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Long-term morphologic and hydrologic effects on benthic invertebrates in a minor channel of the Paraná River floodplain (Argentina)

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ABSTRACT

Temporal variability in river morphology, sedimentology and flow are a fundamental control on instream habitat structure and riverine ecosystem biodiversity. However, long-term riverine ecological time-series in a wider temporal context are particularly rare. The present research involves long-term data series of riverine physical habitat and benthic macroinvertebrate ecology in the Correntoso River (secondary channel of the Paraná River floodplain).

An anthropogenic morphological alteration was identified at the river inlet. As a consequence, a large sedimentation area was originated at the river inlet, preventing the inflow of suspended sand to the Correntoso. However, the natural morphological evolution during the last decades, probably led by three large floodings (1983, 1992 and 1997–8), reconfigured the inlet morphology, allowing the inflow of suspended sand into the channel. These phenomena allowed the sandy sedimentation a few kilometers downstream, redefining its bottom sediment condition over the years. This long-term process prompted great changes on benthic invertebrate ecology, causing a significant fauna depletion.

This research demonstrates the value of long-term data series in ecological studies as well as the importance of an interdisciplinary point of view. Linking physical processes to ecology is particularly useful to aid understanding of the ecological legacy of anthropogenic modification and natural evolution on river systems.

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1. Introduction

This study is framed into the field of eco-geomorphology. Researches under this theme operate at the interface of ecology, hydrology and geomorphology, integrating these well advanced disciplines (Dunbar and Acreman, 2001; Fagherazzi et al., 2004; Wood et al., 2007). This multidisciplinary concept also considers morphological changes induced by anthropological action and its ecological consequence.

It is relatively well known that river discharges may influence instream organisms and communities in multiple ways (flow disturbance), through changes in channel morphology and habitat characteristics, erosion and deposition of sediments, accidental organisms drift, transport and delivery of food resources, etc. (Lake, 2003; Matthaei et al., 2003; Rabeni et al., 2005). Hence, variations in the hydrological levels and discharges have a great influence on the benthic invertebrate assemblage (Daufresne et al., 2004; Bêche et al., 2006; Jackson and Fureder, 2006; Bonada et al., 2007; Dewson et al., 2007; Griswold et al., 2008; Monk et al., 2008; Durance and Ormerod, 2009; Poff et al., 2010; Blettler et al., 2012). Due to this high sensitivity of aquatic organisms, the influence of long-term hydrological changes has been investigated with increasing intensity in the last decades (e.g. Poff, 2002; Palmer et al., 2008, 2009). This kind of hydrological research has been also carried

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out in the Paraná River basin (Marchese and Ezcurra de Drago, 1992; Marchese et al., 2002; Drago et al., 2003; Blettler et al., 2008; Behrend et al., 2009).

However, attempts to quantify macroinvertebrate community response to river flow variability and morphological evolution are currently limited in terms of their temporal and geographical coverage (e.g. Suren and Jowett, 2006). Reasons for this knowledge gap could be the lack of an appropriate framework that enables different disciplines to collaborate in an interdisciplinary setting (Petts, 2000) and the requirement of long-term ecological time-series involving one or more decades (Monk et al., 2006). In this sense, this study comprises an extensive dataset of morphologic, sedimentologic, hydrologic and hydraulic measurements coupled with benthic samplings at the Correntoso River, a minor secondary channel of the large Paraná River floodplain. This database involves the period from 1987 to 2000, including regular as well

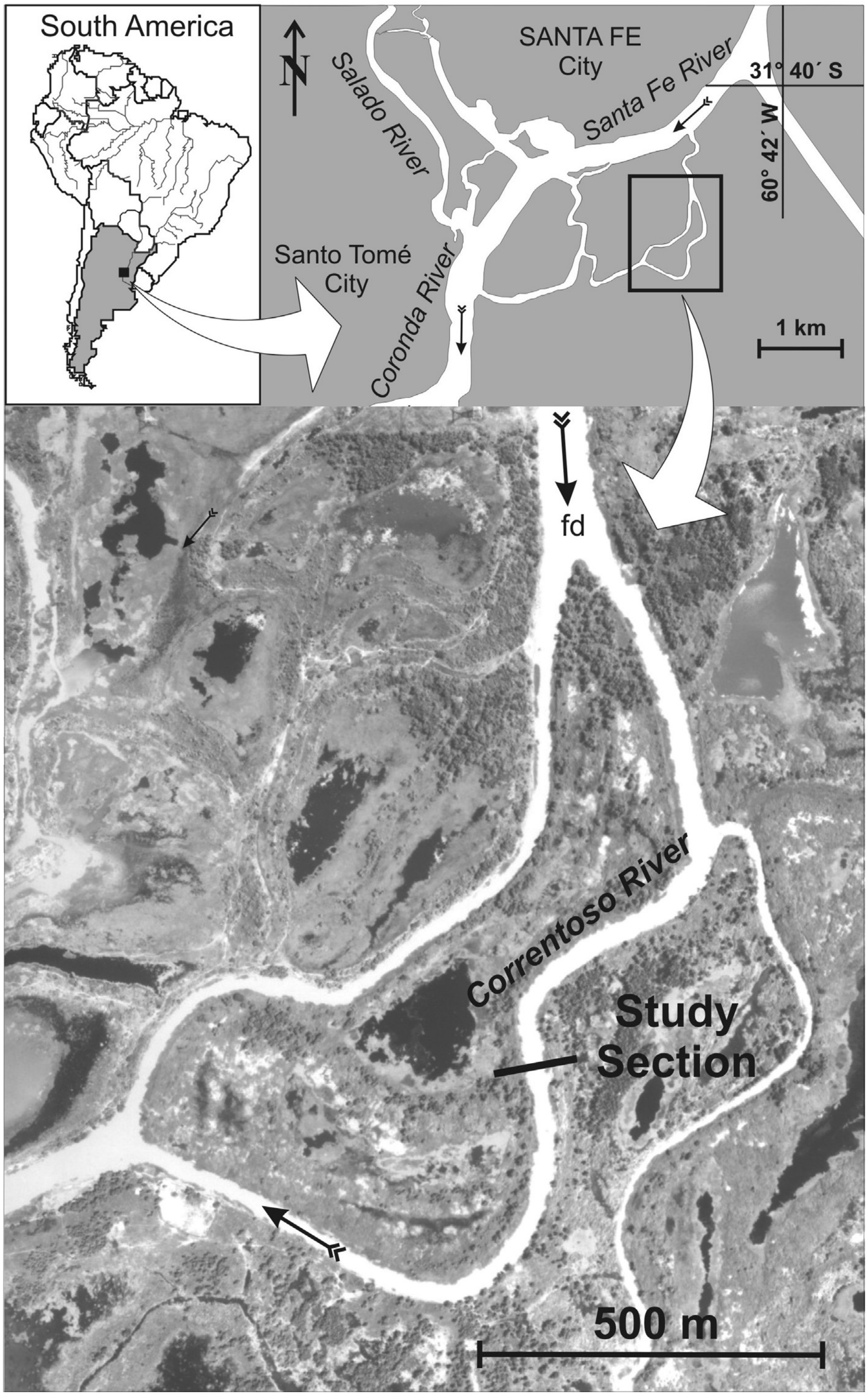

Fig. 1. Location of the study area and details of the sampling stations at the selected straight section.

as extraordinary discharge variations like La Niña and El Niño Southern Oscillation phenomena (ENSO) and remarkable river morphological changes.

The specific aim of this study is to detect the effects of morphological evolution and hydrological fluctuations on benthic invertebrate assemblages in a secondary channel during a period of 13 years. For this reason, the sediment dynamic of the riverine system was also considered. In this sense, it is here hypothesized that the morphological evolution of the river during the last decades coupled with hydrodynamic fluctuations (ENSO phenomena) induced gradual sedimentological changes along the channel i.e. sedimentation of the suspended sand which, in turn, produced an ecological impact on the benthic fauna, promoting its density reduction and the replacement of certain species.

2. Materials and methods

2.1. Study area

The Paraná River is ranked ninth among the largest rivers of the world according to its mean annual discharge to the ocean (18,000 $m^3 s^{-1}$; Latrubesse, 2008). The Middle Paraná River floodplain is characterized by many secondary channels with different discharges (50–2000 $m^3 s^{-1}$) and lakes with different origin and morphometry (Drago, 2007). The Correntoso River is a secondary channel of relatively low hierarchy located in the Middle Paraná River (32° 41′ S; 60° 42′ W) with a mean discharge of 94 $m^3 s^{-1}$, 55 m wide and 5 m deep (Drago et al., 2003; Paira and Drago, 2007). It rises in the Santa Fe River, 2.5 km downstream Santa Fe city harbor and joins the Coronda River 6 km downstream (Fig. 1). Santa Fe and Coronda are also secondary channels of the Paraná floodplain but of a higher hierarchy.

The sampling area is located in a straight reach, 1.6 km downstream the river mouth. Three sampling stations were located on a transversal transect (see Fig. 1), two of them on the banks and the other one on the central area of the channel.

2.2. Dataset

As mentioned above, the whole database was developed at the National Institute of Limnology, Physical Limnology and Benthos laboratories, in Argentina from 1987 to 2000. This database compiles information about water chemistry (mainly regarding water quality), hydrology measurements, hydraulic variables, bed sediments, geomorphology and biology (density, richness and diversity of benthic invertebrates). Fig. 2 shows the water stage at Santa Fe port gauge during the studied period. Each sampling date is also indicated on the water level line. Note that El Niño (ENSO) and La Niña (the opposite climate phenomenon) occurred twice and once, respectively (1992, 1997/8 and 1999) during the studied period.

In all cases, the ecological data comes from samples taken following the same standard sampling procedure. Thus, three benthic samples (sub-replicates) were taken at each sampling station using a clamshell bucket (trade mark: Tamura), filtered through a 200 μm sieve and fixed in 5% formaldehyde in the field. The invertebrates were later hand-picked in the laboratory under a 10x stereoscopic microscope and stored in a 70% ethanol solution. All benthic taxa were identified and counted under microscope (ind. m^{-2}). The taxonomic determinations were made to species level for Turbellaria (Noreña, 1995; Noreña et al., 2005), for Oligochaeta (Brinkhurst and Marchese, 1992), and for Diptera Chironomidae (Trivinho-Strixino and Strixino, 1995). The determinations of other taxa were made till genus and morphospecies level (taxonomic species based on morphological differences from related species).

A total of 459 samples were used in this study along 13 years on the selected straight section of the Correntoso River. Simultaneously with benthic macroinvertebrate samples, the following physical and chemical parameters were measured: sand percentage (%), maximum flow velocity ($m s^{-1}$), local depth (m), conductivity ($\mu S cm^{-1}$), pH, temperature (°C) and transparency (Secchi disk; m). Using the available physical information other hydraulic/morphologic variables were estimated: mean flow velocity ($m s^{-1}$), discharge ($m^3 s^{-1}$), and bed level (m). See the Appendix for methodological details and results. Morphological information was also obtained through the comparative analysis of six aerial and satellite photographs of the Correntoso River inlet from 1954 to 2008. Due to this analysis, a man-induced morphological alteration was detected. Through the review of the historical files (Historical Archive of Santa Fe city), it was then identified as a dredging area. Many newspapers from the 1960s were examined in order to obtain more useful information about this artificial dredged area.

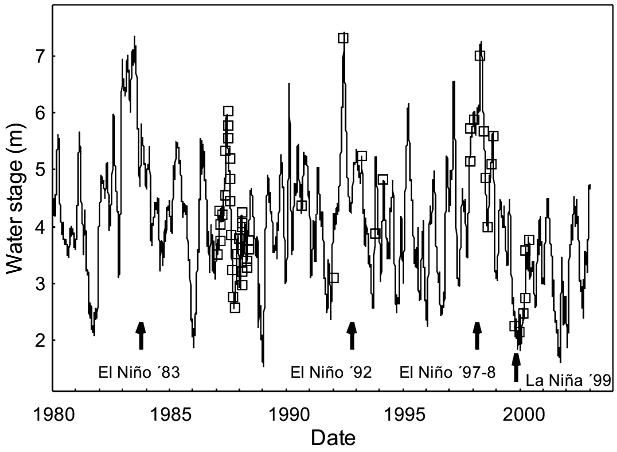

Fig. 2. Daily water stages recorded during the studied period of time (Santa Fe port). Note that every sampling date is marked.

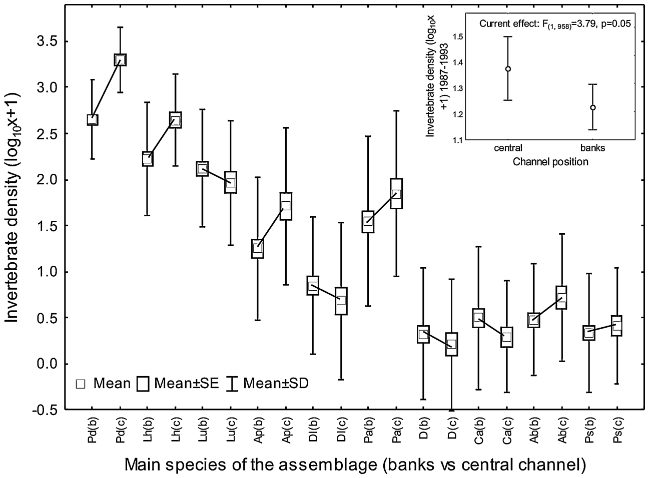

Fig. 3. Box plots of the more abundant invertebrate species showing comparisons between banks and central strip stations. The inset graph shows the ANOVA result of this comparison but taking into account the total invertebrate density. Vertical bars denote 0.95 confidence intervals. Pd = *Paranadrilus descolei*; Lh = *Limnodrilus hoffmeisteri*; Lu = *Limnodrilus udekemianus*; Ap = *Aulodrilus pigueti*; Dl = *Dero* (*Aulophorus*) *lodeni*; Pa = *Pristina Americana*; D = *Dero* sp. I; Ca = *Campsurus violaceous*; Ab = *Ablabesmyia* sp. I; and Ps = *Pisidium sterkianum*.

2.3. Statistical analysis

Due to the non-normal distribution of the benthic data, they were logarithmically transformed [$\log_{10}(x+1)$] and afterward tested again for normality (Shapiro and Wilk, 1965) and homogeneity of variance (*F*max; Sokal and Rohlf, 1981). Subsequently, the analysis of variance one way test (ANOVA) was carried out to determine differences (significance <0.05) between: benthic densities at banks and central strip positions, benthic densities before and after 1990, bed levels before and after 1990, and water levels also before and after 1990. As will be demonstrated later, 1990 depicts a key year in this study. In order to test temporal differences in benthic assemblage patterns, multivariate analyses were used. Multivariate statistic analyses are widespread used in wildlife and ecology researches (McGarigal et al., 2000). The canonical analysis of principal coordinates (CAP; Anderson, 2003), is a constrained ordination procedure that initially calculates unconstrained principal coordinate axes, followed by canonical discriminant analysis on the principal coordinates to maximize separation between predefined groups (Anderson and Robinson, 2003; Anderson and Willis, 2003). CAP is considered more flexible than direct canonical discriminant analysis because any dissimilarity measure can be utilized, using permutations of the observations to test the significance among the defined groups of CAP. Bray–Curtis similarity index (Bray and Curtis, 1957) and 999 permutations were used (Manly, 1997).

In order to reduce the dimensionality of the data (number of variables), patterns of correlation of the environment variables were summarized by principal component analysis (PCA). Axes with eigenvalues greater than 1 were retained for interpretation (Kaiser–Guttman criterion; Jackson, 1993). To identify the attributes that most contributed to the retained axes, Pearson correlations between the scores of the PCA axis and the original data matrix were conducted. Correlation values indicated the importance of each attribute to the ordination.

Additionally, scatter and box plots were used to show particular relationships between variables as well as Pearson correlations and regressions between particular variables.

The R (R Core Team, 2012) and CAP (Anderson, 2003) statistical software packages enabled all the computations.

3. Results

A total of 74 species and morphospecies were counted and identified in the studied period. The benthic invertebrate assemblage was mainly composed by *Paranadrilus descolei* (clearly the dominant species), *Limnodrilus hoffmeisteri*, *Limnodrilus udekemianus*, *Aulodrilus pigueti* (sub-family Tubificinae), *Dero (Aulophorus)lodeni*, *Dero* sp. I, *Pristina americana* (sub-family Naidinae), *Ablabesmyia* sp I (family Chironomidae), *Pisidium sterkianum* (family Sphaeriidae), *Campsurus violaceous*, *Campsurus* sp. I (family Polymitarcyidae), *Bothrioneurum americanum* (sub-family Rhyacodrilinae), and *Limnoperna fortunei* (Bivalvia, family Mytilidae).

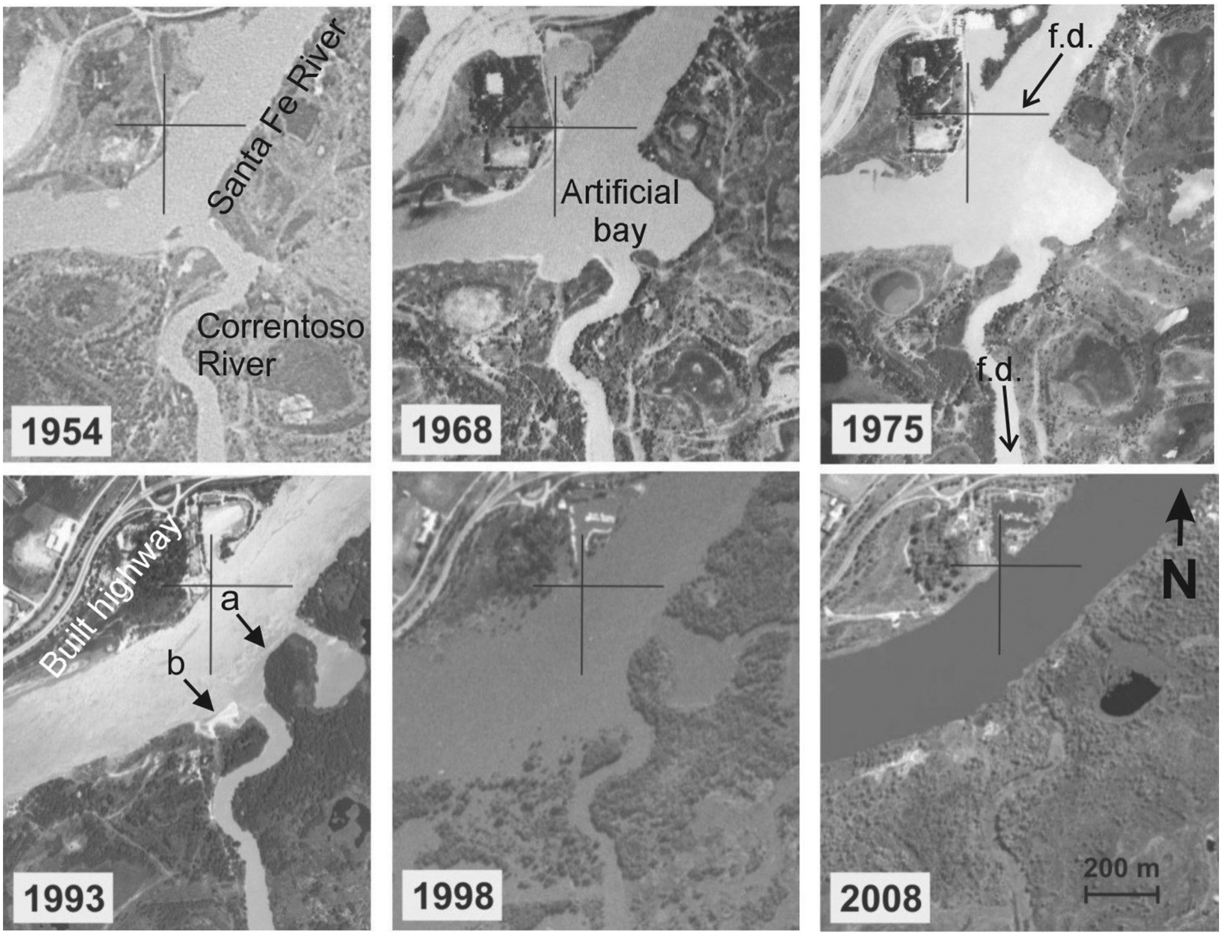

Fig. 4. Sequence of aerial pictures (aircraft) and satellite image (QuickBird) at the Correntoso River inlet from 1954 to 2008. The water level for each picture was, 1954: no available data, 1968: 1.2 m, 1975: 3.42 m, 1993: 3.91 m, 1998: 7.08 m, and 2008: 2.6 m at Santa Fe port. Courtesy of the Argentinean Air Force, II Aerial Brigade. f.d.: flow direction.

Table 1
Density, number of species and diversity values for samplings performed before and after 1990 on banks and central strip areas.

Sampling location	Density (ind m^{-2})	H index	Richness
Central strip	4320	0.46	32
Banks	1569	0.64	42
Before 1990	4320	0.54	26
After 1990	773	1.04	43

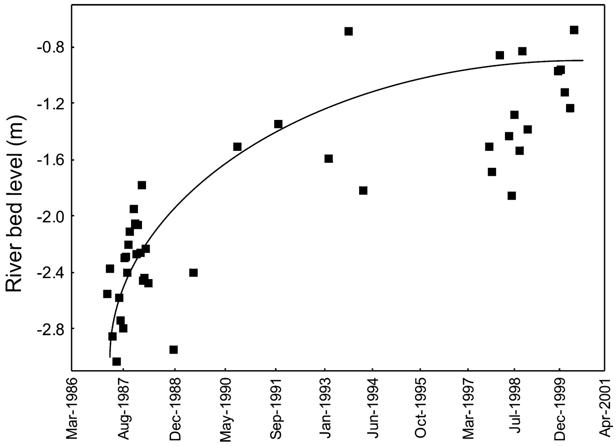

Fig. 5. Evolution of the Correntoso River bed quota during the period of study.

The remarkable occurrence of the alien mussel species *L. fortunei* at the central strip of the channel with significant mean densities (130 ind. m^{-2}) in November 1997 is to be noted.

Table 1 shows comparisons of density, richness and diversity (H index) between samplings among banks and central strip locations performed before and after 1990. The appraisal between banks and the central strip was made only considering samples obtained before 1994. This limitation was due to the lack of available samples at both banks after 1994.

Fig. 3 shows the density box plots of the comparisons between banks and central strip stations, taking into account only the ten most abundant species. When the total invertebrate densities between banks and central strip stations are compared (through ANOVA) a lightly but significant difference arises (Fig. 3, inset panel).

As mentioned above, this relationship was performed considering only the period from 1987 to 1994.

Morphological evolution at the Correntoso River inlet (located 1.6 km upstream from the studied reach) is shown in Fig. 4. It was assessed through the comparative analysis of six aerial and satellite photographs taken in 1954, 1968, 1975, 1993, 1998 and 2008. Due to this analysis a non-natural morphological alteration was identified, and therefore more information was necessary in order to explain it. According to the collected information from 1960s newspapers (Historical Archives of Santa Fe city) and interviews with the Port and Waterways Government Agency staff (Santa Fe province), a series of sediment dredging on the Correntoso River inlet was performed from January 1963 to November 1964, removing 1,300,000 m^3 of fluvial sediments. The purpose of this dredging was to fill out (reclamation) and stabilize the right bank of the Santa Fe River in order to build up the flooding protection required for the construction of “Avenida Circunvalación Mar Argentino” highway. This highway links Santa Fe with Santo Tomé cities, bordering 4.5 km of Santa Fe River right bank. The mentioned river dredging created a relatively large “artificial bay” at the inlet of the river (see 1968 and 1975 pictures). Furthermore, 1993 and 1998 pictures reveal a sedimentation process due to a natural morphological evolution of the river inlet, probably increased by the large flooding (ENSO) in 1983. It is postulated herein that this morphological evolution changed the diversion angle of water and sediments from the Santa Fe River to the Correntoso River. Note also that the Santa Fe River curve changed through time, becoming less pronounced (see complete sequence of pictures). Finally, 2008 image shows the river inlet and channel completely clogged by floating as well as rooted macrophytes.

Fig. 5 shows an average reduction of the river bed level of ≈1 m through the studied period (for methodological details see the Appendix). This bed level diminution started around 1990 and was emphasized along the following ten years, making 1990 a key year in this study.

Fig. 6 shows the relationships between the percentages of sand in bed sediments against the bed and water levels, before and after 1990. The reduction of bed levels is associated with higher amounts of sand in bed sediments after 1990 (A). ANOVA results (not shown in the figure) confirm this statement ($p = 0.001$). Fig. 6B depicts the relationship between sand percentages and water stages. The higher percentages of sand in sediments for all water stages after 1990 are clearly seen.

The PCA ordination (Fig. 7) of physical and chemical variables explained almost 70% of the data variance by the first two principal component axes, following Kaiser–Guttman axes selection. Axis 1 (eigenvalue = 4.7) accounted for 48% of the variance. Environmental

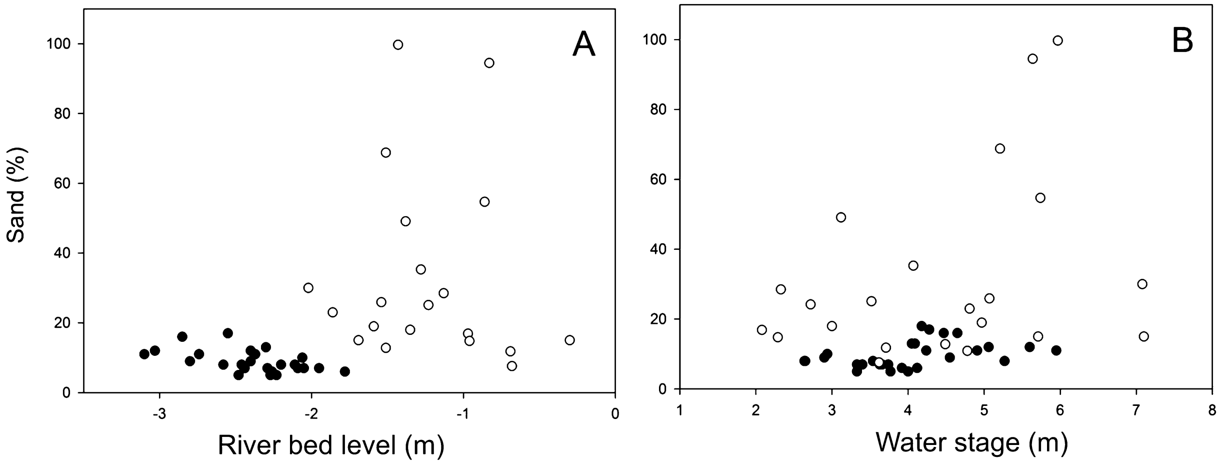

Fig. 6. Percentage of sand in sediments versus water level (A) and bed quote values (B), before 1990 (black circles) and after 1990 (white circles).

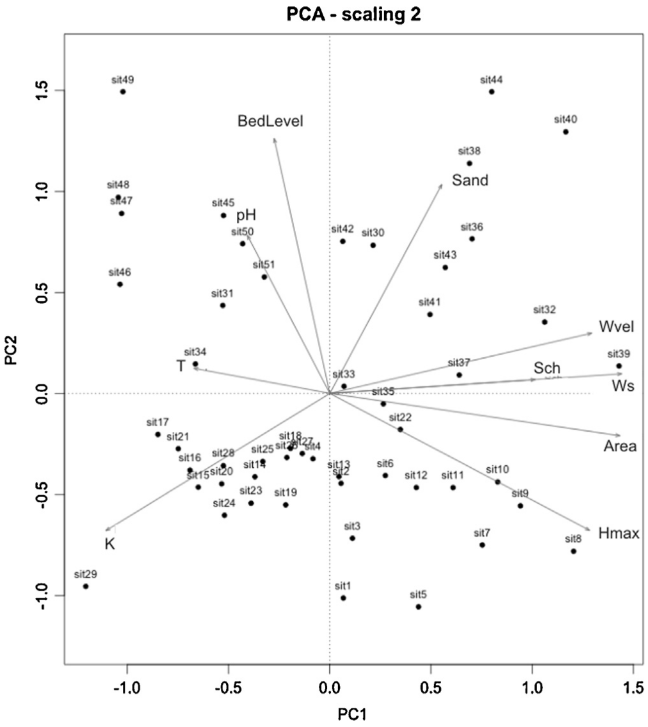

Fig. 7. Plot of score distributions along the Principal Components Analysis (PCA) axes for the physical variables (see Table 2 for score values). T = temperature, sand = percentage of sand in sediments, Wvel = water velocity, Ws = water stage, Sch = Secchi disk, Area = area, Hmax = maximum depth and K = water conductivity. Sit1 to Sit30 = dates from February 1987 to September 1990. Sit31 to Sit51 = October 1991 to May 2000.

variables, water conductivity, water stage, reach area, maximum depths, and water velocity had significantly positive loadings on this axis (with the exception of conductivity; Table 2). The variance explained by axis 2 (eigenvalue = 1.9) was 20%. Significant loadings on axis 2 represented a positive gradient of increasing bed level, pH and sand percentage.

Fig. 8 shows the density box plots of the main species assemblage found at the central strip of the channel, before and after 1990. Note that densities of *P. descolei*, *L. hoffmeisteri*, *L. udekemianus*, *A. pigueti*, *D. lodeni*, *P. Americana* and *Dero* sp. I notoriously decreased after 1990. Conversely, only *C. violaceous*, *B. americanum* and *L. fortunei* increased their densities after 1990. Particularly, this last species comes out as part of the river system in 1997. The inset panel shows the box plot and ANOVA results of the comparison between total invertebrate densities in both periods. Clearly, there is a significant reduction ($p = 0.001$) of the total benthic density after 1990.

Table 2
Structure coefficients of variables measured in the study for the first three principal components of the PCA. Structure coefficients are the correlation between the original variable and the principal component (see text for complementary explanations).

Variable	Principal component 1	Principal component 2
Secchi disk (Sch)	1.01	0.06
Temperature (T)	−0.67	0.12
Conductivity (K)	−1.1	−0.67
Percentage of sand (sand)	0.55	1.03
Water stage (Ws)	1.44	0.09
pH	−0.4	0.78
Reach area (Area)	1.43	−0.2
Maximum depth (Hmax)	1.28	−0.67
Water velocity (Wvel)	1.29	0.29
Bed level	−0.27	1.26

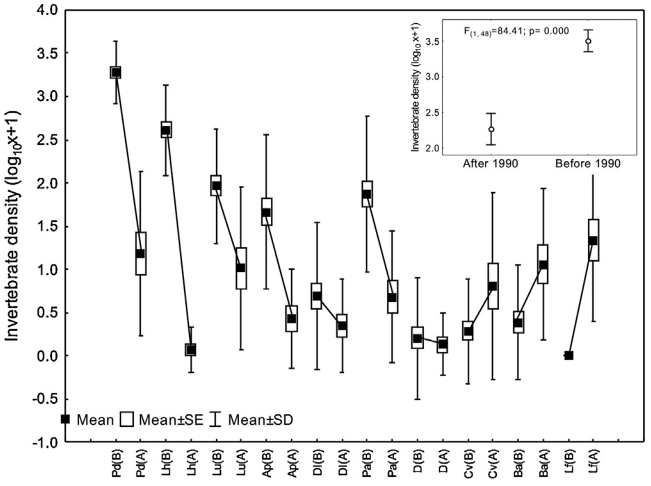

Fig. 8. Box plots of the invertebrate densities at the central strip of the Correntoso channel. More abundant species are considered and compared between them before and after 1990. The inset graph shows the ANOVA result of the same comparison but taking into account the total invertebrate density. Vertical bars denote 0.95 confidence intervals. Pd = *Paranadrilus descolei*; Lh = *Limnodrilus hoffmeisteri*; Lu = *Limnodrilus udekemianus*; Ap = *Aulodrilus pigueti*; Dl = *Dero* (*Aulophorus*) *lodeni*; Pa = *Pristina Americana*; D = *Dero* sp. I; Cv = *Campsurus violaceous*; Ba = *Bothrioneurum americanum*; and Lf = *Limnoperna fortunei*.

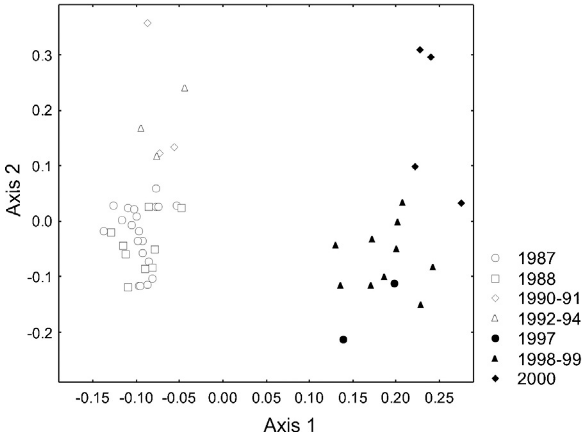

Fig. 9. Constrained ordination plot of the first two canonical axes produced by the Canonical Analysis of Principal coordinates (CAP) showing two significant and different groups of invertebrates ($p = 0.001$), since 1987–1994 and 1997–2000.

The CAP result indicates that there is a significant difference ($T = 3.103$, $p = 0.001$) in the composition and relative abundance of invertebrates before 1994 and after 1997 (Fig. 9). However, the incomplete data recorded from 1990 to 1997 (three samplings from 1990 to 1992, two in 1993, and only one in 1994) should be noted, together with the absolute lack of data from March 1994 to October 1997 (Fig. 2).

4. Discussion

The general benthic invertebrate assemblage found in this study is coincident with that reported by Ezcurra de Drago et al. (2007) for minor channels of low hierarchy in the Paraná River floodplain. According to Marchese and Ezcurra de Drago (1992), Marchese et al. (2002) and Blettler and Marchese (2005) in secondary channels of the Paraná floodplain with a mean discharge > 500 m^3 s^{-1} (Drago et al., 2003), the benthic assemblages inhabiting the central strip and banks are remarkably dissimilar from each other. While this dissimilarity was also recorded in the Correntoso (Table 1), it was scarcely notorious concerning the species composition. The most densely represented species at both locations are detailed in Fig. 3. This fact would be due to the significantly smaller discharge of the Correntoso (94 $m^3 s^{-1}$) in relation with the discharge cited above (>500 $m^3 s^{-1}$), required for great benthic assemblage differences. The low discharge reduces the morpho- and sedimentological differences between banks and central strip habitats, making them similar bottom environments (for instance, there is a similar sand percentage at both locations). In spite of this, some species like *P. descolei*, *L. hoffmeisteri*, *A. pigueti*, *P. americana* and *Ablabesmyia* sp. 1 were clearly more abundant at the central strip (Fig. 3).

As Fig. 4 shows, a deep anthropic impact modified the physical conditions of the Correntoso River in the early1960s. The morphological analysis, taking into account the aerial pictures sequence (Fig. 4) and daily water stages during the studied period (Fig. 2), suggests a morphological evolution of the river inlet tending to fill the man-made dredged bay. This phenomenon was coupled by a slight straightening of the Santa Fe River channel (see 1993, 1998 and 2008 pictures), with its likely thalweg migration. The 1993s picture shows an advanced sedimentation-filling, with emergence of sand bars with the successive vegetal colonization (arrow "a"). Sand bars are usually colonized by pioneer species like *Salix humboldtiana* and *Tessaria integrifolia* in a successional process, which is relatively common and well known in the Paraná floodplain (Marchetti and Aceñolaza, 2011). Note that slightly downstream another sand sediment bar, not yet colonized by vegetation, is located (arrow "b"). Additionally, satellite images from 1988 and 1990 were also analyzed (not shown herein due to their low resolution; 1 pixel = 30 × 30 m). Both images showed similar inlet geometry to 1993 picture, suggesting more favorable conditions for suspended sand inflow from the Santa Fe River around 1990. Finally, 2008 image shows the river inlet almost completely plugged and covered by floating and rooted macrophytes, making it a quasi-lentic environment.

At this part of the discussion and considering the above morphological description, it is suitable to analyze the hydrological fluctuations which occurred during the last decades. In the Middle Paraná the four recorded largest floods (driven by ENSO events) occurred in 1905, 1983, 1992 and 1997/8 (Robertson et al., 2001; Barros et al., 2006). With the exception of 1905 flood, all the others took place during the decades considered in this study for the morphological analysis (Fig. 4). The 1983 flood was the largest ever recorded in the Paraná River system, with discharges larger than 30,000 $m^3 s^{-1}$ with maximum up to 60,000 $m^3 s^{-1}$. It transported enormous amounts of sand throughout the system, being the total bed sand transport more than twice the average; Alarcón et al. (2003) surely contributing largely to the filling of the artificial bay and to the buildup of the new Correntoso River inlet above described (1993 image in Fig. 4). Considering the daily water levels (Fig. 2) 1992 and 1997/8 floods can be compared, as they have similar maximum levels (7.43 m and 7.26 m, respectively) and monthly discharges (26,787 $m^3 s^{-1}$ and 22,999 $m^3 s^{-1}$, respectively; Barros et al., 2006), although a clear difference exits in their durations. Indeed, 1992 flood lasted 155 days with levels higher than the overflow level (≈4.5 m in Santa Fe port gauge; Paira and Drago, 2006), whereas 1997/8 flood remained 271 days over that level, i.e. a flooding time almost 60% larger. The 1997 ENSO event began and continued during the first part of 1998 and caused large discharges in the Paraná River during that period (Barros et al., 2006). However, it was followed by negative rainfall anomalies over most of the basin during 1999 prompting drought conditions and small flows.

Considering the morphological evolution and hydrological fluctuations above explained, it is proposed herein that the artificial bay at the Correntoso river inlet has acted like a sedimentation basin with decreasing flow velocity. Thus, this depositional area, allowed the formation of sandy bars. In addition, these phenomena acting in conjunction could also help to explain the bed level reduction (Fig. 5) and the increasing sand percentages on the Correntoso River bed after 1990 (Fig. 6A and B). The natural morphological evolution of the system, given mainly by ENSO phenomena, partially filled with sandy sediments the artificial bay (see Fig. 4). This event reconfigured the inlet geometry, enabling a higher entry of suspended sands into the Correntoso channel. However, as the average discharges in the Correntoso were reduced after 1990, these sediments finally deposited along its channel mainly throughout the central strip, including the straight section studied, 1.6 km downstream the river inlet.

The flow conditions in the Correntoso River changed around 1990, reducing its flow velocities and discharges (see Appendix for quantitative information, Table A1 and Fig. A2). Reductions in flow velocities and discharges imply decreases in the flow capacity to transport suspended sands with the consequent sand deposition. This phenomenon coupled with the gradual but continual morphologic evolution of the river inlet (above described) explains the bed level reduction and sand deposition along the channel from 1990 onwards. Thus, the river bed was partially refilled (≈1 m high) with sediments composed by 32% of sand. It is worth noting that before 1990 the sand bed percentages at the same place were only 9.5%; i.e. more than 3 time less (see Figs. 6A and B, and 7).

Considering all the above information, it is postulated herein that the close interaction of morphologic evolution, extraordinary hydrologic events and bed sedimentology led to strong invertebrate ecological changes in the Correntoso River, which began around 1990. Thus, densities of the species assemblage notoriously decreased after 1990 (Fig. 8, inset plot). However, three particular species increased their densities: *C. violaceous*, *B. americanum* and *L. fortunei* (Fig. 8). *C. violaceous* is a gathering collector and probably the most important feeding group in secondary channels in the Paraná floodplain. It has been previously collected in bottom sediments with low organic matter content, without hypoxia periods and flowing waters (Ezcurra de Drago et al., 2007). Herein, *C. violaceous* and *B. americanum* increased their densities with the increasing supply of sands from the Santa Fe River (Figs. 7 and 8). On the contrary, the densities of *P. descolei*, *L. hoffmeisteri*, *L. udekemianus*, *A. pigueti* and *P. Americana*, showed a remarkable decrease after 1990 (Fig. 8), also probably due to the bed composition changes. Though more studies are needed, some of these species have the potential to be used as biotic indicators of physical alterations in the environment in secondary channels of the Paraná River system.

The mussel *L. fortunei* appeared for the first time at the Correntoso River in November 1997 (Fig. 8) and deserves special attention considering that it is an alien species. This filtering collector was found in the Middle Paraná River floodplain since 1996, quickly reaching high population densities (Darrigran et al., 1999; Darrigran and Ezcurra de Drago, 2000). The alluvial plain provides a great diversity of substrates colonized by *L. fortunei* during high water phases, supporting its exponential development (Montalto et al., 1999). In agreement with this, it was observed herein that during ENSO 1998 this species reached the highest population densities. Viewing these features it is not possible to know the reasons for the presence of *L. fortunei* in the Correntoso River: either the shifting bed conditions after 1990 prompted its appearance or, simply, it invaded and colonized the Paraná floodplain after 1996.

In spite of the deep morphological and sedimentologic changes starting around 1990, the CAP results (Figure 9) showed a significant benthic fauna depletion since 1997. This multivariate analysis clearly arranged two invertebrate groups along a time gradient which are significantly different from each other ($p = 0.001$). One of them gathers the benthic fauna present in the channel bed between 1987 and 1994 and the other corresponds to those invertebrates found between 1997 and 2000.

Once again, considering all the above information a lack of an exact correspondence between sedimentologic and fauna changes arises (see Figs. 5, 6 and 9). However, it could be explained if three key facts are taken into account. Firstly, there is not data enough to find clear tendencies or to set conclusive statements between 1990 and 1996 (a transitional period?) with only 5 available benthic sampling events (equivalent to 15 sub-replicates). Secondly, the effect of sedimentologic/morphologic changes and hydrodynamic fluctuations on benthic organisms should not be treated like an instantaneous reaction to physical active forces (action–reaction law), but rather as an ecological relationship with a considerable delay between action and reaction. This delay is given by a certain time reaction and tolerance degree (ecological resistance) by organisms to environmental changes. Thirdly and perhaps the most important: the duration of the ENSO 1997/8 event, previously explained. The large extension of this flooding event (271 days) was a key factor to definitely imprint more sandy conditions to the Correntoso channel bed (Fig. 6B), i.e. washing downstream the bed fine sediments. This flooding event should be viewed as the end of gradual morphologic and hydrologic processes triggered by the original human impact during the 1960s at the river inlet. This chain of disturbances was the key structuring force for the channel bed ecology, which likely started in 1990 but was very noticeable after 1997. These results ratify seminal concepts about the importance of floods and morphologic processes for lotic ecology and time scales of environmental-ecological fluctuations (Lake, 2000; Plachter and Reich, 1998; Ward, 1998; Harris et al., 2000; Ward and Tockner, 2001).

The PCA results support the statements about the existence of remarkable environmental changes after 1990 (Table 2 and Fig. 7). Actually, the plot shows a temporal environmental gradient with large variations starting that year. The differences of sand content in bed sediments, water depths, and water conductivity values are noteworthy. However, all conductivity values are within the tolerance range for benthic macroinvertebrates of the Middle Paraná floodplain (75–540 μS cm^{-1}; Ezcurra de Drago et al., 2007). Whereby, it is not an explanatory variable for the invertebrate changes recorded in this study.

Summarizing, at a basic level the floodplain system is best viewed as a dynamic and complex environment where processes of large-patch and long-term creation/recreation events operate together. These processes and events result from a balance between rejuvenation periods (flood pulses), morphological evolution and human impacts, coupled with sediment changes and stabilization. In the Correntoso River system this balance led to a shifting mosaic of physical habitats colonized by biota according to its characteristics at different time scales.

5. Conclusions

(i) In spite of an ecological dissimilarity between the central strip and banks was recorded in the Correntoso River, it was only significant for densities but slightly notorious respecting the species composition.

(ii) The man-made dredging zone at the Correntoso River inlet created a large sedimentation area preventing the inflow of suspended sand. However, the natural morphological evolution during the next decades reconfigured the inlet morphology, allowing the gradual supply of increasing sand rates into the channel. Coupled with this fact a reduction of 60% in discharges after 1990 (from 7.2 to 4.7 m^3 s^{-1}, at 6 m Santa Fe Port) resulted in suspended sand sedimentation, turning the bed sediment composition into a more sandy condition.

(iii) Three large floods (1983, 1992 and 1997–8) consequence of ENSO phenomena would have deeply influenced the natural morphological evolution of the river inlet.

(iv) The interaction of human and natural long-term processes (as described in ii and iii), had a great ecological impact on the benthic fauna in the Correntoso River promoting its density reduction (from 4320 to 770 ind. m^{-2}) and the species replacement ($T = 3.103$, $p = 0.001$).

(v) Due to their ecological requirements, several benthic species were detected as potentially suitable bio-indicators of physical alterations in secondary channels of the Paraná River system: *C. violaceous*, *B. americanum*, *P. descolei*, *L. hoffmeisteri*, *L. udekemianus*, *A. pigueti* and *P. Americana.*

(vi) This research shows the value of long-term data series in ecological studies provided that the different spatial and temporal scales inherent to each process are properly considered.

(vii) The interdisciplinary point of view linking fluvial geomorphology, hydrology, sedimentological and ecological engineering used in this study is remarked. It is particularly useful (if not essential) to aid understanding of the environmental legacy of anthropogenic modifications in river systems.

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Appendix A. Hydraulic characterization of the studied reach

Mean flow velocities ($\bar{u}$) and depths (h) measured at the central station of the studied cross section (Fig. A1) enabled to estimate hydraulic changes through time and to appraise the suspended sand sedimentation along the Correntoso River channel.

Mean velocities and unit discharges ($q = \bar{u}h$) against water stages (as measured in the Santa Fe port gauge) are shown in Fig. A2a and b, respectively. The reductions of velocities and discharges after 1990

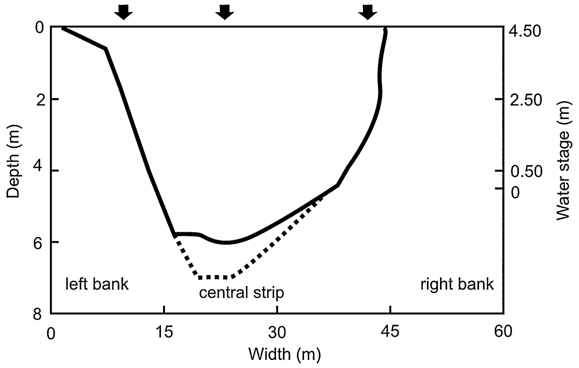

Fig. A1. Cross section and sampling stations at the studied reach (see Figure 1 for location). Dotted line: section before 1990. Full line: section after 1990.

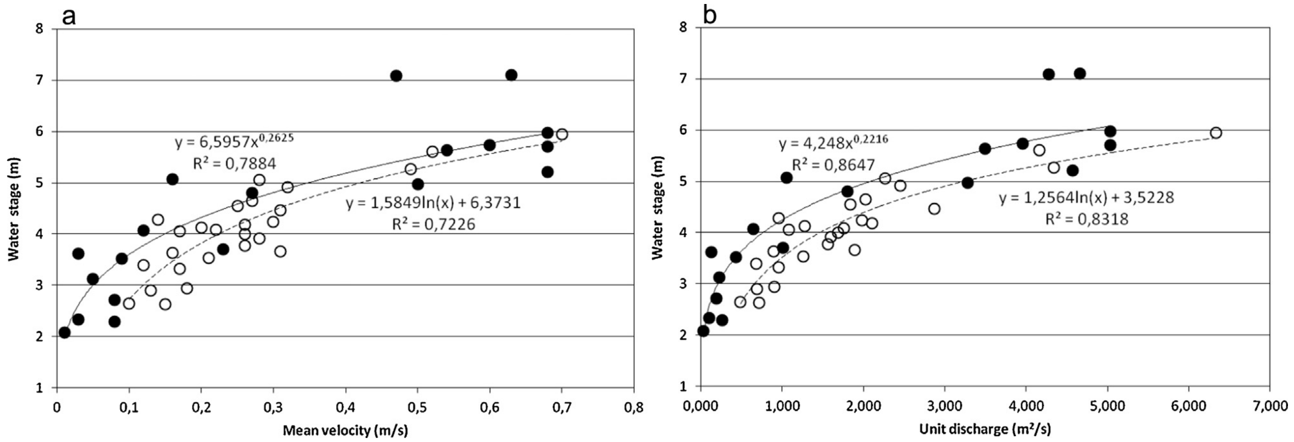

Fig. A2. (a) Mean velocities measured at the central station of the studied cross section against water stages. White circles: velocities before 1990 Full circles: velocities after 1990. (b) Unit discharges measured at the central station of the studied cross section against water stages. White circles: discharges before 1990. Full circles: discharges after 1990. Best fitness equations are included.

Table A1
Average values of mean flow velocities, unit discharges and suspended sand transport parameter of Van Rijn (2007), computed before and after 1990 for different water stages at the central station of the studied cross section. Reductions after 1990 are included.

Water stage (m)	Before 1990			After 1990			$\Delta\bar{u}$	Δq	$\Delta(\bar{u}-u_c)^3$
	$\bar{u}$ (m s^{-1})	q (m^2 s^{-1})	$(\bar{u}-u_c)^3$ (m^3/s^3)	$\bar{u}$ (m s^{-1})	q (m^2 s^{-1})	$(\bar{u}-u_c)^3$ (m^3/s^3)	(%)	(%)	(%)
2	0.063	0.30	–	0.011	0.033	–	82.5	89	–
3	0.12	0.66	–	0.050	0.21	–	58.3	68	–
4	0.22	1.46	–	0.15	0.76	–	32	48	–
5	0.42	3.24	0.0049	0.35	2.07	0.001	17	36	80
6	0.79	7.18	0.16	0.70	4.71	0.091	11	34	43

(full circles) are clearly seen. The average values of these reductions for different water stages were computed with the best fitness equations included in Fig. A2a and b (Table A1).

Diminutions in flow velocities and discharges imply decreases in the flow capacity to transport suspended sands which were appraised with the empirical relationship:

$$g_s \propto (\bar{u} - u_c)^3 \qquad \text{(A1)}$$

where: g_s = suspended transport; $\bar{u}$ = depth average velocity (m s^{-1}); u_c = critical depth-average velocity = 0.25 m s^{-1}. Relation (1) was set by Van Rijn (2007) with high-quality field data from rivers around the world. Depths and sizes of suspended sands ranged between 1 and 15 m and 60–600 μm, respectively. Szupiany et al. (2012) reported frequent median diameters between 80 and 150 μm of suspended sand particles in the middle reach of the Paraná River system, which may be considered as those entering in the Correntoso channel from the Santa Fe River (see Fig. 1). When the transport parameter $(\bar{u} - u_c)^3$ is computed with the average velocity values of Table A1 it is noted that perceptible suspended transport of sands would begin from a water stage of 4 m on. Moreover, a reduction of less than ≈20% of flow velocities at these stages after 1990 means decreases of suspended sand transport between 40% and 80%.

With stages lower than ≈4 m, most sand entering in the Correntoso River would be transported as bed load according to the widely known Hjulström (1935) diagram of critical average velocities for erosion and deposition of different particle sizes. The diagram predicts deposition of bed load when flow velocities fall to 0.61–1.15 m s^{-1} and particle diameters between 80 and 150 μm. Note in Table A1 that velocity values reduce near this lower limit of deposition for water stages in the range of 2–3 m after 1990.

Summarizing, the above analysis combining measurements and classic concepts of fluvial hydraulics prove quantitatively that flow conditions in the Correntoso River were changing around 1990 in such a way as to favor the sand deposition from the bed load and/or suspension after that year. This result should be viewed within the context of an increasing sand supply from the Santa Fe River due to the gradual morphologic alterations of the Correntoso River inlet above described in the text.

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