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Effects of decadal changes in the hydrological regime of the middle reach of the Paraná River (Argentina) on fish densities

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Abstract Changes in fish densities recorded over 14 years (1996–2009) were studied for effects of long-term variation of the hydrologic regime. We collected field data with an echo sounder in scour holes of minor channels draining an area of floodplain in the middle reach of the Paraná River. Fish densities in 2000–2009 were significantly lower than in the previous decade. The decrease was associated with a marked reduction of water levels, flood magnitudes and connectivity of channels with the nearby floodplain lakes. This distortion of the flood pulse likely had an effect on the life history strategies of the fishes. The effects of damming in the upstream basin and other man-made perturbations are minor in the middle reach. However, the decadal alterations of regime are intimately linked to climate fluctuations in the Paraná River basin during the past century. Tendencies of observed fish densities are similar to results reported in literature on the influence on fishes for similar long-term alterations of the flood regime in river flood plain systems.

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Introduction

Most subtropical plain rivers have a seasonal hydrologic regime with alternating periods of low and high water. These fluctuations in water levels are one of the key environmental factors that drive the structure of aquatic communities both spatially and temporally through many ecological mechanisms (Lowe McConnell 1987; Junk et al. 1989; Bayley 1995). Junk et al. (1989), in particular, the "flood pulse concept" highlights the importance of periodic inundation and drought in a river flood plain system since it allows the lateral exchange of water, nutrients and organisms between the river channel and the connected floodplain. It follows that hydrology and hydrochemistry of the parent river are crucial to sustain biodiversity in these systems.

Accessibility to aquatic floodplain habitats for organisms depends on timing of the flood pulse. Access increases during high water levels, and organisms spread randomly across the plain (Saint-Paul et al. 2000). On the contrary, the availability of habitats decreases during low water periods, when most channels lose their connection with fluvial lakes (Rodríguez and Lewis 1994). The importance of this rhythmic phenomenon for fishes is well known. The duration and magnitude of flood disturbance introduce ecological changes to which fish have to adjust (Levin 1992; Grigg 1996; Lake 2003). Moreover, the evolution of life history strategies (Winemiller 2004; Arrington and Winemiller 2006) may be perturbed, affecting the reproduction and success of fish recruitment (Welcomme 1979; Vazzoler and Menezes 1992; Gomes and Agostinho 1997; Richards et al. 2002; Agostinho et al. 2004; Thomaz et al. 2007; Bailly et al. 2008).

According to Agostinho et al. (2004), migratory species in the upper Paraná River were favored during floods longer than 75 days since these pulses promote access to the structural complexity of marginal areas, thereby increasing colonization rates (Junk et al. 1989; Fernandes et al. 2009). The opposite effects of 291 days of low water were reported by Espínola (2005) between April 2001 and January 2002, which included the historical minimum of 1.17 m. This latter hydrological condition might have influenced the normal reproductive cycle of *Cichla kelberi* (tucunaré) since no larvae were observed following the high water period. Eggs and larvae drawn downstream have limited access to lateral habitats during abnormal periods of low water, and population recruitment for the following years is negatively affected even if adults successfully reproduce in tributaries (Agostinho et al. 2008). Dams may also modify the flood pulse with consequences for the fish community. For example, releases from the Porto Primavera dam, in the upper Paraná River were stopped during the fish spawning period in December 1998, drastically reducing the downstream discharge. The numbers of young-of-the-year fishes in the subsequent period were close to zero, despite successful spawning (high density of larvae) and a flood duration that exceeded 100 days (Agostinho et al. 2004).

Similar long-term investigations (during one decade or more) are not frequent due to lack of empirical data to assess impacts on fish densities over such time scales (Górski et al. 2011). Studies of this kind are scarce in rivers of South America. Most of them have been carried out in the upper reach of the Paraná River (e.g. Bailly et al. 2008; Fernandes et al. 2009). These contributions refer essentially to dams' damping effects on the flood pulse. Nearly all of them report impacts on fish through a reduction of peaks and probabilities of large floods and the subsequent decrease in connectivity between lotic–lentic habitats. A positive relation between species richness and total capture per unit effort (CPUE) of long-distance migratory species with the duration of floods and connectivity is stressed.

More long-term studies about the influence of the physical environment on the structure of fish community exist in North America. Geheber and Piller (2012) and Quinn and Kwak (2003) have studied the effects of extreme hydrologic events and damming on fish and noted the necessity of historic time data-series to highlight such effects. Fish diversity decreased significantly in the upper White River (Arkansas, USA) after Beaver Dam became operational around 1964–65 (Quinn and Kwak 2003). The conclusion was reached after comparing samplings before (1962–63) and after (1965–66; 1968 and 1995–1997) the construction.

A huge reduction in fish catches was observed in the Volga River following long-term flow alterations due to damming (Górski et al. 2011). Those authors remarked that disturbance of the normal flood pulse should be viewed as an additional negative factor apart from the known blockage of fish migration routes by damming.

The flood pulse may also be perturbed by changes in the precipitation regime due to climate fluctuations that lead to long dry and wet periods. There has been little study of the effects of this long-term disturbance on the ecology of river flood plain systems, (Junk and Wantzen 2004) though it has been recognized as a crucial topic to be investigated (OECD 2010; Gehrke et al. 2011). The sparse long-term available information on many fish communities is also an obstacle to performing studies linking climate changes and fish (Gehrke et al. 2011).

This paper deals with the last topic by using a unique set of echo sounder records obtained over 14 years (1996–2009) in the floodplain of the Paraná River middle reach. A number of deep scour holes formed in minor channels of the floodplain were measured. The analysis of the 14 years data set was done in the context of the climate fluctuations reported for the Paraná River basin during the last 100 years.

Methods

Study area

The area of studies lies near Santa Fe city (Fig. 1) in the floodplain of the Paraná River middle reach. This area is bounded by the Paraná River itself and an important secondary channel, the Coronda River. The surface is rather flat with a gentle longitudinal slope (1–5 cm/km)

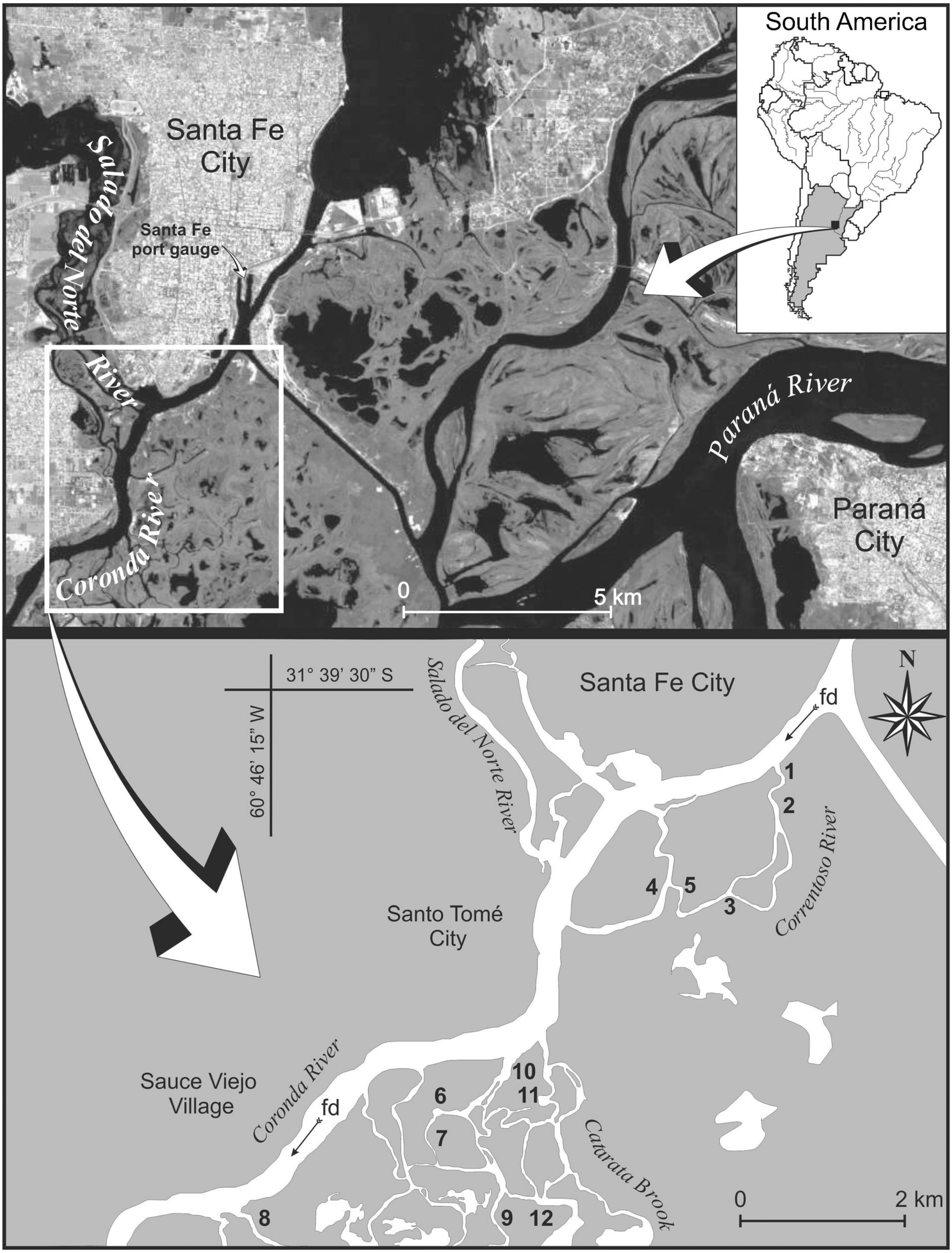


Fig. 1 Study area and sites recorded with echo sounder. See Table 1 for details

and transverse slopes one order of magnitude larger (10 cm/km between the Paraná/Coronda Rivers and a depressed central section).

The plain is dissected by numerous minor channels and covered by lakes, swamps and residual flood plain channels. All of them are intermittently connected depending mainly on the water levels of the Coronda River, which in turn receives its discharges from the Paraná River through a system of channels and lakes located north of the study area. During a flood, water flows from the Coronda River through the inlets of several minor channels, like the Catarata Brook and is distributed into the flood plain. The lakes become increasingly connected with the rising water levels in the minor channels until the entire surface is inundated with the overflow from the channels' banks (Drago 2007).

Silting and/or avulsion of channels and changes in the shapes and depths of the alluvial lakes are typical geomorphic processes observed in these types of floodplains (Paira and Drago 2007). The formation of the Catarata Brook, for instance, began from breaching the Coronda River levees. The rather steep transversal slope of the plain prompted breaching during large floods allowing the overflowing water to reactivate a residual floodplain channel downstream of the levee (Drago 2007).

Deep holes are common along the flood plain channels as a result of scouring processes and other mechanisms. The deep pools located on the outside of meander curves are well known and widely cited in the literature (Richards 1982; Ikeda and Parker 1989). These kinds of holes have maximum depths between 4 and 10 m in the study area (2, 5–9, 11 in Fig. 1; b in Fig. 2). Deeper scour holes, which range from 10 to 20 m deep, locate downstream of channel confluences (3, 4 and 12 in Fig. 1; c in Fig. 2). Finally, "levee toe scour holes", as reported by Drago et al. (2003) and recently described by Ramonell et al. (2007), may also be present immediately downstream of a levee at the inlet of a flood plain channel. These holes may be about 200 m long and up to 20 m deep (1 and 10 in Fig. 1; a in Fig. 2). Paira and Drago (2007) suggest that the high kinetic energy and turbulence of water when entering the flood plain after breaching (Fig. 2) is partly dissipated by scouring a "levee toe hole", i.e. they propose that these holes formed out of an erosive mechanism similar to that in a cascade foot.

Available data

Our study is based on available bathymetric records obtained from a number of minor channels draining the area of Fig. 1. The measurements were taken between

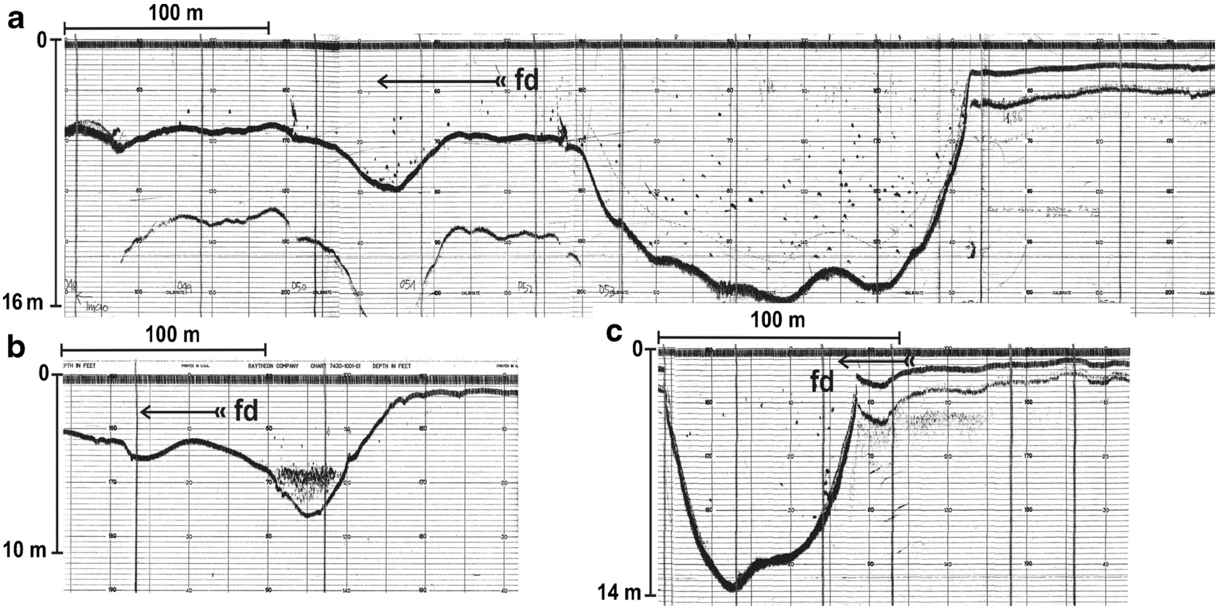


Fig. 2 Types of scour holes. **a** levee toe (*10* in Fig. 1). **b** meander (*5* in Fig. 1). **c** confluence (*12* in Fig. 1). Echo sounding longitudinal profiles (*fd*: flow direction)

1996 and 2009 with a single beam echo sounder (Raytheon model DE-719C of 208 kHz) (Drago et al. 1999). The echo sounder charts (Fig. 2) were carefully examined in order to compute volumes, depths and fish densities. These latter data, together with other information, are listed in Table 1.

Hydrologic regime

The variations of water levels during 1996–2009 were taken from daily records in the Santa Fe port gauge and in light of well-documented changes in the hydrologic regime of the Paraná River system over the past century. Levels were supplied by the National Directorate of Waterways of Argentina. Monthly maximum and minimum levels were obtained along with the decade's average levels (1990–1999 and 2000–2009).

To highlight linkages between differences in the hydrologic regime and the opportunities of water to inundate the floodplain, two procedures were used. First, the records of monthly maximum water level divided by bank-full water level were obtained for an average year within 1990–1999 and 2000–2009 periods, respectively. Second, the days of potamophase (days with water levels higher than bankfull level), limnophase (days with levels lower than bankfull level) and connectivity (total days of potamophase divided by total days of limnophase), were computed yearly with the *f*FITRAS function from the PULSO software (Neiff and Neiff 2003). This software is used to study phenomena that repeat following a sigmoidal function over long periods, such as the seasonal fluctuations of river levels.

The 4.50 m level in the Santa Fe port gauge was used as the reference level from which flow begins to flood the adjacent plain in the study area (bank-full level). Similarly, the 2.30 m level in the same gauge is the top mark from which the isolation phase begins for most lakes in the alluvial plain (Drago 1980; Paira 2003).

Table 1 Details of the available data on the studied scour holes (*L* levee toe; *C* confluence; *M* meander)

Code	Scour hole	Date	Gauge level (m)	Volume (m^3)	Number of transects	Max. depth (m)	Fish density (ind/m^3)
1	L	05/96	4.8	580	1	11.7	0.086
2	M	05/96	4.8	1,014	1	11.8	0.085
3	C	05/96	4.8	940	2	10.5	0.076
4	C	10/99	2.19	1,337	1	9.7	0.079
5	M	05/00	3.24	483	1	8.2	0.030
3	C	08/03	2.39	2,560	4	8.8	0.018
6	M	08/05	2.28	1,253	1	9.1	0.013
7	M	08/05	2.28	1,429	1	9.7	0.006
8	M	08/05	2.28	1,782	1	11.2	0.019
9	M	08/05	2.28	5,496	2	14.3	0.004
10	L	06/09	1.98	6,514	1	15.5	0.017
11	M	06/09	1.98	1,472	1	9.2	0.019
12	C	06/09	1.98	4,133	3	13.1	0.011
10	L	07/09	3.14	14,438	2	16.3	0.011
11	M	07/09	3.14	682	1	8.5	0.029
12	C	07/09	3.14	3,570	2	13.1	0.007

Determination of fish density

Fish densities at each scour hole were computed by applying the echo trace method; that is, the number of fish echoes that appear in an echogram as echo traces was counted and divided by the sampled volume of water (Forbes and Nakken 1972; Mathisen 1980; Burczynski 1982; Oldani and Tablado 1985; Tablado et al. 1988; CARU-INAPE-INIDEP 1990; Moreno-Amich 1990).

The number of transects (echograms) obtained in a given environment make up a sample. By knowing the distance travelled by the boat, the angle of the transducer beam and the depths as given by the echograms, the sample water volume at each transect can be calculated according to the following formula (Mathisen 1980; Burczynski 1982; Fig. 3):

$$v_i = \left(\frac{1}{3}\right) * Di * tg\left(\frac{A}{2}\right) * (H_1 * H_1 + H_2 * H_2 + H_1 * H_2) \tag{1}$$

where: V_i: volume of transect i, D_i: distance travelled by the boat at the given transect, tg: symbol of tangent, A: angle of the transducer beam, H_1: initial depth, and H_2: final depth.

Before computing densities, the available bathymetric records were analyzed for types of scour holes, completeness of data (river stage, date, station location) and especially for echo traces clear definition. After this examination, two out of 12 available echo sounder records were discarded.

Error analysis in fish densities due to the number of transects

Since the number of transects for each scour hole was different (see Table 1), reliability of fish densities in holes with a lower number of transects may be questioned, i.e. the magnitude of density errors due to this fact may distort the analysis.

To gain an insight into this topic, density data were divided into two groups: the ones gathered before the year 2000 and those gathered after, in order to minimize the incidence of the most important independent variable, the water level.

The formula suggested by Wetzel and Likens (1991) was then applied:

$$E = \frac{S^2}{n\overline{X}} \tag{2}$$

where: E = error in fish densities for one group resulting from considering n=1; 2; …; n transects; S^2 = variance of point densities computed for one group, and $\overline{X}$ = mean density for one group. This formula implies

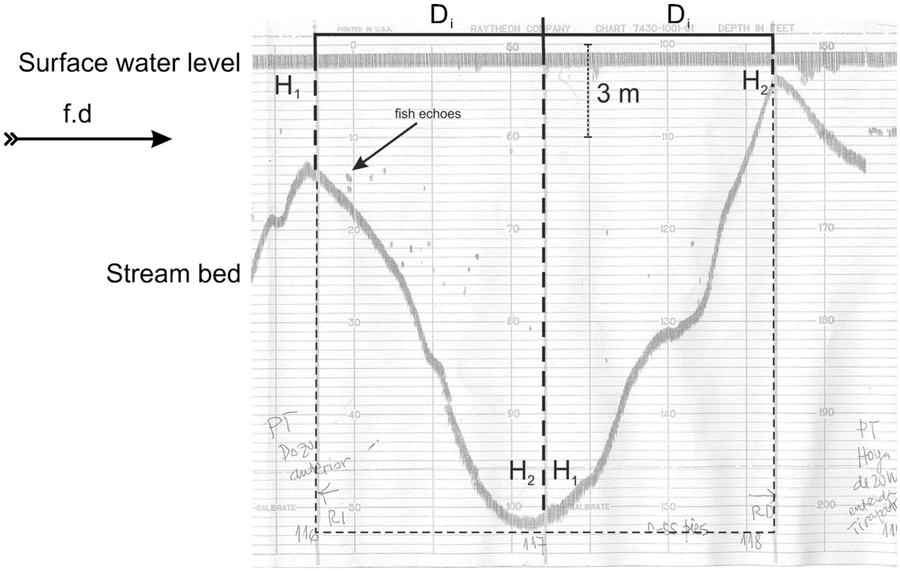


Fig. 3 Echo sounder chart in the Tirapatrás brook (*8* in Fig. 1) obtained following the main flow direction (*fd*). Note the echo traces into the hole denoting the fish presence. Values of depths $H_{1–2}$ and distances D_i are used in Eq. (1) to compute the sampled water volumes

independence of the events, a condition that is satisfied by our measurements, since they were made at random irrespective of the type of scour hole.

The results obtained for densities recorded after 2000 are shown in Table 2. Note the low error in density computations (less than ≈1 %) irrespective of the available number of transects at each hole.

Statistical analysis

A one-way analysis of variance was applied to analyze the differences between both hydrologic periods. The statistical software Statistica 7.0 (StatSoft 2005) was used.

Fish density data were tested with a two-way permutational analysis of variance (Anderson 2001; Mc Ardle and Anderson 2001) to determine differences in scour holes and periods. This test enables also to assess interactions between habitats and periods and is particularly valuable with data from unknown population distributions, serious outliers, small sample sizes and absence of parametric methods to answer the hypotheses of interest (Mc Peek and Kalisz 1993; Kabacoff 2011). Models were run on a Euclidean distance-based analysis with 1,000 random permutations without restrictions (Manly 1997). The statistical software MULTIV version 2.4 was used (Pillar 2004). A significance level of $p<0.05$ was accepted as indicating significance for every computation. Relationships between fish densities and water levels and years were also appraised by means of a simple regression analysis.

Table 2 Density errors computed with 1; 2; …; *n* transects before and after 2000

	After 2000			
	Number of transects			
	1	2	3	4
E (%)	0.45	0.23	0.15	0.11
S^2	0.00007			
$\overline{X}$	0.015			

Note the low errors (less than ≈1 %) in densities obtained from the different numbers of transects. It was also verified that errors for the data recorded previously to 2000 computed with a variance (S^2) two orders of magnitude larger, that is, a conservative criterion, were less than ≈10 %

Results

Hydrologic features

Average values of 4.30 m and 3.20 m were computed for the decades 1990–1999 and 2000–2009, respectively, from water levels records in the Santa Fe port gauge (Fig. 4). Moreover, significant differences ($F_{=1}$= 2471.5; p=0.001) exist between daily water levels from the two periods. Regarding floods, Fig. 4 shows they were larger and more frequent during 1990–1999, with two extraordinary events in 1992 and 1998 when levels peaked at 7.5 and 7 m, respectively. The monthly average maximum level/bank-full level ratios clearly depict the distinct effects of floods on water levels in each period (Fig. 5). The seasonal character of floods is also noticeable in this figure. A high water level period beginning in December with peaks in early-autumn (March–April) typically distinguishes the average water regime of the Paraná River in its middle reach (Giacosa et al. 2000).

Figures 4 and 5 also give some information to explain the hydrologic functioning of the alluvial plain. Most of its lakes were connected to the nearby channels almost at all times during the 1990s and there were few occasions when the hydrometric levels decreased below the minimum for connection (2.30 m). Unlike the 1990s, hydrometric levels from 1999 to 2000 onwards were below 4.5 m most of the time and frequently under 2.30 m (levels reached 5.5 m and 6 m only twice, in 2003 and 2007, respectively), i.e. a great number of lakes lost their connection with the plain channels during this period of low water. Connectivity values depict the above behavior quantitatively since averages of 0.58 and 0.06 were computed for each decade, i.e. a difference of 10 times. The total number of days of potamophase and limnophase came to 1,347 and 2,305 throughout 1990–1999 and 210 and 3,443 throughout 2000–2009, respectively. Figure 6 shows the annual variations in connectivity values.

Considering these hydrologic features, the first decade (1990–1999) will be referred to hereafter as the "humid" period and the second one (2000–2009) as the "dry" period.

Fish densities

No significant differences existed among average fish densities grouped according to type of scour hole (F_2= 0.57; p=0.91; Fig. 7).

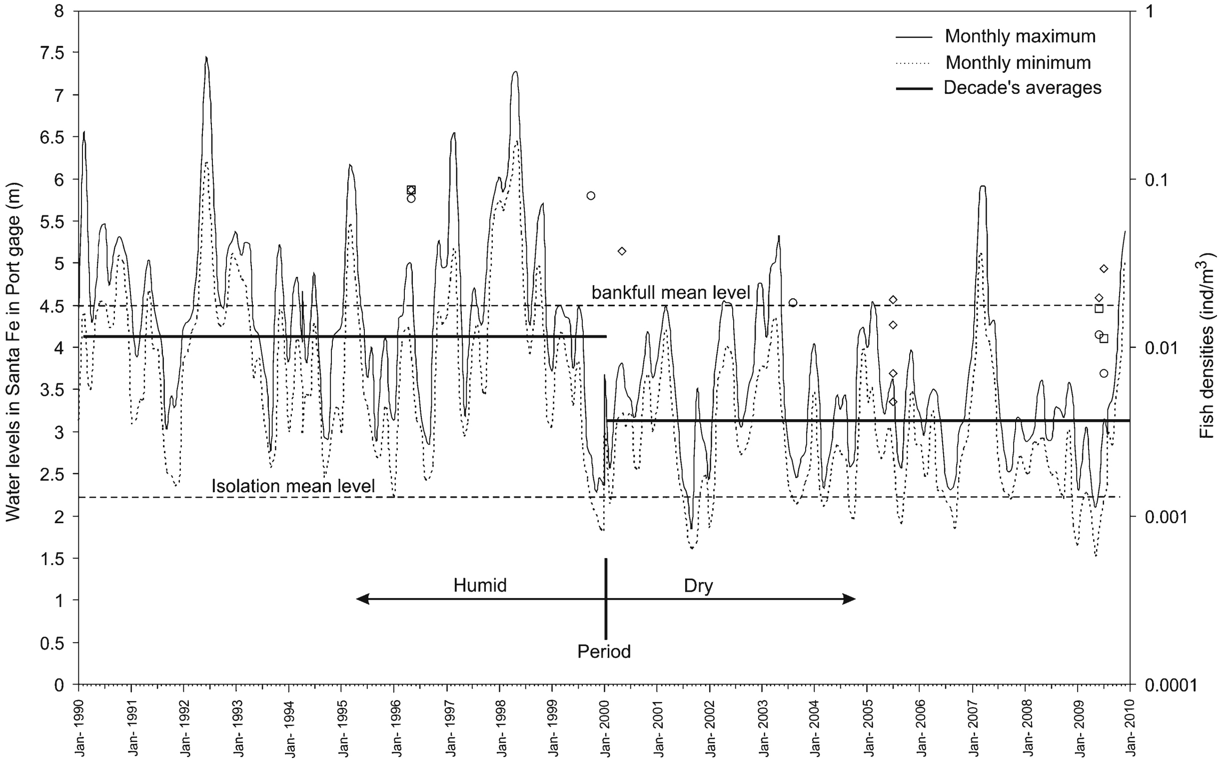
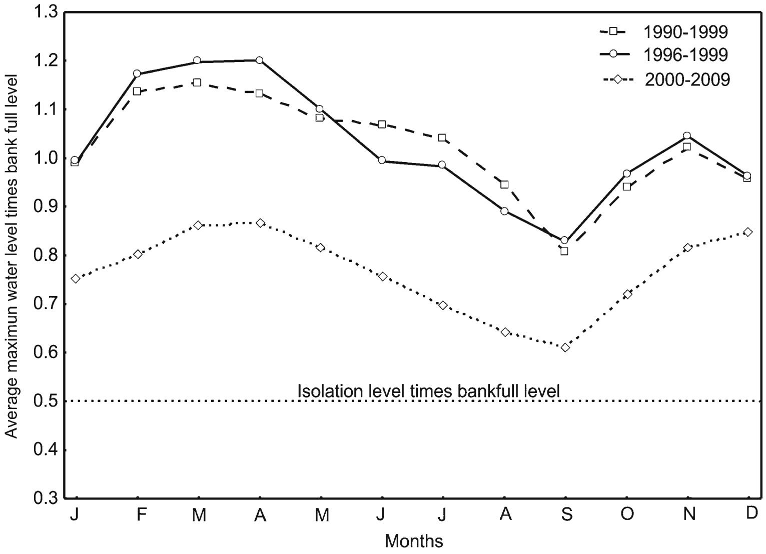


Fig. 4 Monthly water levels (maximum and minimum) during 1990–2009; "bank full" refers to the mean level when overflow of channels begins and "isolation" refers to the mean level when most lakes become disconnected from the plain channels in the area of studies. Fish densities in meander (*triangle*), confluence (*circle*), and levee toe (*white square*) scour holes are included

When densities were viewed in light of water levels and connectivity variations (Figs. 4 and 6), larger values were recorded in the "humid" period (high degrees of connectivity) than in the "dry" period (low degrees of connectivity). Indeed the difference in the average densities between the two periods was statistically significant (F_1=14.30; *p*=0.0003; Fig. 8). The interactions between habitats and periods were not

Fig. 5 Monthly average maximum water levels/bank full level ratios along 1990–1999 and 2000–2009



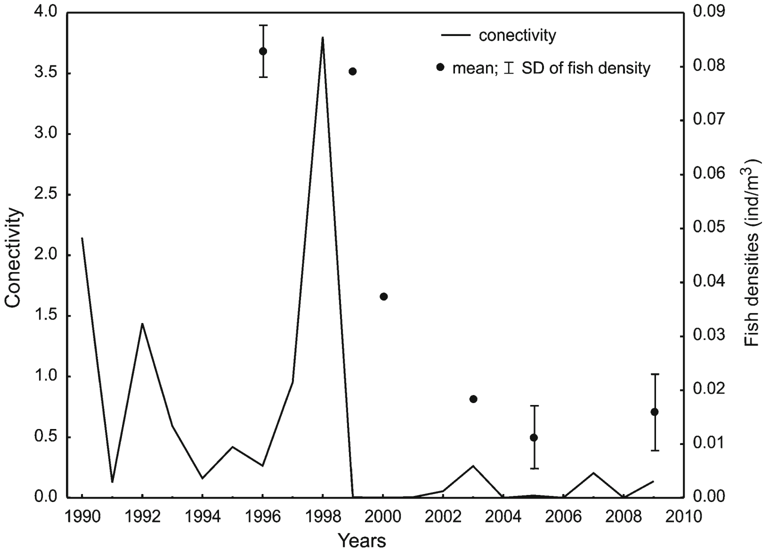


Fig. 6 Variations in connectivity (*left*) and fish density (*right*) along the period of study

show significant (F_{15}=14.47; *p*=0.95). Although density data have a certain degree of seasonal dependency, the two way permutational analysis of variance indicated a low probability of a type I error existence.

Accordingly fish densities were significantly and negatively correlated with years (*r*=–0.87; *p*=0.00001; Fig. 9a) and positively with hydrometric levels (*r*=0.73; *p*=0.0011; Fig. 9b).

Potential man-made alterations of fish densities

Damming, water quality deterioration and overfishing are widely known potential causes for fish density reduction. The possible incidence of any of these factors on fish densities in the middle reach of the Paraná River might be as important as obscuring the role of long-term climate changes. This possibility is briefly discussed below.

Damming

A total of 40 dams have been built in the upper basin of the Paraná River over the 40 years before 2000 (Rodrigues et al. 2005; Agostinho et al. 2007a). As the main purpose of these dams is power generation, their reservoirs are kept almost filled most of the time.

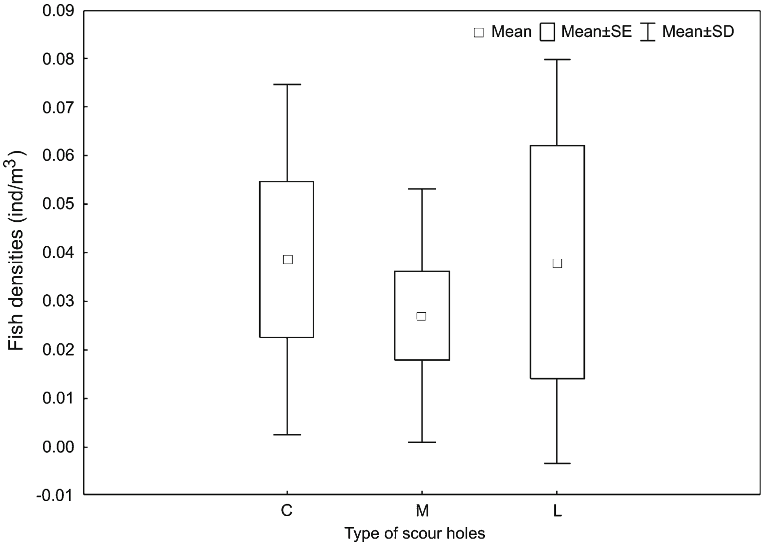
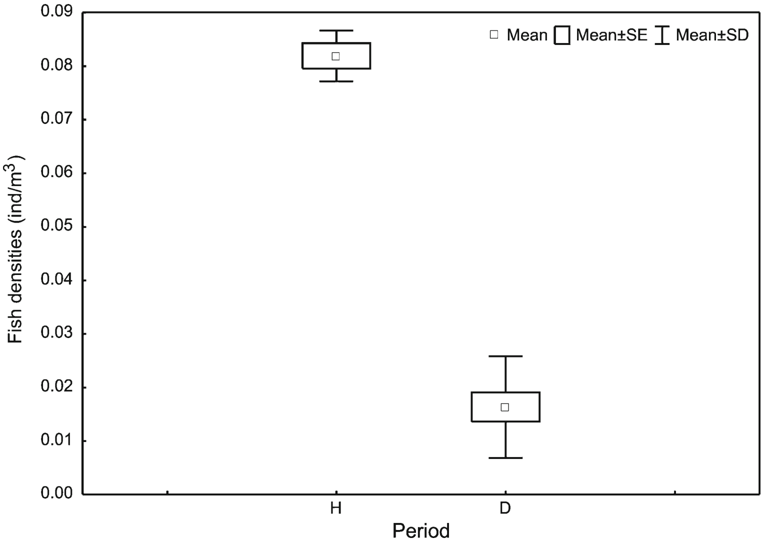


Fig. 7 Box plot with average densities of fish grouped according type of scour hole (*L*: levee toe; *C*: confluence; *M*: meander)

Fig. 8 Box plot with average densities of fish recorded in the humid (*H*) and dry (*D*) periods



This mode of operation minimizes negative effects resulting from long low-water periods since discharges larger than the supply from precipitations are released; the only limitation being the water volume stored in the reservoir. According to estimates from the Sub-Secretary of Water Resources of Argentina the total capacity of all dams was 120,000 hm^3 in 2009. Though this volume is important during low water stages, it is comparable to an ordinary flood. It is thus inferred that the capacity of dams to reduce the peak discharges is very small due to both their operational mode and the magnitude of floods, i.e. damming does not significantly perturb the flood pulse in the Paraná River basin (World Bank 1996; Cacik and Paoli 2000; Paoli and Cacik 2000; Giacosa et al. 2000; Paoli 2011a, b).

As the dams were all built in the upper basin, blockage of fish migration routes has a deep negative influence on fish community in this region (Agostinho et al. 1994, 2008). No quantitative studies exist to assess this effect on migrating fish in the middle reach of the Paraná River. However, it is important to note that a free fluvial corridor of more than 1,500 km without damming is available for them, mostly coinciding with their current migration routes (Bonetto and Pignalberi 1964; Bonetto et al. 1971; Baigún et al. 2003). The corridor spans the lower basin of the Paraná and includes its middle and lower reaches. The Paraguay River, the main tributary at the beginning of the middle reach, provides 2,500 km of un-dammed channels. Thus it would be reasonable to hypothesize that

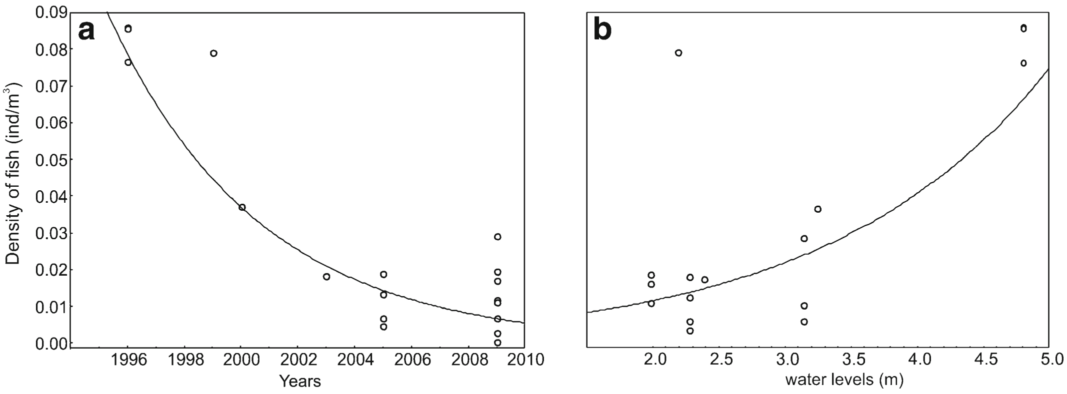


Fig. 9 Correlations of fish densities with time (**a**) and water levels (**b**)

blockage has a minor effect on migrating species in such a large fluvial area.

Water quality

The hydrochemistry of lotic habitats (main channel and secondary/minor floodplain courses) in the middle reach of the Paraná River is adequate for fish life as well as aquatic biota in general, according to international standards for water quality (Hammerly 2011). A key parameter, like the oxygen concentration, has values higher than 75 % in the main channel. This value may go down significantly only during extreme events, like the 1982–83 extraordinary flood when a minimum of 55 % of dissolved oxygen was measured (pH=5). Concentrations recovered rapidly after the peak discharges, reaching values larger than 80 % (pH=7) (Hammerly 2011).

In lentic habitats of the flood plain, similar parameters of water quality vary naturally within a wider range due to factors such as the degree of connectivity with the nearby channels, morphologic features and the vegetation cover (Drago and Vasallo 1980; Hammerly 2011).

Water pollution is appreciable along the right bank of the lower Paraná and de la Plata rivers between Rosario and Buenos Aires cities. A large part of the Argentinian population and industry are concentrated along these 450 km. Baigún et al. (2003) concluded that development of coastal fisheries along that strip is not possible unless contamination is reduced. Nonetheless, an alternative would exist for this activity from the center of the river and in more remote areas where good conditions for fish life prevail. Hammerly (2011), remarked that during the normal stages of the Paraná River, parameters of quality for drinking water are maintained within international standards around important cities like Santa Fe, Paraná and Rosario.

To summarize, pollution should not be a problem as to seriously perturb the aquatic biota in the lower part of the Paraná River basin. In localized sites, contamination is indeed important, but that involves a small portion of the whole area.

Overfishing

Fisheries along the riverine corridor of the Paraguay-Paraná and de la Plata Rivers are moderately exploited in comparison to other tropical and sub-tropical regions (Quirós 2004). Different models to appraise overfishing along this corridor were applied in a recent study (Bechara et al. 2007). In spite of their rather large errors, all models indicated low and moderate exploitation rates. Moreover, though fishing activities has rapidly developed, there is no evidence of a reduction in richness or diversity in the fish community (Quirós et al. 2007).

The inaccuracy of these estimates has been noted by several different authors but they all agree that fisheries would not be severely exploited in the lower basin of the Paraná River. Thus, overfishing was not considered, for the moment, a factor capable of distorting significantly the statements of this study.

Discussion

The water level variations observed in the Santa Fe port gauge between 1990 and 2009 have to be analyzed, taking into account the hydrologic changes recorded in the Paraná River basin during the 20th century. Several authors (e.g. García and Vargas 1998) showed that climate variability over the past century involved at least two hydrologic scenarios that affected a large part of the basin. The first one lasted nearly 40 years, between 1930 and 1970, with low precipitation levels and river discharges. Conversely, after 1970 increased precipitations and discharges took place in the basin. Very large flows associated with the El Niño (ENSO) phenomenon occurred. This “humid” period was particularly noticeable until approximately 1999–2000 when water levels, discharges, frequency and magnitude of floods decreased again. Though climatologists do not yet have enough evidence as to state with certainty that the latter “humid” period is over (Saurral and Barros 2009), a decade with lower precipitations, water levels and flows began around 2000. Consequently, the studied period between 1996 and 2009 involves the transition between two clearly distinct hydrological pictures.

This change would be related to an impact on fish densities recorded over that period. Densities for the “humid” decade (1990–1999) were significantly higher than for the “dry” one (2000–2009). Other potential anthropogenic causes for differences in density values such as damming, deterioration of water quality and overfishing would not had reached such an importance at that moment as to underestimate the "climate" explanation. Dams built in the upper basin of the Paraná River, for example, proved to have minor effects on the flood pulse in its middle reach thus supporting the idea of climate as the main driving variable associated with long-term changes in the hydrologic regime (World Bank 1996; Cacik and Paoli 2000; Paoli and Cacik 2000; Giacosa et al. 2000; Paoli 2011a, b).

Migratory fishes in the Paraná River, such as large Siluriformes (*Pseudoplatystoma coruscans* (surubí pintado); *P. fasciatum fasciatum* (surubí atigrado), and Characiformes [*Prochilodus lineatus* (sábalo)]; *Salminus brasiliensis* (dorado); *Leporinus obtusidens* (boga), swim long distances upstream to reproduce and spawn in lotic habitats during a high water phase, which normally takes place during the spring–summer time. Eggs and larvae are swept downstream by flow and colonize lakes connected to the main and secondary channels of the floodplain where their growth begins. Adults migrate downstream as well for feeding, taking advantage of the huge richness and production of the alluvial plain (see Rossi et al. 2007 for a complete discussion on the topic). As in other river floodplain systems the synchronization of increases in water levels, temperature and photoperiod triggers spawning and gonadal maturation of migratory species. For instance, access to the diverse habitats of the floodplain is crucial for the larvae of *P. lineatus*, the most common species, since they begin their first feeding and growth in the slow water areas of open channels and lakes where there is refuge and plenty of food (Rossi et al. 2007). Most fish species in the upper Paraná River display a comparable strategy as well since the South American basins have very similar flood regimes (Godoy 1975; Suzuki et al. 2004; Agostinho et al. 2007b).

In light of these life history strategies of migratory fishes and the disturbance in the flood pulse features after 2000, the significant decrease in fish densities throughout the following decade is the likely result of a perturbation in their regular reproductive cycle. That is, climate fluctuations led to a diminution in the magnitude and frequency of floods, lower water levels and a huge reduction of connectivity and availability of alluvial plain habitats (Figs. 5 and 6) with negative consequences on fish community.

Within the few studies on this topic, Laë (1994) reported that a long dry period between 1969 and 1970 and 1985 reduced flooding in the central delta of Niger River. This was the main reason for a decline in fish catches, from 90 000 ton yr^{-1} to 45 000 ton yr^{-1}.

The available dataset allowed us to highlight the inter-decadal differences in fish densities but there are obvious limitations when a study is intended at shorter time scales, i.e. on the order of an annual flood pulse. The scattering of fish density point data in Figs. 4, 6 and 9 could partly be due to these year-to-year alterations of water levels.

Concluding remarks

Changes of fish densities recorded over 14 years in minor channels of the middle reach of the Paraná River floodplain are related to long-term disturbances in the hydrologic regime. Densities before 2000 were significantly higher than values observed in the following decade. The diminution was associated with a marked reduction in the magnitude of floods and connectivity of channels with the nearby floodplain lakes, that is, the flood pulse varied in such a way that would have affected the life strategies of fish.

The changing hydrologic condition identified over the studied period is intimately linked to climate fluctuations reported for the Paraná River basin during the past century. Thus this study shows that a connection exists between climatic factors and fish through the flood pulse concept.

The available biologic data set used in the study is rather unique in a large fluvial system like the middle reach of the Paraná River. It was carefully analyzed with different statistic methods (two-way permutational variance and regressions), to test its usefulness to satisfy the study purposes.

Viewed as a whole the results clearly show the existence of the density differences irrespective of the tests used in the statistical analysis. Although further data are needed to gain a better insight, observed tendencies regarding fish densities agree with results reported in literature about other long-term alterations in flood regimes and their influence on fish in river-floodplain systems. Reasons associated with man-made impacts would not be as important as to account for changes in fish densities and to distort the conclusions.

In view of the results, some questions arise like the one concerning the eventual impact on fish densities of the "dry" period verified in the basin between 1930 and 1970, i.e. did the perturbation of the flood pulse in this period imply a reduction in the overall fish densities with respect to the previous and following "humid" decades? Several factors such as increasing human impacts perturbing the basin conditions possibly make it difficult to reach a definite answer. Nevertheless, it seems to be clear that the long-term alterations of flow, say 10 years or more, due to climate variability are a superimposed component on the year-to-year variations of flow regime and as such they should be properly considered in policies aimed to provide effective resource management.

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