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Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes

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In southern Brazil, cold (*La Niña*) and warm (*El Niño*) episodes of the *El Niño* Southern Oscillation (ENSO) phenomenon cause drought and high rainfall, respectively. The low precipitation and freshwater outflow associated with *La Niña* during 1995–1996 were associated with an increase in the abundance of marine species in the Patos Lagoon estuary. During the 1997–1998 *El Niño*, high precipitation and river discharge were associated with low abundance of marine species in the estuary. ANOVA results showed a higher abundance during *La Niña* than *El Niño* for estuarine resident (RES) and estuarine dependent (DEP) fishes. During *La Niña* catch per unit of effort (CPUE) of RES increased from the marine to estuarine area, but during *El Niño* CPUE increased at the marine area and diminished during summer and autumn in some estuarine sites. DEP fishes had an opposite abundance pattern. During *La Niña*, these fishes were abundant at the coastal marine area and along some estuarine sites, but during *El Niño*, CPUE remained almost the same at the marine area but dropped along some estuarine sites. These different abundance patterns for dominant fish groups yielded a positive interaction between stations and climatic events. With higher river discharge and the consequent decline of dominant euryhaline fishes, such as *Mugil platanus* and *Atherinella brasiliensis*, freshwater species increased in abundance and richness in the shallow waters of the estuary. The ENSO phenomenon influences precipitation and estuarine salinity in southern Brazil and thereby seems to have a strong influence on recruitment, immigration, and emigration dynamics of fish species living within and adjacent to estuarine habitats.

Key words: *La Niña*; *El Niño*; ENSO; fish assemblage; estuary; Patos Lagoon.

INTRODUCTION

The *El Niño* Southern Oscillation (ENSO) is associated with a warming of surface waters that occurs at irregular intervals in the eastern tropical Pacific. A severe ENSO affects not only the Pacific marine environment, but also continental systems worldwide (Trillmich & Ono, 1991). Cold (*La Niña*) and warm (*El Niño*) episodes of ENSO in the Pacific cause drought and abundant rainfall, respectively, in southern Brazil, Uruguay and north-eastern Argentina (Philander, 1990). The intensity of the 1995–1996 *La Niña* was moderate, but the 1997–1998 *El Niño* was, by some measures, the strongest on record, with major climatic impacts felt around the world (McPhaden, 1999). In estuaries and riverine sytems, ENSO can affect salinity, temperature and water circulation

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patterns, disrupting seasonal cycles of primary production (Lehman & Smith, 1991; Ciotti *et al.*, 1995; Yin *et al.*, 1997) and changing fish assemblages and fisheries (Vera & Sanchez, 1997; Swales *et al.*, 1999; Smolders *et al.*, 2000; Sanchez-Velaso *et al.*, 2000).

The ENSO phenomenon seems to influence variability of phytoplankton production and biogeochemical cycles in the Patos Lagoon estuary and adjacent coastal areas in southern Brazil. According to Ciotti *et al.* (1995), highest chlorophyll *a* concentrations in coastal waters of southern Brazil coincide with large freshwater discharge after periods of strong *El Niño* events in the Pacific Ocean.

Shallow waters of the Patos Lagoon estuary are important nursery grounds for several commercially important species (Vieira & Castello, 1996). Thus, it is important to understand the extent to which ENSO phenomena influence recruitment and abundance patterns of juvenile fishes. The aim of this study is to describe relative abundance, size distributions and recruitment patterns of dominant species in shallow waters of Patos Lagoon estuary during the 1995–1996 *La Niña* and 1997–1998 *El Niño* events. The results will be compared with data from the shallow-water fish assemblage of the Patos Lagoon estuary obtained with a similar sampling design during non-ENSO years (Bemvenuti, 1987; Vieira, 1991*a*; Chao *et al.*, 1985).

MATERIALS AND METHODS

STUDY SITE

Patos Lagoon (32° S; 49° W; Fig. 1) is the largest choked lagoon in the world. According to Kjerfve (1986), choked lagoons have a single entrance channel and small ratios of entrance-channel cross-sectional area to lagoon surface area. Patos Lagoon is 10 360 km^2 and connects in its southern extreme to the South Atlantic via a 20 km entrance channel 0·5–3 km in width. Estuarine-dependent and marine organisms that use the estuary for reproduction and feeding enter and leave through this channel (Chao *et al.*, 1985). Physicochemical dynamics of Patos Lagoon estuary are determined by topographical and meteorological conditions, with the tidal range within the estuary limited to low diurnal amplitude (mean=0·47 m). Wind patterns and precipitation in the watershed determine the salinity regime in the estuary (Costa *et al.*, 1988).

The fish assemblage of Patos Lagoon is seasonally dynamic and receives species from both adjacent fresh and marine waters. The estuarine ichthyofauna is composed of *c.* 110 species, but most of them are present in the estuary only for a portion of the year (Chao *et al.*, 1985). Some species, such as *Atherinella brasiliensis* (Quoy & Gaimard) and *Jenynsia multidentata* (Jenyns), remain in the estuary throughout their lives. Many marine fishes use the Patos Lagoon estuary as nursery grounds (Vieira & Castelo, 1996; Garcia & Vieira, 1997). Patos Lagoon and the adjacent coastal area support one of the most important fisheries in the warm-temperate south-western Atlantic. About 3500 artisanal (Reis & D'Incao, 2000) and 3000 industrial fishermen are temporarily or permanently involved in fishing activities in this region (Haimovici *et al.*, 1996).

FIELD SAMPLING

Stations were located in shallow waters (mean depth <1·5 m) because of the inherent limitations of the sampling gear. Station C1 (32°09·654′ S; 52°05·936′ W) was located in a coastal marine area adjacent to Patos Lagoon, and four other stations (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) were located within the estuary (Fig. 1).

Fish were sampled using a 9 m beach seine (13 mm bar mesh in the wings and 0·5 mm in the centre 3 m section) that was pulled to cover an area of *c.* 60 m^2. Five hauls were

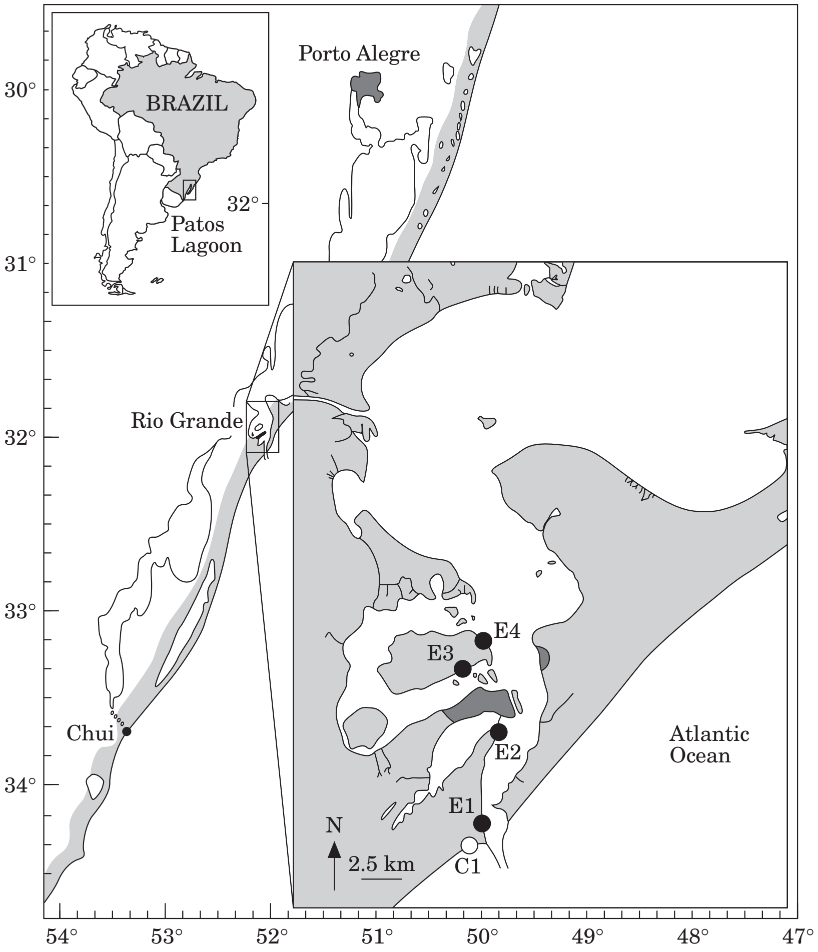

FIG. 1. Patos Lagoon estuary (●) and marine coastal adjacent area (○) studied showing the fixed beach seine stations.

made monthly at each beach station from August 1996 to November 1998. Specimens were preserved in 10% formalin and later identified, counted and measured to the nearest mm. Each month, air and water temperature, water transparency (Secchi disc) and salinity were measured at each station. Also, precipitation was recorded at a local meteorological laboratory (Fundação Universidade do Rio Grande, FURG).

Juveniles <50 mm of the family Clupeidae were not identified to species level. Meristic characters were clearly visible on individuals >50 mm, which were identified as *Brevoortia pectinata* (Jenyns), *Ramnogaster arcuata* (Jenyns) and *Platanichthys platana* (Regan).

DATA ANALYSIS

Several authors have demonstrated that rainfall tends to be above the median in *El Niño* years, and tends to be below in *La Niña* years in southern Brazil (Lau & Sheu, 1988; Ropelewski & Halpert, 1989; Rao & Hada, 1990; Pisciottano *et al*., 1994; Diaz *et al*., 1998; Grimm *et al*., 1998; Kane, 1999). The duration of the 1995–1996 *La Niña* and 1997–1998 *El Niño* (Figs 2 and 3) was estimated from local atmospheric data and the occurrence of ENSO conditions in the eastern tropical Pacific (McPhaden, 1999; Changnon & Bell, 2000).

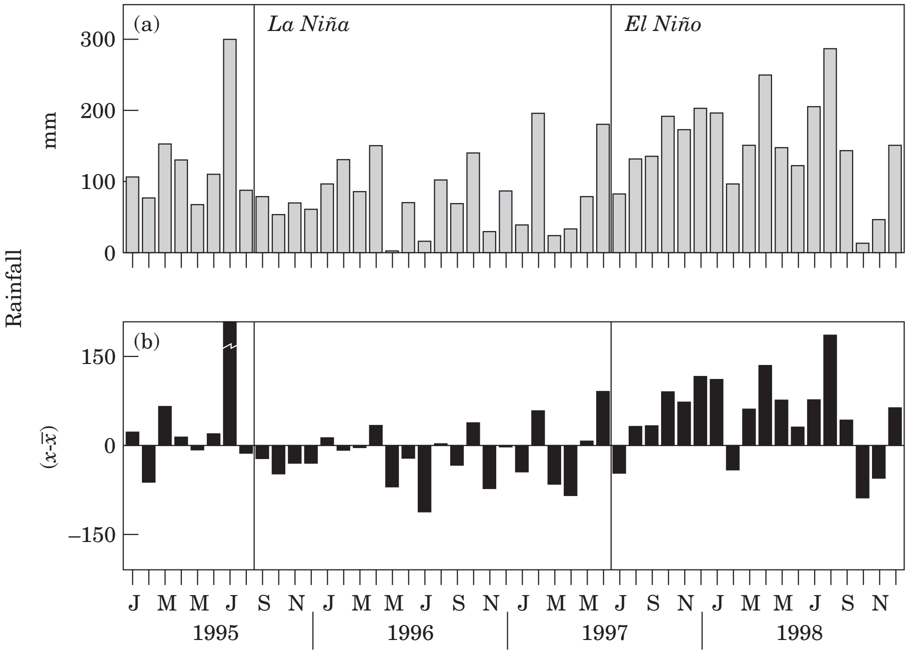

FIG. 2. Monthly rainfall from 1995 to 1998 at Rio Grande city, Patos Lagoon estuary. (a) Monthly rainfall; (b) difference between monthly rainfall (x) from 1995–1998 and mean monthly rainfall ($\bar{x}$) from 11 years (1988–1998). Data recorded from the Meteorological Laboratory, Rio Grande University.

The meteorological effects of the 1995–1996 *La Niña* and 1997–1998 *El Niño* in the Patos Lagoon estuary were revealed by monthly rainfall and salinity patterns between January 1995 and December 1998. This short-term data set was compared with a long-term database of monthly average rainfall from 1988–1998 (11 years) and salinity from 1978–1983 and 1996–1998 (8 years) in the Patos Lagoon estuary. Monthly values (x) from the short-term data set (January 1995 to December 1998) were contrasted with monthly averages ($\bar{x}$) using $x-\bar{x}$.

Based on the life-cycle stages during which marine and freshwater species migrate into the estuary, Vieira & Castello (1996) proposed seven ecological categories for the fishes of Patos Lagoon estuary (estuarine resident, marine dependent, marine opportunistic, marine occasional visitor, anadromous, freshwater opportunistic, and freshwater or tropical marine occasional visitors). This classification was based on a long-term survey carried out with beach seines and trawls (Chao *et al*., 1985). During the present study, only beach seines were employed and the sample area (mean depth <1·5 m) was restricted in the shallow waters of the estuary. As a result, 43·6% of the *c*. 110 fish species known to occur in Patos Lagoon estuary (Chao *et al*., 1985) were captured. For example, the anadromous catfishes *Netuma barba* (Lacepède) and *Netuma planifrons* Higuchi, Reis & Araújo usually inhabit deep regions of the estuary and are rarely caught in shallow waters. Thus, the two *N. barba* specimens captured in the present survey were pooled with the estuarine-dependent group. Considering that some categories were essentially absent in the survey of shallow habitats, Vieira & Castello's seven categories were reduced to the following four: (1) estuarine resident (RES) (typically occurring and breeding in estuaries); (2) estuarine dependent (DEP) (marine or freshwater spawning species found predictably in large numbers in estuaries during certain periods of their life-cycle); (3) marine vagrant (MAR) (typically inhabiting marine environments and rarely occurring in estuaries); (4) freshwater vagrant (FRE) (typically inhabiting freshwater environments and rarely occurring in estuaries).

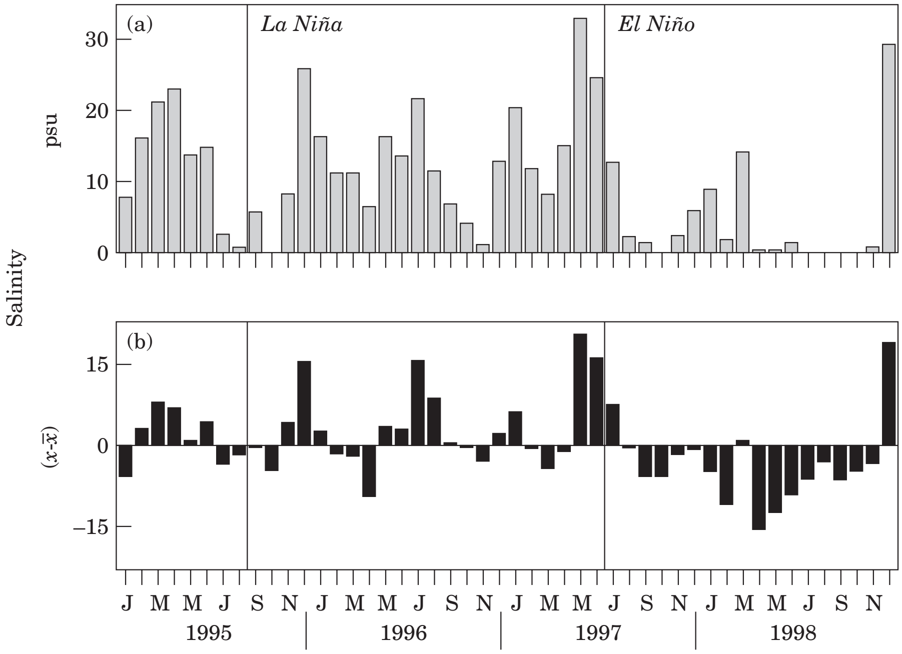

FIG. 3. Average monthly salinity from 1995 to 1998 at Rio Grande city, Patos Lagoon estuary. (a) Monthly average; (b) difference between monthly average (x) from 1995–1998 and monthly average ($\bar{x}$) from 8 years (1978–1983 and 1996–1998).

In order to assess temporal abundance patterns samples were grouped by seasons: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December).

The frequency of occurrence (%) was calculated as the ratio of the number of occurrences of a specie divided by the total × 100. Numerical abundance (%) was calculated as the total abundance (n) of a specie, divided by the total abundance (N) of all species captured × 100. The relative importance (RANK) for each specie was obtained by multiplying numerical abundance by frequency of occurrence.

Biological data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Cochran test and standard deviations-means plots) prior to their use in statistical tests (Underwood, 1997). In all cases where log-transformed data were processed using analysis of variance (three-way ANOVA Model I), the assumptions of normality and homogeneity of variances were met. In order to have a balanced ANOVA design, four seasons were used for each climatic period: *La Niña* (winter–spring 1996, summer–autumn 1997) and *El Niño* (spring 1997, summer–autumn–winter 1998). Newman–Keuls test was used for *post-hoc* comparisons after ANOVA.

In cases where the assumptions of an ANOVA could not be met, a non-parametric Mann-Whitney *U*-test was used. Spearman rank correlation was performed on environmental parameters (rainfall and salinity) and abundance data for each species group. Species abundance catch per unit effort (CPUE), and size (total length, L_T, mm) data were analysed graphically by plotting CPUE (individuals per sample) by L_T. This approach reveals recruitment patterns of the dominant species (Vieira, 1991*a*).

RESULTS

ENVIRONMENTAL PARAMETERS

Comparing the monthly rainfall and salinity with the long-term monthly average of the region revealed two distinct patterns (Figs 2 and 3). Low rainfall coincided with high estuarine salinity between September 1995 and May 1997 which can be attributed to the 1995–1996 *La Niña*. A rainy period associated with low estuarine salinity that occurred between July 1997 and September 1998 can be attributed to the 1997–1998 *El Niño*.

RELATIVE ABUNDANCE AND SPECIES COMPOSITION

RES and DEP fishes were dominant groups and together represented >90% of captures during both climatic events, whereas MAR and FRE occurred in low abundance and were infrequent. Except for FRE, groups showed greater CPUE during *La Niña*. FRE had higher relative abundance and frequency of occurrence during *El Niño* (Table I).

Overall abundance of RES was about five times lower during *El Niño* (13·50 individuals per haul) than *La Niña* (64·03), even though relative importance of this group showed similar values during both climatic events (*La Niña*=43·4%, *El Niño*=43·6%). Dominant fishes in this group were *A. brasiliensis*, *Odonthestes argentinensis* (Valenciennes) and *J. multidentata*. These species were less frequently captured during *El Niño*, and their relative abundance showed large interspecific variation during both climatic periods. Whereas *A. brasiliensis* occupied the same abundance rank during both periods, *J. multidentata*, dropped from fourth to twelfth position during *El Niño*.

CPUE of DEP fishes collectively was about five times lower during *El Niño* (15·40 individuals per haul) than *La Niña* (81·23) (Table I), but the relative importance of this category in both climatic events was similar (*La Niña*, 55·1%; *El Niño*, 49·9%). Dominant DEP species were *Mugil platanus* Günther, *Micropogonias furnieri* (Desmarest), *Mugil curema* Valenciennes and fishes of the family Clupeidae. The three species of mullet showed a distinct abundance pattern in both climatic events. *Mugil platanus* was dominant during *La Niña* and *El Niño*, but during *El Niño*, *M. curema* changed from third to ninth and *Mugil gaimardianus* Desmarest from ninth to fourteenth rank position (Table I).

FRE were more abundant during *El Niño* (n=140; U=1206; P<0·01), with the most important species being *Parapimelodus nigribarbis* (Boulenger) and *Astyanax eigenmanniorum* (Cope). MAR were more abundant during *La Niña* (n=140; U=1306; P<0·01), and *Ulaema lefroyi* (Goode) and *Menticirrhus littoralis* (Holbrook) were the most dominant representatives of this group (Table I).

Correlation between abundance and environmental parameters was similar for both RES and DEP groups. Abundance was significantly negatively correlated with rainfall and significantly positively correlated with salinity. FRE fish abundance was significantly positively correlated with rainfall, and negatively correlated with salinity. MAR fishes revealed opposite trends with rainfall and salinity (Table II).

SPATIAL AND TEMPORAL VARIATION

In general, abundance trends based on individual beach stations were similar to those obtained using pooled data, e.g. a higher abundance for all species groups during *La Niña* than *El Niño*, with the exception of FRES (Figs 4 and 5). During *La Niña* CPUE of RES increased from the marine station (C1) to the estuarine ones (E1 to E4), but during *El Niño* CPUE increased at the C1 station

TABLE I. Number of individuals (*n*), number of individuals per seine haul (CPUE), numerical abundance, frequency of occurrence and relative importance (RANK) of the fishes captured during 1995–1996 *La Niña* and 1997–1998 *El Niño* events. Fishes are classified as estuarine resident, estuarine dependent, freshwater vagrants and marine vagrants

	La Niña					*El Niño*				
	n	CPUE	Numerical abundance (%)	Frequency of occurrence (%)	RANK	*n*	CPUE	Numerical abundance (%)	Frequency of occurrence (%)	RANK
Estuarine-resident (RES)	13 927	64·03	43·44			4438	13·5	43·62		
Atherinella brasiliensis	10 619	48·52	32·92	83·87	1	3256	9·83	31·76	59·52	1
Odontesthes argentinensis	1175	5·40	3·66	36·41	6	1043	3·25	10·50	27·19	4
Jenynsia multidentata	2010	9·55	6·48	32·26	4	43	0·14	0·44	5·14	12
Gobionellus schufeldti	113	0·52	0·35	19·35	10	54	0·16	0·52	9·37	10
Genidens genidens (Valenciennes)						40	0·12	0·38	3·63	13
Syngnathus folletti Herald	10	0·05	0·03	1·84	15	2	0·01	0·02	0·60	23
Estuarine-dependent (DEP)	17 630	81·23	55·12			5060	15·46	49·95		
Mugil platanus	6667	30·83	20·91	59·91	2	1783	5·59	18·06	41·99	3
Clupeidae	2055	9·36	6·35	32·72	5	2150	6·49	20·97	37·16	2
Micropogonias furnieri	345	1·58	1·07	21·66	7	608	1·82	5·89	45·62	5
Mugil curema	8075	37·24	25·27	34·56	3	210	0·64	2·06	6·95	9
Lycengraulis grossidens (Agassiz)	95	0·43	0·29	6·45	11	238	0·71	2·28	25·38	6
Mugil gaimardianus	390	1·77	1·20	13·36	9	42	0·13	0·42	1·51	14
Anchoa marinii Hildebrand						20	0·06	0·19	2·42	15
Paralichthys orbignyanus (Valenciennes)	2	0·01	0·01	0·92	20	5	0·02	0·05	1·51	18
Menticirrhus americanus (L.)	1	0·01	0·01	0·46	22	2	0·01	0·02	0·60	24
Netuma barba						2	0·01	0·02	0·60	25
Freshwater vagrants (FRE)	2	0·01	0·01			656	1·95	6·31		
Parapimelodus nigribarbis						237	0·71	2·30	13·60	8
Astyanax eigenmanniorum						313	0·93	3·00	12·99	7
Oligosarcus jenynsii (Günther)						51	0·15	0·49	9·67	11
Oligosarcus robustus Menezes						19	0·06	0·19	2·42	16
Pimelodus maculatus Lacepède						17	0·05	0·16	1·51	17
Cyphocharax voga (Hensel)						4	0·01	0·04	1·21	19

Table I. *Continued*

	La Niña					*El Niño*				
	n	CPUE	Numerical abundance (%)	Frequency of occurrence (%)	RANK	*n*	CPUE	Numerical abundance (%)	Frequency of occurrence (%)	RANK
Geophagus brasiliensis Kner	2	0·01	0·01	0·92	21	2	0·01	0·02	0·60	26
Crenicichla lepidota Heckel						2	0·01	0·02	0·60	22
Rhamdia spp						3	0·01	0·03	0·60	21
Loricariichthys anus (Valenciennes)						2	0·01	0·02	0·60	27
Hyphessobrycon bifasciatus Ellis						3	0·01	0·03	0·30	30
Hyphessobrycon luetkenii (Boulenger)						1	0·01	0·01	0·30	32
Cnesterodon decemmaculatus (Jenyns)						1	0·01	0·01	0·30	34
Hoplias malabaricus (Bloch)						1	0·01	0·01	0·30	35
Marine vagrants (MAR)	463	2·12	1·47			11	0·04	0·11		
Ulaema lefroyi	353	1·60	1·09	15·67	8					
Menticirrhus littoralis	48	0·23	0·15	7·37	12	2	0·01	0·02	0·60	28
Trachinotus marginatus	22	0·10	0·07	5·99	13					
Citharichthys spilopterus	14	0·06	0·04	3·69	14	3	0·01	0·03	0·60	20
Trachinotus falcatus (L.)	3	0·01	0·01	1·38	19	1	0·01	0·01	0·30	36
Oncopterus darwinii Steindachner	4	0·02	0·01	1·84	17					
Umbrina canosai Berg	8	0·04	0·03	1·38	16					
Prionotus punctatus (Bloch)	3	0·01	0·01	1·38	18					
Trichiurus lepturus L.						2	0·01	0·02	0·60	29
Gobionellus oceanicus (Pallas)	1	0·01	0·01	0·46	23	1	0·01	0·01	0·30	33
Symphurus jenynsi Evermann & Kendall						2	0·01	0·02	0·30	31
Trachinotus carolinus (L.)	2	0·01	0·01	0·46	27					
Eucinostomus argenteus Baird & Girard	1	0·01	0·01	0·46	24					
Epinephelus spp	1	0·01	0·01	0·46	25					
Eucinostomus melanopterus (Bleeker)	2	0·01	0·01	0·46	28					
Diapterus rhombeus (Cuvier)	1	0·01	0·01	0·46	26					
Total	32 022	147·39		28 species		10 165	30·95		36 species	

TABLE II. Spearman correlation and level of significance ($P<0{\cdot}05$) between abiotic factors (rainfall and salinity) and relative abundance of the four species groups. Monthly samples were aggregated by seasons yielding $n=9$ from 1996–1998

	Resident estuarine	Dependent estuarine	Freshwater vagrants	Marine vagrants
Rainfall	− 0·733*	− 0·750*	0·854**	− 0·661
Salinity	0·800*	0·667*	− 0·695*	0·831**

*$P<0{\cdot}05$, **$P<0{\cdot}01$.

and diminished during summer and autumn mainly at the E3 and E4 estuarine sites (Fig. 4). The different abundance pattern of RES fishes along the site stations during both climatic events led to a positive interaction between sites × years (Table III).

DEP fishes had an opposite abundance pattern. During *La Niña*, these fishes were abundant at the coastal marine station (C1) and principally at the E2 and E4 estuarine sites. But, during *El Niño*, CPUE remained almost the same at the C1 station but dropped at the E2 and E4 sites (Fig. 4). The different abundance pattern of dependent fishes along the site stations during both climatic events led to a positive interaction between sites × years factor (Table III).

Vagrant species revealed different patterns. MAR fishes were only abundant inside the estuary during summer and autumn during *La Niña* when salinity was higher, whereas FRE fishes were abundant during spring and summer of *El Niño* when salinity was lower. FRES fishes tended to be most abundant at northern estuarine sites and rarest at the coastal marine station (Fig. 5).

SIZE STRUCTURE

Most estuarine fishes corresponded to immature size classes ranging from 20 to 130 mm L_T. Some species were represented by all size classes (juvenile to adults) in beach seine hauls (*A. brasiliensis*, *J. multidentata*, *Gobionellus schufeldti* Jordan & Eigenmann), but catches of other species were comprised of juveniles and sub-adults (*M. platanus*, *M. curema*, *O. argentinensis*, *M. furnieri*, *Trachinotus marginatus* Cuvier) (Fig. 6).

The size distribution of the RES group was broad, bimodal and dominated (CPUE) by *A. brasiliensis* and *O. argentinensis*. During *El Niño*, *A. brasiliensis* was very abundant in the marine coastal area and seemed to replace *O. argentinensis* [Fig. 6(a)]. DEP fishes had a narrow unimodal distribution dominated by *M. platanus* and *M. curema*. *Mugil platanus* (0+ year class, 20–30 mm) were abundant inside Patos Lagoon estuary during *La Niña*, but not during *El Niño* [Fig. 6(b)].

MAR fishes had different size distributions in the estuary and marine coastal area. Inside the estuary, this group showed a bimodal size distribution that was strongly influenced by *U. lefroy*, whereas in the adjacent coastal marine area, the distribution was more unimodal and dominated by *T. marginatus*. During *El Niño*, abundance of all size classes declined significantly in the marine coastal area [Fig. 6(c)]. FRE fishes had an essentially bimodal distribution dominated

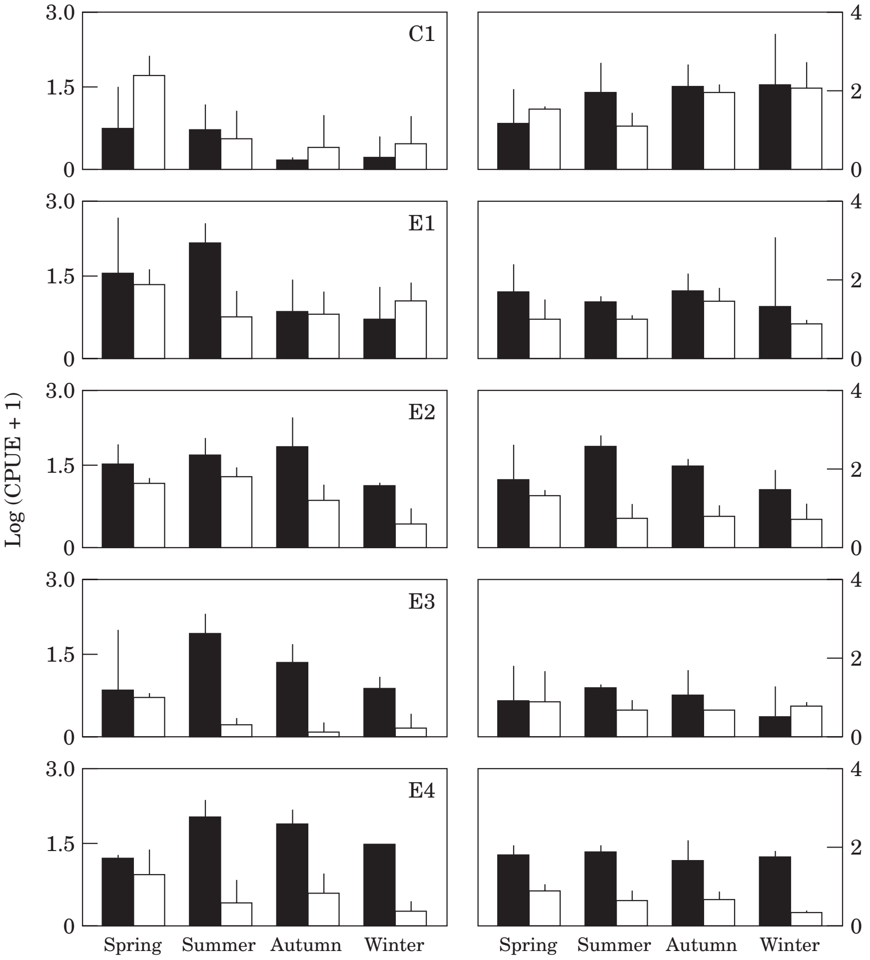

FIG. 4. Log (CPUE+1)+95% CI by season where CPUE is the average number of individuals per seine haul at each station site (C1–E4) and for resident (left column) and dependent (right column) species groups during 1995–1996 *La Niña* (■) and 1997–1998 *El Niño* (□) events.

by juveniles and sub-adults of *A. eigenmanniorum* and *P. nigribarbis*. During the 1997–1998 *El Niño*, sub-adult, *P. nigribarbis*, were captured at the coastal marine station [Fig. 6(d)].

RECRUITMENT OF DOMINANT SPECIES

Atherinella brasiliensis, was less abundant at the E3 and E4 estuarine sites during summer and autumn of the *El Niño*, but this species had higher abundance at the coastal marine station during spring, autumn and winter (Fig. 7, Table IV). Individuals of age 0+ years (20–60 mm L_T) had higher abundance (CPUE) inside the estuary during summer and autumn of the *La Niña*, but their abundance declined during the *El Niño* period (Fig. 8).

Overall, *M. platanus* was less abundant inside the estuary during the *El Niño*, especially at the E2, E3 and E4 estuarine sites (Fig. 7; Table IV). At the coastal marine station (C1) juvenile *M. platanus* (<55 mm L_T) were more abundant

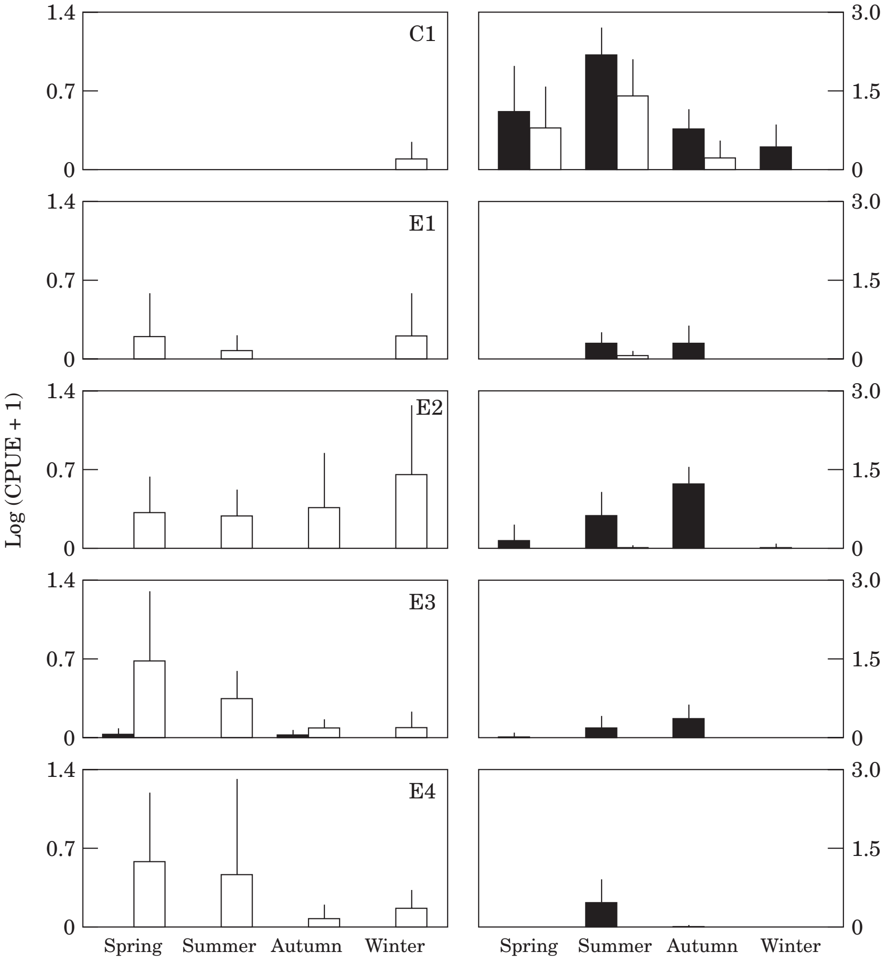

FIG. 5. Log (CPUE+1)+95% CI by season where CPUE is the average number of individuals per seine haul at each station site (C1–E4) and for freshwater (left column) and marine (right column) species groups during 1995–1996 *La Niña* (■) and 1997–1998 *El Niño* (□) events.

during autumn and winter seasons of both *La Niña* and *El Niño*. But within the Patos Lagoon estuary, juveniles become less abundant during *El Niño* (Fig. 9).

DISCUSSION

FRESHWATER DISCHARGE IN THE ESTUARY

By affecting freshwater discharge, salinity and the movement of biota between estuarine and marine coastal areas, 1995–1996 *La Niña* and 1997–1998 *El Niño* episodes strongly influenced ecosystem dynamics in the Patos Lagoon estuary. The high precipitation associated with *El Niño* cause higher freshwater outflow to the continental shelf, increasing the export of nutrients and primary production (Ciotti *et al.*, 1995). During *La Niña*, nutrient-rich salt water enters the estuary and enhances phytoplankton primary production (Abreu *et al.*, 1995).

TABLE III. Results of three-way ANOVA of relative abundance (CPUE) variation of the resident and dependent estuarine fishes. Individual values were $\log_{10}$ transformed

Source	d.f.	SS	MS	*F*	*P*	Newman–Keuls
Resident estuarine						
Years	1	8·39	8·39	54·17	**	*La Niña*>*El Niño*
Sites	4	6·62	1·66	10·70	**	E1=E4=E2>C1=E3
Seasons	3	4·90	1·63	10·56	**	Su=Sp>Au>Wi
Years × sites	4	7·45	1·86	12·03	**	
Years × seasons	3	4·40	1·47	9·48	**	
Sites × seasons	12	3·56	0·30	1·91	*	
Years × sites × seasons	12	2·95	0·25	1·59	0·11	
Dependent estuarine						
Years	1	9·56	9·56	51·73	**	*La Niña*>*El Niño*
Sites	4	10·01	2·50	13·53	**	C1>E4=E1=E2>E3
Seasons	3	0·67	0·22	1·20	0·31	
Years × sites	4	5·15	1·29	6·96	**	
Years × seasons	3	1·77	0·59	3·20	*	
Sites × seasons	12	3·78	0·31	1·70	0·08	
Years × sites × seasons	12	2·10	0·17	0·94	0·50	

The factors are years (*La Niña*, *El Niño*), sites (C1, E1, E2, E3, E4) and seasons (Su, summer; Au, autumn; Wi, winter; Sp, spring). $*P<0·05$, $**P<0·01$. Newman–Keuls' test: $P<0·05$.

Variable freshwater outflow and winds driven by *El Niño* events should influence the survival and growth of juvenile fishes that use estuarine areas as nursery grounds (Yin *et al.*, 1997).

Fish abundance declined in the shallow waters of Patos Lagoon estuary during the 1997–1998 *El Niño*. Higher freshwater outflow caused by *El Niño* seemed to reduce recruitment and survival of fishes in this estuary. Even fishes that dominate shallow marginal waters of the estuary during non-ENSO years (Chao *et al.*, 1985), such as *A. brasiliensis* and *M. platanus,* showed below-average abundance during *El Niño*. The exception was the freshwater group. With the higher freshwater outflow during *El Niño*, some riverine fishes temporally expanded their ranges into the estuary.

ENSO-induced changes in fish assemblage structure have been reported elsewhere. Godínez-Domínguez *et al.* (2000) showed that the 1997–1998 *El Niño* episode altered the normal patterns of seasonal occurrence for estuarine species in Bahía de Navidad, Mexico, as well as there being an unusually high abundance of uncommon species. These authors considered ENSO events to be an interannual driving variable that enhances fish diversity in inshore waters. Davis (2000) noted that elevated sea level and water temperature caused by the 1997–1998 *El Niño* episode in southern California negatively affected recruitment of dominant tidepool species, and positively affected abundance of rare fishes. In pelagic ecosystems, fish larvae can respond in different ways to *El Niño*-induced changes. Sánchez-Velaso *et al.* (2000) observed that *Sardinops caeruleus* (Girard) larvae were almost absent during the 1997–1998 *El Niño* in the Gulf of California, when sea surface temperature increased by 4° C. *Engraulis mordax*

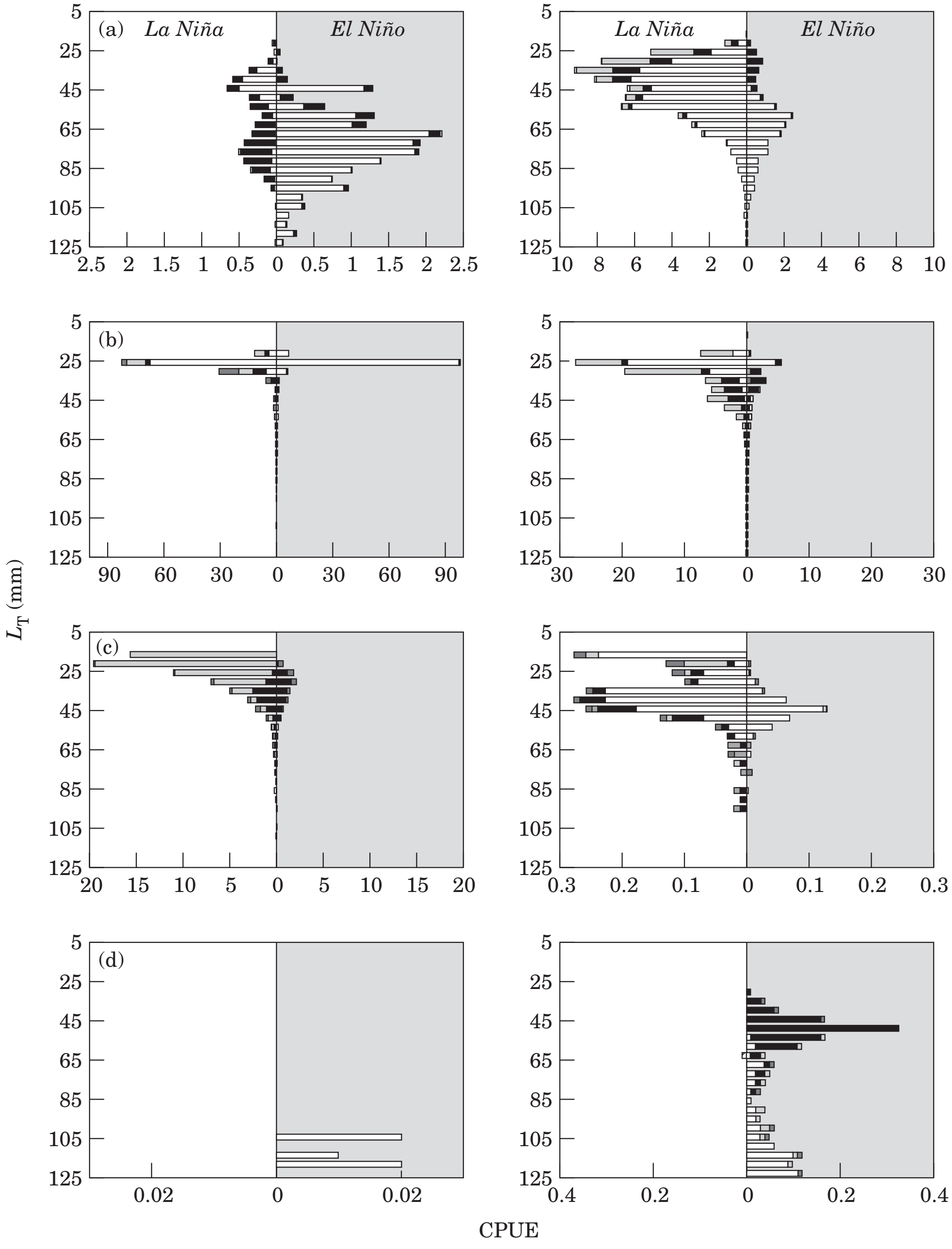

FIG. 6. CPUE (average number of individuals per seine haul) by L_T of the four species groups: (a) estuarine residents, (b) estuarine dependents, (c) marine vagrants and (d) freshwater vagrants in marine coastal (left column) and estuarine (right column) areas during 1995–1996 *La Niña* and 1997–1998 *El Niño* events. (a) □, *Atherinella brasiliensis*; ■, *Odontesthes argentinensis*; ▩, *Jenynsia multidentata*; ▨, *Gobionellus schufeldti*; ▤, others; (b) □, *Mugil platanus*; ■, Clupeidae; ▩, *Mugil curema*; ▨, *Micropogonias furnieri*; ▥, *Lycengraulis grossidens*; ▤, others; (c) □, *Ulaema lefroyi*; ■, *Menticirrhus littoralis*; ▩, *Trachinotus marginatus*; ▨, *Citharichthys spilopterus*; ▤, others; (d) □, *Parapimelodus nigribarbis*; ■, *Astyanax eigenmaniorum*; ▩, *Oligosarcus jenynsii*; ▤, others.

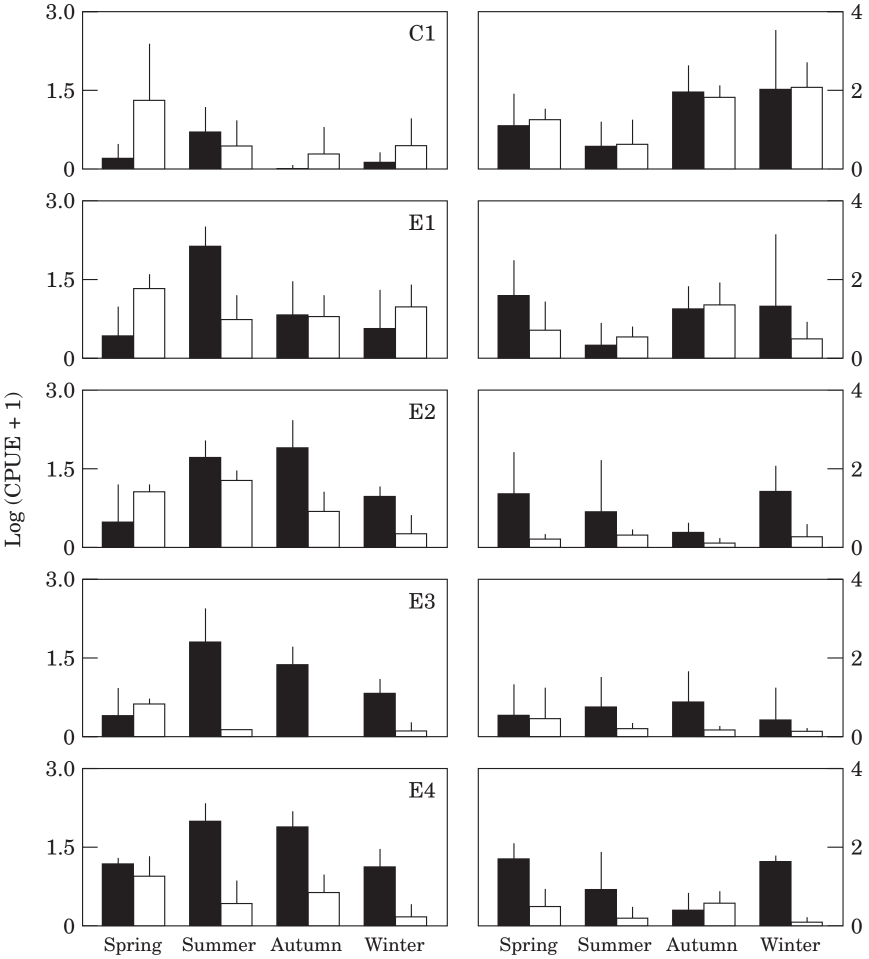

FIG. 7. Log (CPUE+1)+95% CI by season where CPUE is the average number of individuals per seine haul at each station site (C1–E4) for *Atherinella brasiliensis* (left column) and *Mugil platanus* (right column) during 1995–1996 *La Niña* (■) and 1997–1998 *El Niño* (□) events.

Girard larvae were more abundant during the same period, probably because this species better tolerates environmental changes and extremes.

In some regions, *El Niño* events produce droughts, with fish populations of tropical floodplain rivers particularly affected (Swales *et al.*, 1999; Mol *et al.*, 2000; Smolders *et al.*, 2000). According to Mol *et al.* (2000), the stochastic effects of ENSO-associated droughts represent an important non-equilibrium component in the ecology of fish communities in tropical rivers.

The strong salinity gradient and the rapid changes that can occur in temperature, turbidity and other environmental factors pose physiological and ecological challenges for estuarine organisms. Relatively few species can be considered true estuarine residents (Haedrich, 1983; Vieira & Musick, 1993, 1994). In highly dynamic salinity regimes, the elevated energy costs of osmotic stress are offset by abundant food resources and predation refuge in shallow estuarine waters (Day *et al.*, 1989; Kennish, 1990; Santos & Bianchini, 1996). Although overall fish

TABLE IV. Results of three-way ANOVA of relative abundance (CPUE) variation of *Atherinella brasiliensis* and *Mugil platanus*. Individual values were $\log_{10}$ transformed

Source	d.f.	SS	MS	*F*	*P*	Newman–Keuls
Atherinella brasiliensis						
Years	1	4·39	4·39	30·24	**	*La Niña*>*El Niño*
Sites	4	6·24	1·56	10·75	**	E4=E2=E1>E3=C1
Seasons	3	4·84	1·61	11·12	**	Su>Au=Sp>Wi
Years × sites	4	7·52	1·88	12·96	**	
Years × seasons	3	10·53	3·51	24·19	**	
Sites × seasons	12	3·35	0·28	1·92	*	
Years × sites × seasons	12	2·43	0·20	1·40	0·19	
Mugil platanus						
Years	1	6·01	6·01	19·60	**	*La Niña*>*El Niño*
Sites	4	12·44	3·11	10·14	**	C1>E1=E4=E2=E3
Seasons	3	3·68	1·23	4·00	*	Wi=Sp=Au>Su
Years × sites	4	2·64	0·66	2·15	0·08	
Years × seasons	3	1·57	0·52	1·71	0·17	
Sites × seasons	12	9·16	0·76	2·49	**	
Years × sites × seasons	12	3·49	0·29	0·95	0·50	

The factors are years (*La Niña*, *El Niño*), sites (C1, E1, E2, E3, E4) and seasons (Su, summer; Au, autumn; Wi, winter; Sp, spring). *$P<0·05$, **$P<0·01$. Newman–Keuls' test: $P<0·05$.

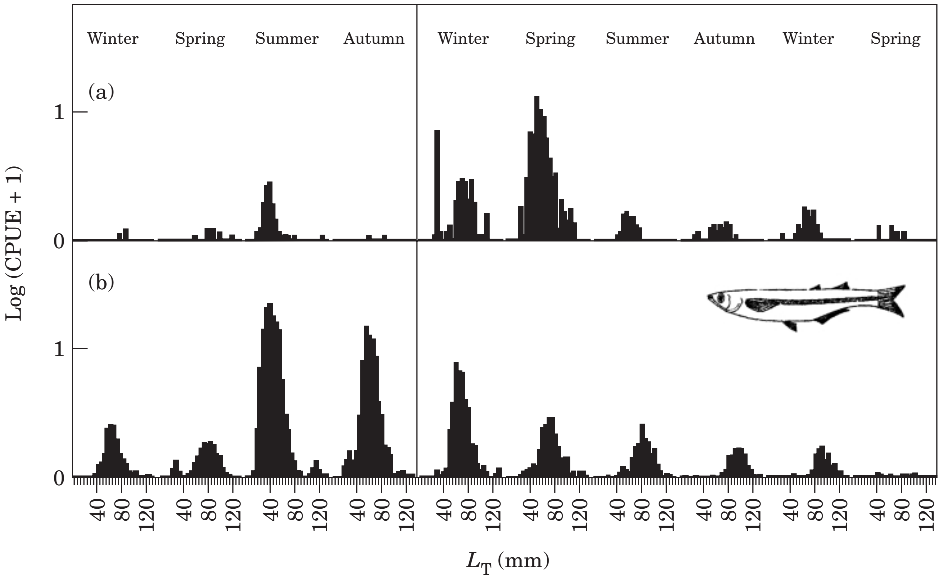

FIG. 8. Seasonal variation in log (CPUE+1) where CPUE is the average number of individuals per seine haul by L_T for *Atherinella brasiliensis* in marine coastal (a) and estuarine (b) areas during 1995–1996 *La Niña* (left column) and 1997–1998 *El Niño* (right column) events.

abundance (CPUE) declined almost five-fold during the 1997–1998 *El Niño*, relative importance of estuarine-resident fishes was similar during the two climatic periods. For example, *A. brasiliensis* remained the dominant species in

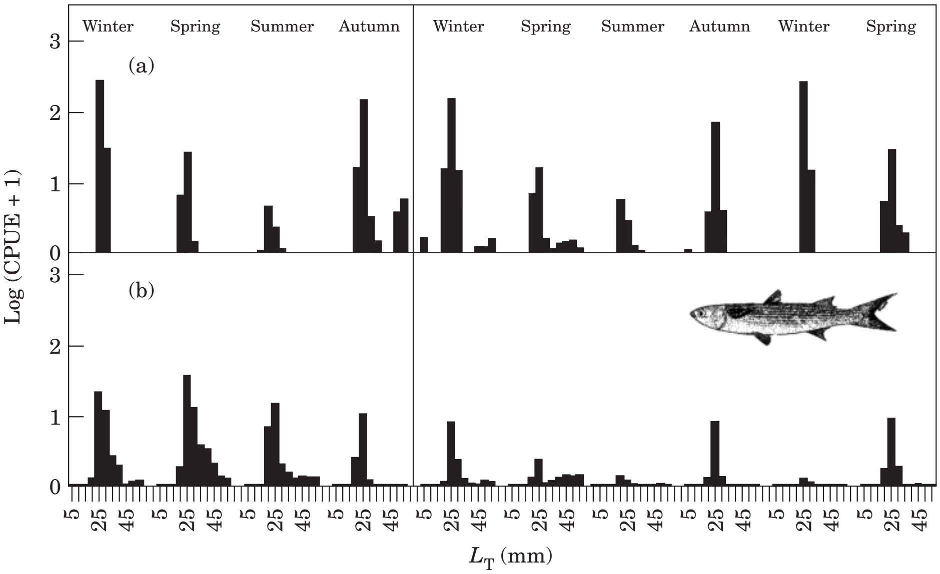

FIG. 9. Seasonal variation in log (CPUE+1) where CPUE is the average number of individuals per seine haul by L_T for *Mugil platanus* in marine coastal (a) and estuarine (b) areas during 1995–1996 *La Niña* (left column) and 1997–1998 *El Niño* (right column) events.

shallow waters of the Patos Lagoon estuary even during the high freshwater outflow associated with *El Niño*, probably a function of its spawning strategy, high mobility and tolerance of extreme salinity fluctuations (Bemvenuti, 1987).

Freshwater outflow in the northern region of Patos Lagoon estuary ranges from 700 to 3000 $m^3\ s^{-1}$. Discharges >3000 $m^3\ s^{-1}$, which frequently occur during *El Niño* events, result in an estuarine plume that extends into the adjacent coastal marine area (Garcia, 1996). A similar pattern can be found in other aquatic systems. Sun & Furbish (1997) showed that *El Niño* and *La Niña* are responsible for up to 40% of annual precipitation variations and up to 30% of river discharge variations in Florida. In this ecosystem, large amounts of fresh water recharge into the estuary in an *El Niño* year and less fresh water recharges into an estuary in a *La Niña* year. Therefore, the annual precipitation and stream discharge amount can be predicted from the sea surface temperature (SST) variation in the tropical Pacific associated with ENSO episodes. Indeed, the projection of the 1997–1998 *El Niño* event reached different rivers located in the tropical and sub-tropical Atlantic. The major river outflows (Amazon, Orinoco and Congo) have strong signatures associated with this ENSO event with plumes of apparently high chlorophyll *a* >10 mg m^{-3} near their deltas (Signorini *et al.*, 1999).

During the 1997–1998 *El Niño*, the estuarine plume seemed to affect fish abundance and assemblage composition in the coastal marine area of the Patos Lagoon estuary. During *El Niño*, estuarine-resident *A. brasiliensis*, were more abundant at the coastal marine site. Even the freshwater catfish *P. nigribarbis*, normally an inhabitant of rivers and upper reaches of Patos Lagoon (>50 km from the estuary's mouth), was captured in the adjacent coastal marine area during *El Niño*. The higher CPUE of estuarine-resident and freshwater-vagrant fishes in the coastal region during 1997 and 1998 suggests that high freshwater discharges associated with *El Niño* transported fishes from the estuary into coastal marine areas.

The role of freshwater discharge in flushing estuarine-resident and freshwater species from estuaries, and obstructing movement of early life stages of estuarine-dependent fishes into estuaries have been documented in other locations. According to Marais (1982), freshwater outflow strongly affects fish populations depending on severity of flooding, configuration of the estuary, and the extent to which normal fish food resources are affected.

In the Gamtoos and Sundays Estuary, South Africa, flood conditions were associated with low salinity and high turbidity throughout the estuary, and were negatively correlated with abundance of mullets (Marais, 1983). Although larvae and juveniles of some estuarine-resident fishes have adaptations to avoid advection into the sea (Whitfield, 1999), extremely high freshwater discharge has the potential to transport any fish species from the estuarine system. For instance, Melville-Smith *et al.* (1981) showed how larvae of estuarine-resident *Gilchristella aestuaria* Gilchrist (Clupeidae) in Sundays Estuary (South Africa) rely on tidal transport to avoid being swept out to sea. The larvae remain in the middle and upper reaches of the estuary where zooplankton and other food resources are most abundant, with marine areas outside the mouth avoided until the juvenile stage. During flood events, the effectiveness of this adaptive behaviour is exceeded, and large numbers of *G. aestuaria* larvae are flushed into the sea.

DOMINANT SPECIES

Atherinella brasiliensis and *M. platanus* are the most abundant fishes in the shallow waters of the Patos Lagoon estuary (Chao *et al.*, 1985). However, the two species have different life history strategies: *A. brasiliensis* completes its entire life cycle inside the estuary (Bemvenuti, 1987), whereas *M. platanus* spawns in the sea and uses shallow waters of the estuary as a nursery ground (Vieira, 1991*b*).

According to Vieira (1991*b*), juvenile *M. platanus* occur year-round in estuarine and adjacent marine habitats of the Patos Lagoon estuary, and the species appear to be well-adapted to large fluctuations in temperature and salinity. The importance of *M. platanus* in the fishery of southern Brazil (Reis & D'Incao, 2000) and the dominance of juveniles in the shallow waters of Patos Lagoon estuary suggest that this ecosystem functions as an important nursery ground (Vieira & Scalabrin, 1991).

Based on data obtained in non-ENSO years, Vieira (1991*b*) proposed the following model to describe the life cycle of *M. platanus* in southern Brazil. Spawning occurs in northern offshore grounds and eggs and larvae drift towards the surf zone by wind-generated surface currents. After they reach *c.* 20 mm L_T, early juveniles gradually migrate to the bottom and begin to feed on benthic microalgae and microfauna. In the surf zone, they move with longshore currents that run southward most of the year, resulting in passive transport toward the mouth of the Patos Lagoon estuary. Once close to the estuary, net upstream circulation at the bottom transports recruits into the estuary where they subsequently disperse into shallow areas.

During the 1995–1996 *La Niña* and 1997–1998 *El Niño*, *M. platanus* recruits (<55 mm L_T) were always abundant in the surf zone adjacent to the mouth of the Patos Lagoon estuary during winter and spring, as predicted by Vieira's (1991*a*) life cycle model. Under the drought conditions caused by *La Niña*, which was characterized by saltwater intrusion into the estuary and lower freshwater discharge, juvenile *M. platanus* moved into the shallow waters of the Patos Lagoon estuary in great numbers. However, during the 1997–1998 *El Niño*, juvenile *M. platanus* did not appear in great abundance in the Patos Lagoon estuary probably due to high freshwater discharge caused by *El Niño*. It is hypothesized that low recruitment of *M. platanus* into the estuary during the 1997–1998 *El Niño* could negatively impact the artisanal fishery that is so heavily dependent on mullets.

Atherinella brasiliensis is a small euryhaline species (maximum 160 mm L_T) that spawns during summer in the shallow waters of the Patos Lagoon estuary. During non-ENSO years, Bemvenuti (1987) showed that *A. brasiliensis* of 0+ years (<70 mm L_T) move toward the estuary's mouth where they remain until they attain *c.* 70–100 mm L_T. During this period, they occasionally migrate in low abundance into marine coastal waters. During spring, sub-adults and adults (>100 mm L_T) migrate towards the northern region of the estuary in preparation for spawning.

The 1997–1998 *El Niño* episode seemed to disrupt the recruitment of juvenile *A. brasiliensis* in the Patos Lagoon estuary. During the 1995–1996 *La Niña*, their recruits were captured in higher abundance than in the 1997–1998 *El Niño* episode. The apparent failure in the recruitment of *A. brasiliensis* during the 1997–1998 *El Niño* might have been caused by the inability of sub-adults and adults to reach the shallow waters in the northern region due to high freshwater discharge along the longitudinal axis of the estuary. High discharges caused by *El Niño* could have transported a large fraction of the *A. brasiliensis* population outside the estuary, and hindered their return to the estuary. Evidence supporting this hypothesis was the unusual abundance, when compared with non-ENSO years (Bemvenuti, 1987), of *A. brasiliensis* at the coastal site during winter and spring of the 1997–1998 *El Niño* period.

Relationships between ENSO-induced environmental changes and abundance fluctuations in fish communities and fisheries have been reported for others coastal areas. Vera & Sánchez (1997) suggested that changes in abundance and composition of fish catches from the coastal shelf off the Nexpa River, Mexico, may depend, in part, on cyclical annual changes associated with the California Current and ENSO episodes. In the south Pacific, Lu *et al.* (1998) showed that recruitment of albacore *Thunnus alalunga* (Bonnaterre) often is low for those generations spawned during ENSO events. Low recruitment appears to be related to lower ocean primary production, spawning success and larval survival during these periods.

It is concluded that the shallow-water fish assemblage of the Patos Lagoon estuary showed different species composition and recruitment patterns of dominant species during the 1995–1996 *La Niña* and 1997–1998 *El Niño* episodes. Low precipitation and freshwater outflow associated with *La Niña* enhanced the entrance of juveniles of marine species into nursery grounds of the estuary. During high precipitation and river discharge associated with *El Niño*, abundance of marine species was significantly lower in the estuary. With higher river discharge and the consequent declined of dominant estuarine fishes, such as *M. Platanus* and *A. brasiliensis*, freshwater species increased in abundance and species richness in the shallow waters of the estuary. Given that some of the species most negatively affected by *El Niño* are important in industrial and artisanal fisheries, ENSO phenomena must be evaluated for future fisheries management. Because ecosystem perturbations caused by ENSO phenomenon can be fully understood only in a broad temporal scale (Grant *et al*., 2000), long-term monitoring is essential.

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