



Effects of 1997–1998 El Niño on the dynamics of the shallow-water fish assemblage of the Patos Lagoon Estuary (Brazil)

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Received 18 June 2001; received in revised form 4 October 2002; accepted 9 October 2002

Abstract

High rainfall associated with El Niño events significantly increases runoff and stream discharge in southern Brazil. High freshwater discharge changes salinity, temperature, and water circulation patterns that can affect the fish estuarine assemblage. Using long-term data obtained from standardized surveys, we analyzed fish assemblage structure and dynamics in shallow waters of the Patos Lagoon estuary in southern Brazil before, during, and after the 1997–1998 El Niño event. Overall, the relative abundance of all the fish groups in the estuary was about five times lower during the El Niño than before and after. Freshwater vagrants were the only group with greater abundance during El Niño. Fish species richness was higher in the estuary during the El Niño event, when many freshwater species expanded their ranges into the Patos Lagoon estuary, than before or after the El Niño. El Niño-induced assemblage changes were not highly persistent, and the estuarine fish assemblage returned to its pre-El Niño state within 18 months after the El Niño period. Densities of many marine and estuarine fishes increased to pre-El Niño levels within 3–6 months of the end of the El Niño period. We suggested that the rapid recovery of fish estuarine populations after the 1997–1998 El Niño may have been caused by one or some combination of: (a) enhanced productivity stimulated by nutrients contained in newly deposited alluvial sediments, and (b) enhanced larvae transport in the large saltwater intrusion that followed the El Niño event. Clearly, fish population dynamics and assemblage structure of the Patos Lagoon estuary can neither be interpreted nor predicted on a long-term basis without explicit consideration of El Niño Southern Oscillation patterns.

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Keywords: assemblage structure; El Niño Southern Oscillation; El Niño; estuary; freshwater outflow; Patos Lagoon; population dynamics; Recruitment

1. Introduction

El Niño Southern Oscillation (ENSO) events are relatively discrete climatic patterns that occur at intervals of 3–7 years. The El Niño phenomenon refers to a warming of the tropical Pacific basin in association with a weakening of the trade winds. The latest El Niño event in 1997–1998 was, by some measures, the strongest on record, with major climatic impacts felt around the world (McPhaden, 1999a,b). ENSO phenomena provide tremendous opportunities for natural ecological

comparisons at multiple hierarchical levels over broad geographic scales, and can effectively serve as a regional or global ecological field experiment (Grant, Grant, Keller, & Petren, 2000; Polis, Hurd, Jackson, & Pinero, 1997).

Ecological effects attributed to the 1997–1998 El Niño episode were observed in a variety of ecosystems and across multiple levels of biological organization: river geochemistry (Villar & Bonetto, 2000), reef corals (Glynn, Colley, Ting, Mate, & Guzman, 2000; Spencer, Teleki, Bradshaw, & Spalding, 2000), pelagic systems (Gonzales, Sobarzo, Figueroa, & Nothig, 2000; Sanchez-Veloso, Shirasago, Cisneros-Mata, & Avalos-Garcia, 2000), fish communities (Davis, 2000; Swales, Storey, Roderick, & Figa, 1999), and bird and mammal

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populations (Bradshaw, Davis, Lalas, & Harcourt, 2000; Grant et al., 2000; Lyver, Möller, & Thompson, 1999). Globally, El Niño phenomena vary widely in intensity and have both negative and positive aspects (Arntz, 1986).

Through its influence on regional precipitation, ENSO phenomena originating in the southeastern Pacific could directly influence fish assemblages and fisheries in rivers and coastal waters over a large portion of the earth (Fiedler, Methot, & Hewitt, 1986; Godínez-Domínguez, Rojo-Vázquez, Galván-Piña, & Aguilar-Palomino, 2000; Mysak, 1986; Sanchez-Velaso et al., 2000; Swales et al., 1999). El Niño episodes cause higher than average rainfall in southern Brazil, Uruguay, and northeastern Argentina (Grimm, Ferraz, & Gomes, 1998; Philander, 1990; Ropelewski & Halpert, 1987, 1989), which directly affects runoff and stream flow in major rivers of the region (Diaz, Studzinski, & Mechoso, 1998; Mechoso & Iribarren, 1992). Higher river discharge changes salinity, temperature, and water circulation patterns in estuaries and coastal waters (Binett, Reste, & Diouf, 1995; Crivelli et al., 1995; Livingston, 1991; Winemiller & Leslie, 1992), which in turn can affect biogeochemistry and primary production (Ciotti, Odebrecht, Fillmann, & Möller, 1995; Yin, Harrison, Goldblstt, John, & Beamish, 1997). An association between river discharge, estuarine productivity, and fisheries has been reported in many regions of the world (Caddy & Bakun, 1995; Deegan et al., 1986; Martins, Pardal, Lillebo, Flindt, & Marques, 2001). Based on a long-term study of the Apalachicola Bay system, Gulf of Mexico, Livingston, Niu, Lewis, and Woodsum (1997) showed that productivity, community composition, and food web structure change in response to reduced freshwater outflow during prolonged drought.

Our study analyzes recruitment patterns, species composition, and fish assemblage structure and dynamics in shallow waters of the Patos Lagoon estuary before, during, and after the 1997–1998 El Niño event based on data obtained from a long-term standardized survey. The continental shelf of extreme southern Brazil is one of the most productive fishing areas in Brazil (Reis & D’Incao, 2000). The Patos Lagoon estuary is an important nursery area for several commercially important fish species from this region (Chao, Pereira, & Vieira, 1985; Vieira & Castello, 1996). It is, therefore, critically important to understand the extent to which El Niño events affect the recruitment and abundance patterns of juvenile and adult fishes in this ecosystem. We show strong patterns of association between dynamics of physical parameters and fish populations. Our study also reveals that by several months after the El Niño several resident- and estuarine-dependent fish populations returned to densities at or above pre-El Niño levels.

2. Materials and methods

2.1. Study site

Located along the coastal plain of Rio Grande do Sul in southern Brazil, Patos Lagoon (32°S 49°W) is the largest choked lagoon in the world. This estuary is 250 km long and 60 km wide, covering an area of 10,360 km² (Fig. 1). According to Kjerfve (1986), choked lagoons have a single entrance channel and small ratios of entrance-channel cross-sectional area to lagoon surface area. The brackish area is restricted to the southern portion of the lagoon (ca. 10% of total area), and the lagoon is connected to the ocean by a single inlet about 4 km long and 740 m wide at the mouth. The lagoon’s drainage basin covers 201,626 km² (Asmus, 1996). Wind patterns and fluvial discharge control circulation, salinity distribution, and water levels. Seasonal freshwater discharge varies considerably (47–30,300 m³ s⁻¹), and during El Niño years, runoff greatly exceeds average values. Winds are predominantly NE–SW in the region (Garcia, 1996).

The ichthyofauna of the Patos Lagoon estuary is composed of about 110 species, but only a few are frequent and abundant throughout the year (Chao et al.,

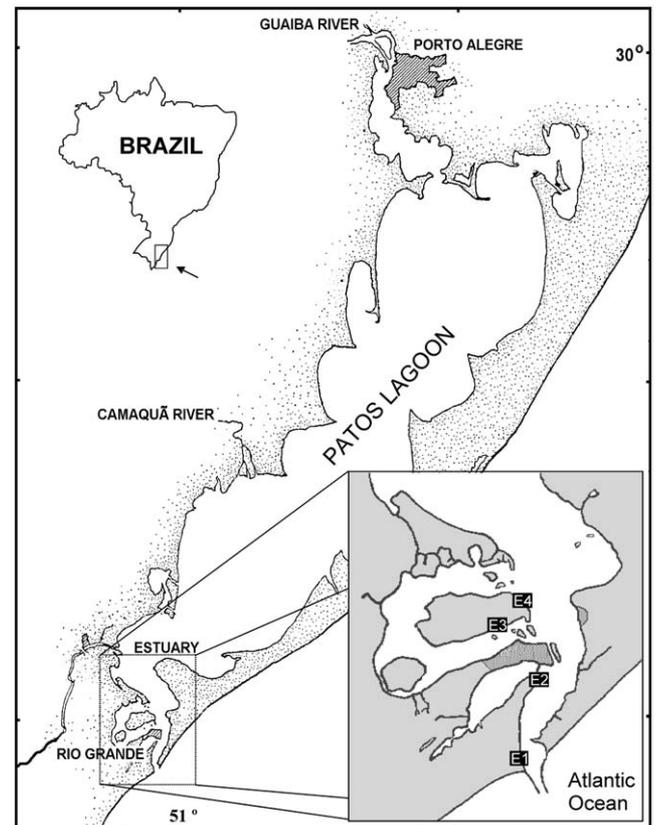


Fig. 1. Patos Lagoon showing the beach sampling stations located within its estuarine area (E1, 32° 09.047' S, 52° 06.133' W; E2, 32° 03.649' S, 52° 05.272' W; E3, 32° 00.967' S, 52° 08.089' W; E4, 31° 59.553' S, 52° 05.970' W).

1985). Some fishes, such as the Brazilian silverside, *Atherinella brasiliensis* (Chernoff, 1986), complete their entire cycle within the estuary, whereas marine species, such as the mullet, *Mugil platanus* (Günther, 1880), use the estuary as a nursery ground during specific periods of their life cycles (Vieira & Castello, 1996). Patos Lagoon and the adjacent coastal area support one of the most important fisheries in the warm-temperate southwestern Atlantic. About 3500 artisanal (Reis & D’Incao, 2000) and 3000 industrial fishermen are temporarily or permanently involved in fishing activities in this region (Haimovici, Castello, & Vooren, 1996).

2.2. Field sampling

Survey stations were located in shallow waters (mean depth, <1 m) of the estuary, where fishes can be efficiently sampled with a seine net (Fig. 1). Fish were sampled using a 9-m beach seine (13 mm bar mesh in the wings and 5 mm in the center 3-m section) that was pulled quarter circle to the shore covering an area of about 60 m². Five hauls were made, monthly, at each beach station from August 1996 to April 2000. Specimens were preserved in 10% formalin and later identified, counted, and measured for total length (TL) to the nearest mm. Each month, air and water temperature, water transparency (Secchi disk), and salinity were measured at each station. Precipitation was recorded daily at a local meteorological laboratory (Fundação Universidade do Rio Grande).

2.3. Data analysis

ENSO strongly influences rainfall patterns in southern Brazil (Grimm et al., 1998). Rainfall tends to be above the median from November to February during El Niño years (Kane, 1999; Lau & Sheu, 1988; Pisciotano, Diaz, Cazes, & Mechoso, 1994; Rao & Rada, 1990; Ropelewski & Halpert, 1989; and see Diaz et al., 1998 for relationships with the Atlantic Ocean). The duration of the 1997–1998 El Niño (Fig. 2) was estimated from local meteorological and hydrological data plus the occurrence of El Niño conditions in the eastern tropical Pacific (Changnon & Bell, 2000; Kane, 1999; McPhaden, 1999b; Slingo, 1998).

The meteorological effects of the 1997–1998 El Niño in the Patos Lagoon estuary were determined by comparing each monthly environmental parameter (August 1996 to April 2000) with a long-term database of monthly averages. Monthly values (x) from the short-term data set were contrasted with monthly averages (μ) using $x - \mu$. The short-term rainfall data were compared with a database from 13 years (1988 to 2000) of monthly precipitation in Rio Grande City, Patos Lagoon estuary (Meteorology Lab, Fundação Universidade do Rio Grande). Hydrological data (temperature of water, trans-

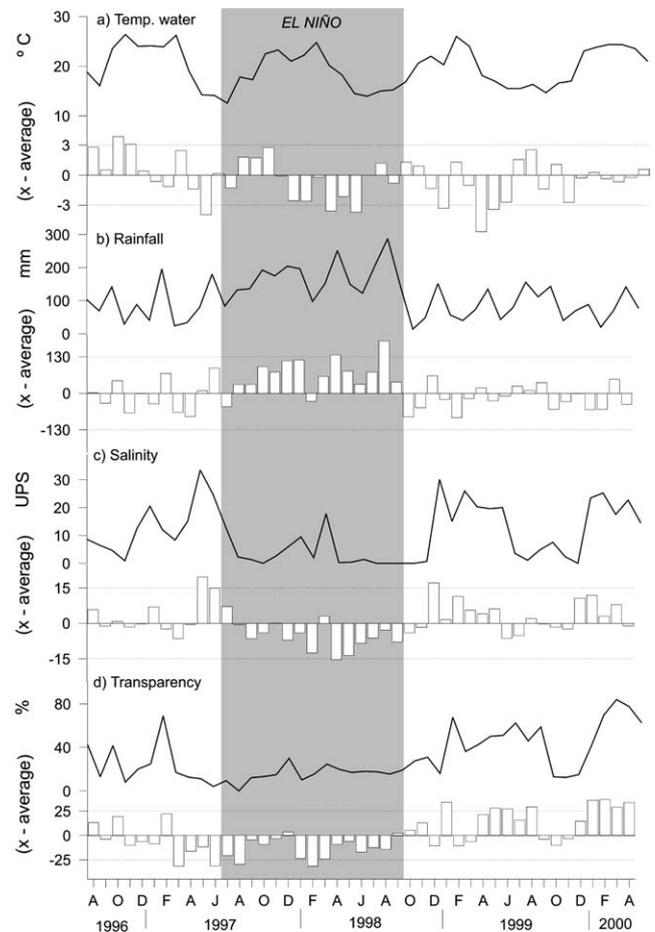


Fig. 2. Monthly values of (a) water temperature, (b) rainfall, (c) salinity, and (d) water transparency showing variation associated with El Niño. Lines represent monthly average from August 1996 to April 2000. Bars represent difference between each monthly average from 1996 to 2000 and each monthly long-term average (rainfall, 13-year from 1988 to 2000; water temperature, salinity, and transparency, 10-year from 1978 to 1983 and from 1996 to 2000).

parency, and salinity) were compared with a 10-year database (1978–1983 and 1996–2000) of monthly samples from the Patos Lagoon estuary.

Our samples were dominated by four life history categories (Garcia, Vieira, & Winemiller, 2001; Vieira & Castello, 1996):

- Estuarine resident (RES): typically occurring and breeding in estuaries;
- Estuarine dependent (DEP): marine- or freshwater-spawning species found predictably in large numbers in estuaries during certain periods of their life-cycle;
- Marine vagrant (MAR): typically inhabiting marine environments and rarely occurring in estuaries;
- Freshwater vagrant (FRE): typically inhabiting freshwater environments and rarely occurring in estuaries.

In order to have a balanced ANOVA design that allows comparisons without confounding months, we

used only data collected from October to April each year. This resulted in four periods: 'pre' (October 1996–April 1997), 'El Niño' (October 1997–April 1998), 'post1' (October 1998–April 1999), and 'post2' (October 1999–April 2000). Variation in the abundance (catch per unit effort, CPUE) of fishes between periods and months was analyzed by a repeated-measures ANOVA. We average the five seine hauls in each fixed beach station to create monthly means, using the 7 months (October to April) within periods (pre, El Niño, post1, post2) as the repeated measure, and the four estuarine beach stations as their true replicates. We used the Huynh-Feldt statistic to control the assumption of sphericity (Kneib & Scheele, 2000; Zar, 1996). The associated probability provided by this statistic was coincident with the *F*-statistic in our repeated measures analyses, showing conformity to the required assumption of sphericity.

In all the cases, the biological data (log-transformed) met the assumptions of normality (Kolmogorov–Smirnov (K–S) test) and homogeneity of variances (Cochran test). In order to assess recruitment patterns of the dominant species, CPUE and size (TL) were analyzed graphically by plotting CPUE by size class (Vieira, 1991a).

Relationships between fish assemblages and environmental variables at sampling stations were analyzed with canonical correspondence analysis (CCA; ter Braak, 1986), using the software package CANOCO. We used a Monte Carlo permutation test to assess the statistical significance of relationships. Species with mean frequency of occurrence <1 were omitted to avoid a disproportionate effect of rare species on the analysis. The environmental variables used were monthly rainfall (mm), salinity, water temperature (°C), and water transparency (percentage) of the maximum possible Secchi depth (1 m).

In the CCA ordination diagram, the relative importance of environmental variables in explaining variability in species/samples dispersion is indicated by the length and angle of arrows in the species and sample ordination plots. The angle and length of the arrow relative to a given axis reveals the correlation of the variable with that canonical axis (environmental gradient). The position of a species on an axis reveals its associations with the environmental gradient (i.e. increasing abundance with high or low values for the environmental variable).

The richness and evenness (i.e. equitability) components of species diversity were analyzed individually. The species-richness component was calculated by rarefaction method (Hurlbert, 1971; Sanders, 1968). This approach provides a standardized measure of species diversity adjusted for sample size effects, thus permitting comparison between assemblages with different densities of organisms or samples obtained with different efforts. Evenness was analyzed by the *E4* ratio method of Hill

(1973). This index converges to one when a single species dominates abundance, and it is relatively unaffected by the addition of rare species (Ludwig & Reynolds, 1988). Variation in the rarefaction richness and Hill's evenness between periods and months were analyzed in the same way as mentioned before for ANOVA abundance analysis. These data met the assumptions of normality (K–S test) and homogeneity of variances (Cochran test) without transformation.

3. Results

3.1. Environmental parameters

Between July 1997 and September 1998, rainfall in the region of Patos Lagoon estuary was consistently higher than the long-term average, whereas salinity and water transparency were lower than the average (Fig. 2). Salinity fell to <1 values during this period. Salinity was significantly negatively correlated with rainfall ($R = 0.675$; $p < 0.001$; $n = 25$ seasonal averages from Fall 1994 to Fall 2000). Rainfall was not significantly correlated with either water temperature ($R = 0.174$; $p = 0.404$; $n = 25$ Fall 1994 to Fall 2000) or water transparency ($R = 0.467$; $p = 0.068$; $n = 16$ Winter 1996 to Fall 2000). The high rainfall and low estuarine salinity between July 1997 and September 1998 can be attributed to the 1997–1998 El Niño. This period coincided with the occurrence of the 1997–1998 warm ENSO in the eastern tropical Pacific (Changnon & Bell, 2000; McPhaden, 1999a,b; Slingo, 1998) and with the predicted excess rainfall in southern Brazil (Grimm et al., 1998; Kane, 1999).

3.2. Species relative abundance and diversity patterns

A total of 99,039 fishes, representing 58 species, were captured in 885 samples obtained over the study period. Estuarine-resident and estuarine-dependent fishes were dominant groups (Table 1), whereas freshwater vagrants and marine vagrants were less frequent and occurred in relatively low densities (Table 2). The estuarine-resident *A. brasiliensis* and the estuarine-dependent mullets, *M. platanus* and *M. curema* (Valenciennes, 1836), were the most abundant species, and together accounted for 50.9% of the grand total catch. Overall, the abundance (CPUE) of all the ecological groups in the estuary was about five times lower during the El Niño (28.35 individuals per haul) than non-El Niño periods (pre-El Niño = 137.79; post-El Niño = 166.83). Freshwater vagrants were the only group that had greater abundance and frequency of occurrence during El Niño (Fig. 3).

The repeated measures ANOVA of the CPUE of two dominant groups (estuarine resident and estuarine dependent) showed significant main effects for periods

Table 1

Number of individuals per haul (CPUE) of estuarine resident and estuarine dependent at the estuarine area before (pre), during (El Niño), and after (post) the 1997–1998 El Niño event

	Pre	El Niño	Post
Estuarine resident	63.89	16.64	57.69
<i>Atherinella brasiliensis</i>	45.89	10.17	44.25
<i>Jenynsia multidentata</i>	8.40	0.11	7.40
<i>Odontesthes argentinensis</i>	5.33	2.45	4.57
<i>Platanichthys platana</i>	3.48	1.04	0.21
<i>Ramnogaster arcuata</i>	0.28	2.49	1.18
<i>Gobionellus shufeldti</i>	0.47	0.19	0.07
<i>Genidens genidens</i>		0.20	
<i>Syngnathus folletti</i>	0.04	0.01	0.01
Estuarine dependent	71.60	9.69	103.42
<i>Mugil platanus</i>	28.86	4.22	62.67
<i>Mugil curema</i>	33.75	0.55	19.03
<i>Brevoortia pectinata</i>	5.42	2.02	12.06
<i>Mugil gaimardianus</i>	1.63	0.15	5.57
<i>Micropogonias furnieri</i>	1.47	1.95	3.92
<i>Lycengraulis grossidens</i>	0.47	0.76	0.11
<i>Paralichthys orbignyanus</i>	0.01	0.02	0.05
<i>Menticirrhus americanus</i>	<0.01	0.01	0.02
<i>Netuma barba</i>		0.01	
Total	135.50	26.33	161.11

and months (Table 3). Overall, both dominant groups of fishes had significantly lower CPUE during El Niño when compared with pre and post (1 and 2) periods. Post-hoc multiple comparisons (Newman–Keuls test, $\alpha = 0.05$) detected that CPUE values at the El Niño period, during the warmer months of January to April, differed from those at the pre (January to March), post1 (January and March), and post2 (January to April). The different abundance patterns of the estuarine resident among the periods and months resulted in a positive interaction (periods \times months) main effect (Fig. 4).

Rarefaction richness ($E[S]$) and evenness ($E4$) parameters differed significantly among periods (Table 4). Post-hoc multiple comparisons (Newman–Keuls test, $\alpha = 0.05$) showed that a higher number of species ($E[S]$) were captured at the El Niño, especially between November and February. Similarly, the relative abundance was more evenly distributed among species at the El Niño in November and January, which resulted in lower values of $E4$ (Fig. 5).

3.3. Size structure

Fishes ranged in size from 20 to 130 mm (Fig. 6). The size distribution of the estuarine-resident group during non-El Niño periods was weakly bimodal and dominated by juvenile fishes (20–60 mm). The size distributions of estuarine-resident fishes were significantly different when the pre-El Niño period was compared with the post-El Niño period (K–S test, $z = 1.39$, $p < 0.05$), with the former showing a more strongly bimodal distribution and lower abundance of the

Table 2

Number of individuals per haul (CPUE) of freshwater vagrants and marine vagrants at the estuarine area before (pre), during (El Niño), and after (post) the 1997–1998 El Niño event

	Pre	El Niño	Post
Freshwater vagrant	0.01	1.90	0.59
<i>Astyanax eigenmanniorum</i>		0.75	0.29
<i>Parapimelodus nigribarbis</i>		0.81	0.02
<i>Oligosarcus jenynsii</i>		0.18	
<i>Phalloceros caudimaculatus</i>			0.16
<i>Oligosarcus robustus</i>		0.04	0.03
<i>Geophagus brasiliensis</i>	0.01	0.01	0.04
<i>Pimelodus maculatus</i>		0.06	
<i>Cyphocharax voga</i>		0.02	
<i>Poecilia vivipara</i>			0.01
<i>Rhamdia</i> sp		0.01	
<i>Hyphessobrycon bifasciatus</i>			0.01
<i>Phallopterychus</i> sp			0.01
<i>Crenicichla lepidota</i>		0.01	0.01
<i>Loricariichthys anus</i>		0.01	
<i>Cnesterodon decemmaculatus</i>			0.01
<i>Macropsobrycon uruguayanae</i>		0.01	
<i>Hyphessobrycon luetkenii</i>			0.01
<i>Hoplias malabaricus</i>		0.01	
Marine vagrant	2.28	0.12	5.14
<i>Trachinotus marginatus</i>	0.09		0.19
<i>Anchoa mitchilli</i>		0.07	2.42
<i>Ulaema lefroyi</i>	1.47		1.51
<i>Menticirrhus littoralis</i>	0.20	0.01	0.10
<i>Umbrina canosai</i>	0.03		0.66
<i>Harengula clupeiola</i>	0.30		
<i>Eucinostomus gula</i>			0.17
<i>Citharichthys spilopterus</i>	0.07	0.01	0.04
<i>Oncopterus darwini</i>	0.02		<0.01
<i>Prionotus punctatus</i>	0.01		0.01
<i>Trachinotus falcatus</i>	0.01	0.01	<0.01
<i>Stellifer rastriifer</i>			0.01
<i>Trichiurus lepturus</i>		0.01	0.01
<i>Gobionellus oceanicus</i>	0.01	0.01	0.01
<i>Eucinostomus melanopterus</i>	0.01		
<i>Symphurus jenynsi</i>	0.01		
<i>Trachinotus carolinus</i>	0.01		
<i>Epinephelus</i> sp	0.01		0.01
<i>Sardinella brasiliensis</i>	0.01		
<i>Porichthys porosissimus</i>			0.01
<i>Eucinostomus argenteus</i>	0.01		
<i>Diapterus rhombeus</i>	0.01		
<i>Lagocephalus laevigatus</i>			0.01
Total	2.29	2.02	5.72

smallest recruits (Fig. 6a). Otherwise, estuarine-dependent fishes had a narrow unimodal distribution, dominated by juvenile fishes (20–30 mm) that did not differ from pre- (K–S test, $z = 1.11$, $p = 0.17$) and post- (K–S test, $z = 1.25$, $p = 0.09$) El Niño periods (Fig. 6b).

During El Niño, freshwater vagrant fishes inside the estuary had a bimodal distribution dominated by 40–80 mm fishes and individuals >100 mm. After the El Niño event, the freshwater vagrants size distribution was significantly different (K–S test, $z = 1.525$, $p = 0.019$) with predominately 40–80 mm fishes (Fig. 6c). Marine vagrant fishes had a weakly bimodal size distribution during the

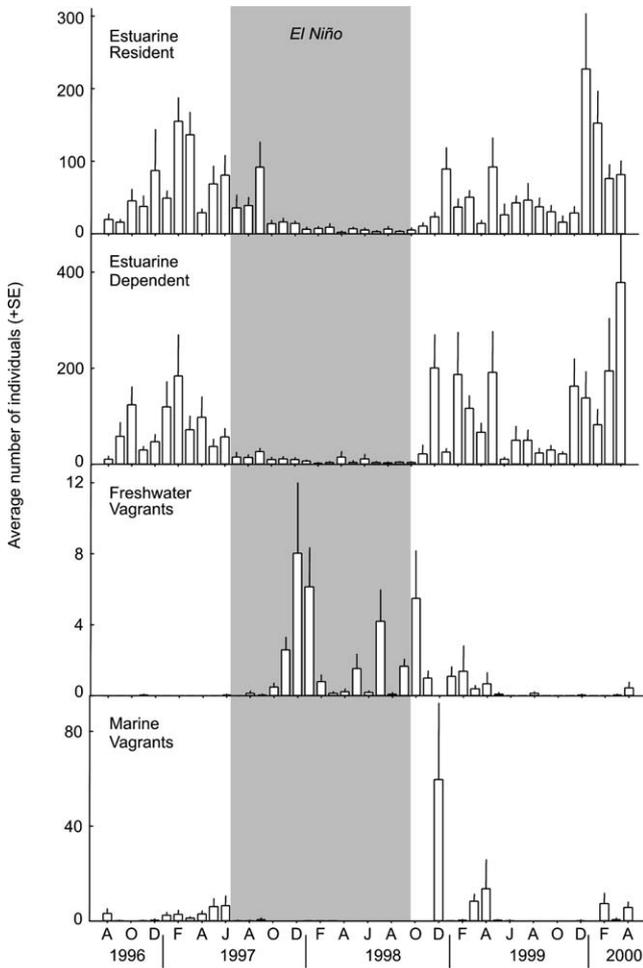


Fig. 3. Monthly mean fluctuations of the average number of individuals and standard error of the four fish groups (estuarine residents, estuarine dependents, freshwater vagrants, and marine vagrants) from August 1996 to April 2000. The 1997–1998 El Niño is delimited from July 1997 to September 1998.

pre that contrasted with a strongly unimodal distribution at the post period. During the El Niño, the abundance of all size classes declined in the estuary (Fig. 6d).

3.4. Species composition and environmental variables

In the CCA analysis, the first axis (eigenvalue = 0.169) alone modeled 62.4% of the total explained variance, showing a high species–environment correlation (0.785). Salinity and transparency were strongly correlated with the first axis, whereas rainfall and water temperature were correlated with the second axis (Table 5).

From the ordination diagrams (Fig. 7a, b), we can infer that the first axis is a salinity gradient in which months with high salinity and water transparency samples cluster at the left side of the ordination plot, and those showing lower salinity and water transparency cluster at the right side. The second axis contrasts months with high water temperature and low rainfall (bottom side) with low water temperature associated with high

Table 3 Results of repeated measures ANOVA of relative abundance (CPUE) variation of estuarine-resident and estuarine-dependent fishes in relation to periods (pre, El Niño, post1, post2) and months (October to April)

Source	df	SS	MS	F	p
<i>Estuarine resident</i>					
Periods	3	13.03	4.35	10.56	**
Months	6	3.78	0.63	4.87	**
Periods × months	18	7.59	0.42	2.27	*
Residual	54	10.00	0.18		
<i>Estuarine dependent</i>					
Periods	3	15.76	5.25	12.72	**
Months	6	4.28	0.71	3.21	*
Periods × months	18	8.75	0.49	2.26	*
Residual	54	11.62	0.21		

Individual values were log₁₀-transformed. Significant values, *p < 0.05; **p < 0.01.

rainfall (upper side). Samples collected during the El Niño cluster at the upper-right side of the ordination plot (Fig. 7b). These samples were associated with higher rainfall, and lower salinity and water transparency.

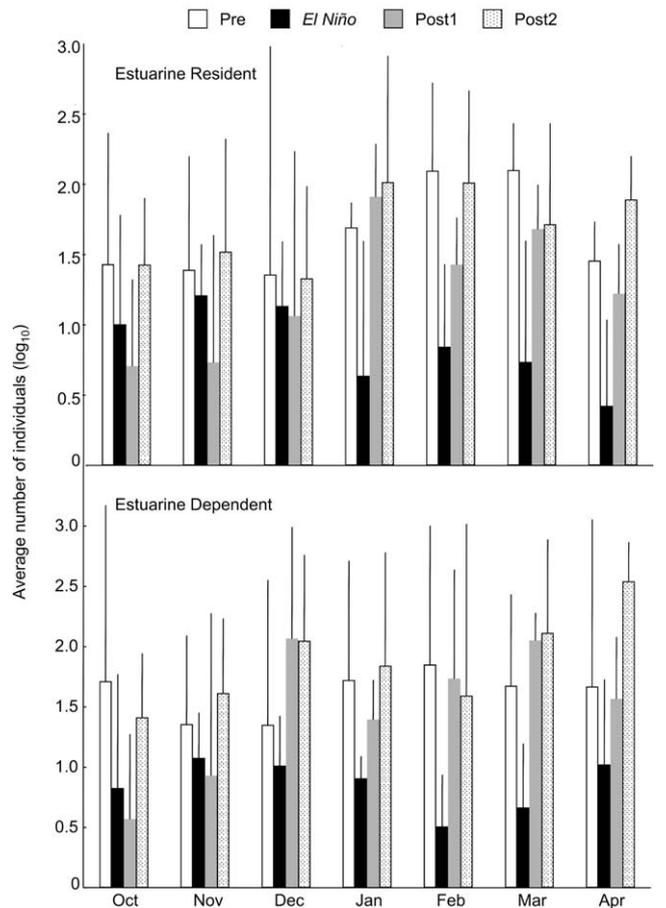


Fig. 4. Average number of individuals and standard error for estuarine-resident and estuarine-dependent fish groups between October to April during four periods: pre (October 1996–April 1997), El Niño (October 1997–April 1998), post1 (October 1998–April 1999), and post2 (October 1999–April 2000).

Table 4
Results of repeated measures ANOVA of species richness (rarefaction, $E[S]$) and evenness ($E4$ ratio method of Hill) parameters in relation to periods (pre, El Niño, post1, post2) and months (October to April)

Source	df	SS	MS	F	p
Richness ($E[S]$)					
Periods	3	67.735	22.578	7.883	**
Months	6	7.073	1.179	0.678	0.669
Periods \times months	18	76.174	4.232	2.668	**
Residual	54	85.667	1.586		
Evenness ($E4$)					
Periods	3	0.043	0.014	4.390	*
Months	6	0.024	0.004	1.471	0.243
Periods \times months	18	0.173	0.009	1.153	0.331
Residual	54	0.452	0.008		

Significant values, * $p < 0.05$; ** $p < 0.01$.

Freshwater vagrants (*Parapimelodus nigribarbis* (Boulenger, 1889), *Oligosarcus jenynsii* (Günther, 1864), *Astyanax eigenmanniorum* (Cope, 1894)) were most abundant in samples positioned at the upper-right side of the diagram in association with samples collected during high rainfall periods of El Niño. The cichlid *Geophagus brasiliensis* was the only freshwater vagrant associated with high salinity and water transparency samples collected during non-El Niño months. In contrast, marine vagrants (especially *Ulaema lefroyi* (Goode, 1874), *Menticirrhus littoralis* (Holbrook, 1855), and *Trachinotus marginatus* (Cuvier, 1832)) were most abundant in samples clustered at the left side of the ordination plot in association with high salinity and water transparency samples that belong to the pre and post periods (Fig. 7a, b).

The two dominant fish groups (estuarine resident and estuarine dependent) cluster between the vagrant species, showing higher association with samples characterized by intermediate environmental values. Among these fishes, *Odontesthes argentinensis* (Valenciennes, 1835), *Gobionellus shufeldti* (Jordan and Eigenmann, 1887), and *Micropogonias furnieri* (Desmarest, 1823) were more associated with low salinity and high rainfall samples, whereas *Mugil curema* (Valenciennes, 1836) and *Mugil gaimardianus* (Desmarest, 1831) cluster near samples with high salinity and water transparency. The two most abundant fishes (*Atherinella brasiliensis* and *Mugil platanus*) occupied the origin of the diagram, which reflected their high association with the grand mean of each environmental variable (Fig. 7a).

4. Discussion

During the 1997–1998 El Niño, rainfall exceeded the average for southern Brazil (Kane, 1999) and in the Patos Lagoon estuary, salinity and water transparency were significantly lower than average. Qualitatively similar effects of increased discharge from the Patos Lagoon

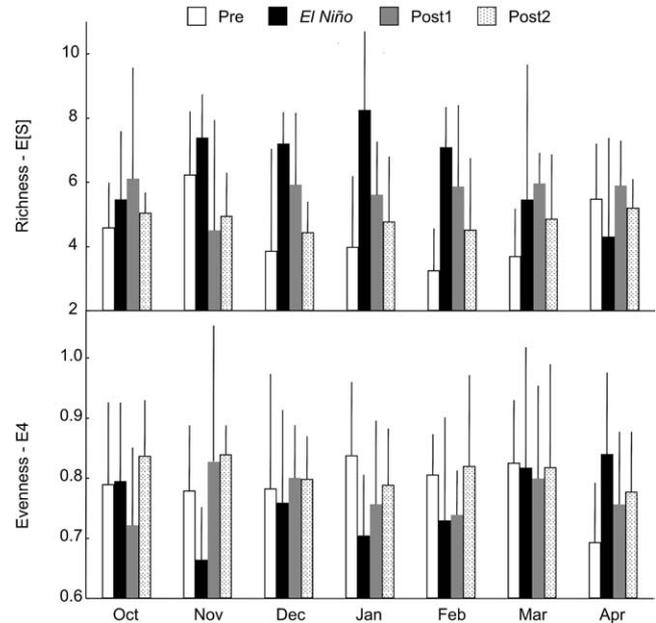


Fig. 5. Average number of individuals and standard error for specie richness (rarefaction, $E[S]$), based on a standard sample size of 50 individuals, and evenness ($E4$ ratio method of Hill) between October and April during four periods: pre (October 1996–April 1997), El Niño (October 1997–April 1998), post1 (October 1998–April 1999), and post2 (October 1999–April 2000).

were observed during the 1987 ENSO (Ciotti et al., 1995; Lima, Garcia, & Möller, 1996).

The hydrological processes that control water exchange between the Patos Lagoon and the adjacent marine area also aid in transporting larvae and juvenile fishes into and out of the estuary. Most coastal fishes spawn in marine waters adjacent to the estuary during late spring and early summer, which coincides with the period of maximum saltwater intrusion into the estuary. Larvae and juveniles are transported or migrate into the estuary where they find shelter and food in the shallow, unvegetated intertidal flats and beds of submersed macrophytes (Chao et al., 1985; Garcia & Vieira, 1997; Muelbert & Weiss, 1991). The normal entrance of juvenile marine fishes into the estuary was strongly disrupted during the 1997–1998 El Niño event. During winter and early spring, estuarine-dependent fishes, such as mullets, were abundant in the surf zone adjacent to the mouth of the Patos Lagoon estuary. However, under conditions of high freshwater discharge triggered by El Niño and limited saltwater intrusion into the estuary, few juvenile estuarine-dependent fishes apparently moved into the shallow waters of the Patos Lagoon estuary.

4.1. Recruitment of dominant species

According to Vieira (1991b), juveniles (<50 mm) of three common mullet species (*Mugil platanus*, *M. curema*, and *M. gaimardianus*) use shallow-water habitats of the Patos Lagoon estuary. The low abundance of juvenile

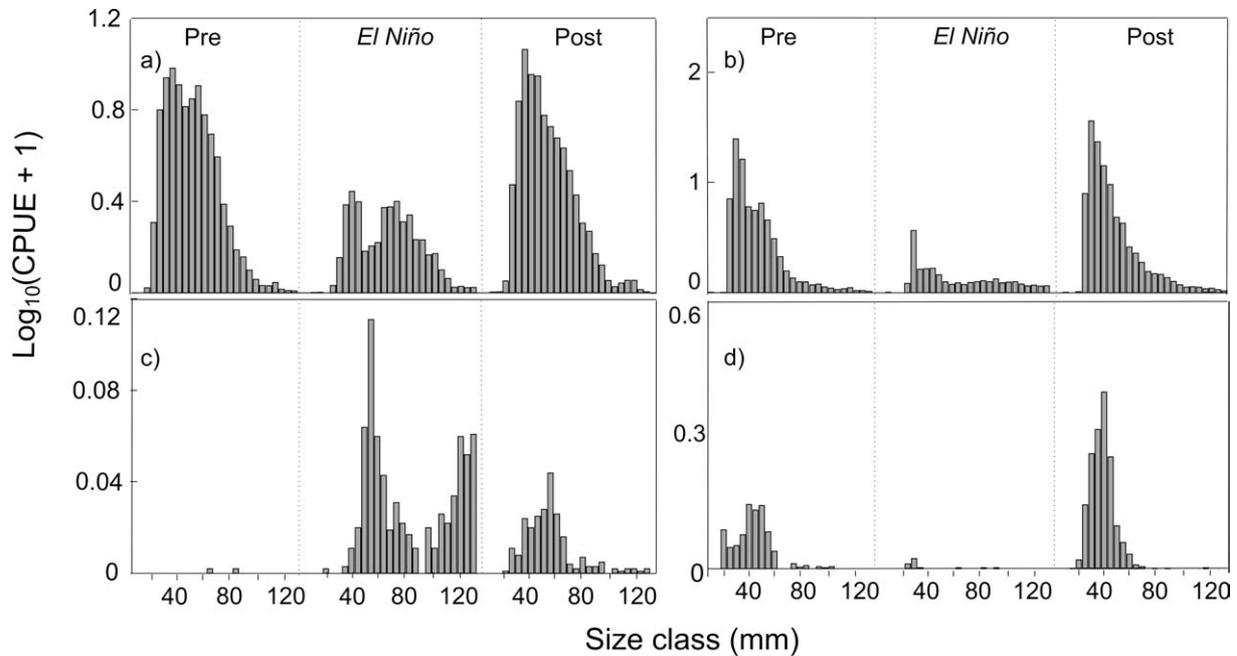


Fig. 6. CPUE (average number of individuals per seine haul) by size class (mm TL) of the four fish groups: (a) estuarine residents, (b) estuarine dependents, (c) freshwater vagrants, and (d) marine vagrants captured before (August 1996–June 1997), during (El Niño; July 1997–September 1998), and after (October 1998–April 2000) the 1997–1998 El Niño event.

mulletts in the Patos Lagoon estuary during the 1997–1998 El Niño suggests that high freshwater outflow may have rendered ineffective the mechanism of passive immigration into the estuary by net upstream movement of high-salinity bottom waters. We hypothesized that the low recruitment of immature mullets into the Patos Lagoon estuary during El Niño events could significantly impact the important artisanal fishery of the mullet adults in this region. [Castello and Möller \(1978\)](#) were the first to observe a relationship between rainfall and recruitment of marine species in the Patos Lagoon estuary. These authors showed that rainfall was negatively correlated with the pink-shrimp (*Farfantepenaeus*

paulensis) production in the estuary, and they suggested that strong freshwater outflow is a severe obstacle for larval penetration.

Juvenile fishes and shrimp exploit vertical stratification of the water column and tidal flow to aid movement into and out of estuaries ([Whitfield, 1999](#)). Vertical stratification in the Patos Lagoon estuary depends on the relative strength of river discharge and wind action that interact to produce either salt wedge, partially stratified or complete mixing of the water column ([Möller & Casting, 1999](#); [Möller, Casting, Salomon, & Lazure, 2001](#)). During river flow exceeding $4500 \text{ m}^3 \text{ s}^{-1}$, the salt water is rapidly flushed out of the estuarine system ([Möller, Paim, & Soares, 1991](#)). This flushing is more important during El Niño events when higher precipitation and freshwater discharged from rivers dominate the estuary for several months. During the 1997–1998 *El Niño*, the estuarine plume extended 30 km along the coast near the Patos Lagoon estuary (O. O. Möller, personal communication). In addition, high freshwater outflow may elevate water depth of the estuary along its longitudinal gradient, which hinders saltwater intrusion. During this situation, only storm conditions can reverse the pressure gradient between the lagoon and the coastal area ([Möller et al., 2001](#)).

In contrast to estuarine-dependent individuals, larvae and juveniles of estuarine-resident fishes must remain within the estuarine system ([Whitfield, 1999](#)), and several species have developed behavioral adaptations to avoid being flushed out of the estuarine area (e.g. [Melville-Smith, Baird, & Wooldridge, 1981](#)). During flood events,

Table 5
Results of CCA performed on the relative abundance (CPUE) of fish species

Axes	1	2	3	4
<i>Biplot scores of environmental variables</i>				
Salinity	-0.953	0.188	-0.234	-0.038
Temperature of water	-0.091	-0.567	-0.512	-0.639
Transparency	-0.510	-0.346	0.691	-0.378
Rainfall	0.304	0.753	0.232	-0.535
<i>Summary statistics for ordination axes</i>				
Eigenvalues	0.169	0.057	0.029	0.015
Species–environment correlations	0.785	0.668	0.519	0.48
Cumulative percentage variance				
of species data	11.8	15.7	17.8	18.9
of species–environment relation	62.4	83.5	94.3	100

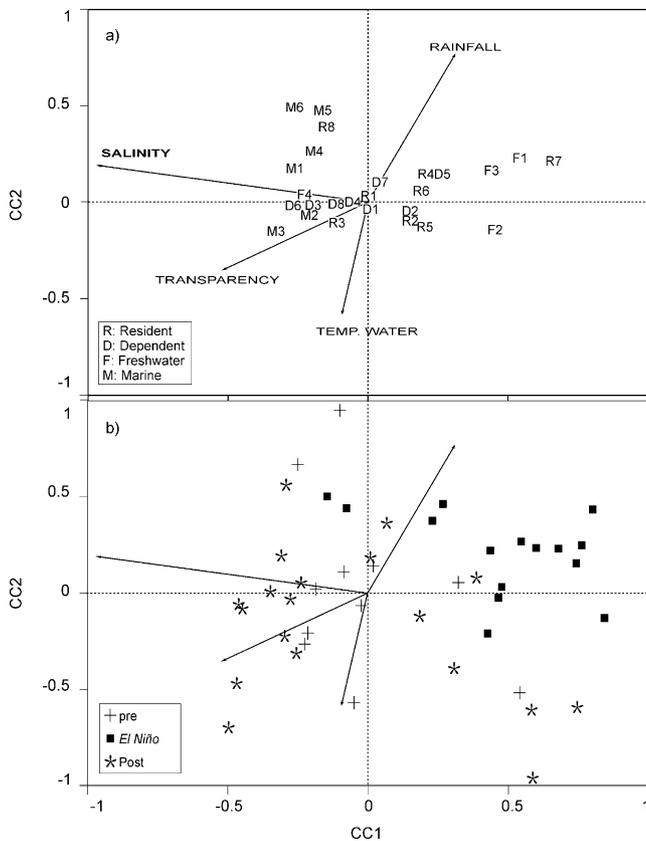


Fig. 7. CCA ordination plot. (a) Association of fish species with each axis is represented by its score (plotted) and correlation between environmental variables and axes are represented by the length and angle of arrows. The species groups were labeled as estuarine Resident (R1, *A. brasiliensis*; R2, *Odontheistes argentinensis*; R3, *Jenynsia multidentata*; R4, *Platanichthys platana*; R5, *G. shufeldtii*; R6, *Ramnogaster arcuata*; R7, *Genidens genidens*; R8; *Syngnathus folletti*), estuarine Dependent (D1, *M. platanus*; D2, *M. furnieri*; D3, *Mugil curema*; D4, *Brevoortia pectinata*; D5, *Lycengraulis grossidens*; D6, *Mugil gaimardianus*; D7, *Paralichthys orbignyana*; D8, *Menticirrhus americanus*), Freshwater vagrants (F1, *P. nigribarbis*; F2, *A. eigenmanniorum*; F3, *O. jenynsii*; F4, *G. brasiliensis*), and Marine vagrants (M1, *U. lefroiyi*; M2, *M. littoralis*; M3, *T. marginatus*; M4, *Citharichthys spilopterus*; M5, *Anchoa marini*; M6, *Umbrina canosai*). (b) sample sites (+, pre; ■, El Niño; * post) and environmental variables (arrows). Each point represents a single sample station and date (five beach seine hauls at the location for a given month). Environmental variables are salinity, rainfall, water temperature, and transparency.

the effectiveness of this adaptive behavior is exceeded, and large numbers of fish larvae are flushed out to sea.

The high freshwater discharge associated with the El Niño event exceeded the behavioral adaptations of some estuarine residents of Patos Lagoon estuary, such as the euryhaline species, *A. brasiliensis*. This small fish (maximum TL = 160 mm) spawns during summer in the shallow waters of Patos Lagoon estuary (Bemvenuti, 1987). Young-of-the-year (<70 mm) move toward the estuary's mouth where they remain until about 70–100 mm. During this period, they occasionally migrate in low abundance into marine coastal waters. During spring, sub-adults and adults (>100 mm TL) migrate

towards the northern region of the estuary in preparation for spawning. High freshwater discharges caused by El Niño transported large numbers of *A. brasiliensis* juveniles outside the estuary. As a result, an unusually high abundance of this species was observed at the adjacent marine coastal area during winter and spring of the 1997–1998 El Niño period (Garcia et al., 2001).

4.2. Diversity

Fish species richness was higher in Patos Lagoon estuary during the El Niño than before and after, and this was strongly influenced by an increase in the number of freshwater fishes. With higher river discharge and the consequent decline of dominant euryhaline fishes, freshwater vagrant species increased in relative abundance and richness in the shallow waters of Patos Lagoon estuary. These riverine fishes temporarily expanded their ranges throughout the estuary. The most frequently captured freshwater fishes during the 1997–1998 El Niño were the freshwater catfish, *P. nigribarbis*, and the characids, *A. eigenmanniorum* and *O. jenynsii*. These species normally inhabited rivers and the uppermost reaches of Patos Lagoon >50 km from the estuary's mouth. Freshwater fishes either migrated or were transported into the estuary by strong freshwater outflow, and some species, such as *P. nigribarbis*, were even captured in adjacent coastal habitats (Garcia et al., 2001). With the return of the usual saltwater intrusion from coastal waters after the 1997–1998 El Niño, freshwater species gradually declined in the estuarine system. This gradual reduction probably was caused by mortality, directly or indirectly associated with physiological stress.

Overall, species evenness index ($E4$) demonstrated a high fish dominance pattern (mean values usually between 0.70 and 0.85) because a few dominant estuarine-resident and estuarine-dependent species (e.g. *A. brasiliensis* and *M. platanus*) remained largely dominant throughout the study. Estuarine fish assemblages, worldwide, typically are dominated by relatively few species (Day, Hall, Kemp, & Yañez-Arancibia, 1989; Kennish, 1990; Whitfield, 1996). However, there was a slight decrease in dominance during 2 months of the El Niño event (November and January), when the decrease in abundance of the dominant fishes coincided with the increase in freshwater fishes.

4.3. Post-El Niño recovery

River flow into estuaries influences not only salinity, but also the export of both macrodetritus (particulate organic matter, POM) and fine POM (FPOM), which can change the biochemical properties of water (Whitfield, 1999). In the Patos Lagoon estuary, interannual chlorophyll *a* oscillation depends on rainfall patterns

in the drainage basin. Phytoplankton biomass and production peaks in the estuary are strongly correlated with high inputs of dissolved inorganic and particulate nitrogen after elevated rainfall. High precipitation in southern Brazil associated with El Niño events is followed by increased estuarine phytoplankton biomass and production (Abreu, Odebrecht, & Gonzalez, 1994; Ciotti et al., 1995; Proença, Hama, & Odebrecht, 1994). Therefore, higher coastal marine and estuarine primary production associated with El Niño may explain the high abundance of resident and marine species following the 1997–1998 event, especially during the second year after the phenomenon.

This production-enhancement hypothesis is corroborated by findings from other estuaries and marine coastal areas. In the St Lucia estuary (South Africa), the density of the estuarine-resident, filter-feeding *Gilchristella aestuaria* (Clupeidae) increased 15-fold during the months immediately following a flood, which could be indirectly linked to greater food resource availability in the form of phytoplankton and zooplankton blooms that followed the flood (Martin, Cyrus, & Forbes, 1992). Livingston et al. (1997) showed that river discharge seems to be the key element controlling food-web structure and dynamics in Apalachicola Bay, Gulf of Mexico. In this system, phytoplankton and benthic algal production respond rapidly to changes in discharges; higher trophic levels respond over a 1–2 years period. The most important influence of freshwater outflow on primary producers was inferred to be changes in water transparency that influenced the relative importance of planktonic vs. benthic primary production.

Others factors could have a synergistic effect on fish abundance in the Patos Lagoon estuary. After the abrupt termination of the 1997–1998 El Niño, cold La Niña conditions were observed in the eastern equatorial Pacific (Mcphaden, 1999a). Cold ENSO episodes cause drought in southern Brazil, Uruguay, and northeastern Argentina (Philander, 1990). During La Niña events, nutrient-rich salt water enters the Patos Lagoon estuary and enhances phytoplankton production (Abreu, Hartmann, & Odebrecht, 1995). Thus, recycling of nutrients in alluvial sediments combined with intrusion of nutrient-enhanced marine water could have stimulated primary production in the Patos Lagoon estuary in 1999–2000. This high production would have stimulated the growth and survival of estuarine-resident and estuarine-dependent fishes, a pattern especially apparent during the second year after the 1997–1998 El Niño.

Other studies have reported rapid recovery of populations and species assemblages after the 1997–1998 El Niño. During this event, Davis (2000) observed several changes in a tidepool fish assemblage in California. The abundance of species that were normally dominant declined during the El Niño event. This decrease was largely attributed to low numbers of larvae recruiting

from the plankton, which may have permitted species that were usually rare to become abundant during the El Niño. However, assemblage changes were not persistent, with the assemblage returning to pre-El Niño conditions almost immediately after the El Niño.

5. Conclusions

The ENSO results in cascades of cause and effect over a broad hierarchy of spatial scales ranging from regional macroclimatic patterns to responses of individual organisms to variation in microhabitats. In southeastern Brazil, high precipitation associated with 1997–1998 El Niño phenomenon significantly affected the hydrology, water quality, and fish assemblages of the Patos Lagoon estuary. Some of the strongest assemblage patterns were clearly caused by species' direct responses to changes in salinity and freshwater outflow, both inside and outside the estuary. The observed increase in freshwater fishes within the estuary was perhaps predictable. However, the reduced abundance of several important estuarine-dependent and marine species with broad physiological tolerances was not predicted. The complex life cycles of these species involves movement among multiple coastal habitats during specific stages of development. The greater freshwater outflow during El Niño probably resulted in greater water-current velocity and vertical mixing at the estuary mouth, and reduced salinity in the marine coastal area. These changes in and around the mouth of the estuary may have transported many estuarine-residents and freshwater species out the estuary, and obstructed the movement of early life stages of estuarine-dependent fishes into the estuary. El Niño-associated changes in freshwater discharge from rivers probably affected estuarine productivity as well, with indirect consequences for fish population and assemblage dynamics. The greatest effects of nutrient additions from high freshwater discharge were observed among fishes during the period after the El Niño phenomenon when the estuarine fish assemblage quickly returned to its pre-El Niño state, but with higher abundance of many estuarine-resident and -dependent species. Our study reinforces the general viewpoint that recruitment in most marine coastal fish populations is strongly influenced by interannual climatic and oceanographic variation. The ability to predict population and assemblage dynamics in estuarine systems like Patos Lagoon is strongly contingent on capabilities to forecast ENSO phenomena.

Acknowledgements

We thank Lisiane A. Ramos, for collecting data between August 1996 and August 1997, and numerous colleagues who assisted in the field, especially Marcelo B. Raseira and Daniel Loebmann. We are grateful to

Mark A. Hixon, Clarisse Odebrecht, and two anonymous referees for providing valuable comments, as well as Luis E. Pereira and Marlise Bemvenuti for help with species identification, and Hernan Lopez for assistance with CCA analysis. The Laboratory of Meteorology (Fundação Universidade do Rio Grande) kindly provided precipitation data. The study received financial support from the Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior—CAPES (Brazil), the Conselho Nacional de Desenvolvimento Científico 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).

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