches of the lagoon. Following prolonged drought, intrusion of marine waters ultimately eliminates freshwater taxa.

Our study revealed associations among physical factors that likely control composition and abundance of freshwater fishes in Patos Lagoon. Such factors interact on multiple scales: local (e.g., salinity gradient, water level), regional (rainfall in the drainage basin leading to intermittent pulses of freshwater discharge), and global (wet and dry episodes trigged by ENSO events). This hierarchy of environmental interactions poses special challenges for management of fishery resources.

There is growing concern about the potential vulnerability of the Patos Lagoon ecosystem to accidentals introduction of non-indigenous fishes. Several exotic species (e.g., carps, Nile tilapia, channel catfish) have been cultivated in rice-field aquaculture and sportfishing ponds within the drainage basin (Poli et al. 2000). Escape of non-indigenous species from aquaculture has been recorded in Brazilian inland waters (Agostinho & Julio 1996, Orsi & Agostinho 1999). In some cases, elsewhere, this resulted in extirpation of native fishes, although in other cases invading species have been established without documented impacts on native fauna (Moyle & Light 1996). Our findings reinforce concerns that, during periods of elevated freshwater discharge, exotic species transported from ponds could survive for extended periods throughout the lagoon. Carp already have been captured within the estuarine zone (AMG, JPV, unpubl. data). Potential effects (both positive and negative) of such invading species on the native ichthyofauna of Patos Lagoon are currently unknown. Our findings reinforce the idea that management of the lagoon's fish populations must consider dynamics over sufficiently broad spatial and temporal scales.

Acknowledgements

We thank Lisiane A. Ramos for collecting data between Aug. 1996 and 1997 and the numerous colleagues who assisted in the field. We are grateful to Erica Caramaschi and Frances Gelwick for providing valuable comments, Luis R. Malabarba for provide an updated taxonomic list of characiforms in the Patos Lagoon system, and Luis E. Pereira and Marlise Bemvenuti for help with species identification. The study received financial support from the Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior – CAPES (Brazil), the Conselho Nacional de Desenvolvimento Cientifico e Tecnológico – CNPq (Brazil), Brazilian Long Term Ecological Research (LTER), and the Inter American Institute for Global Change Research (IAI) through a fellowship granted by SACC/Consortium (CRN-019). Alice Grimm also acknowledges the support from IAI-CRN055.

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