



Climate-induced year-class fluctuations of whitemouth croaker *Micropogonias furnieri* (Pisces, Sciaenidae) in the Río de la Plata estuary, Argentina–Uruguay

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ABSTRACT

The whitemouth croaker, *Micropogonias furnieri*, is exploited by coastal fisheries in the Plata estuary. Its age structure shows the predominance of certain year classes, which are indicative of recruitment variability. The estuary is affected by river discharge variations associated with climatic signals (El Niño Southern Oscillation and others). We hypothesize that recruitment may correlate: (i) negatively with runoff (low runoff would promote the stronger retention of ichthyoplankton); (ii) positively with temperature (higher temperatures should enhance larvae survivorship and/or expand the spawning season); and (iii) positively with the wind zonal component (stronger onshore winds should facilitate the retention of ich-

thyoplankton). A time series of the relative cohort strengths was constructed for the 1938–2000 period from the age frequencies based on otolith readings. We performed a spectral analysis of the biological and physical series, and we searched for co-movements between them, which suggested the presence of mechanistic links. The results showed co-movements for recruitment, runoff and air temperature series at approximately 6.5, 3.4 and 2.4 yr; the temperature reinforced the runoff effects on recruitment at the 6.5-yr peak, and it weakened them at the 3.4- and 2.4-yr peaks. Wind variability was not relevant for the time scales studied. To explore the mechanisms of retention, we modeled the effects of the runoff fluctuations on the dispersal of the eggs. Both the statistical and modeling results supported the hypothesis that the effects of extreme river discharges on retention may regulate croaker recruitment by promoting high (low) recruitment during low (high) discharge periods.

Key words: El Niño Southern Oscillation, modeling, recruitment, retention, river discharge, time series analysis

INTRODUCTION

It is well accepted that recruitment in most fish populations varies from year to year. Order-of-magnitude differences in year-class success are typical and they constitute a major source of the success and failure of fisheries (Shepherd *et al.*, 1984; Cowan and Shaw, 2002). Fish populations vary in response to fishing and as a response to density-dependent and density-independent processes that determine recruitment, growth and natural mortality (e.g., Rothschild and Shannon, 2004; Bakun, 2010).

The effects of the parental stock size and the subsequent recruitment have been studied for many decades. The two fundamental stock-recruit models are those of Beverton and Holt, which assumes that recruitment constantly increases toward an asymptote with an increasing abundance of spawners (density-dependent mortality may be explained by food competition), and the contrasting model by Ricker, which

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assumes a declining recruitment above a certain spawner population size (the recruitment decline is explained by the cannibalism of the young by the adults) (e.g., Hilborn and Walters, 1992).

Those models, and some variants, have been used to manage fish stocks over the last 50 yr. More recently, the models have been criticized for practical and theoretical reasons; for instance, the abundance of spawners is not directly proportional to the production of eggs. This is because fishing changes the size and age structure of the stocks, which leaves fewer age classes with smaller individuals that have lower relative fecundity, produce lower quality eggs and/or have shorter spawning seasons (e.g., Jakobsen *et al.*, 2009). Another limitation of the stock recruitment models is that they do not account for changing environmental conditions. Although the effects of the abundance of spawners on recruitment cannot be discarded, most of the natural (non-fishing) variability is presumably related to the density-independent effect of the fluctuating environments (Shepherd *et al.*, 1984; Sissenwine, 1984; Bakun, 2010). Many studies that have attempted to link recruitment with environmental conditions have shown significant correlations, but a major shortcoming of those studies is that they are primarily data exploration exercises, and their correlations cannot be viewed as a test of a previously stated hypothesis (Sissenwine, 1984; Hinrichsen, 2009). However, they have been used as a basis for building hypotheses, which facilitates the future development of process-oriented studies (Shepherd *et al.*, 1984).

Hjort (1914) proposed that the variable year-class success is most likely determined during the early life of marine fishes. Since this work was completed, two important corollaries have evolved. The first is that recruitment depends on the match or mismatch of the annual reproductive cycle of the fish and the annual production cycle of the larval fish prey (Cushing, 1975). Most process-oriented research has been focused on the feeding/starvation of larvae (e.g., Cushing, 1975; Lasker, 1975; Rothschild and Osborn, 1988; Platt *et al.*, 2003). The second corollary is that recruitment depends on water dynamics, which maintains pelagic eggs and larvae in or transports them to areas that are suitable for larvae survival. Most marine fishes tend to spawn at specific times and places within predictable and distinct circulation features. Several studies that have investigated the impacts of transportation processes on recruitment have focused on larvae that drift to estuarine nurseries (e.g., Vinagre *et al.*, 2007, 2009).

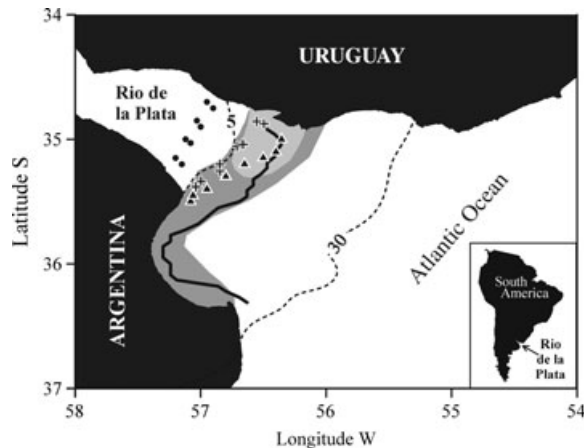
Due to the net seaward movement of estuarine waters, the export of early life-history stages from the

estuaries has been argued to be a major problem for estuarine spawners (Boehlert and Mundy, 1988). This lack of efficient retention mechanisms has been proposed to explain why fishes do not typically spawn inside estuaries (e.g., Dando, 1984; Haedrich, 1992). However, there are evident risks in drifting from marine spawning grounds to nurseries at estuaries, one being the high variability in recruitment strength (e.g., Martinho *et al.*, 2009). Unlike most estuaries, spawning activity is rather common in the Río de la Plata estuary, in which the existence of retention mechanisms has been proposed (Acha *et al.*, 1999; Simionato *et al.*, 2008; Braverman *et al.*, 2009). This ecosystem, which is located at 35°S on the Atlantic coast of South America, is one of the most important estuarine environments in the continent. The reproduction of fish in this area is a very frequent phenomenon, and several species spawn planktonic eggs along its bottom salinity front (Acha *et al.*, 2008 and references).

The whitemouth croaker, *Micropogonias furnieri*, is the dominant species in terms of its biomass in that estuary. This species is the main target of the coastal fisheries of Argentina and Uruguay, and it accounts for approximately 20% of the coastal species catches in Argentina (Carozza *et al.*, 2004). The joint landings by both countries ranged from 49 800 to 56 500 t yr⁻¹ from 2005 to 2009 (<http://www.minagri.gob.ar/site/index.php> and <http://www.dinara.gub.uy>). The species has a long lifespan (up to 39 yr in the region), and its age structure shows the predominance of certain year classes, indicative of recruitment fluctuations, that display variability at periods of between 4 and 7 yr (Carozza *et al.*, 2004). An empirical study that determined statistical relationships between the strength of the cohorts and the Southern Oscillation Index (<http://www.cpc.ncep.noaa.gov/data/indices>) showed that the spectral composition of both series was similar, and they contained peaks at 5–7-yr intervals (Klippel and Haimovici, 2000).

Whitemouth croakers spawn well inside the estuary at the bottom salinity/turbidity front (Fig. 1) (Macchi and Christiansen, 1996; Acha *et al.*, 1999), which is where their larvae are retained (Braverman *et al.*, 2009). In this way, the reproductive success of *M. furnieri* appears to be linked to the dynamics of the estuarine waters. The estuary is characterized by a semi-permanent salt-wedge regime (Guerrero *et al.*, 1997), its fast reaction to atmospheric forcing (Simionato *et al.*, 2006, 2007, 2010; Meccia *et al.*, 2009), its low tidal amplitude (Simionato *et al.*, 2004) and its weak seasonality in river discharge (Guerrero *et al.*, 1997). At larger temporal scales, however, the system is under the effects of large river discharge variations,

Figure 1. The Río de la Plata estuary. Dashed lines represent spring-summer mean bottom isohalines (redrawn from Guerrero *et al.*, 1997). Thick line represents modal position of the turbidity front (redrawn from Framiñan and Brown, 1996). Light grayed region represents whitemouth croaker (*Micropogonias furnieri*) spawning ground (redrawn from Acha *et al.*, 1999). Dark grayed area shows spatial pattern of larvae distribution (redrawn from Braverman *et al.*, 2009). Dots (groups 1 and 2), crosses (groups 3 and 4) and triangles (groups 5 and 6) show the particles' launching positions for low, mean and high runoff conditions, respectively.



which are primarily associated with the El Niño Southern Oscillation (ENSO) cycle (e.g., Depetris *et al.*, 1996; Robertson and Mechoso, 1998). During El Niño events, an excess of rainfall was observed in the Plata basin, and a shortage was observed during La Niña years, which produced positive and negative discharge anomalies, respectively (Depetris *et al.*, 1996; Robertson and Mechoso, 1998). Winds in the area also show a strong interannual variability (Simionato *et al.*, 2005) and a portion of this variability has been related to the ENSO cycle (Meccia *et al.*, 2009). These data led us to hypothesize that the ENSO-related and other climatic signals may drive recruitment variability through river discharge fluctuations and/or wind interannual variability that act upon the retention mechanisms for eggs and larvae. As an alternative, we hypothesized that the water temperature changes were linked to climate variability, which may affect the growth, and consequently the survivorship, of the larvae, or it may act on the adults, affecting the extent of the reproductive season.

To investigate the degree to which the observed variability of the fish recruitment could be attributed to the interannual variability in the runoff, wind and/or temperature, we compiled information on the ages of individuals based on otolith ring counts. A series of cohort strengths (age distribution within the

population) was constructed for the period from 1938 to 2000 and compared with the historic hydrological, wind and air temperature records. Different spectral analysis methods were employed to study the relationship between the recruitment and climate variability of those series.

Finally, to explore qualitatively the mechanisms that were involved in the retention processes, we modeled the effects of the runoff fluctuations on the dispersal of the eggs. We performed a set of process-oriented numerical experiments, in which neutral particles that resembled planktonic fish eggs (or early larvae) were released along the probable positions of the frontal zone that resulted from different runoff scenarios, and we tracked them in different wind conditions.

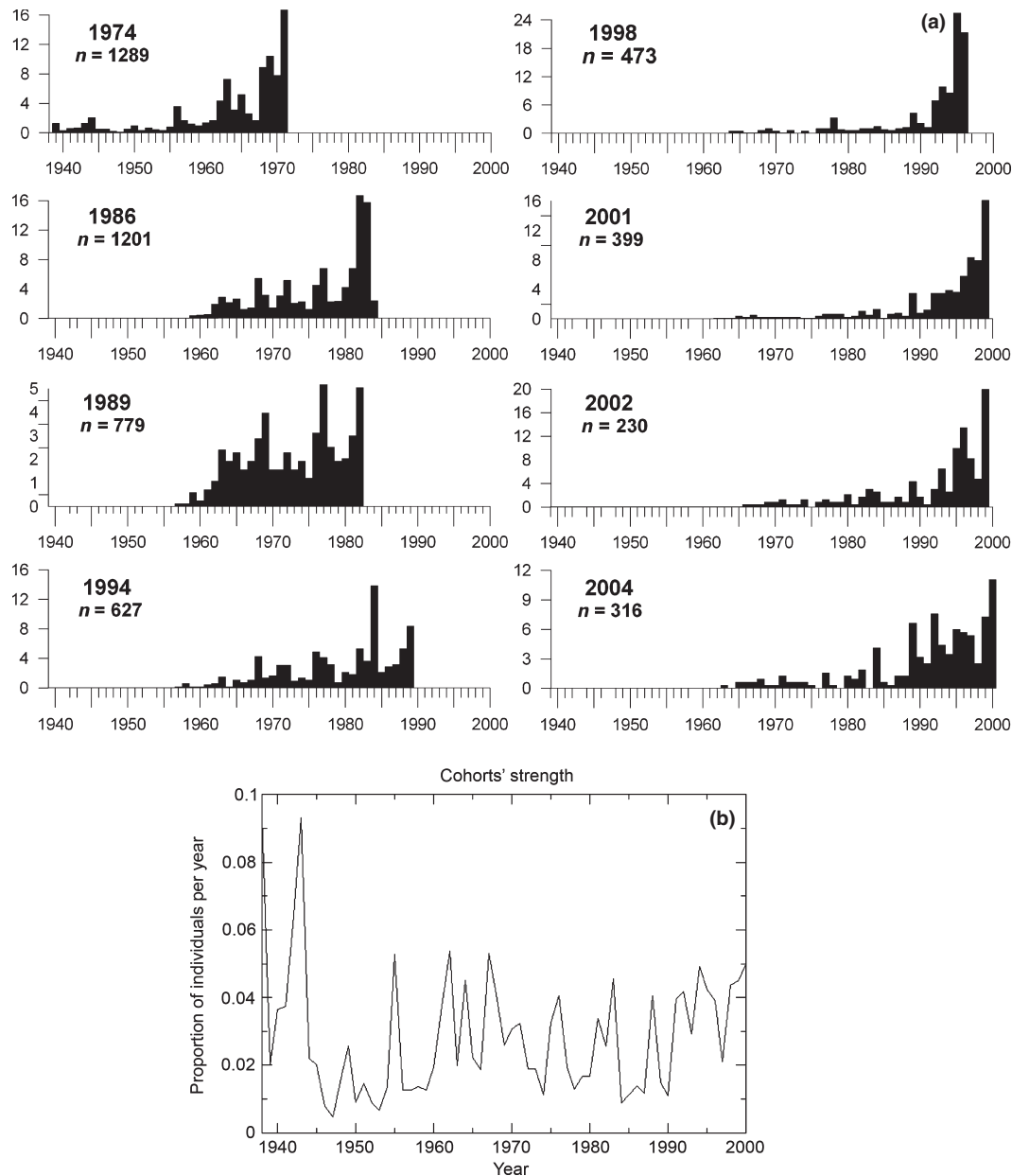
MATERIAL AND METHODS

Data

Four data sources, one of which was biological (the age structure of the fishes) and three of which were environmental (runoff, temperature and wind), were used.

A biological time series for the period from 1938 to 2000 was constructed from age frequencies that were estimated from samples randomly collected in eight different years (1974, 1986, 1989, 1994, 1998, 2001, 2002 and 2004) (Fig. 2a). The age data were provided by the Fish Ageing Lab of the National Institute for Fisheries Research and Development (INIDEP), Argentina. The age estimations were based on the annuli counts from sagittal otoliths of 5314 individuals. Whitemouth croakers were collected during fisheries research cruises in 1989, 1998, 2001, 2002 and 2004, and the commercial fishery in 1986 and 1994. The total length, total weight and sex of the fish were determined and their sagittal otoliths removed. The otoliths were subsequently cleaned and stored dry. The right otoliths were polished to reach the core in the plane of the *sulcus acusticus* (sagittal plane), toasted, and read under a dual discussion microscope (10–15× magnification) with reflected light. Two readers independently aged each otolith, and disagreements were resolved by performing a third reading with both readers. To expand the time series backward, we included data on age structure published by Haimovici (1977). These data were obtained from the commercial fishery during 1974. The otolith sagittae were sectioned along the sagittal plane and polished. The readings were performed under a dissecting microscope with reflected light, two independent readings on each otolith. Only the readings that coincided were considered.

Figure 2. (a) Relative abundances of *Micropogonias furnieri* pseudo-cohorts in different years (1974–2004). (b) Series of cohorts' strengths (proportion of individuals per year) for the period 1938–2000 constructed from data in a.



The youngest individuals considered were 3 yr old, and this age class corresponded to the assumed recruitment. The oldest individuals in the samples were 27–41 yr old. The estimated ages were subtracted from the sampling year to estimate the year class, which is the year during which the individuals were born. The effect of natural mortality was removed to detect the contribution of the older cohorts. The estimates of N_0 (initial number of individuals in the

cohort) were made by assuming an exponential decay model as follows:

$$\text{if } N_t = N_0 e^{-Zt} \quad (1)$$

$$\text{then } \ln N_0 = \ln N_t + Zt \quad (2)$$

where N_t is the number of individuals at time t and Z_t is the instantaneous rate of total mortality. Z_t was esti-

mated from the catch curves (Ricker, 1975) by employing a regression analysis (Zar, 1999). Because there were no age-based mortality estimations for *M. furnieri*, we assumed that M (natural mortality) was constant for the ages from which Z was estimated (the estimations of M ranged between 0.13 and 0.17; Carozza *et al.*, 2004). This procedure was applied to the eight age-frequency distributions and, due to the relatively long life span of the species (approximately 40 yr), several cohorts were repeatedly sampled. Next, the relative strength of each cohort was estimated as the mean frequency that was weighted by the inverse of variance (Fig. 2b). The longevity of the species permitted us to make inferences on a wide time frame; however, the employed methodology may have generated several errors in the age estimations of the older fish.

Because the croaker spawning season lasts from November to April (Macchi and Christiansen, 1996), the analysis of the three environmental data series was limited to that period of the year. The means for that period were calculated for every year to build a 62-yr time series.

The monthly estimates of the Río de la Plata runoff from 1938 to 2000 were provided by the Instituto Nacional del Agua, Argentina. The estimates were based on the discharge series of the Paraná River at Paraná City and of the Uruguay River at Concordia City, which are both located several hundred kilometers upstream of their confluence to the estuary. The estimates considered the propagation time to the head of the estuary and the input of the minor tributaries that are downstream of those cities; the resulting data therefore represent the total runoff to the Río de la Plata estuary at its head (Borús *et al.*, 2008).

No long-term water temperature measurements in the Río de la Plata estuary were available, and the satellite SST observations, which began in the 1980s, are very recent. A series of air temperature readings collected at the Central Observatory of Buenos Aires (COBA), which is located on the southern margin of the upper estuary, covered the period of interest (1938–2000). Because the Río de la Plata estuary is very shallow and almost vertically homogeneous in temperature (Guerrero *et al.*, 1997), the air temperature can be regarded as a proxy for the water temperature. To validate this assumption, we compared the (normalized) SST anomalies at the Plata frontal zone (Reynolds and Smith, 1994; taken from <http://ingrid.ldeo.columbia.edu>) and the (normalized) air temperature at COBA for the period from 1982 to 2000. Although the shortness of the series limited the statistical examination, a cross-spectrum analysis (data not shown) revealed coherence in the cycles of vari-

ability for both series. Moreover, recent results based on direct observations of both variables from an oceanographic buoy anchored in the maximum turbidity zone over the course of more than 1 yr, confirmed the very high coherence of both signals in the seasonal, intra-seasonal and synoptic time scales (Simionato *et al.*, in press). Based on those results and the fact that we are interested in the cycles of variability of the times series, we decided to employ air temperature as a proxy for water temperature.

There were not enough direct observations of the velocity of the winds over the estuary during the analyzed period. Four daily fields of surface wind components from the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalyses (<http://www.cdc.noaa.gov>) were selected as an alternative source. The information consists of a set of gridded data with a spatial resolution of 2.5° (approximately 250 km) and a temporal resolution of 6 h (Kalnay *et al.*, 1996). Discussions regarding their quality over the Southern Hemisphere can be found in Simmonds and Keay (2000) and evaluations of their performance over the Río de la Plata area are presented in Simionato *et al.* (2007). To build a time series that was representative of wind variability in the region, the data were spatially averaged over the area that spanned from 38° to 34°S and 53° to 59°W .

Statistical methods

We analyzed the time series in the frequency domain to highlight the relevant temporal scales of the different physical and biological processes. Because the series were relatively short, we applied independent spectral methods (Multi-Taper Method, MTM, and Singular Spectrum Analysis, SSA) to obtain good estimations of the distribution of the variance of every series in terms of the frequency (or power spectral density) and to verify the results. We first detected significant oscillations of the MTM and SSA. Secondly, we filtered and reconstructed the time series, which included only the meaningful signals (reconstructed components, RCs). Finally, we analyzed the reconstructed series using the maximum entropy method (MEM), which provided a more precise determination of the involved frequencies. Because the series were short (only 63 yr), the MTMs were performed using $p = 2$ (i.e., a bandwidth of $4/63$ cycles per yr) and $K = 3$ (p = half-bandwidth; K = number of tapers). The robust red noise assumption was used, and the adaptive MTM spectra were constructed. The spectra were smoothed with a window of 0.1 cycles per yr, and a red noise model was fitted to the smoothed

spectrum to obtain the curves that were associated with the 50, 90, 95 and 99% confidence levels. The signals were defined as the parts of the spectrum lying above the confidence levels. The SSA were computed for $M = 12$ (M = window width), and the stability of the periodicities found was checked for changes in this parameter. The calculations in this paper used the Toeplitz form of the autocorrelation matrix (Vautard *et al.*, 1992).

Due to the different nature of the variables and to avoid differential effects of their different variance on the results, all the data series were normalized by subtracting the mean and dividing the result by the standard deviation. Therefore, the series and results are expressed in standard deviation units. The statistically significant long-term trends and/or long-period periodicities that could not be resolved due to the series shortness were reconstructed via SSA and subtracted from the original series. The MTM and SSA analyses were then repeated for the detrended series to test the significance of the peaks in the absence of the highly energetic trends. The statistical significance of the SSA pairs was determined by using the Chi-squared and Monte Carlo tests against a red noise hypothesis (Allen and Smith, 1996). The complete descriptions of those methods, their application to geophysical signals and the theory involved can be found in Ghil *et al.* (2002) and the references therein.

We utilized multichannel SSA (M-SSA) for the simultaneous analysis of several variables. The oscillatory pairing criterion was applied to the resulting SSA pairs following Vautard *et al.* (1992). Broomhead and King (1986) proposed the use of M-SSA for multivariate time series, such as those that we analyzed here, based on the context of nonlinear dynamics. This analysis has been applied to many fields, including the intra-seasonal variability of large-scale atmospheric fields (Plaut and Vautard, 1994), and to ENSO for both observed data (e.g., Unal and Ghil, 1995) and coupled general circulation model simulations (Robertson *et al.*, 1995). The four statistical methods were implemented using the SSA-MTM toolkit of Dettlinger *et al.* (1995) and Ghil *et al.* (2002).

We first analyzed the variability of every series independently to identify their significant oscillations. Next, we identified co-movements (i.e., the tendency of two variables to evolve at similar frequencies) by pairing the biological series with each of the physical variables. Finally, we considered the variables all together, and although this methodology may appear to be redundant, given the shortness of the series and the noisy nature of the variables (particularly the biological variable), it provides more confidence in the results.

We have initially hypothesized the existence of the following: (i) a negative correlation between the cohort strength and runoff because a low runoff would promote a stronger ichthyoplankton retention and *vice versa*; (ii) a positive correlation between temperature and cohort strength because higher temperatures should enhance larval survivorship and/or expand the spawning season and *vice versa*; and (iii) a positive correlation between cohort strength and the wind zonal component, because stronger easterly (onshore) winds should facilitate the ichthyoplankton retention and *vice versa*.

The model and settings

We employed the Estuary, Coastal, and Ocean Model (ECOM), a three-dimensional hydrodynamic computer code developed by HydroQual (Blumberg, 1996) for application in marine and freshwater systems. The model domain was set between $58^{\circ}36'W$ to $50^{\circ}W$ and $38^{\circ}30'S$ to $30^{\circ}S$, and the variable horizontal resolution was set between 3.5 and 7.5 km and 10 vertical sigma levels. The finest horizontal resolution was set over the Río de la Plata estuary and its maritime front, where the grid spacing (Δx and Δy) was <4 km. The highest vertical resolution was set near the surface and bottom. The boundary conditions at the sea surface were wind forcing and zero salt and heat fluxes. The initial conditions for the release of the particles (see below) were obtained to initiate the model from rest and to spin it up until the stabilization of the salinity frontal zone at its observed location in the spring–summer (the spawning season) for the mean, high and low continental discharge conditions. Following Simionato *et al.* (2001, 2008), the frontal zone was modeled to be dependent only on salinity. The mean discharge of the Paraná and Uruguay Rivers during the last decades of the 20th century ($25\,000\text{ m}^3\text{ s}^{-1}$) was considered to represent the mean runoff, and the values of $50\,000$ and $10\,000\text{ m}^3\text{ s}^{-1}$ were used as the representative high and low runoff conditions, respectively. After 150 days of integration, the simulations accurately reproduced the salinity patterns when they were compared to the observational results (Guerrero *et al.*, 1997). For more details about the model and the settings, see Simionato *et al.* (2008).

Numerical experiments

Micropogonias furnieri spawns at the bottom salinity front in a stratified region where its eggs remain below the halocline (Acha *et al.*, 1999). Neutral buoyancy particles were launched at the model bottom layer to simulate the dispersion of the planktonic eggs under different runoff conditions and at different spawning

locations (Fig. 1). Groups 1 and 2, which were located upstream, represent spawning areas under low runoff conditions; groups 3 and 4 represent spawning areas under mean discharge conditions, and groups 5 and 6 represent spawning areas under high discharge conditions. The particles were launched along the 5 and 10 isohalines produced by the model with the aim of studying the sensitivity to small changes in the initial position. For groups 5 and 6, because the estuary basin widens and the bottom salinity front is very narrow at the outer area, the launching units were placed along a north–south line that was approximately between Montevideo and Punta Piedras, and we will refer the northernmost regions being represented by group 5 and the southernmost regions by group 6.

The atmospheric circulation in the region is characterized by high wind direction variability in short-time scales, mainly related to the changes from a dominant northerly to a prevailing southerly component over a scale of approximately 3–4 days. Persistent events with dominant easterly or westerly components are much less frequent (Simionato *et al.*, 2005). Following Simionato *et al.* (2008), the modeling strategy was designed to develop short-term simulations in which the effect of the winds from 16 directions (22.5° apart) on the particle advection and dispersion was analyzed. In this manner, 16 different simulations were performed for each of the runoff conditions, which included all six of the groups of particles that were launched in every simulation. The wind speed was set to 6 m s^{-1} , representing the mean and the mode for all of the seasons in the NCEP/NCAR reanalyzed climatology at 35.24°S 54.37°W (Simionato *et al.*, 2008). The wind speed and direction were gradually

changed from their initial spring–summer value on 1 day by applying a linear ramp, and the particles were released after 24 h of the simulation. The particles were tracked over a 3-day period.

Given a particular forcing situation, the launch of the particles facilitated the study of their dispersal due to the dispersive properties of the environment and to advection. To quantify those results, we computed the root mean square distance to the source (RMSDS) of every particle group at the end of the 3-day simulation.

RESULTS

Time series analyses

Significant variability at interannual periods (between 2 and 8 yr) was observed in all four of the analyzed data series. In addition, some of the series exhibited long-term trends and/or variability in decadal time scales (e.g., 31.5 yr in the cohort time series and approximately 26 yr in the wind series).

Cohort strength scales of variability

The MTM analysis identified significant peaks at low frequencies (31.5 yr; 90% confidence) and at bands that were centered at approximately 6 yr (95% confidence), 2.9 yr (95% confidence) and 2.5 yr (90% confidence) (Fig. 3a,b; Table 1).

Reconstructed components (RCs) were calculated using SSA (Fig. 4a–d). The first pair of eigenmodes, which accounted for 39% of the variance, were identified as a trend (Fig. 4a). The next three pairs of eigenmodes, which displayed periodicities of approximately 6.2, 2.6 and 3.6 yr, accounted for almost 55%

Figure 3. (a) Multi-Taper spectrum of the cohorts' strength time series. Thin lines are median, 90, 95, and 99% significance levels against a red-noise null hypothesis. Significant peaks were found at bands around 31.5 yr (90% of confidence), 6 yr (95% of confidence), 3 yr (95% of confidence) and 2.5 yr (90% of confidence). (b) Same for the detrended series.

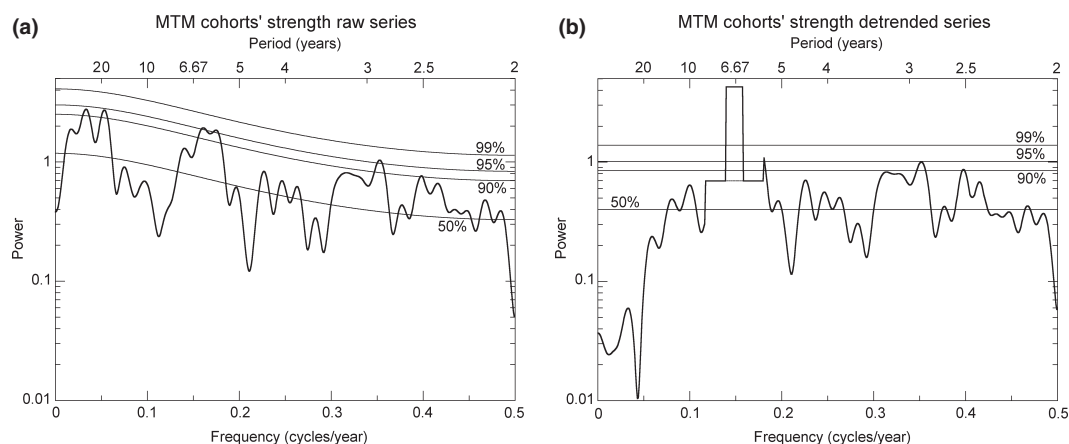


Table 1. Time series analysis.

	Multi-taper method	SSA reconstructed components		
	Significant peaks, Years (%)	Significant peaks, Years (%)	Explained variance (%)	MEM reconstructed components (Years)
Cohorts'strenght	6.9 (95)	6.2 (95)	28.0	6.2
	3.6 (99)	3.6 (80)	9.7	3.6
	2.5 (90)	2.6 (80)	17.0	2.4
Runoff	6.9 (95)	6.8 (95)	16.8	6.3
	3.6 (99)	3.6 (95)	25.7	3.6
	2.5 (90)	2.4 (80)	12.0	2.4
Air temperature	7.6 (90)	8.4 (95)	17.0	8.7
	3.2 (95)	3.4 (95)	21.1	3.4
	2.4 (95)	2.3 (90)	14.0	2.3
Wind	3.5 (90)	3.5 (95)	17.9	3.4

SSA, singular spectrum analysis; MEM, maximum entropy method.

In brackets, confidence level of the estimations.

of the total variance, and they were significant at the 95, 80 and 80% confidence intervals, respectively, based on the application of the Chi-squared and Monte Carlo tests (Table 1). The lower significance levels associated with the last two oscillatory pairs may be attributable to inadequate sampling at the annual resolution and/or the shortness of the series. However, both SSA pairs met the oscillatory pairing criteria, and because their periods corresponded approximately to those found using the MTM, the results of the two independent methods taken together provide strong evidence that those spectral peaks, which were near 2.5 and 3.5 yr, are real. To better determine the frequency of the identified oscillations, MEM was applied to the RCs. This method determined that the three oscillations were located at 6.2, 3.6 and 2.4 yr. The reconstruction of the cohort strength time series in terms of the three RCs (Fig. 4e) was robust in visual terms and accounted for 86.6% of the detrended series variance. Consequently, most of the series variance can be explained in terms of three quasi-oscillations with periods at approximately 6.2, 3.6 and 2.4 yr and a decadal variability component.

Runoff scales of variability

The MTM analysis indicated significant periodicities at approximately 6.9 (95% confidence), 3.6 (99% confidence) and 2.5 yr (90% confidence) and a long-term trend component that accounted for 25% of the variance; this trend was removed via SSA. The SSA revealed three pairs of eigenmodes that accounted for almost 55% of the total variance (72.6% of the detrended series variance), and they were significant at the 80–95% confidence interval based on the Chi-squared

and Monte Carlo tests (Table 1). The three SSA pairs passed the oscillatory pairing criteria, and their periods approximately corresponded to those that were found using MTM, which suggests that the spectral peaks are robust. The MEM of the RCs located the peaks at 3.6, 6.3 and 2.4 yr.

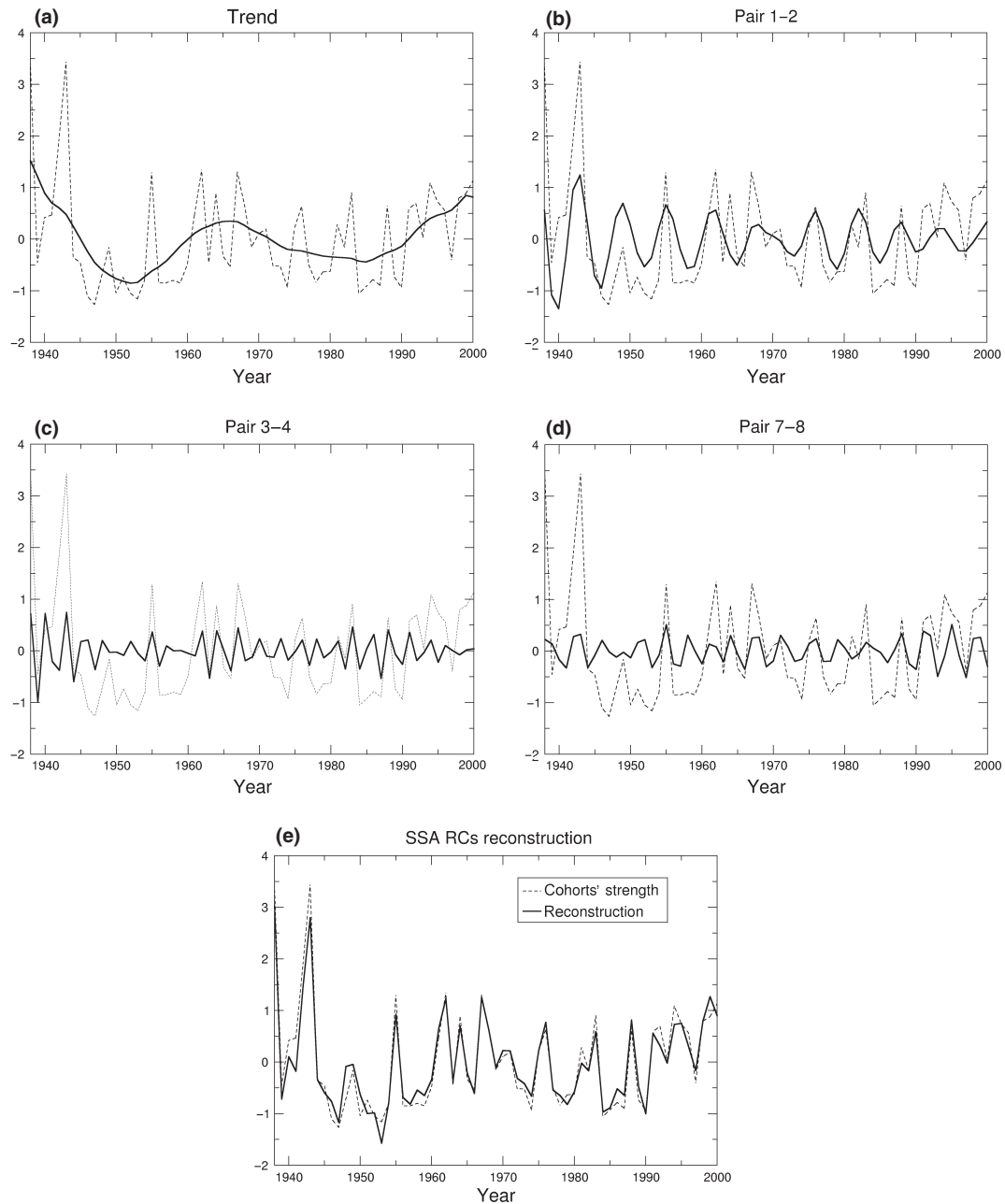
Temperature scales of variability

The MTM analysis showed significant peaks of variability at periods that were located at approximately 7.6 (90% confidence), 3.2 (95%) and 2.4 (95%) yr. The SSA revealed a trend, which accounted for 28.9% of the variance, and three pairs of eigenmodes, which accounted for more than 50% of the total variance (82.8% of the detrended series variance); they were significant at the 90–95% confidence intervals based on the application of the Chi-squared and Monte Carlo tests (Table 1). All three SSA pairs met the oscillatory pairing criteria, and their periods corresponded approximately to those that were found using MTM, which suggests that the spectral peaks were real. The MEM of the RCs located the peaks at approximately 3.4, 8.7 and 2.3 yr.

Wind scales of variability

The MTM of the meridional wind component displayed neither a trend nor any significant peak in the variability. The significant peaks of the zonal wind component (90% level of confidence) were identified at bands that were centered at 26.0 and 3.5 yr. The first band reflected a decadal variability component and it was removed. The SSA of the detrended series showed that eigenmodes 3 and 4 corresponded to an oscillation with a period of

Figure 4. Trend and reconstructed components (RC's) from the oscillatory pairs (thick solid) of the cohorts' strength time series, and unfiltered annual anomalies (thin solid). (a) RC's 1–2 of an SSA of the unfiltered annual time series with a 10-yr window. (b–d) SSA of the detrended time series with a 12-yr window. The 6.2, 2.5 and 3.5 yr are RC's 1–2, 3–4 and 7–8 respectively. (e) Reconstruction from the RC's (thick solid) of the cohorts' strength time series and the unfiltered annual anomalies (thin solid). Series are normalized, units are of standard deviation.



approximately 3.5 yr; this accounted for 21.5% of the variance of the detrended time series (15.0% of the total variance) and was significant at the 95% confidence interval based on the Chi-squared and Monte Carlo tests (Table 1).

Cohort strength and runoff

The cohort strength and the river runoff (during the spawning season) displayed periodicities at the same frequency bands. A comparison of both of the detrended series revealed a negative correlation for almost

every period of the record, with the exception of the mid-1970s and the early 1980s (Fig. 5a); no apparent correlation between the components was regarded as a trend (Fig. 5b).

To explore the relationships between those variables, M-SSA was applied jointly to the detrended series. The first six eigenvalues form three significant oscillatory pairs corresponded to periods of approximately 6.5, 3.6 and 2.4 yr; the first two were significant at a 95% confidence interval, and the third was significant at a 90% confidence interval. They accounted for 26.2, 20.7 and 16.5% of the joint variance, respectively (for $M = 12$).

An anticorrelation between runoff and cohort strength was clearly observed in the RCs that corresponded to the three pairs (Fig. 6a,c,f). High (low) continental discharges were related to the low (high) strength of the cohorts. Although the most energetic oscillatory pair for the runoff corresponded to approximately 3.6 yr, the joint analysis with cohort strength indicated that 6.5 yr was the most important period for the combined variability, which suggests that additional effects contributed to this relationship.

Cohort strength and temperature

The air temperature time series also displayed significant quasi-oscillations in nearly the same bands as the cohort strengths. To identify statistically significant co-movements between those variables, an M-SSA was jointly applied to the detrended series (the trends did not display significant correlations; Fig. 6d). The first six eigenvalues formed three significant oscillatory pairs, which corresponded to periods of approximately 6.5, 3.3 and 2.5 yr (Fig. 5c,d). They accounted for 22.9, 15.9 and 12.8% of the joint variance, respectively (for $M = 12$). The Chi-square test revealed that the first two pairs were significant at a 95% confidence interval, whereas the third was only significant at the 80% confidence interval.

An anticorrelation between both series was observed in the RCs that corresponded to the pairs that were associated with the cycles of approximately 3.3 and 2.5 yr (Fig. 6d,g). High (low) air temperatures were apparently associated with the low (high) strength of the cohorts. Nevertheless, for the cycle that contained periods of approximately 6.5 yr, the

Figure 5. Comparisons between cohorts' strength (full line) and runoff (a) and (b) or air temperature (c) and (d). Runoff and air temperature series in dashed line. (a) and (c) show the detrended series; (b) and (d) show the trends fitted via SSA. Series are normalized, units are of standard deviation.

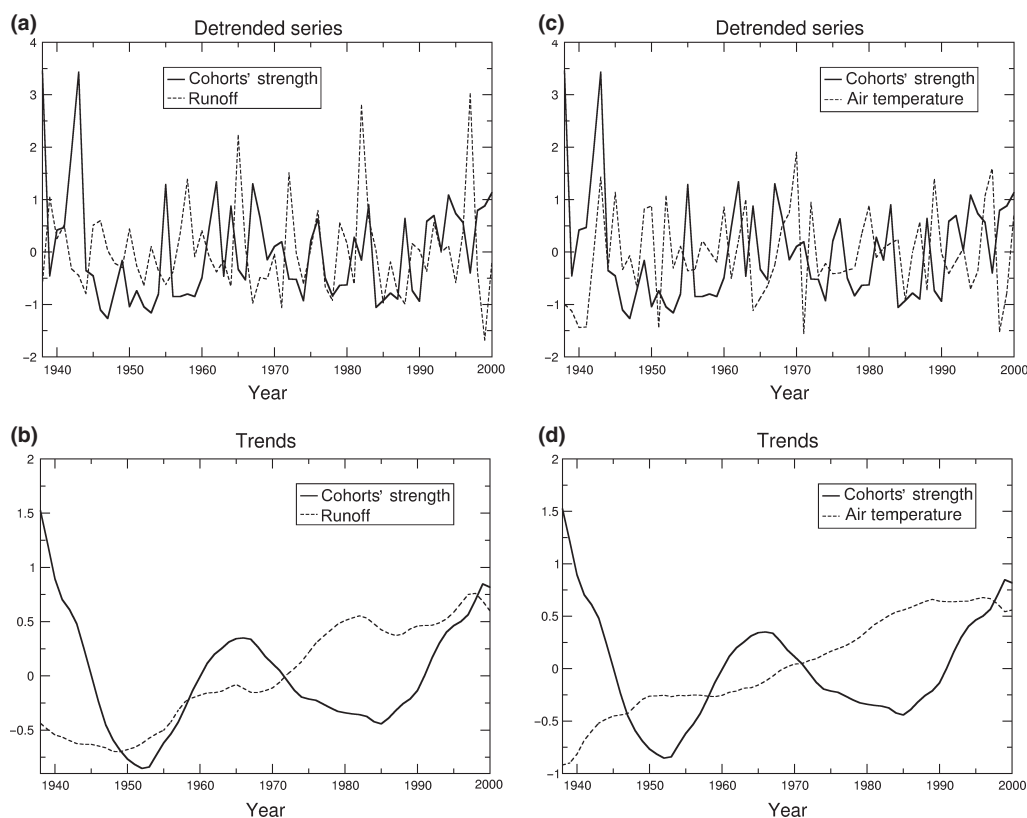
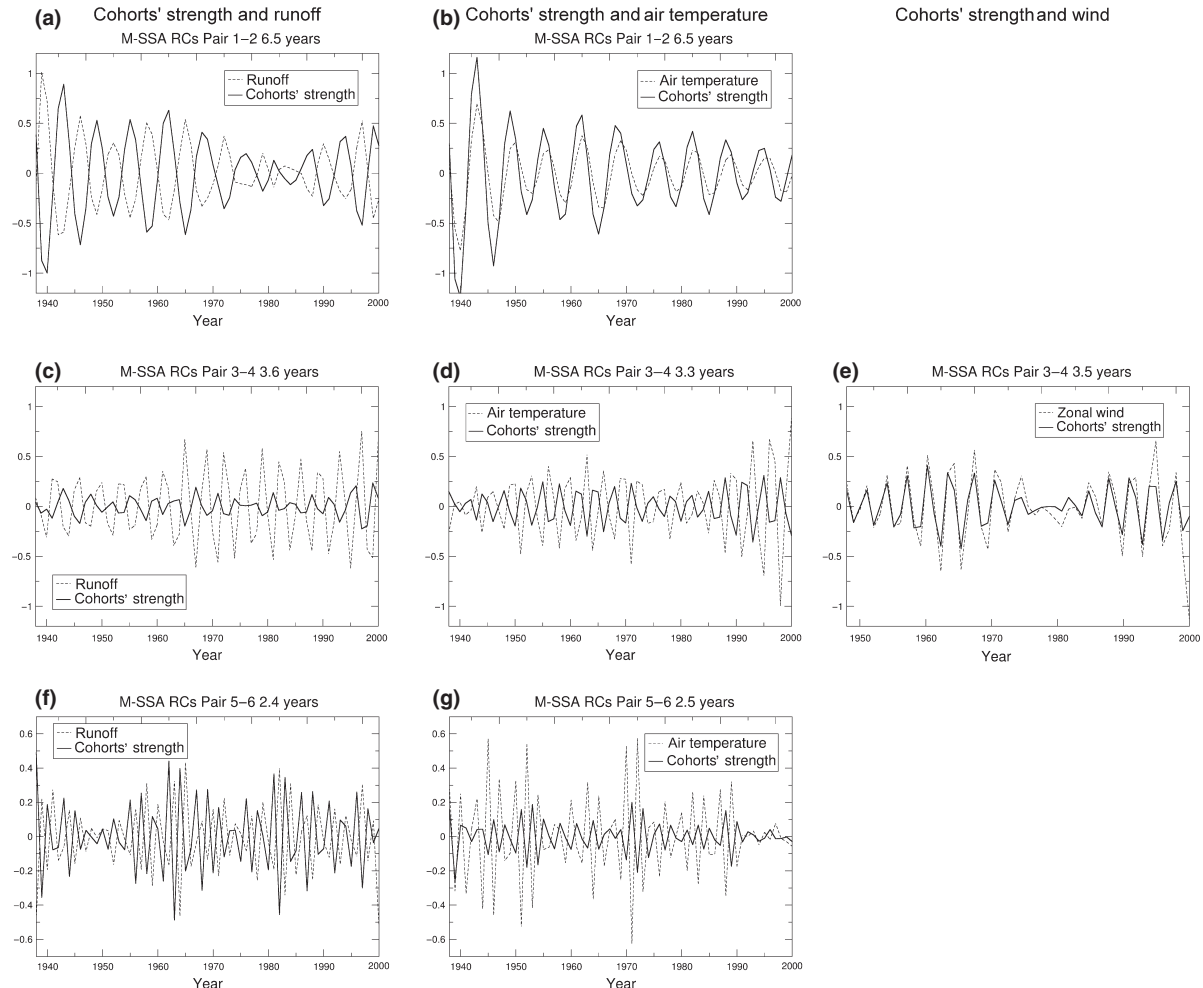


Figure 6. Reconstructed components (RC's) for the cohorts' strength (dashed line) and the environmental variables (solid line) from the Multichannel Singular Spectrum Analysis (M-SSA). The upper (a) and (b), central (c); (d) and (e) and lower panels (f) and (g) show the RC's of the first, second and third oscillatory pairs identified, respectively. Series are normalized; results are in standard deviation units. Environmental variable in the first column (a); (c) and (f) correspond to runoff; in the second column (b); (d) and (g) to air temperature; and the in third column (e) to zonal wind.



signals were almost in phase, and the strength of the cohorts slightly led temperature (Fig. 6b). This result suggests that temperature was only a beneficial factor for the cohorts for this last cycle. As observed for the runoff, although the most energetic cycle for air temperature was centered at 3.3 yr, the joint analysis with cohort strength identified 6.5 yr as the most important cycle. This is the only cycle for which temperature and cohort strength were positively correlated.

Cohort strength and wind

To determine whether a relationship existed between the variables, M-SSA was applied together to the detrended series. The third and fourth eigenmodes

formed an oscillatory pair at a period of 3.4 yr, which accounted for 17.9% of the variance ($M = 12$) and was significant at a 95% confidence level (data not shown). The relationship between the oscillation that was extracted from the zonal wind by the SSA (data not shown) and the oscillation that was derived from the M-SSA (Fig. 6e) with cohort strength was remarkable. Therefore, our results revealed a statistically significant relationship between the quasi-oscillation that was identified for the cohort strengths at a period of approximately 3.5 yr and the zonal wind component. The high (low) strength of the cohorts was associated to the easterly (westerly) wind anomalies that were detected on interannual time scales (Fig. 6e).

Integrated analysis of cohort strength, runoff, temperature and wind

Three of the series displayed significant periodicities around similar bands, which were centered at approximately 6.5 or 7, 3.5 and 2.5 yr. Cohort strength displayed statistically significant common variability with runoff and air temperature. However, the RCs (which represent quasi-oscillations) that were obtained from the combination of the cohort strength series with either runoff or temperature (left and central panels of Fig. 6, respectively) were slightly different; this difference was probably related to the shortness of the time series and the fact that SSA is highly data-adaptive. To identify statistically significant co-movements in the three series, a new M-SSA was applied to all of the normalized detrended series together.

The M-SSA revealed the first six eigenvalues form three significant oscillatory pairs, which corresponded to periods of 6.5, 3.4 and 2.4 yr. They accounted for 18.5, 16.5 and 12.1% of the joint variance, respectively ($M = 12$). The Chi-square test revealed that all of these values were significant at a 95% confidence level.

The results of the RCs (data not shown) were consistent with those that were obtained in the previous sections. For the cycles of approximately 3.4 and 2.4 yr, an anticorrelation was observed between the runoff air temperature and cohort strength. High (low) runoff and air temperatures were related to low (high) cohort strength. Nevertheless, although the cohort strength and runoff were negatively correlated in the cycle of approximately 6.5 yr, the cohort strength and air temperature were almost in phase, and the biological series slightly led temperature in this cycle. The zonal wind component showed only one cycle, and its period was approximately 3.4 yr. In this cycle, a positive correlation with cohort strength was observed; this was in contrast to the behavior of the temperature/runoff peak observed at 3.4 yr.

Modeling experiments

The extreme runoff conditions that were modeled showed that a river flow that was higher than normal displaced the front downriver and generated stronger salinity gradients. Conversely, during low runoff conditions, the front was displaced to an upriver position and showed weaker gradients (data not shown).

After 3 days of simulation, the final positions of the particles in the three discharge scenarios and the six groups that were launched at the bottom salinity front were different for the four main wind directions

(northeasterly, southwesterly, southeasterly and northwesterly) (Figs 7–10). The dispersion was higher when the particles were launched further downstream. The runoff condition appeared to only strongly affect those groups that were launched far upstream (groups 1 and 2); for these groups, the dispersion seemed to increase with the discharge, in other words, the dispersion of the particles seemed to be more sensitive to the launching position than to the runoff. To quantify these results, we computed the root mean square distance to the source (RMSDS) of every particle group at the end of the 3-day simulation; this magnitude measured the distance that was traveled by the particles after those days and their dispersion. For every runoff condition, dispersion clearly increased when the particles were launched further downstream (Fig. 11). An important rise in the RMSDS between groups 1 and 2, and groups 3 and 4, and an increment that was associated to very small changes in the initial position for most of the wind directions between groups 1 and 2, and groups 3 and 4, were observed. Moreover, the runoff condition only significantly affected the dispersion of the groups that were launched upstream (groups 1 and 2), whereas the dispersion pattern for the other four groups remained almost the same. Finally, for every group of particles and runoff scenarios, the dispersal was larger for the winds that originated from the first quadrant than the winds that originated in the third quadrant (Fig. 11).

DISCUSSION

Our results suggest that the effects of environmental changes that are related to climate variability during the critical early development of the croakers may propagate through the entire life span of a croaker's cohort. It is important to stress that we worked with a relative measure of the recruitment and not with its absolute values. We have shown that climate variability can drive oscillations in recruitment; however, fishing pressure on this stock has increased continuously, especially during the 1990s, which has diminished the stock size (Carozza *et al.*, 2004). The impacts of the decrease in the stock size (which we did not analyze) may decrease the absolute intensity of the recruitments during that period.

Because we employed air temperature data instead of water temperature data and introduced a putative bias that was associated with age estimations in the older fishes of this long-lived species, we could not draw definitive conclusions. Notwithstanding, the coherency in the pattern of variability of the biological and environmental series was remarkable.

Figure 7. Final positions of particles from groups 1, 2, 3, 4, 5 and 6 launched at the bottom after 3 days of simulation, for NE wind. Larger circles represent initial positions. Lines representing the 5, 7.5 and 10 m isobaths have been superimposed. Gray tones correspond to different launching units, each one composed by 100 particles.

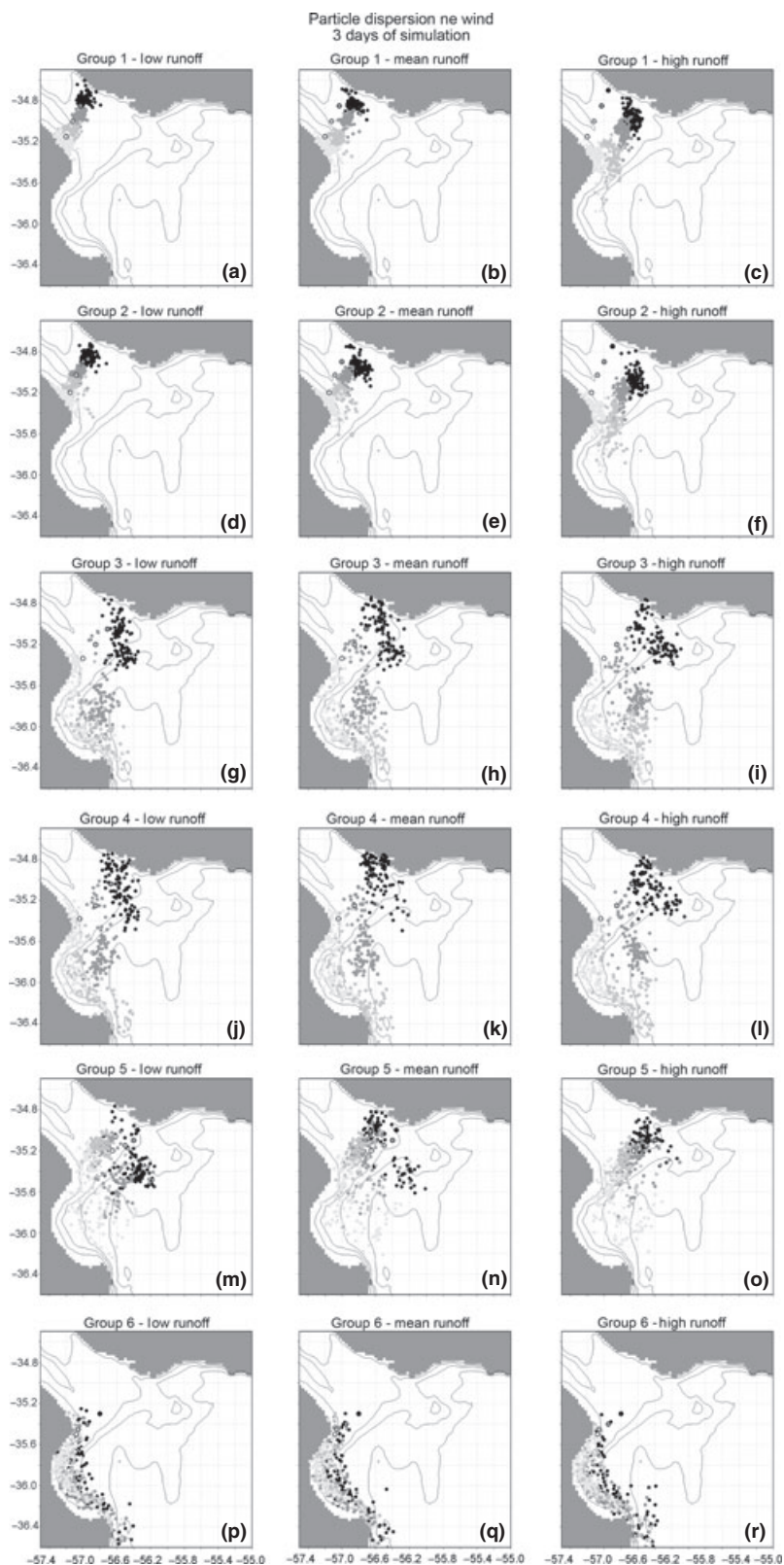


Figure 8. Same as Fig. 7, for SW wind.

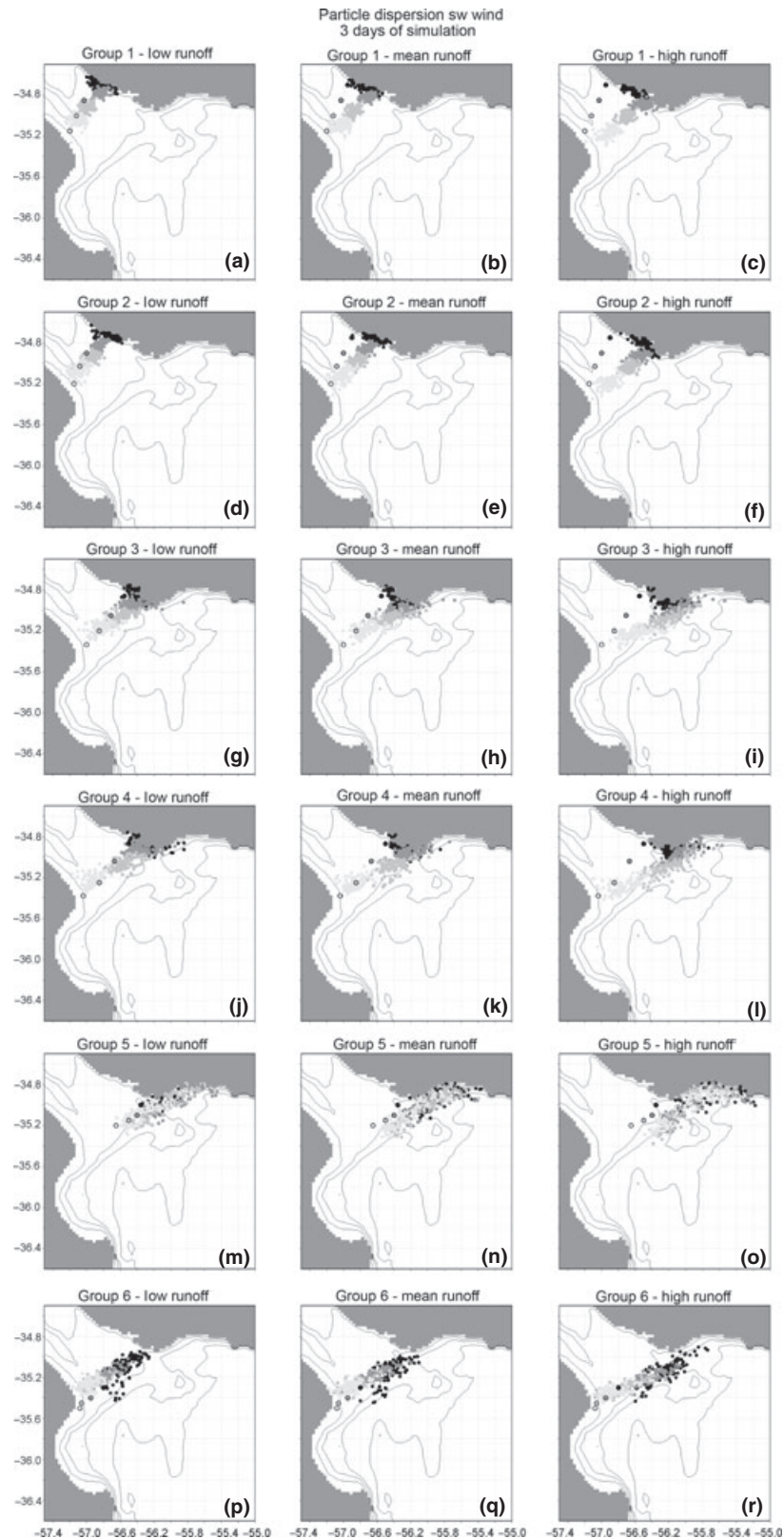


Figure 9. Same as Fig. 7, for SE wind.

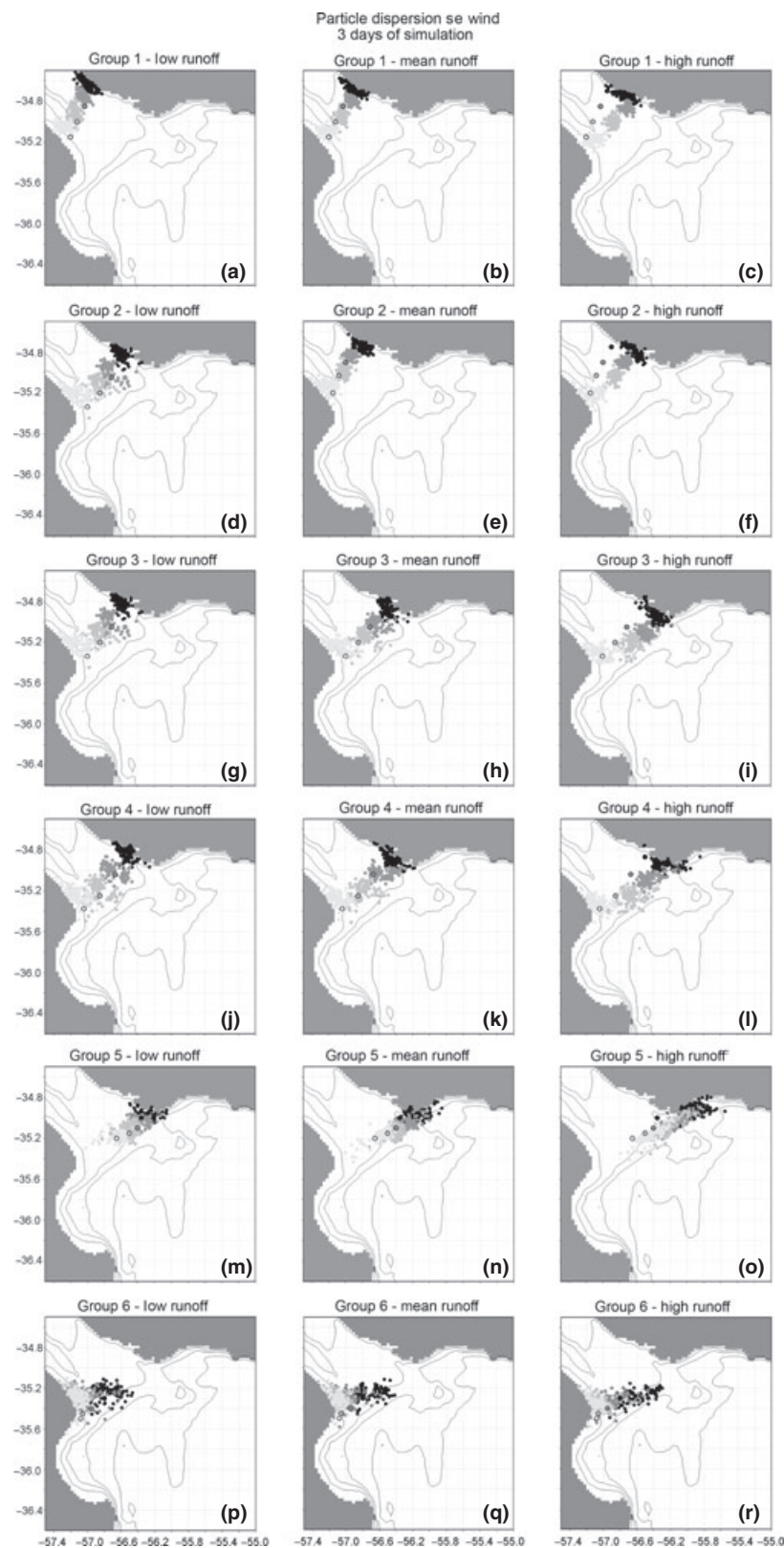


Figure 10. Same as Fig. 7, for NW wind.

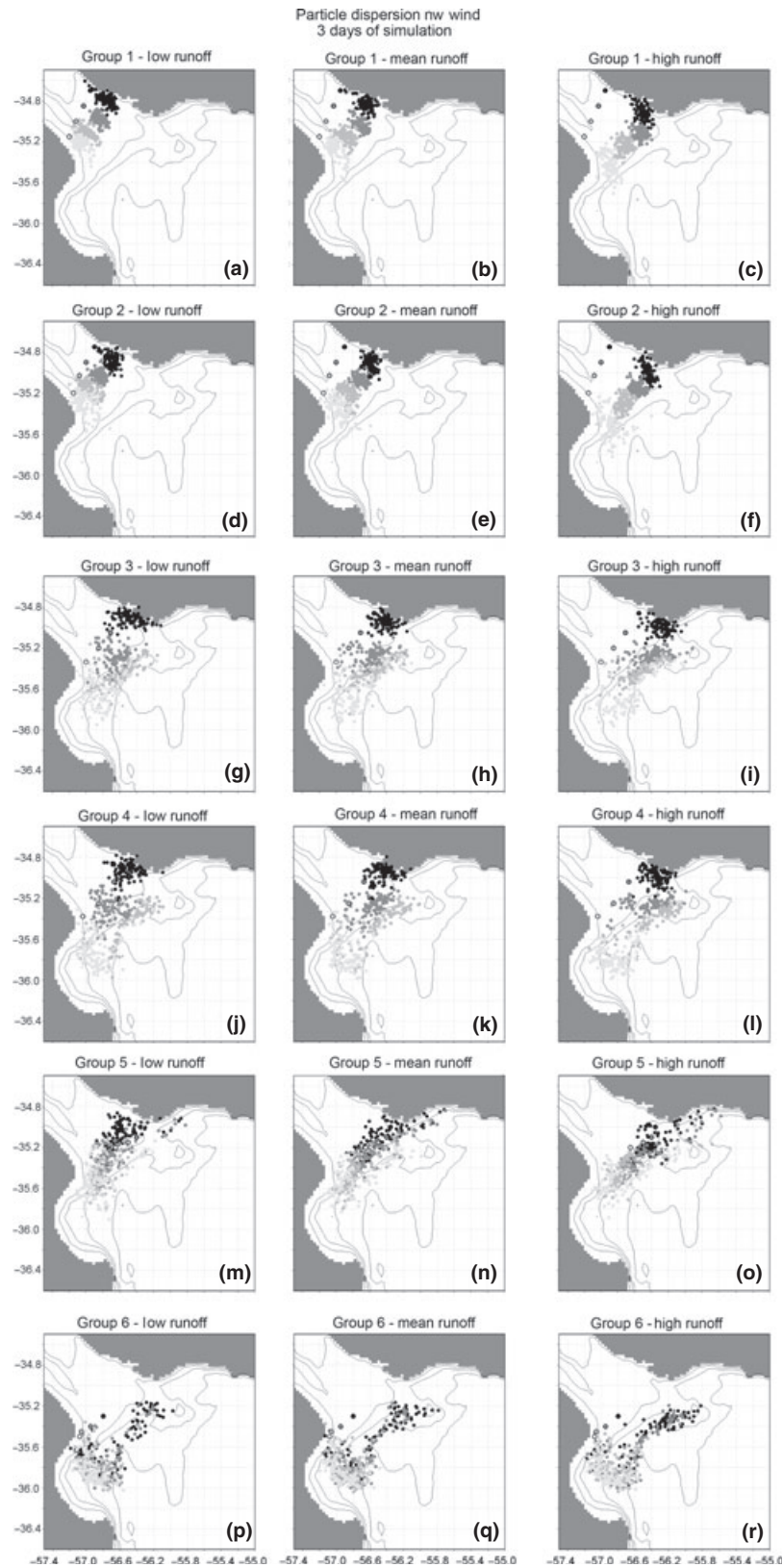
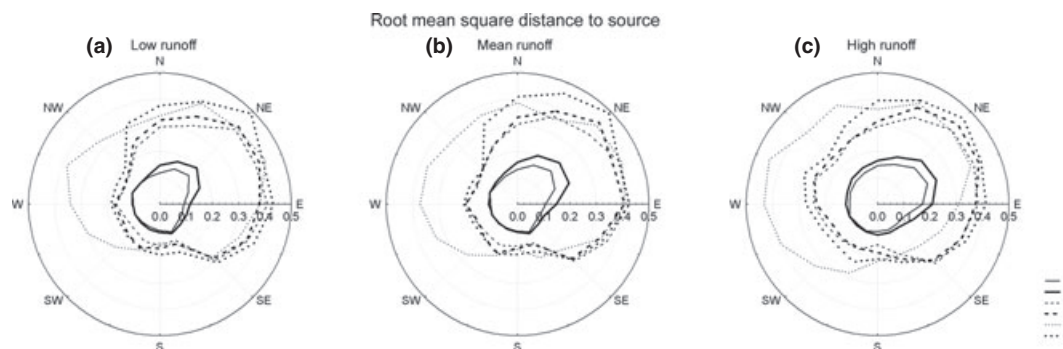


Figure 11. Root mean square distance to the source (RMSDS) of every particle group at the end of the 3rd day of simulation.

Runoff fluctuations and recruitment

Three of the time series that were analyzed (recruitment, river discharge and air temperature) showed statistically significant common variability at approximately 6.5, 3.4 and 2.4 yr. Similar quasi-oscillations were detected for the discharge of one of the main tributaries to the Río de la Plata, which is the Uruguay/Negro River; this river exhibited peaks at 6.3, 3.5 and 2.5 yr. The first of those oscillations was associated with SST anomalies that existed over the tropical Pacific and North Atlantic Oceans. The 3.5 and 2.5 peaks were related to the ENSO cycle, in which the warm (cold) phase leads to anomalously high (low) stream flows (Robertson and Mechoso, 1998).

Retention areas are important for maintaining population coherency in the highly dispersive aquatic environment, and the retention of eggs and larvae in favorable areas has been hypothesized to be an important determinant of marine fish year-class strength (Iles and Sinclair, 1982; Bernatchez and Martin, 1996). Our results support the hypothesis that climate-induced extreme river discharges can affect the retention properties of the estuary (high runoff promotes low retention and *vice versa*) to regulate croaker recruitment.

Albeit estuaries are generally considered to be highly advective environments (Boehlert and Mundy, 1988), several researchers have shown that croakers reproduce in a retentive area that lies inside the Plata estuary (Acha *et al.*, 1999; Simionato *et al.*, 2008; Braverman *et al.*, 2009). Macchi *et al.* (1996) and Jaureguizar *et al.* (2008) showed that gravid females concentrate to spawn near the bottom salinity front. Because some evidence has shown that runoff fluctuations can generate horizontal displacements of the front (Berasategui *et al.*, 2004; Nagy *et al.*, 2008), we hypothesize that spawning adults move following the

frontal spatial variations. As a consequence, the eggs would be released further upstream (low discharge) or downstream (high discharge), which may potentially result in a strengthening or weakening of retention. The results of the numerical experiments supported this hypothesis; changes in runoff or the spawning location modified the spreading of the planktonic eggs (particles in the model). The highest retention resulted from the combination of upstream spawning and a low runoff condition and *vice versa*. The results of the model also demonstrated that spawning position has a larger impact on retention compared with the runoff magnitude. Therefore, the major influence of the discharge fluctuations would be achieved through displacements of the front that, in turn, induce the down- or up-river movements of the spawning gravid females (the direct effects of the runoff variability, however, are important for those particles that were launched up-river, which reinforced the process). If this hypothesis is true, we would assume that environmental homing (*sensu* Brochier *et al.*, 2009) at the bottom salinity front is a key element in the reproductive strategy of the whitemouth croaker. We did not demonstrate the existence of homing in this species; this possibility seems to be a logical extension of our results based on the knowledge of croaker life history.

Temperature variability and recruitment

The effects of temperature changes on cohort strength were most important in the period of approximately 6.5 yr, in which the higher than normal temperatures seemed to reinforce the low discharge effects in the production of the strongest cohorts. Although this was the strongest peak in the cohort series, it was not the most energetic peak of the runoff series (Table 1). This may be because the 6.5-yr peak was the only peak in which temperature reinforced the effects of river discharge on the cohorts.

High temperatures may act to increase the larval growth rate and survivorship (e.g., Jones, 2002). The faster growing cohorts have been shown to experience lower cumulative mortality rates because they spend less time in the stage that is vulnerable to predators (Houde, 1996; Cowan and Shaw, 2002). Temperature may also have an effect during the adult phase; values outside the ranges that are normally experienced by a stock will delay maturation at cold temperatures and accelerate maturation at warmer temperatures (Bye, 1990), which can shorten or prolong the reproductive season and affect annual egg production. Temperature can also play more subtle roles, such as affecting prey abundance or the tolerance to certain salt or oxygen concentrations. For the 3.4- and 2.4-yr peaks, the lower than normal temperatures acted in opposition to river discharge, but they could not neutralize its outcomes. Those peaks, which negatively affected cohort strength, seem to be forced by a climatic phenomenon (ENSO cycle) other than that of the 6.5-yr peak (Robertson and Mechoso, 1998; see above).

Wind effects on recruitment

Winds are very important at the seasonal and synoptic time scales in this estuary (Simionato *et al.*, 2005) because they control the surface salinity patterns and mixing processes (Guerrero *et al.*, 1997; Simionato *et al.*, 2001, 2004, 2007, 2010; Acha *et al.*, 2008; Meccia *et al.*, 2009). At the scales that we analyzed (interannual), only the zonal wind component showed co-movements with cohort strength, and this was only observed for the 3.5-yr cycle. In agreement with results that were derived from other methodologies (Meccia *et al.*, 2009), the current results demonstrated the presence of easterly wind anomalies (retention reinforcements) linked to the El Niño phase (high river discharge) and westerly anomalies (retention weaknesses) linked to the La Niña phase (low discharge). In other words, wind variability on the interannual scales should counteract the river discharge effects on retention and would likely reduce its influence.

Climate and recruitment forcing

The major effects of climate on the recruitment of croakers would be driven by river runoff alterations, and changes in temperature play a secondary role.

South America is one of the regions that featured large positive trends in the annual and summer precipitation in the 20th century (Giorgi, 2002). Long-term changes in the annual precipitation patterns for almost all of the southeastern South American regions have been reported by several authors (see the

references in Krepper and Zucarelli, 2010). Regarding the Plata basin, a sustained positive trend that began in 1950 has been demonstrated in the low-frequency variability of rainfall (Krepper and Sequiera, 1998). In addition to the precipitation trends, the Río de la Plata runoff has increased significantly during the 20th century (e.g., Pasquini and Depetris, 2007). However, it can be argued that the recruitment fluctuations that we showed may be driven by extraordinary events rather than by general trends. The climatology of the water excesses and shortages during the 20th century in the Plata basin revealed that almost all of the excess critical periods occurred after 1950, whereas most of the shortage-critical periods occurred before 1950 (Krepper and Zucarelli, 2010). With respect to our hypothesis, this would indicate that recruitment of croakers during the first half of the 20th century could have been higher than that of the second half; however, our time series is not large enough to test this hypothesis. Regarding future scenarios, the extent to which alterations that are associated with global climate change can impact the retention properties of the estuary and the resulting consequences for its populations are unclear; these issues cannot be addressed without a high degree of speculation. Significant future climate change effects on river discharges of the Plata basin cannot be discounted because the regional precipitation has already demonstrated a substantial positive trend in the past. However, the future scenarios for the next 50 yr over the majority of the Plata basin contain too much uncertainty because the outputs of the global climate models considerably underestimate the present mean precipitation and they also differ among themselves (Barros *et al.*, 2005). Moreover, the role of the large basin in absorbing a potential precipitation excess is uncertain. However, a continual increasing pattern of positive anomalies could intensify the declining trend of the stock size that is produced by fishing pressure.

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