Estuaries Vol. 27, No. 6, p. 905–914 December 2004

Comparison of 1982–1983 and 1997–1998 El Niño Effects on the Shallow-water Fish Assemblage of the Patos Lagoon Estuary (Brazil)

A. M. GARCIA[1,*], P. VIEIRA[1], K. O. WINEMILLER[2], and A. M. GRIMM[3]

[1] *Fundação Universidade Federal de Rio Grande (FURG), Departamento de Oceanografia, Laboratório de Ictiologia, C. P. 474–Rio Grande, RS, Brasil*

[2] *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258*

[3] *Department of Physics, Federal University of Paraná, PR, Brazil*

ABSTRACT: Meteorological impacts of El Niño events of 1982–1983 and 1997–1998 were observed in locations throughout the world. In southern Brazil, El Niño events are associated with increased rainfall and higher freshwater discharge into Patos Lagoon, a large coastal lagoon that empties into the Atlantic Ocean. Based on interdecadal meteorological and biological data sets encompassing the two strongest El Niño events of the last 50 yr, we evaluated the hypothesis that El Niño-induced hydrological changes are a major driving force controlling the interannual variation in the structure and dynamics of fishes in the Patos Lagoon estuary. High rainfall in the drainage basin of the lagoon coincided with low salinity in the estuarine area during both El Niño episodes. Total rainfall in the drainage basin was higher (767 versus 711 mm) and near-zero salinity conditions in the estuarine area lasted about 3 mo longer during the 1997–1998 El Niño event compared with the 1982–1983 event. Hydrological changes triggered by both El Niño events had similar relationships to fish species composition and diversity patterns, but the 1997–1998 event appeared to have stronger effects on the species assemblage. Although shifts in species composition were qualitatively similar during the two El Niño events, distance between El Niño and non-El Niño assemblage multivariate centroids was greater during the 1996–2000 sampling period compared with the 1979–1983 period. We provide a conceptual model of the principal mechanisms and processes connecting the atmospheric-oceanographic interactions triggered by the El Niño phenomena and their effect on the estuarine fish assemblage.

Introduction

The El Niño phenomenon refers to a warming of the tropical Pacific basin in association with a weakening of the trade winds that occur at intervals of 3–7 yr. El Niño events vary in intensity. The 1982–1983 and 1997–1998 El Niño episodes were comparable in magnitude and represented the strongest warming observed since 1950 (Glantz 2001). Meteorological changes induced by El Niño events are felt around the world, with important implications for the dynamics of aquatic ecosystems (Caviedes 2001; Enfield 2001) ranging from coral reefs (Glynn et al. 2001) to upwelling regions (Brodeur et al. 1985; Jiménez et al. 2001; Roy and Reason 2001).

Some authors suggest that recent El Niño events were stronger and more frequent than those in the past (Tudhope et al. 2001). Although predictions cannot be conclusive because they may depend on atmospheric processes that are not well understood, Timmermann et al. (1999) showed that, under a scenario of increasing greenhouse-gas concentrations, El Niño-like conditions would become more frequent. The frequency and intensity of El Niño events and their effects may also be influenced by the phases of interdecadal modes of sea surface temperature variation (Mestas-Nuñez and Enfield 1999, 2001). If El Niño events increase in severity and duration in response to global change, it will become critically important to understand how meteorological and hydrological patterns associated with El Niño events affect ecosystems.

Patos Lagoon (32°S, 49°W) represents an appropriate ecosystem to evaluate how disturbances induced by El Niño can affect the dynamics and structure of fish estuarine assemblages. El Niño episodes have affected the western coasts of the Americas frequently over the last 5,000 yr (Rollins et al. 1986), which coincides with the geomorphologic age (5,000–6,000 yr) estimated for the Patos Lagoon system on the Atlantic coast of southern Brazil (Knoppers and Kjerfve 1999). High rainfall in southern Brazil during El Niño events (Grimm et al. 1998, 2000) increases freshwater discharged

---

* Corresponding author: tele: +55 53/233-6752; fax: +55 53/233-6601; e-mail: amgarcia@mikrus.com.br

© 2004 Estuarine Research Federation

into Patos Lagoon several-fold (Garcia 1996). This lagoon is one of the world's largest coastal aquatic ecosystems (10,360 km^2 with a drainage basin of 201,626 km^2), and its estuarine zone serves as a nursery ground for coastal fishes (Vieira and Castello 1996), including species that support important fisheries in the southwestern Atlantic Ocean (Haimovici et al. 1996; Reis and D'incao 2000).

Previous studies showed that El Niño can affect the primary productivity in the southern Brazilian coastal area and the fish assemblage of Patos Lagoon estuary. The moderate 1987–1988 El Niño increased freshwater discharge into the estuary and coastal marine area, and affected phytoplankton production and biogeochemical cycles in the coastal area (Ciotti et al. 1995; Lima et al. 1996). Garcia et al. (2001) demonstrated that the fish assemblage had opposite trends in fish abundance and diversity between cold (1995–1996 La Niña) and warm (1997–1998 El Niño) ENSO episodes. Based on a larger data set, Garcia et al. (2003a) showed that the 1997–1998 El Niño-induced changes were not highly persistent, with the fish assemblage returning to its pre-El Niño state within 18 mo following the El Niño. Differences in sampling protocols, methods of data analysis, and lack of replication (i.e., more than one El Niño event analyzed simultaneously) hinder efforts to construct predictive models of El Niño effects on the fish assemblage of Patos Lagoon estuary.

Garcia et al. (2001, 2003a) proposed that the high rainfall associated with El Niño events significantly increases runoff and freshwater discharge in the drainage basin of Patos Lagoon, which, in turn, changes salinity patterns within the estuary. This hypothesis was based on rainfall data obtained from a single meteorological station located in the estuarine area (Rio Grande City). Due to the spatial variability of El Niño effects in southern South America (Grimm et al. 2000), there is uncertainty as to whether the rainfall pattern observed at a given station would be an accurate predictor of El Niño-induced changes in rainfall over the entire Patos Lagoon drainage basin.

Based on an interdecadal biological data set encompassing the two strongest El Niño events of the last 50 yr, and an regional rainfall data set that includes 81 sample stations scattered around the drainage basin, we evaluated the hypothesis that El Niño-induced hydrological change is a major driving force controlling interannual variation in the distribution and abundance of fish species in Patos Lagoon estuary. We addressed the following questions in the present study. Did El Niño-induced changes in rainfall and salinity occur with the same magnitude during both El Niño events? Did species composition, abundance patterns, and fish diversity reveal similar trends during both El Niño events? Did rainfall and salinity conditions prior to the onset of the El Niño events influence the magnitude of responses? Based on current findings and those from previous studies, we developed a conceptual diagram showing the main mechanisms and processes linking atmospheric-oceanographic interactions triggered by El Niño phenomena to the fish assemblage structure in Patos Lagoon estuary.

Materials and Methods

STUDY SITE

The southern 10% of Patos Lagoon (250 km long and 60 km wide) has the geomorphologic features of a bar-built estuary, and its upper limnic area (30 km wide) gradually narrows into a channel (700 m wide) connected with the south Atlantic Ocean. Apart from a navigation channel, about 80% of the estuarine zone is less than 2 m deep (Fig. 1). The estuarine ecosystem is a nursery ground for several abundant fish and shrimp species (Vieira and Castello 1996; Reis and D'incao 2000).

Tidal influence in the estuary is minimal (mean tidal amplitude is 0.47 m). Wind and seasonal pulses of freshwater inflow influence patterns of water circulation and salinity (longitudinally and vertically). The lagoon has a drainage basin formed by rivers characterized by a mid latitude flow regime: high discharge in late winter and early spring followed by low to moderate discharge through summer and autumn (Möller et al. 2001). During El Niño events, rainfall in southern Brazil (Grimm et al. 2000) is above average, and the mesohaline zone can be displaced to the inner continental shelf (Möller et al. 2001).

FIELD SAMPLING

Fishes were sampled using a 9 × 1.5 m beach seine (13 mm bar mesh in the wings and 5 mm in the center 3-m section) that was pulled to cover an area approximately 60 m^2. Survey stations were located in shallow waters of the Patos Lagoon estuary (Fig. 1). The number of survey stations varied between the two sampling periods, with four to six survey stations during 1979–1983 and four during 1996–2000. Each sample was composed of three beach seine hauls. Seven samples (21 hauls) were made during each season within two periods: winter 1979 to spring 1983 (the one exception was summer 1983 with 15 hauls) and winter 1996 to spring 2000. Samples were grouped by seasons as follows: summer (January–March), autumn (April–June), winter (July–September), and spring (October–December). Salinity was measured monthly at each station, and precipitation was re-

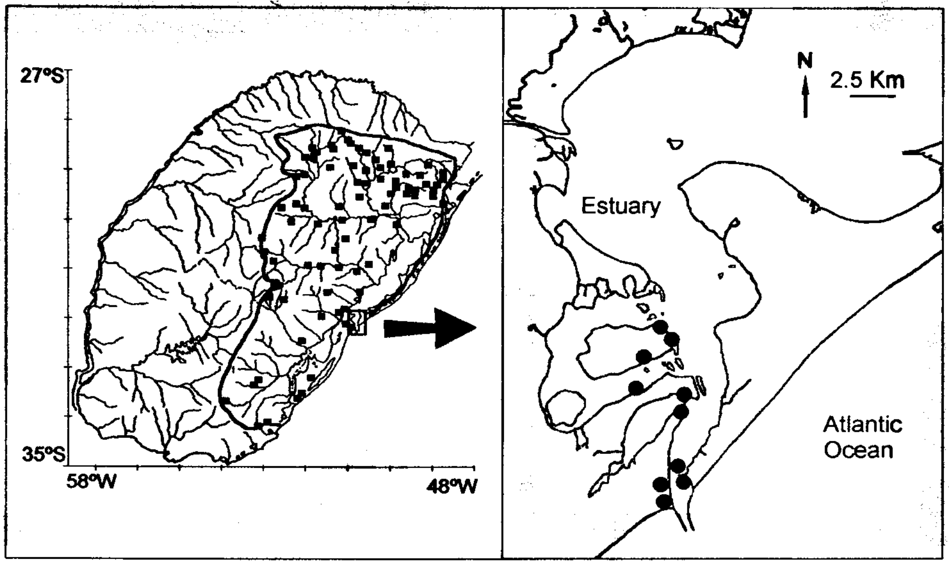


Fig. 1. Drainage basin of the Patos Lagoon (bold line) with the spatial distribution of the 81 meteorological stations (filled squares), and the estuarine area showing beach survey stations (dots).

corded daily at 81 meteorological stations located along the lagoon drainage basin.

DATA ANALYSIS

Environmental Parameters

Meteorological effects of the two El Niño periods on the Patos Lagoon estuary were determined by comparing individual seasonal rainfall and salinity values (winter 1979 to spring 1983 and winter 1996 to spring 2000) with a long-term database of seasonal averages. Seasonal values (x) from the short-term data were contrasted with seasonal averages (μ) using x − μ. Rainfall data were compared with a database of 22 yr (1979–2000) of precipitation in the Patos Lagoon drainage basin. A mean rainfall series for the basin was calculated for this period from the data of 81 stations (Fig. 1). Salinity data were compared with a 10-yr database (1978–1983 and 1996–2000) of monthly values obtained from 10 sample stations located at the Patos Lagoon estuary. Based on the rainfall and salinity distributions and anomalies in Patos Lagoon, we used the following seasons to set the temporal limits of El Niño events: spring 1982 to winter 1983 (1982–1983 El Niño) and spring 1997 to winter 1998 (1997–1998 El Niño).

Diversity Indices

Species richness was calculated by the rarefaction method (Sanders 1968; Hurlbert 1971). This approach provides a standardized measure of species diversity adjusted for the effect of sample size, permitting comparison between assemblages with different densities of organisms or samples obtained with different amounts of effort. Evenness was analyzed by the Evar index proposed by Smith and Wilson (1996), which has equal sensitivity to rare and abundant species. This index converges to one when species abundances are equal. Species diversity was estimated using the Shannon-Wiener index. Variation in diversity, richness, and evenness were analyzed by one-way analysis of variance.

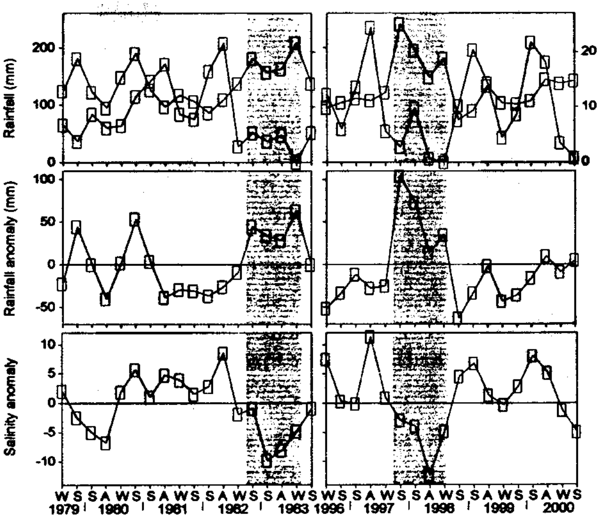
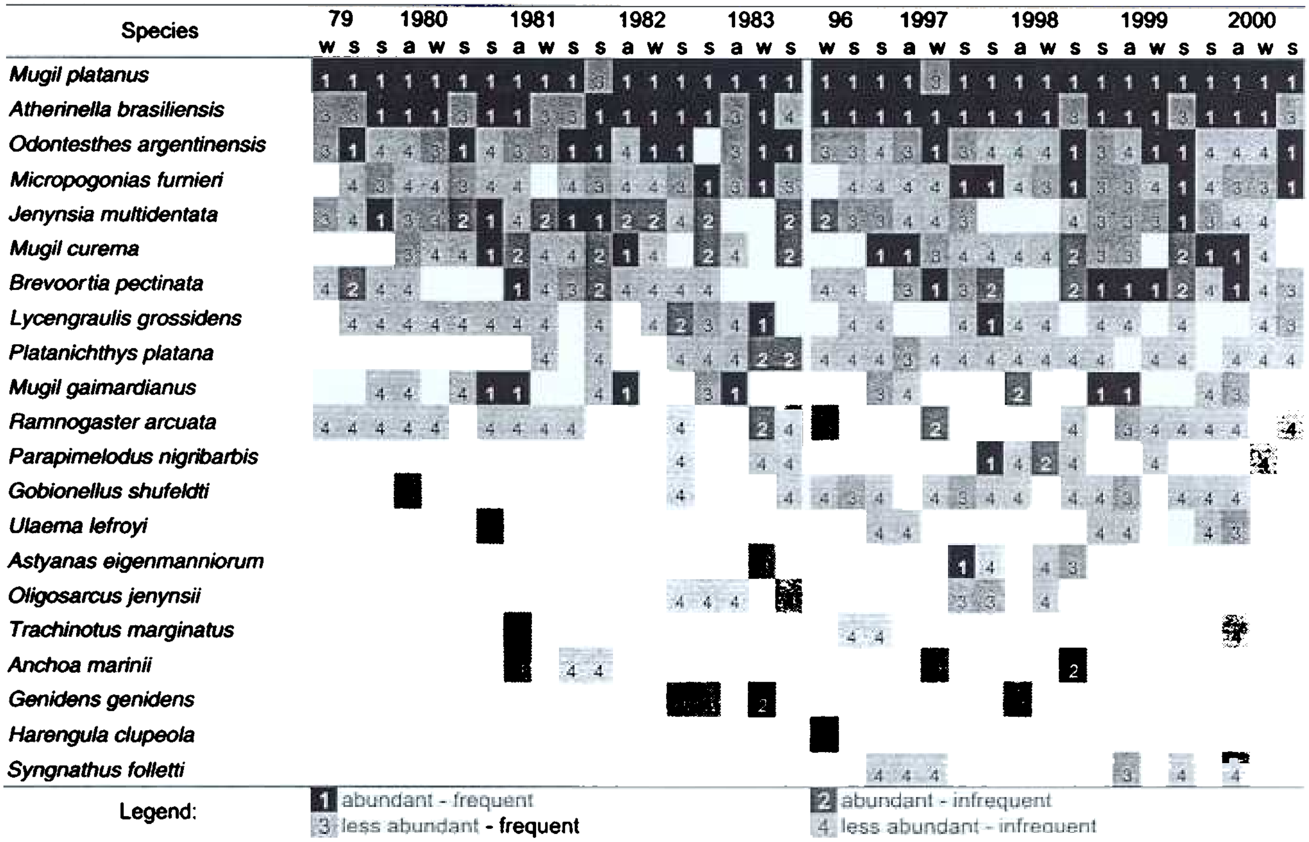


Fig. 2. Seasonal fluctuation in the two sampling periods (1979–1983 and 1996–2000) of average rainfall in the drainage basin of Patos Lagoon and average salinity in its estuarine area, rainfall anomalies, and salinity anomalies. Anomalies represent difference between each seasonal value from 1979–1983 and 1996–2000 and each seasonal long-term average (rainfall: 22 yr from 1979 to 2000 and salinity: 10 yr from 1978 to 1983 and 1996 to 2000). The shaded area represents El Niño periods.

TABLE 1. Relative importance (based on percent numerical abundance and frequency of occurrence) of the most representative fishes captured during the two sampling periods (1979–1983 and 1996–2000). w—winter, s—spring, s—summer, a—autumn. See legend below and details in the material and methods.



Species	79		1980				1981				1982				1983				96		1997				1998				1999				2000			
	w	s	s	a	w	s	s	a	w	s	s	a	w	s	s	a	w	s	w	s	s	a	w	s	s	a	w	s	s	a	w	s	s	a	w	s
Mugil platanus	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1
Atherinella brasiliensis	3	3	1	1	1	3	1	1	3	3	1	1	1	1	1	3	1	4	1	1	1	1	1	1	1	1	1	3	1	1	1	3	1	1	1	3
Odontesthes argentinensis	3	1	4	4	3	1	4	3	3	1	1	4	1	1		3	1	1	3	3	4	3	1	3	4	4	4	1	3	4	1	1	4	4	4	1
Micropogonias furnieri		4	3	4	4	3	4	4		4	3	4	4	3	1	3	1	3		4	4	4	4	1	1	4	3	1	3	3	4	1	4	3	3	1
Jenynsia multidentata	3	4	1	3	3	2	1	4	2	1	1	2	2	4	2			2	2	3	3	4	4	3				4	3	3	3	1	3	4	4	
Mugil curema				3	4	4	1	2	4	4	2	1	4		2	4		2			1	1	3	4	4	4	4	2	3	3		2	1	1	4	
Brevoortia pectinata	4	2	4	4				1	4	3	2	4	4	4	4				4	4		3	1	3	2			2	1	1	1	2	4	1	4	3
Lycengraulis grossidens		4	4	4	4	4	4	4	4		4		4	2	3	4	1			4	4			4	1	4	4		4	4		4			4	3
Platanichthys platana									4		4			4	4	4	2	2	4	4	4	3	4	4	4	4	4	4	4		4	4		4	4	4
Mugil gaimardianus			4	4		4	1	1			4	1			3	1					3	4				2			1	1			4	3		
Ramnogaster arcuata	4	4	4	4	4		4	4	4	4				4			2	4	■				2					4		3	4	4	4	4		4
Parapimelodus nigribarbis														4			4	4							1	4	2	4			4				4	
Gobionellus shufeldti				■										4				4	4	3	4		4	3	4	4		4	4	3		4	4	4		
Ulaema lefroyi							■														4	4							4	4			4	3		
Astyanas eigenmanniorum																	■							1	4		4	3								
Oligosarcus jenynsii														4	4	4		■						3	3		4									
Trachinotus marginatus								■												4	4													4		
Anchoa marinii								■		4	4												■					2								
Genidens genidens														■	■		2									■										
Harengula clupeola																			■																	
Syngnathus folletti																					4	4	4							3		4		4		

Legend:
1 abundant - frequent
3 less abundant - frequent
2 abundant - infrequent
4 less abundant - infrequent

These data met the assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Cochran test). We used the following periods to achieve a balanced design without confounding seasonal samples: spring 1979 to winter 1980, spring 1980 to winter 1981, spring 1981 to winter 1982, spring 1982 to winter 1983, spring 1996 to winter 1997, spring 1997 to winter 1998, spring 1998 to winter 1999, and spring 1999 to winter 2000. El Niño years were represented by spring 1982 to winter 1983 and spring 1997 to winter 1998.

Discriminant Function Analysis (DFA)

Species classified as infrequent and less abundant were omitted to avoid a disproportionate effect of rare species on the DFA. We used the following procedure to sort out rare species. The frequency of occurrence (FO%) for each species was calculated as the ratio of the number of occurrences of a species divided by the total (× 100). The percent numerical abundance (PN%) was calculated as the total abundance (n) of a species, divided by the total abundance (N) of all species captured (× 100). Fishes showing FO% > 50 by season were considered frequent species, whereas fishes showing PN% > the ratio (100/number of species) were considered abundant. These criteria selected 21 fish species (out of 63) as the most representative for use as predictor variables in DFA.

We performed stepwise DFA to select variables (F values of 1 for entry and 0 for removal) that yielded the most significant linear combination for discrimination between groups. Four groups were determined a priori as follows: El Niño and non-El Niño during the 1979–1983 period, and El Niño and non-El Niño during the 1996–2000 period. A tolerance value of 0.01 was used as the criterion for assuming that variables were not redundant (a tolerance value of 0.01 means that the variable is 99% redundant with other variables already included in the model). Data (log relative abundance + 1) were checked for normality (normal probability plots) and homogeneity of variances (Cochran test and standard deviations-means plots) prior to use

TABLE 2. Indices of diversity (Shannon-Wiener, H'), equitability (Evar), and richness (Rarefaction, E[Sn]; adjusted sample equals 155 individuals) calculated for each season during the two sampling periods (1979–1983 and 1996–2000). The bold represents El Niño periods.

Year	Season	H'	Evar	E(Sn)
1979	winter	0.30	0.10	4.42
	spring	0.73	0.49	7.92
1980	summer	0.46	0.09	5.63
	autumn	0.43	0.13	7.41
	winter	0.36	0.10	4.93
	spring	0.69	0.13	8.25
1981	summer	0.61	0.08	6.02
	autumn	0.81	0.18	11.61
	winter	0.32	0.09	4.80
	spring	0.64	0.11	7.48
1982	summer	0.93	0.14	13.16
	autumn	0.76	0.11	8.82
	winter	0.57	0.08	5.79
	spring	**0.67**	**0.20**	**11.54**
1983	**summer**	**0.76**	**0.13**	**10.33**
	autumn	**0.47**	**0.15**	**7.45**
	winter	**0.93**	**0.16**	**11.00**
	spring	0.76	0.11	9.21
1996	winter	0.66	0.13	6.99
	spring	0.58	0.14	8.12
1997	summer	0.44	0.11	7.80
	autumn	0.58	0.11	8.19
	winter	0.72	0.10	7.20
	spring	**0.76**	**0.21**	**12.60**
1998	**summer**	**0.87**	**0.25**	**13.29**
	autumn	**0.63**	**0.18**	**9.05**
	winter	**0.79**	**0.31**	**10.39**
	spring	0.76	0.13	11.04
1999	summer	0.74	0.10	9.62
	autumn	0.71	0.10	8.66
	winter	0.75	0.12	7.19
	spring	0.75	0.11	8.85
2000	summer	0.65	0.10	7.61
	autumn	0.71	0.10	8.98
	winter	0.30	0.16	6.35
	spring	0.70	0.25	9.04

in the analysis. Only a few species did not meet these assumptions, but we retained them in the analysis because DFA is fairly robust to these violations, especially when sample size is large and the design is balanced (Underwood 1997).

Results

Environmental Parameters

Comparison of seasonal rainfall and salinity with long-term seasonal averages revealed similar trends within both sampling periods (1979–1983 and 1996–2000). High rainfall in the drainage basin of Patos Lagoon coincided with low salinity in the estuarine area, which can be attributed to the strong El Niño events of 1982–1983 and 1997–1998. The magnitudes of meteorological (rainfall) and hydrological (salinity) effects differed between the two El Niño events. Total rainfall in the drainage basin was higher (767 versus 711 mm) and near-zero salinity conditions in the estuarine area lasted about 3 mo longer during the 1997–1998 El Niño compared with the 1982–1983 El Niño (Fig. 2). Rainfall was above its historic average across all seasons in both El Niño periods, being particularly strong during spring and summer of the 1997–1998 El Niño. High rainfall anomalies during both El Niño events were preceded by extended periods of below-average rainfall (Fig. 2). In contrast with rainfall trends, salinity was below its historic average across all seasons during both El Niño events, especially during summer and autumn of 1982–1983 and autumn of 1997–1998 (Fig. 2).

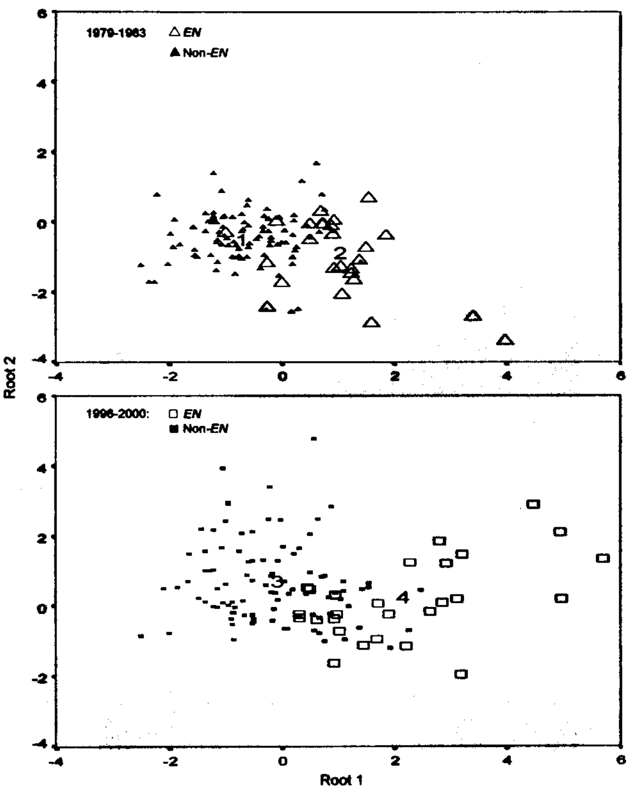


Fig. 3. Scatter plot of the individual scores for the two first discriminant functions (Root 1 and 2) for the two sampling periods 1979–1983 and 1996–2000. Centroid groups are represented as (1) Non-El Niño, (2) El Niño during the 1979–1983 period, (3) Non-El Niño, and (4) El Niño in 1996–2000.

Species Composition and Diversity

A total of 87,901 fishes, representing 63 species, was captured in 750 beach seine hauls made over the study period. Most species, especially marine and freshwater vagrants, had low abundance and frequency in samples. Based on percent numerical abundance and frequency of occurrence, 21 species were identified as the most important assemblage elements (Table 1).

Dominance by a few species was reflected in low

TABLE 3. Summary of the discriminant function analysis (DFA) and canonical coefficient of the predictor variables selected by the stepwise forward method. * $p < 0.01$. Data were $\log_{10}$ transformed.

Axes		2	
Summary statistics for ordination axes			
Eigenvalues	0.821	0.351	0.197
Cumulative percentage variance	60.0	85.6	100.0
Wilks' Lambda	0.340	0.618	0.836
Chi-square	257.0	114.4	42.8
df	54	34	16
Significance	*	*	
Standardized canonical coefficient			
Jenynsia multidentata	−0.525	−0.088	−0.308
Odontesthes argentinensis	−0.502	−0.105	0.154
Mugil platanus	−0.161	0.082	−0.117
Mugil curema	−0.148	0.433	0.025
Mugil gaimardianus	−0.094	−0.411	0.216
Brevoortia pectinata	−0.069	0.434	−0.344
Ulaema lefroyi	−0.016	0.289	0.200
Ramnogaster arcuata	−0.008	−0.160	0.320
Astyanax eigenmanniorum	0.388	0.153	−0.495
Oligosarcus jenynsii	0.312	0.075	−0.148
Parapimelodus nigribarbis	0.280	0.203	−0.148
Atherinella brasiliensis	0.263	0.272	0.324
Lycengraulis grossidens	0.253	−0.369	−0.033
Genidens genidens	0.196	−0.090	0.260
Platanichthys platana	0.057	0.220	0.273
Micropogonias furnieri	0.039	0.015	0.403
Harengula clupeola	0.036	0.246	0.153
Gobionellus shufeldti	0.004	0.267	0.167

values of assemblage evenness (Evar index usually less than 0.15) among survey periods. Evenness tended to increase during El Niño events, with statistically significant higher values observed during the 1997–1998 event ($n = 14$, $F = 10.598$, $p < 0.01$). There was also an increase in the number of species (obtained by the rarefaction method) captured during both El Niño events, with the 1997–1998 episode yielding significantly higher values ($n = 14$, $F = 4.302$, $p < 0.05$; Table 2).

FISH COMPOSITION DURING EL NIÑO VERSUS NON-EL NIÑO PERIODS

Stepwise DFA derived linear combinations of 18 variables (species) to discriminate among the four periods (El Niño and non-El Niño during 1979–1983, and El Niño and non-El Niño during 1996–2000). Three species (*Trachinotus marginatus, Anchoa marinii,* and *Syngnathus folletti*) were redundant (tolerance > 0.01) and eliminated from the data set of 21 dominant species. The two first canonical functions explained 85.6% of the variance, but the first root alone account for 60% and had higher discrimination power (Wilks' lambda = 0.34; Table 3). The distance between El Niño and non-El Niño group centroids along the first axes was greater during 1996–2000 (2.13 to −0.20) than 1979–1983 (1.00 to −0.675). The second root modeled a weak trend of interdecadal differences between 1979–1983 (centroids: −0.43 and −1.00) and 1996–2000 (0.17 and 0.65; Fig. 3).

The three species most associated with non-El Niño conditions (positive canonical coefficients given in Table 3) were *Jenynsia multidentata, Odontesthes argentinensis* (both estuarine residents), and *Mugil platanus* (estuarine dependent; Fig. 4). The three species most associated with El Niño conditions (negative canonical coefficients) were the freshwater vagrants *Astyanax eigenmanniorum, Oligosarcus jenynsii,* and *Parapimelodus nigribarbis* that occurred in the estuarine area almost exclusively during El Niño events (Fig. 5).

Discussion

COMPARING THE STRENGTH OF EL NIÑO EVENTS

Meteorological and hydrological patterns associated with the 1982–1983 and 1997–1998 El Niño events had similar relationships to fish species composition and diversity patterns, but the 1997–1998 event appeared to have stronger effects on the fish assemblage. Evenness values tended to increase during both episodes; this was caused by decreases in number of dominant species and increases in vagrant fishes. Species richness also increased during both El Niño events when several freshwater species expanded their ranges into the estuary, but this difference was only statistically significant during the 1990s. The present interdecadal study, with

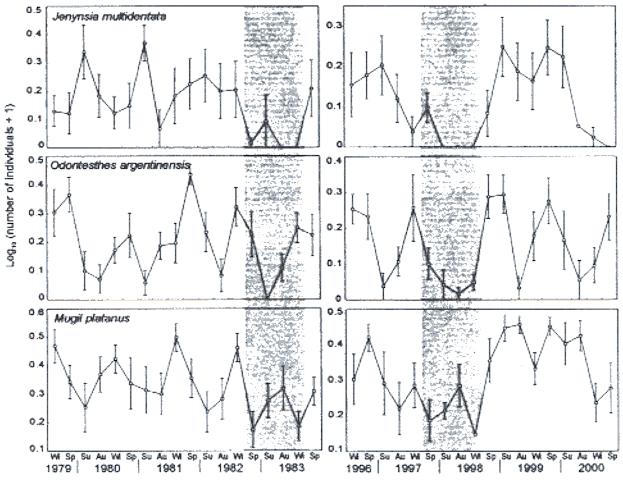


Fig. 4. Seasonal fluctuation in relative abundance of *Jenynsia multidentata, Odontesthes argentinensis*, and *Mugil platanus* in the two sampling periods (1979–1983 and 1996–2000). These species had higher negative standardized coefficient in the first discriminant function (Root 1, see Table 3), showing greater association with non-El Niño periods. The shaded area represents El Niño periods.

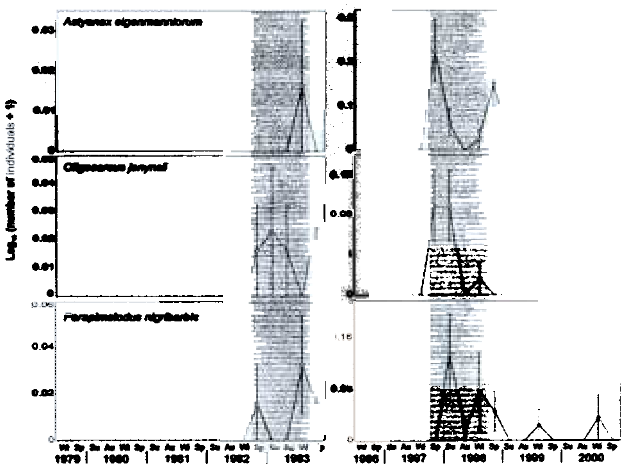


Fig. 5. Seasonal fluctuation in relative abundance of *Astyanax eigenmanniorum, Oligosarcus jenynsii*, and *Parapimelodus nigribarbis* in the two sampling periods (1979–1983 and 1996–2000). These species had higher positive standardized coefficients in the first discriminant function (Root 1, see Table 3), showing greater association with El Niño periods. The shaded area represents El Niño periods.

El Niño replication and regional rainfall data set, seemed to corroborate the hypothesis that positive rainfall anomalies triggered by El Niño events play a major role on the interannual variability of the fish assemblage of Patos Lagoon estuary.

Differences in assemblage structure associated with El Niño events were even more apparent in results from DFA. The distance between El Niño and non-El Niño DFA centroids was greater during the 1996–2000 sampling period compared with the 1979–1983 period. Although shifts in species composition had similar patterns during both El Niño events, the temporal changes in species relative abundances were greater during the 1997–1998 episode. Some freshwater fishes (e.g., the freshwater catfish *P. nigribarbis* and the characins *A. eigenmanniorum* and *O. jenynsii*) were more common during El Niño periods. Freshwater vagrants were only caught in the estuarine area during higher freshwater outflow trigged by the elevated rainfall of El Niño episodes. These species achieved greater relative abundance during the 1997–1998 El Niño than the 1982–1983 El Niño.

Differences in the magnitudes of 1982–1983 and 1997–1998 El Niño effects on the fish assemblage of Patos Lagoon estuary probably result from differences in the intensity of associated salinity anomalies. During both El Niño periods, high rainfall within the drainage basin resulted in unusually low salinity in the estuarine zone, but the 1997–1998 El Niño had a greater effect. The 1997–1998 event was associated with near-zero salinity for a period that lasted 3 mo longer than the low-salinity conditions associated with the 1982–1983 event. Such differences in the magnitude of effects associated with the 1982–1983 and 1997–1998 El Niño events have also been reported from studies of Pacific coastal systems of South America. Sánchez et al. (2000) demonstrated that both events had comparable effects on the coastal marine ecosystem off Peru, although the 1997–1998 produced more extreme conditions. Arcos et al. (2001) showed that the 1982–1983 and 1997–1998 El Niños led to changes in diet and habitat use by jack mackerel (*Trachurus symmetricus murphyi*) off the coast of Chile. These patterns were only evident during moderate to strong El Niño events and little change occurred during weak events.

A Simplified Conceptual Model of El Niño Effects on the Fish Assemblage

A conceptual model summarizes mechanisms and processes associated with El Niño phenomena and their effects on the ichthyofauna of Patos Lagoon estuary (Fig. 6), and synthesizes information scattered within regional literature (Ciotti et al. 1995; Lima et al. 1996; Grimm et al. 1998; Garcia et al. 2003a; Costa et al. 2003).

The warming of the sea surface temperatures in the eastern equatorial Pacific Ocean (shaded area in Fig. 6 no. 1) during El Niño episodes enhances the convection and rainfall in this area, producing anomalous heating in the troposphere. This generates perturbations in the atmospheric divergent Hadley and Walker circulations, as well as anomalous Rossby waves that propagate poleward and

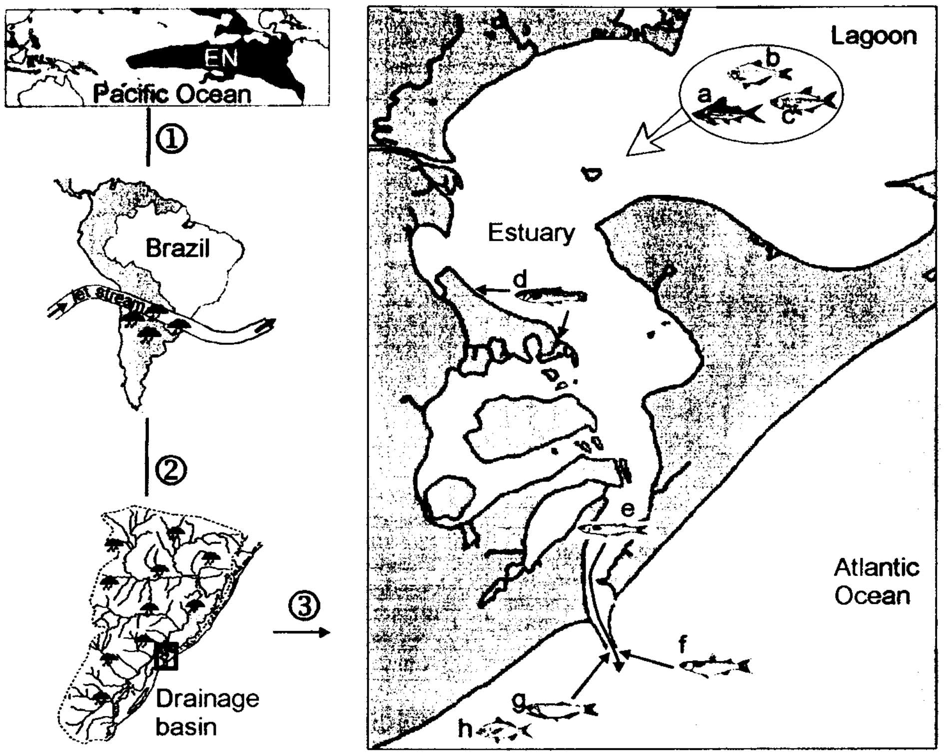


Fig. 6. A simplified conceptual diagram showing the linkages between El Niño events in the Equatorial Pacific Ocean and the estuarine fish assemblage of Patos Lagoon in southern Brazil (see detailed explanation in the Discussion).

eastward. These atmospheric perturbations affect rainfall in southern Brazil especially in austral spring and the next winter. They produce a cyclonic circulation anomaly over southern South America, with an anticyclonic one northeast of this region. These anomalies strengthen the subtropical jet (a belt of strong upper-level westerly winds) and produce a cyclonic vorticity advection over southern Brazil. These aspects favor the intensification of mesoscale systems and cyclogenesis over this region (Grimm el al. 1998, 2000).

The above average rainfall triggered by El Niño events over the large drainage basin (201,626 km^2) of Patos Lagoon greatly increases freshwater outflow into the lagoon (10,360 km^2; no. 2 in Fig. 6). Freshwater outflow in the northern region of Patos Lagoon estuary normally ranges from 700 to 3,000 m^3 s^{-1}. But during El Niño events, discharges > 3,000 m^3 s^{-1} frequently occur and the estuarine plume can extend several kilometers into the adjacent coastal marine area (Garcia 1996; Möller personal communication).

This elevated freshwater outflow affects hydrology, water quality, and the fish assemblage in the estuarine area (971 km^2; no. 3 in Fig. 6). Water levels along the estuarine margin increase, water transparency tends to fall, and near-zero salinity conditions can last for several months (Costa et al. 2003; Garcia et al. 2003b). Freshwater from the middle to upper lagoon expands towards the estuarine zone carrying with them several freshwater fishes (e.g., *P. nigribarbis, A. eigenmanniorum,* and *O. jenynsii*) that spread throughout the estuary, and in some cases, are even caught in the adjacent marine coastal area. This increase in the number of freshwater fishes is the main factor leading to high fish diversity usually associated with El Niño events (Garcia et al. 2003a). High freshwater discharge also decreases the relative abundance of those fishes occurring year-round and breeding in the estuary. Two phenomena seem to explain these trends. Vegetation-affiliated fishes (e.g., *J. multidentata*) have greater access to flooded vegetated habitats in low and mid marshes during periods of high freshwater discharge, and may be less abundant at shoreline sample stations used for seine surveys (dilution hypothesis; Garcia et al. 2004). For other species (e.g., *Atherinella brasiliensis*), pelagic juveniles are transported in large numbers out of the estuary into adjacent marine coastal waters (flushing hypothesis; Garcia et al. 2001). In contrast to estuarine resident fishes, marine species that predictably use estuarine areas as juveniles (e.g., *M. platanus*) or occasional marine visitors (e.g., *A. marinii, Ulaema lefroyi*) enter the estuary in lower numbers during periods of high freshwater discharge. Apparently the high freshwater outflow through the narrow mouth of the estuary (only 700 m wide) impairs physical mechanisms that allow passive movement of these fishes into the estuary (i.e., net upstream movement of high-salinity bottom waters).

Recruitment of marine organisms into nursery areas of Patos Lagoon estuary may be severely curtailed during high freshwater outflow indirectly triggered by El Niño events. Mullet (*M. platanus*) and pink shrimp (*Farfantepenaeus paulensis*), which together sustain the increasingly impoverished artisanal estuarine fishery in this region (Reis and D'incao 2000), are among those estuarine-dependent species that could be negatively affected by sustained, high freshwater discharge (see discussion in Garcia et al. 2003a). The degree of association between fishery catches of adult stocks and juvenile recruitment into the estuary is currently unknown, particularly for the mullet. According to Tyler (1992), management of commercially exploited fish stocks is severely hampered without some understanding of the processes that drive recruitment variability on a long-term basis.

As emphasized by Jaksic (2001), El Niño phenomena provide natural experiments that reveal connections between atmospheric-oceanographic processes and marine biota that may occur on very broad geographic scales. The causal linkages between El Niño phenomena in the South Pacific and the ichthyofauna of Patos Lagoon estuary are an example of complex, large-scale biophysical interactions. Additional ecosystem components (e.g., nutrient dynamics, productivity) need to be added to the model.

ACKNOWLEDGMENTS

We thank researchers and staff from the FURG Ichthyology Laboratory that collected historical data (1979–1983), Lisiane A. Ramos for collecting data between August 1996 and August 1997, and numerous colleagues who assisted in the field. This 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 the SACC/Consortium (CRN-019). Alice Grimm acknowledges the support of Inter-American Institute for Global Change Research (IAI-CRN055) and of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil).

LITERATURE CITED

ARCOS, D. F., L. A. CUBILLOS, AND S. P. NÚÑEZ. 2001. The jack mackerel fishery and El Niño 1998–98 effects off Chile. *Progress in Oceanography* 49:597–617.

BRODEUR, R. D., D. M. GADOMSKI, W. G. PEARCY, H. P. BATCHELDER, AND C. B. MILLER. 1985. Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. *Estuarine Coastal and Shelf Science* 21:365–378.

CAVIEDES, C. N. 2001. El Niño in History: Storming Through the Ages. University Press of Florida, Gainesville, Florida.

CIOTTI, A. M., C. ODEBRECHT, G. FILLMANN, AND O. O. MÖLLER. 1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. *Continental and Shelf Research* 15:1737–1756.

COSTA, C. S. B., J. C. MARANGONI, AND A. M. G. AZEVEDO. 2003. Plant zonation in irregularly flooded salt marshes: Relative importance of stress tolerance and biological interactions. *Journal of Ecology* 91:951–965.

ENFIELD, D. B. 2001. Evolution and historical perspective of the 1997–1998 El Niño-Southern Oscillation event. *Bulletin of Marine Science* 69:7–25.

GARCIA, A. M., M. B. RASEIRA, J. P. VIEIRA, K. O. WINEMILLER, AND A. M. GRIMM. 2003b. Spatiotemporal variation in shallow-water freshwater fish distribution and abundance in a large subtropical coastal lagoon. *Environmental Biology of Fishes* 68: 215–228.

GARCIA, A. M., J. P. VIEIRA, AND K. O. WINEMILLER. 2001. Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. *Journal of Fish Biology* 59:1218–1238.

GARCIA, A. M., J. P. VIEIRA, AND K. O. WINEMILLER. 2003a. Effects of 1997–1998 El Niño on the dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). *Estuarine, Coastal and Shelf Science* 57:489–500.

GARCIA, A. M., J. P. VIEIRA, K. O. WINEMILLER, AND M. B. RASEIRA. 2004. Reproductive cycle and spatiotemporal variation in abundance of the one-sided livebearer *Jenynsia multidentata*, in Patos Lagoon, Brazil. *Hydrobiologia* 515:39–48.

GARCIA, C. A. E. 1996. Hydrographic characteristics, p. 18–20. *In* U. Seeliger, C. Odebrecht, and J. P. Castello (eds.), Subtropical Convergence Environments: The Coastal and Sea in the Southwestern Atlantic, Volume 1. Springer Verlag, Berlin.

GLANTZ, M. H. 2001. Currents of Change: Impacts of El Niño and La Niña on Climate and Society. Cambridge University Press, Cambridge, U.K.

GLYNN, P. W., J. L. MATÉ, A. C. BAKER, AND M. O. CALDERÓN. 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69:79–109.

GRIMM, A. M., V. R. BARROS, AND M. E. DOYLE. 2000. Climate variability in Southern America associated with El Niño and La Niña events. *Journal of Climate* 13:35–58.

GRIMM, A. M., S. E. T. FERRAZ, AND J. GOMES. 1998. Precipitation anomalies in southern Brazil associated with El Niño and La Niña events. *Journal of Climate* 11:2863–2880.

HAIMOVICI, M., J. P. CASTELLO, AND C. M. VOOREN. 1996. Fisheries, p. 183–196. *In* U. Seeliger, C. Odebrecht, and J. P. Castello (eds.), Subtropical Convergence Environments: The Coastal and Sea in the Southwestern Atlantic, Volume 1. Springer Verlag, New York.

HURLBERT, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. *Ecology* 52:577–586.

JAKSIC, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* 24:241–250.

JIMÉNEZ, C., J. CORTÉS, A. LEÓN, AND E. RUIZ. 2001. Coral bleaching and mortality associated with the 1997–98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). *Bulletin of Marine Science* 69:151–169.

KNOPPERS, B. AND B. KJERFVE. 1999. Coastal lagoons of southeastern Brazil: Physical and biogeochemical characteristics, p. 35–66. *In* G. M. Perillo, M. C. Picolo, and M. Pino (eds.), Estuaries of South America: Their Geomorphology and Dynamics, Volume 1. Springer Verlag, Berlin.

LIMA, I. D., C. A. E. GARCIA, AND O. O. MÖLLER. 1996. Ocean surface processes on the southern Brazilian shelf: Characterization and seasonal variability. *Continental Shelf Research* 16: 1307–1317.

MESTAS-NUÑEZ, A. M. AND D. B. ENFIELD. 1999. Rotated global modes of non-ENSO sea surface temperature variability. *Journal of Climate* 12:2735–2746.

MESTAS-NUÑEZ, A. M. AND D. B. ENFIELD. 2001. Eastern Pacific SST variability: ENSO and non-ENSO components and their climatic associations. *Journal of Climate* 14:391–402.

MÖLLER, O. O. J., P. CASTING, J.-C. SALOMON, AND P. LAZURE. 2001. The influence of local and non-local forcing effects on the subtidal circulation of Patos Lagoon. *Estuaries* 24:297–311.

REIS, E. G. AND F. D'INCAO. 2000. The present status of artisanal fisheries of extreme Southern Brazil: An effort towards community-based management. *Ocean & Coastal Management* 43: 585–595.

ROLLINS, H. B., J. B. RICHARDSON, AND D. H. SANDWEISS. 1986. The birth of El Niño: geoarchaeological evidence. *Geoarchaeology* 1:3–15.

ROY, C. AND C. REASON. 2001. ENSO related modulation of coastal upwelling in the eastern Atlantic. *Progress in Oceanography* 49:245–255.

SÁNCHEZ, G., R. CALIENES, AND S. ZUTA. 2000. The 1997–98 El Niño and its effects on the coastal marine ecosystem off Peru. *California Cooperative Oceanic Fisheries Investigations Reports* 41: 62–86.

SANDERS, H. L. 1968. Marine benthic diversity: A comparative study. *The American Naturalist* 102:243–282.

SMITH, B. AND J. B. WILSON. 1996. A consumer's guide to evenness indices. *OIKOS* 76:70–82.

TIMMERMANN, A., J. OBERHUBER, A. BACHER, M. ESCH, M. LATIF, AND E. ROECKNER. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–697.

TUDHOPE, A. W., C. P. CHILCOTT, M. T. MCCULLOCH, E. R. COOK, J. CHAPPELL, R. M. ELLAM, D. W. LEA, J. M. LOUGH, AND G. B. SHIMMIELD. 2001. Variability in the El Niño-Southern Oscillation through a glacial-interglacial cycle. *Science* 291:1511–1517.

TYLER, A. V. 1992. A context for recruitment correlations: Why fisheries biologist should still look for them. *Fisheries Oceanography* 1:97–107.

UNDERWOOD, A. J. 1997. Experiments in Ecology—Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge, U.K.

VIEIRA, J. P. AND J. P. CASTELLO. 1996. Fish fauna, p. 56–61. *In* U. Seeliger, C. Odebrecht, and J. P. Castello (eds.), Subtropical Convergence Marine Ecosystem. The Coast and the Sea in the Warm Temperate Southwestern Atlantic, Volume 1. Springer Verlag, New York.

SOURCE OF UNPUBLISHED MATERIALS

MÖLLER, O. Personal communication. Laboratório de Oceanografia Física, Departamento de Física, Universidade do Rio Grande, CP 474, 96200-200 Rio Grande RS, Brazil.

Received, October 13, 2003
Revised, June 3, 2003
Accepted, June 8, 2004