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Hydrodynamic and morphologic effects on the benthic invertebrate ecology along a meander bend of a large river (Paraguay River, Argentina–Paraguay)

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ABSTRACT

A detailed hydro-ecological study to identify the effects of bed flow and morphodynamic processes on the distribution (and composition) of benthic invertebrates in a large river is presented herein. A crossing-pool sequence in a meander bend of the Paraguay River (Paraguay–Argentina) was examined. According to the results, there is a link between the benthic fauna, hydraulic and bed sediment size along the bend. The meander pool, with a deep scour hole and the largest bed shear stresses, would be a hostile area for benthic invertebrates, since lower densities were found there. A transversal analysis revealed two different invertebrate assemblages at each of the sampled cross sections: one across the mobile bottom with higher densities but lower diversity, richness and evenness than the other one found close to the banks. On the other hand, a comparison between both Paraguay and Paraná rivers revealed that the first one would seem to have optimal hydraulic conditions for the invertebrate's development, because the hydraulic energy of the Paraná River was too intense for the favorable settlement of benthic organisms at some specific habitats. The overall conclusion of this paper, that morpho-hydraulic features and biotopes are related, is an important step forward in river ecohydrology. With further development of this concept, river management techniques can improve and river rehabilitation projects can be designed with greater confidence.

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1. Introduction

Engineers and scientists have long been attracted to meanders since they are common and widespread elements in natural rivers. An excellent summary of early studies made in the late 19th and first half of 20th centuries about meanders can be found in Leliavsky (1964). Later on, Naot and Rodi (1982), Demuren and Rodi (1986), Odgaard (1984, 1986, 1987), Barkdoll et al. (1999), Duc et al. (2004) made some specific contributions on general aspects of the hydro- and morpho-dynamic of meanders. Darby et al. (2000, 2002) and Darby and Delbono (2002) studied the stability and erosion of meandering rivers' margins. Ikeda et al. (1981), Parker et al. (1982), Parker and Johannesson (1989) and Johannesson and Parker (1989) built mathematical models regarding the meander's origin and evolution. Most of these models are 1D, however 3D models have been developed more recently (Wu et al., 2000; Olsen, 2003; Rüther and Olsen, 2005). Finally, avulsion and rectification of meanders were studied by Drago et al. (2003) and Ramonell and Amsler (2005) in the Paraguay–Paraná hydrosystem.

It is widely known that natural meanders have specific land-form features: (i) the crossing areas at the meander's head and tail (upstream and downstream, respectively) with relatively regular cross-sections; and (ii) the pool area located slightly downstream from the middle point of the bend with a strongly asymmetric cross-section. This asymmetry is characterized by a point bar on the convex side and a deep hole near the concave bank (Carson, 1986; Bridge, 2003; among others). Erosion along the concave bank occurs due to fastest convective water flows and secondary currents (Henderson, 1966). The degree of bank retreat and pool erosion depend on the resistance of the concave bank materials (Nanson and Hickin, 1986), the flow duration and magnitude (Odgaard, 1987, 1989), the radius of curvature (Odgaard, 1987), and the flow capacity to transport bed materials (Neill, 1984). Thus, bend dynamics (amplitude changes and/or downstream migration rates) is a discontinuous process.

Studies linking the distribution, diversity and body morphology of benthic organisms with hydraulic stresses, eco-hydraulic, have been published by Statzner et al. (1988), Wetmore et al. (1990), Lancaster and Hildrew (1993), Growns and Davis (1994), Hart et al. (1996), Kawamura et al. (2003), Mérigoux and Dolédec (2004), Dolédec et al. (1999, 2007; among others) based on measurements made in relatively small streams. On the other hand, the
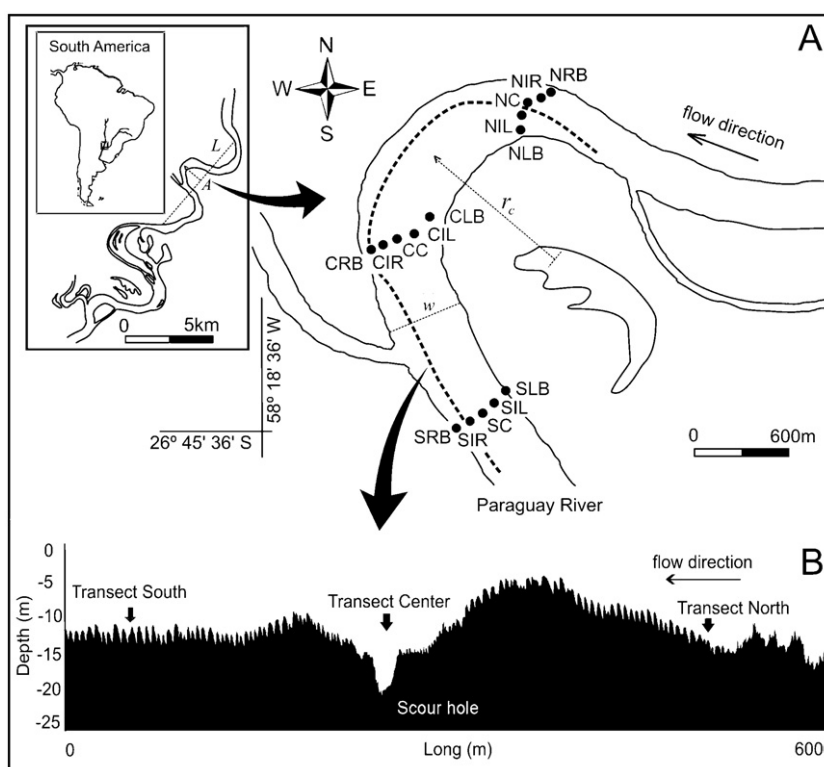
Fig. 1. (A) Location and details of the sampling stations at the selected meander, in a plant view. (B) Longitudinal bathymetric profile showing the position of the studied cross sections.

association between these two aspects in relation with morphology units is relatively unexplored. This is probably attributable to the low attention ecologists have paid to hydraulics, or geomorphologists to biotic interactions. In addition, there is currently poor knowledge regarding meso-scale, such as riffles (or crossings) and pools (Kemp et al., 2000).

As for large rivers, a strong connection between bed hydraulic conditions and invertebrate ecology in the Middle Paraná River and other secondary channels and tributaries (all around its basin) was described by Blettler et al. (2008) and Amsler et al. (2009). In addition, a few years earlier Takeda et al. (2001) and Stevaux and Takeda (2002) reported an inverse cause–effect relationship between discharge and benthic densities in the Upper Paraná River.

Establishing a certain relationship between physical features and the functional composition of invertebrate communities has strong implications for river restoration. This linkage could therefore be used to develop unified biomonitoring tools at different morphological units and scales (e.g., meander bends), thus covering areas at a larger geographical scale (Dolédec et al., 1999). Attempts to protect and partially restore large rivers must be based on ecological knowledge. One promising approach is to designate critical areas for special protection like riverine meanders (Thorp, 1992). Consequently, the present study focuses on the influence of hydro- and morphodynamic processes on the spatial distribution patterns of benthic invertebrates along a large river meander bend. In the context of river restoration the recreation of physical habitat must be achieved through an understanding of both form and function of meanders. Understanding the hydro-geomorphic structure and ecological relationships of rivers at meander level represents a significant potential for optimizing river rehabilitation and management strategies. Actually, if suitable data are available for bed shear stress, velocity, water depth or other key characteristics, a reliable eco-hydraulics model can be developed for invertebrates

(Bockelmann et al., 2004). This paper is a seminal contribution on the subject in a large river like the Lower Paraguay.

2. Methodology

2.1. Sampling site

The studied meander is located on the Lower Paraguay River, 15 km upstream the Bermejo River confluence (26° 45′ 36″S to 58° 18′ 36″W). The Lower Paraguay River is 331 km long from Punta Ita-Pirú (Paraguay) to its confluence with the Paraná River (near Corrientes city, Argentina). Its meandering channel drains by a large alluvial floodplain and it is 575 m wide (2700 m maximum and 260 m minimum) and 9 m depth (Drago, 1990) on average, with a mean discharge of 4000 m³ s⁻¹ (Giacosa et al., 2000). The benthic sampling and flow measurements were performed in October 2007 at three selected cross sections along the meander bend: transect North (crossing zone, at the bend head), Center (pool zone), and South (crossing zone, at the bend tail; Fig. 1A and B).

A low and relatively steady water stage (Q = 1700 m³ s⁻¹) was recorded during the study. The selected bend is characterized by the following morphologic variables: amplitude (A) = 3100 m, average width ($\overline{w}$) = 510 m, average curvature radius (r_c) = 1090 m, and axial wave length (L) = 6200 m. A and L values were measured considering the next upstream bend according to Bridge (2003). Sampling and measurements were made at five stations across each transect. These stations were named according to their positions in the cross section, i.e. left bank (LB), intermediate left (IL), central (C), intermediate right (IR) and right bank (RB); the letters N, C or S refer to the corresponding transect, i.e. N = North; C = Center; S = South (see Fig. 1).

Longitudinal and transversal bathymetric profiles along the bend are shown in Figs. 1B and 2, respectively. Dunes with the
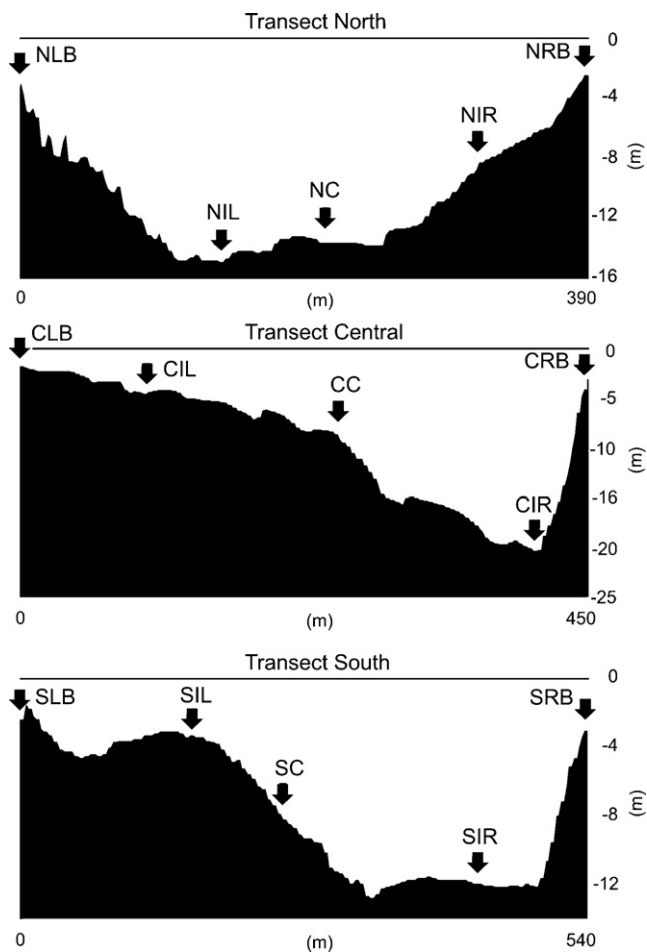
Fig. 2. Bathymetric profiles of the selected meander cross sections showing the location of the sampling stations. Note the marked asymmetric profile of transect Central.

following average dimensions were recorded: 30 m long–0.8 m high (transect North), and 50 m long–1.4 m high (transect South). Note that dunes have smaller dimensions along the scour hole where transect Center was located. Regarding the transversal profile, this transect shown the typical asymmetric cross-section, as was described in the Introduction.

2.2. Flow measurements and benthic sampling

The boat positioning at the selected transects was attained using a Furuno GP-1650WF echo sounder coupled to a GPS, checking the coordinates together with flow depths at each sediment and benthic sample. Details of the river bed topography were previously surveyed through the software package Fugawi Marine version 4.5 (Northport Systems Inc., 2007). Measures of current velocity profiles were obtained by using an electrical propeller current meter, simultaneously with the benthic samples. A total of 9–16 point velocities (depending of the local depth) were recorded in the water column at each verticals, with measurements more closely spaced in the first one meter from the bottom. Each point velocity was the average value of a 100 s measuring interval.

Three benthic sample 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 from Noreña, 1995, and Noreña et al., 2005; for Oligochaeta from Brinkhurst and Marchese, 1992; and for Diptera Chironomidae from Trivinho-Strixino and Strixino, 1995). The determinations for other taxa were made till genus and morphospecies level (taxonomic species based wholly on morphological differences from related species). Additional sediment samples for granulometric analysis (by dry sieving) and organic matter estimation (by ignition and subsequent ash-free dry matter weight; g C%), were taken at the same sites.

The following additional variables were also recorded in order to characterize chemically the environmental health: conductivity (μS cm^{-1}), pH, temperature (°C), dissolved oxygen (mg l^{-1}), transparency as given by the Secchi disk (Secchi disc transparency, m), total dissolved solids (mg l^{-1}), total Alkalinity (mg l^{-1} Ca CO$_3$), bicarbonate (Ca CO$_3$ mg l^{-1}), Carbonate (CO$_3$ Ca mg l^{-1}), Chloride (mg l^{-1}), total Hardness (mg l^{-1} Ca CO$_3$), Calcium (mg l^{-1}), Magnesium (mg l^{-1}), Potassium (mg l^{-1}), Silica (mg l^{-1}) and Sodium (mg l^{-1}).

2.3. Selection and treatment of the hydraulic variables

The characterization of the river hydraulics near the bottom at each station was attained by direct measurements of the local velocity profiles, depths (h), bed sediment particle size distributions (d_{50}), and an estimation of the bed forms height at a given site. These parameters are the necessary inputs to calculate hydraulic variables such as the bed shear stress (τ_0), or its equivalent the shear velocity (U_*), the mobility number (τ_*) and the "mobility-velocity number" (τ_{*U}). This last variable is a modification suggested by Yalin (1977) of the conceptually similar mobility number, but with the practical advantage that its estimation is simpler since it is based on the local mean velocity ($\overline{U}$), instead of τ_0 as necessary for the estimation of τ_* (Table 1).

Regarding τ_*, it is a widely known dimensionless variable in river sciences. It involves the relationship between the tractive forces, trying to move the bed particles as given by τ_0, and the particle weight per unit area, as given by ($\gamma_s - \gamma_w$) and d_{50} (passive force) which resist that movement (see Table 1). The reliable estimation of local values of τ_0 in large natural rivers, or the related variable U_*, is not an easy task. Usually, it can be approached trough the well-known relation (Van Rijn, 1993):

$$u = a \, \log \frac{y}{Z_0} \tag{1}$$

which can be expressed in the more standard form (Kostaschuk et al., 2004):

$$u = a \, \log y + b \tag{2}$$

where, u: current velocity point velocity at a distance y from the bottom; Z_0: $k_s/30$ for rough turbulent flow; k_s: roughness length, b: regression coefficient; and a: regression slope between measured velocity points and log y. Theoretically, it was shown that Eq. (1) is valid to $a = 5.75U_*$, provided that turbulent, steady and uniform flow conditions are properly satisfied (Schlichting, 1979; Yalin, 1977). In this sense, Amsler and Schreider (1986, 1992) and Trento et al. (1990) showed the validity of approaching the vertical velocity distribution by a semi-log function at a large stream like the Paraguay River such as Eq. (1). These authors fitted successfully the general expression, from which Eq. (1) is derived, to a large number of vertical velocity profiles measured in the main channel of the Paraná River. In addition, it was made considering a wide diversity of flow and bed conditions. For methodological details see Amsler et al. (2009).

Table 1
Summary of the hydraulic variables measured or computed in the study (a = regression slope from Eq. (2); ρ = water density; γ_s = specific weight of sediment; γ_w = specific weight of water; $s = \gamma_S/\gamma_w$; g = gravity acceleration; d_{50} = median of the bed sediment size distribution).

Name	Symbol	Units	Formula	Description
Current velocity	U	m s^{-1}	Direct measurement	Velocity measured at each point in the vertical profile
Depth	h	m	Direct measurement	Local depth
Shear velocity	U_*	m s^{-1}	$U_* = \frac{a}{5.75}$	An estimate of turbulence intensity close to the bottom
Shear stress	τ_0	kg m^{-2}	$\tau_0 = U_*^2 \rho$	Bed shear stress derived from the shear velocity
Mobility number	τ_*	None	$\tau_* = \frac{\tau_0}{(\gamma_s - \gamma_w)d_{50}}$	Dimensionless relationship between active forces acting on the bed and particles weight
Mobility-velocity number	τ_{*U}	None	$\tau_* = \frac{\overline{U}^2}{g(s-1)d_{50}}$	Version of τ_* using $\overline{U}$ instead of τ_0

In order to apply the simplified version of Eq. (1), i.e. Eq. (2), it is further necessary to define the proper origin of the measured velocity profiles, the so called hydraulic bottom (or virtual origin), since the regression slope a and, thus, the τ_0 (or U_*) accuracy is deeply influenced by that origin (Perry and Joubert, 1963). Depending of the relative submergence and geometry of the bed form at a given site, the virtual origin can be located anywhere between the crest and trough of these bed forms. The ad hoc procedure advanced by Perry and Joubert (1963) to find that origin, was used herein. Previously to the determinations of the virtual origin, the data of the velocity profiles were smoothed using a simple method. For a detailed description of these methodological procedures, see Amsler et al. (2009).

The fitness of Eq. (2) for the measured velocity profiles on the meander active bed (also called central strip), once defined the virtual origins, are presented in Fig. 3. The values of τ_0 were computed based on the a slopes of the fitted curves. Note that it was not possible to fit a semi-log function for the velocity distributions at SIL station.

2.4. Statistical analysis

As the benthic data of density were not normally distributed, they were logarithmically transformed [$\log_{10}(x+1)$] and then checked their normality (Shapiro and Wilk, 1965) and homogeneity of variance (F_{max}; Sokal and Rohlf, 1981). As normality was verified after log transformation, a parametric statistic was applied.

Table 2
Mean benthic densities at each sampling station. The *N. bonettoi* mean density (more abundant species) was also included herein.

Sampling station	Mean benthic density (ind. m^{-2})	Mean *N. bonettoi* density (ind. m^{-2})
North	20,883	14,929
Center	5636	4749
South	20,279	16,828
Central strip	25,769	20,210
Banks	4633	107
North bank left (NBL)	22,847	289
North intermediate left (NIL)[a]	48,216	43,332
North center (NC)[a]	31,764	30,205
North intermediate right (NIR)	964	771
North bank right (NBR)	627	48
Center bank left (CBL)	498	241
Center intermediate left (CIL)	4643	3647
Center center (CC)	2651	2298
Center intermediate right (CIR)[a]	19,569	17,545
Center bank right (CBR)	819	16
South bank left (SBL)	1671	0
South intermediate left (SIL)	48	16
South center (SC)	1558	434
South intermediate right (SIR)[a]	96,786	83,643
South bank right (SBR)	1334	48

[a] Thalweg track.

Thus, ANOVA one way test was carried out (significance <0.05) to determine differences between means of benthic density along the stations of the thalweg track. The post hoc Fisher test was applied to identify the significant differences between the ANOVA results.

In order to find the eigenvectors which maximize the dispersion (inertia) among the different studied sampling stations (to know the similarity level between them), a Detrended Correspondence Analysis (DCA) was carried out (Hill and Gauch, 1980). This ordination technique allows correcting the "horseshoe effect" of the Principal Component Analysis (see technical details in Hill and Gauch, 1980). The computer program Multi-Variate Statistical Package (MVSP) version 3.1 (Kovach, 2002) was used for multivariate analysis.

3. Results

A total of 33 species and morphospecies were identified in the studied meander bend. The taxonomic groups found were Oligochaeta, Bivalvia, Turbellaria, Copepoda, Diptera (Chironomidae, Tanypodinae and Ceratopogonidae), Nematoda, Hydrozoa and Acari. The sampling points located at the active bed of the channel (i.e. IL, C and IR stations, with the exception of SIL station) presented an assemblage composed principally by *Narapa bonettoi*, *Rhyacodrilus* sp (Oligochaeta); *Myoretronectes paranaensis* (Turbellaria); *Tobrilus* sp (Nematoda); *Potamocaris* sp (Copepoda); among others. The assemblage at banks (i.e. LB and RB stations, together with SIL station) were principally composed by *Limnoperna fortunnei* (Bivalvia); *Cordylophora caspia* (Hydrozoa); *Paranadrilus*

Table 3
Shannon's diversity index, evenness and species richness values at each sampling stations, banks, active bed and selected transects.

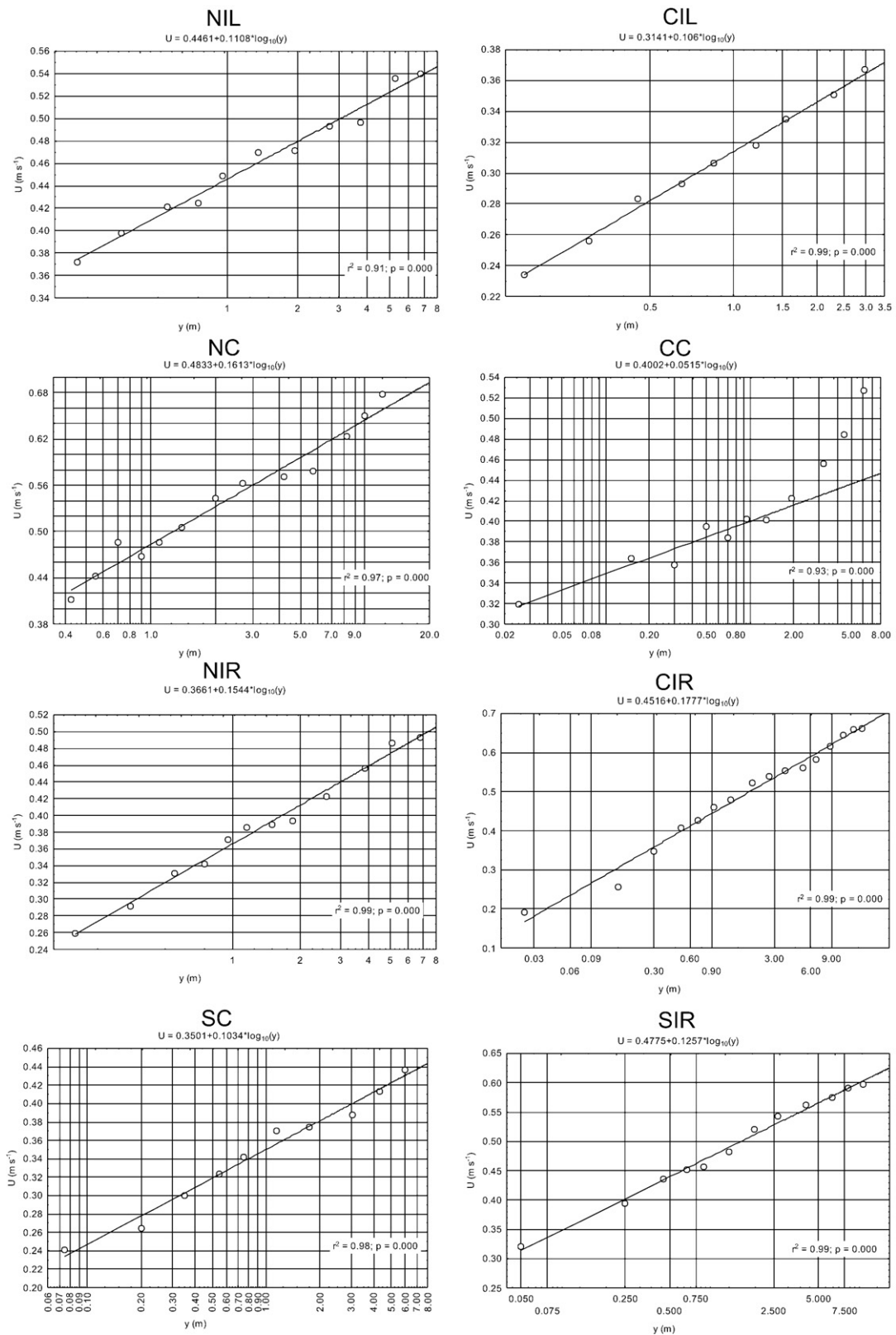| Sampling areas	Diversity index	Evenness	Richness
North	0.39	0.30	20
Center	0.3	0.22	23
South	0.31	0.22	25
Central strip	0.23	0.27	19
Banks	0.5	0.5	30
NLB	0.5	0.2	8
NIL	0.6	0.2	9
NC	0.3	0.1	6
NIR	1.2	0.6	4
NRB	2.0	0.7	8
CLB	2.7	0.7	12
CIL	0.9	0.3	8
CC	0.8	0.3	7
CIR	0.1	0.06	4
CRB	0.7	0.2	6
SLB	2.3	0.8	8
SIL	1.6	1	3
SC	1.2	0.5	6
SIR	0.8	0.3	10
SRB	1.2	0.3	12

Fig. 3. Semi-log plots of the smoothed velocity profiles measured on the active bed of the meander showing the fitness of Eq. (2). The *y* values were determined accounting for the virtual origin concept.
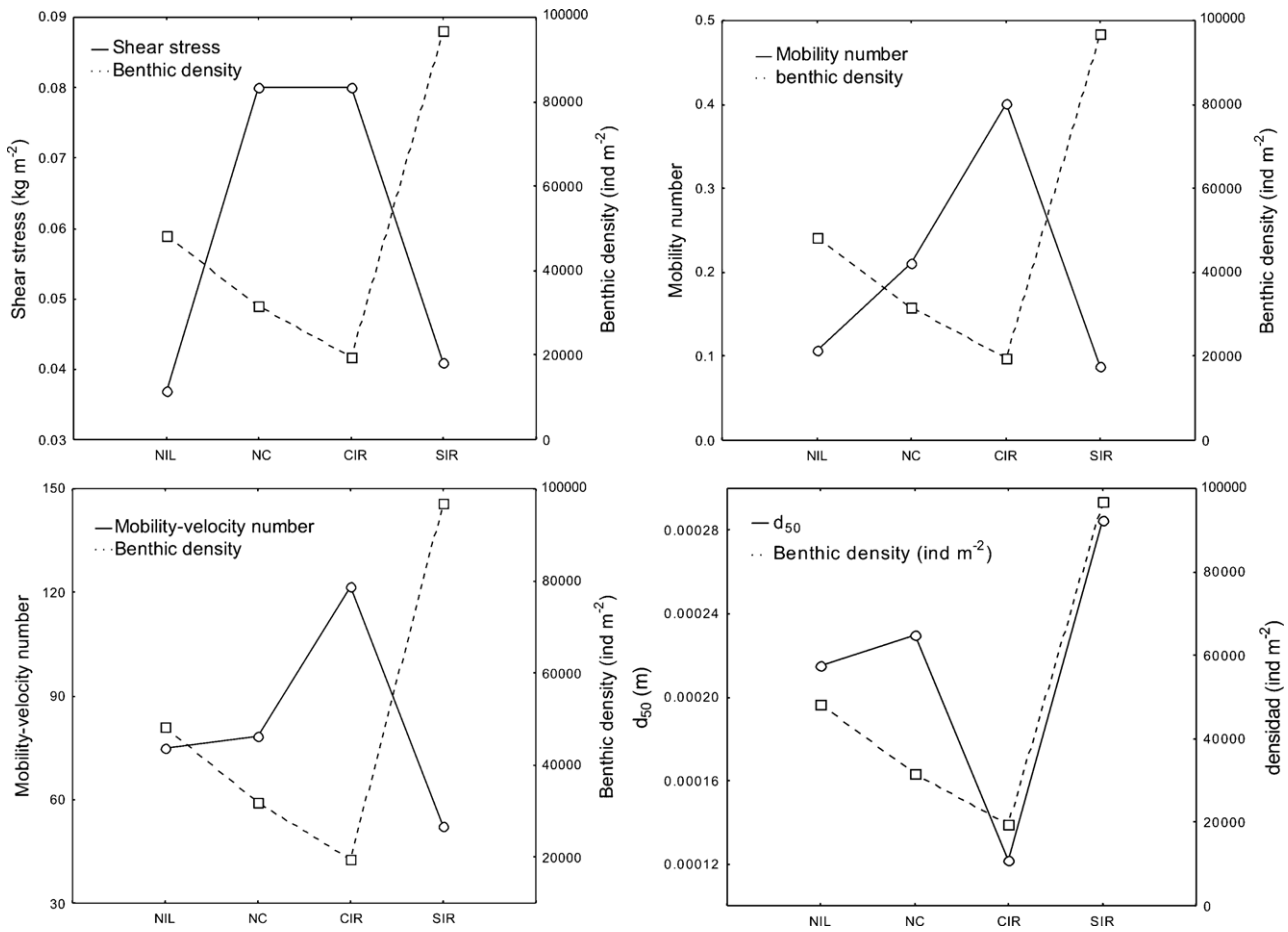
Fig. 4. Relationships between benthic density (ind. m^{-2}) and hydraulic and sedimentological variables (τ_0, τ_*, τ_{*U} and d_{50}) on the thalweg track (i.e. NIL, NC, CIR and SIR stations).

descolei, Pristina Americana, Brinkhurstia americanus and Haplotaxis aedeochaeta (Oligochaeta); among others.

Total invertebrate densities, considering all the sampling stations (15), ranged between 48 (SIL station) and 96,786 ind. m^{-2} (SIR station). Mean densities at each transect was 20,883 (North), 5636 (Center) and 20,279 ind. m^{-2} (South; Table 2). This table also includes separately the densities of N. bonettoi since this species was clearly the most abundant recorded in the study.

The values of the diversity, evenness index and species richness were relatively similar at each transect. However, different values arise when the bank and active bed stations are compared (Table 3). Lower values of these parameters were found mostly at the active bed stations.

Values of sediment organic matter, sand percentages, depths, medians of sand particle size distributions and hydraulic variables are shown in Table 4. Stronger hydraulic conditions were found in the active bed of the channel with maximum values at the meander pool (CIR station shows the highest values of τ_* and τ_{*U}). Note that it was not possible to estimate all the hydraulic variables at the bank stations since the velocity profiles did not follow a logarithmic distribution.

Fig. 4 shows the corresponding relationships between the invertebrate densities with hydraulic and sedimentologic variables along the thalweg track (NIL, NC, CIR and SIR stations). They are inversely related to each other, i.e. the lower densities were found on the sampling stations with stronger hydraulic energy. However, an opposite relation was recorded when the d_{50} values were

considered, i.e. the invertebrate density increases in the places where the median size of grains is larger.

The statistical differences in benthic densities at each sampling station along the thalweg track were explored through the Analysis of Variance (ANOVA; Fig. 5). The significance of the ANOVA
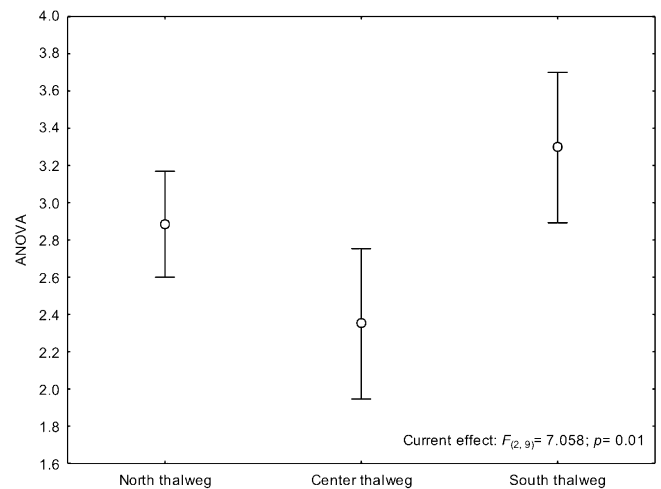

Fig. 5. ANOVA results in the thalweg track at three studied transects (North, Center and South). Vertical bars denote 0.95 confidence intervals.

Table 4
Sediment organic matter, bed sediment and hydraulic variables at each sampling station.

	Organic matter (gC%)	Sand (%)	Depth (m)	Mean velocity (m s^{-1})	Shear stress (kg m^{-2})	d_{50} (m)	Mobility number	Mobility-velocity number
NLB	0.48	53.2	3.4	0.38	0.018	–	–	–
NIL[a]	0.15	97.6	14.7	0.51	0.038	0.00029	0.079	55.5
NC[a]	0.13	99.1	13.1	0.54	0.080	0.00032	0.152	56.3
NIR	0.28	97.3	8.1	0.38	0.074	0.00017	0.262	52.5
NRB	1.30	60.6	1.3	0.32	–	–	–	–
CLB	0.71	83.9	1.5	0.08	–	–	–	–
CIL	0.13	97.5	3.9	0.3	0.035	0.00028	0.075	19.9
CC	0.17	99.2	7.9	0.41	0.008	0.00019	0.026	54.8
CIR[a]	0.10	96.2	19.3	0.5	0.081	0.000175	0.28	84.9
CRB	2.98	24.6	1.3	0.44	–	–	–	–
SLB	2.25	30.2	1.8	0.23	0.003	–	–	–
SIL	1.29	54.0	3.4	0.33	–	–	–	–
SC	0.24	93.2	7.8	0.34	0.033	0.000135	0.148	52.9
SIR[a]	0.16	99.3	11.7	0.5	0.041	0.0004	0.062	37.1
SRB	1.86	41.8	1.5	0.26	–	–	–	–

[a] Thalweg track.

results was tested with the post hoc Fisher LSD (multiple comparison tests). The CIR sampling station showed significant differences compared to the other sampling stations on thalweg track.

The sand concentrations in suspension are shown in Fig. 6A. Note the marked increase of suspended sand in the transect Central at CIR and CRB stations, particularly close to the bottom. The relation between *N. bonettoi* densities and the sand percentage present in the bed sediment at the bank sampling stations is shown in Fig. 6B. It is remarkably the tendency of densities to increase together with the bed sand content.

The first axis of the Detrended Correspondence Analysis (DCA) has explained 41.1% of the inertia, while the second axis just 17.6% (axis 1 + axis 2 = 58.7% of inertia; Fig. 7). Note that, in order to simplify this analysis and its interpretation, the invertebrate species with densities lower than 500 ind. m^{-2} were not considered in this testing. In overall terms, the stations located at the central strip (and thalweg) of the main channel were separated from the stations at both banks. Therefore, a total of only 19 species were selected.

A comparison between *N. bonettoi* and τ_0 values at the active bed channel in both Lower Paraguay and Middle Paraná rivers main channels is shown in Fig. 8. The stronger hydraulic conditions and lower density values were recorded in the Middle Paraná River.

Finally, the results of the overall values of the chemical variables (total Alkalinity, Bicarbonate, Carbonate, Chloride, total Hardness, Calcium, Magnesium, Potassium, Silica, Sodium, conductivity, pH, temperature, dissolved oxygen, transparency and total dissolved solids) shown an optimal water quality, i.e. they are within the natural values range expected at the fluvial system (Depetris and Pasquini, 2007).

4. Discussion

The typical sand-adapted assemblage of invertebrates was recorded at NC, NIL, CC, CIR and SIR stations, which are located along the active bed (i.e. not considering the bank areas) of the studied channel reach (Fig. 7). This assemblage, called herein "active bed assemblage", inhabits the sandy bed along nearly 3500 km (18° latitude) in the Paraguay–Paraná hydrosystem (Marchese and Ezcurra de Drago, 1992; Takeda and Fujita, 2004; Marchese et al., 2005; Ezcurra de Drago et al., 2004, 2007). The Oligochaete *Narapa bonettoi* was clearly the assemblage dominant taxa (Table 2) and the key species of the system (Marchese, 1994). It co-occurred with other species, such as *Myoretronectes paranaensis*, *Potamocaris* sp 1, *Rhyacodrilus* sp 1, *Tobrilus* sp 1, *Lopescladius* sp 1 and *Djalma-batista* sp 1. These species cope with relatively strong bed hydraulic
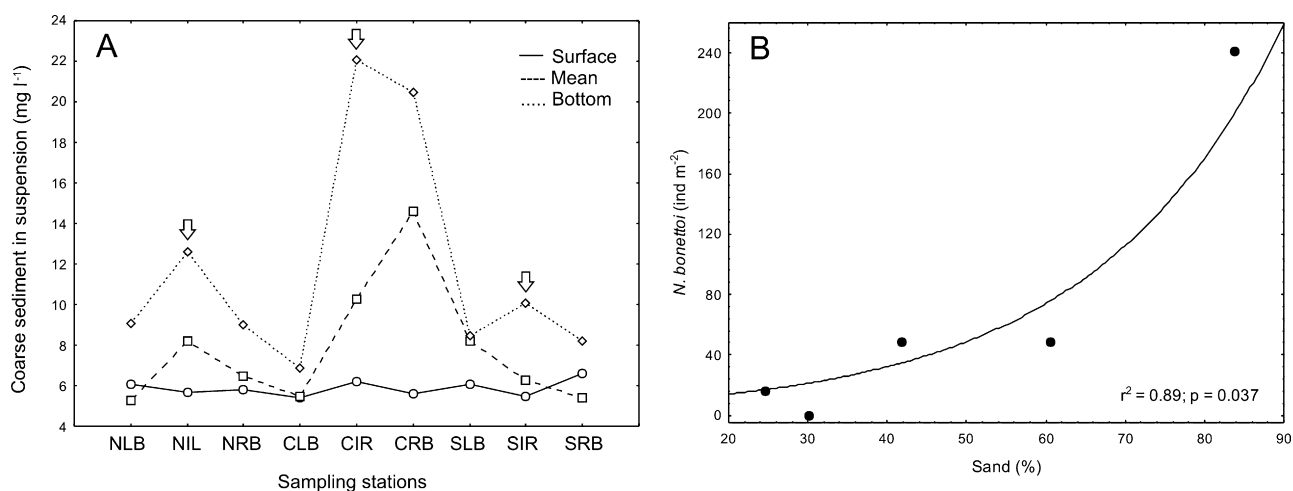

Fig. 6. (A) Fraction of coarse suspended sediments concentration (d > 0.062 mm) over the central strip sampling stations. Surface = suspended sediment concentration at surface water level; Mean = sediment concentration at mean depth on the water vertical; and Bottom = sediment concentration near to the bed. Rows mark the thalweg track. (B) Relation between *N. bonettoi* densities and the bed sand content at the banks.
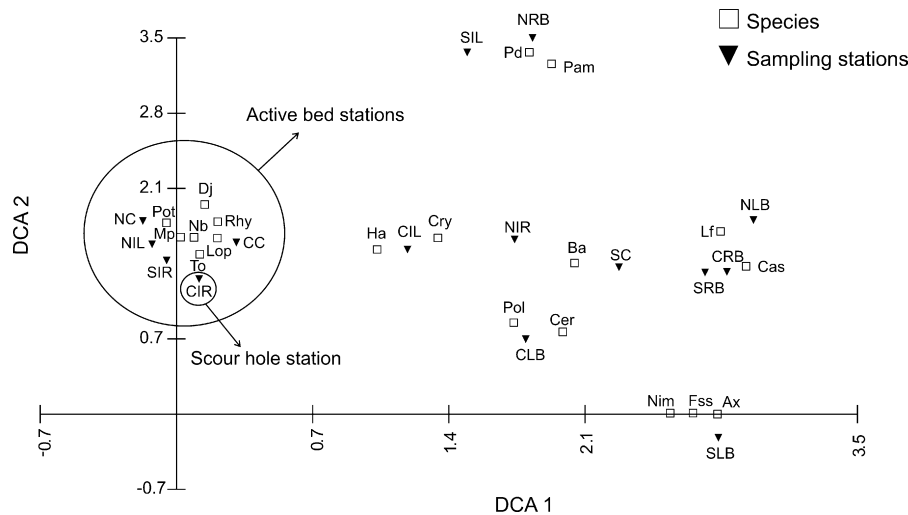
Fig. 7. Plot of Detrended Correspondence Analysis (DCA) along the first two axes for 19 more abundance species collected on the meander (see the axes values in the text). Nb: *Narapa bonettoi*; Mp: *Myoretronectes paranaensis*; To: *Tobrilus* sp; Lf: *Limnoperna fortunei*; Ax: *Axarus* sp; Cry: *Cryptochironomus* sp; Pol: *Polypedilum* sp; Fss: *Fissimentum* sp; Nim: *Nimbocera* sp; Lop: *Lopescladius* sp; Dj: *Djalmabatista* sp; Cer: *Ceratopogonidae* sp; Pot: *Potamocaris* sp; Rhy: *Rhyacodrilus* sp; Ba: *Brinkhurstia americanus*; Ha: *Haplotaxis aedochaeta*; Pd: *Paranadrilus descolei*; Pam: *Pristina Americana*; and Cas: *Cordylophora caspia*.

conditions and they live in sediments with very low organic matter content (Table 4). They are typically r-strategists with a high reproduction rate which, together with their small body sizes, allow a fast colonization of the mobile sands (Marchese et al., 2002).

Concerning the hydrodynamic forces (τ_0, τ_* and τ_{*U}) along the thalweg track, there is an observable increase in the flow intensity along with a decrease in invertebrate density at the hole area (see CIR station in Figs. 1B and 4, Tables 2 and 4). As it was described above (see Section 1), the river flow is typically concentrated in the concave side of a meander bend. It induces the larger bed shear stresses on this areas and the consequent erosion, generating the scour hole and a marked depth and asymmetric cross section (Figs. 1B and 2; see transect Central). Following Constantine et al. (2009), the associated rise in the mobility number explains, in turn, the high level of suspended bed sediment recorded in the area (see Table 4 and Fig. 6A). Continual collisions between suspended sand grains near the bottom could cause the damage and subsequent death of invertebrates inhabiting these areas (Carling, 1995;

Blettler et al., 2008), which explains the lower density recorded at the scour hole. Note as well in Fig. 6A the significant increase in suspended sand concentrations near the bed at CRB station. The reasons for this could be related to the known secondary flow cells usually found on meander bends. They would be co-responsible for the concave bank erosion and the consequent sediment transport to the inner bank to such an extent as to precisely satisfy mass balance under steady conditions and streamwise uniform flow. Thus, bank migration is conceptually replaced with an imposed transverse sediment flow (Parker and Eke, 2009). This transport might be the origin of a redistribution of the invertebrates and would partially explain the relatively high densities recorded at CC and CIL stations (Table 2). This speculation is based on the well established hydrodynamic mechanisms in small and medium meandering rivers, where secondary currents are large enough to transversely transport bed sediments. Nevertheless, according to Szupiany et al. (2009) it should be considered with caution at large spatial scales (i.e. $B/\overline{h} \gtrsim 10$ and $\overline{Q} = 1700\,\text{m}^{-3}\,\text{s}$; $\overline{h}$: mean depth at a cross section, B: channel width, $\overline{Q}$: mean discharge; Latrubesse, 2008). In large meandering rivers, like the Paraguay, this process is still a matter for research.

The crossing areas (Figs. 1 and 2, Transects North and South) are wider and shallower than the pool area (transect Center). Thus, the values of local unit discharges ($q = uh$), τ_0, τ_* and τ_{*U} are lower at crossings (see thalweg track in Table 4). Consequently, the invertebrate densities were higher in these transects than in transect Center (Table 2, Fig. 5).

In short, the above facts have a high ecological significance along the studied meander bend, resulting in the scour hole being rigorous habitat with lower benthic density due to its greater hydraulic energy (when compared to the crossing thalweg areas). However, flow intensities and the organization of turbulent structures are also contributing factors for the dispersal life stages of benthic organisms (McNair et al., 1997), which entails obvious implications when it comes to biomonitoring invertebrates, assessing habitat and designing river rehabilitation projects. Fig. 8 shows a comparison between Lower Paraguay and Middle Paraná rivers main channels, taking into account the *N. bonettoi* density and τ_0 values on the active bed of the rivers. The Paraná River is ranked ninth among the largest rivers in the world (Latrubesse, 2008). The Overall data used herein from this river were obtained from a previous
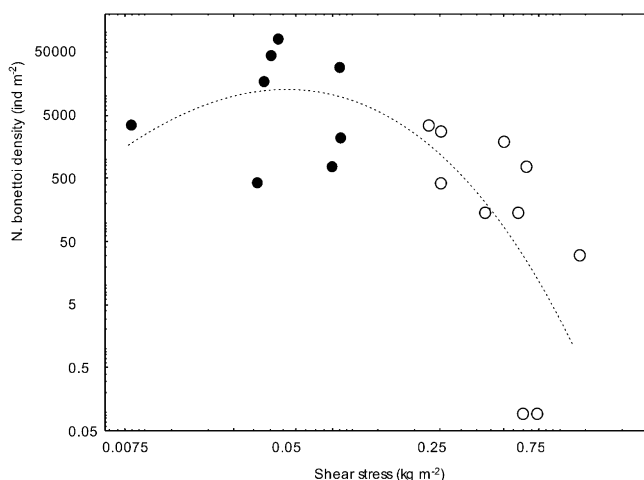

Fig. 8. Relation between *N. bonettoi* density and τ_0 values in the Paraguay and Paraná rivers. Full circle = Paraguay River; empty circle = Paraná River. In order to include in this scatter graph (with logarithmic axes) the points with 0 ind m^{-2} of *N. bonettoi*, it has been represented with the value 0.05 in the Y-axis.

study carried out by Amsler et al. (2009). Fig. 8 revels that in the Paraguay River the density of the species is markedly higher than in the Paraná River. A possible explanation for this trend could be in relation to the different discharges, and consequently bed shear stresses, on both rivers ($\overline{Q} = 4000\,\text{m}^3\,\text{s}^{-1}$ and $\overline{Q} = 16,000\,\text{m}^3\,\text{s}^{-1}$ in Lower Paraguay and Middle Paraná, respectively). Note the decrease in density of $\tau_0 = {\sim}0.55\,\text{kg m}^{-2}$ (Middle Paraná River). Note, as well, that this flow variable never exceeds 0.081 kg m^{-2} in the Lower Paraguay. Thus, the distribution of the species in the scatter graph can be represented through a bell-shaped curve. It means that the species' respond to a hydrologic/hydraulic gradient follows this curve. These kinds of curves are usual in ecological theories (e.g. niche theory). However, there are inherent difficulties in inferring response curves under field conditions. For discussions on the validity of the species' response to these curves, see Austin (1999) and Morin et al. (1986). Nevertheless, these curves are very important for the development of an ecologically-based flow regime. This is particularly useful for assessing impact on the ecological status of the river and for determining the minimum flow requirements of aquatic populations (Brunke et al., 2001; Mouton et al., 2007).

About the analysis in the riparian side, benthic samples collected near the banks (NRB, NLB, CRB, CLB, SRB and SLB stations) are quite different in species composition and density compared with those from the active bed (Fig. 7). The "bank assemblage" (as called herein) is mainly composed of the following species, grouped according to a decreasing density order: *Limnoperna fortunei*, *Cordylophora caspia*, *Paranadrilus descolei*, *Prístina americana*, *Brinkhurstia americanus* and *Limnodrilus hoffmeisteri*. This bank assemblage is well adapted to the typical hydraulic and bed sediment conditions at banks, i.e. slow flowing water which encourages the deposition of the finest particles in suspension. In Table 4, see the mean velocity values measured at these bank sites. All of them are equal or lower than the critical values for suspension initiation of ∼0.1 mm particles (see Figure 4.1.11 in Van Rijn, 1993). In Table 4 also note the remarkably lower percentages of sand content of the river bed near the banks compared to those from the active bed, i.e. the banks are typical areas with an important silt and clay content in their bed material. This fine and very fine sediments are not adequate for *N. bonettoi* ecological requirements. Thus, the tendency to fit the curve in Fig. 6B was expected (for details see Figure 2 in Blettler et al., 2008).

In short, the variable which will explains *N. bonettoi* distribution, i.e. shear stresses or bed sediment texture, will be a function of the area where the species inhabits. That is, the hydraulic factors are the main variable along the thalweg area. On the contrary, the densities of *N. bonettoi* near the banks are principally dependent upon the bed sand contents.

The higher invertebrate diversity, evenness and richness values were recorded at bank stations (Table 3), along with the lowest densities (Table 2). Marchese et al. (2002), Ezcurra de Drago et al. (2004, 2007), and Blettler and Marchese (2005) have found the same assemblage and similar ecological characteristics (density, evenness and richness) at riparian zones of the Paraná–Paraguay hydrosystem.

A number of sampling stations showed peculiarities which deserve a special discussion. In this sense, Fig. 3 reveals, in the velocity profile, whose values were obtained at CC station, the presence of the "wake effect" phenomenon (Schlichting, 1979). This fact due to the break of the slope angle and can be recognized in the logarithmic velocity point's distribution. For this reason, the bed hydraulic variables at this station were calculated with Eq. (2) and considering only the first eight velocity points measured closest to the bed. These points were later used to approach the real bed hydraulic forces (Trento et al., 1990). The wake phenomenon is closely associated with flow perturbations near the re-attachment

point at the lower stoss-side of dunes and it can be highly turbulent and intermittent (Best and Kostaschuk, 2002; among others), in spite of a relatively low average bed shear stress (Raudkivi, 1963; Kostaschuk, 2000; see Table 4, CC station). Considering the explanation above, the CC station is thought to be located at the re-attachment point in the lower stoss-side of a dune. Consequently, the high and fluctuating turbulence at this site could explain the lower benthic density recorded in CC sampling station, when compared with the nearby CIL and CIR stations. This lower invertebrate density on the low stoss-side of dunes has been reported by Amsler et al. (2009) in bed forms of the Paraná River.

On the other hand, according to Fig. 2, the SIL station would be located on a "sediment bump" (a possible bar to embryo?). This zone could be understood as a deposition area out of its bed's material composition: 54% of very fine sand, 30% of silt and 16% of clay. The bed's sediment distribution is similar to that recorded on both meander banks (Table 4). This would not only explain the similarities in composition between benthic assemblage in SIL and that one in bank stations (Fig. 8), but also the striking low density of *N. bonettoi* there (Table 2).

Finally, transect South revealed a similar benthic density between riparian stations (SLB and SRB) and central station (SC) (Table 2). However, when the composition of invertebrate species at these sites is analyzed in detail, it found that similarity is only borne at density level. Actually, the invertebrate species living there are completely different, i.e. riparian stations are dominated by taxa such as *L. fortunei*, *Axarus* sp, *Polypedilum* sp 1, *Fissimentum* sp 1 and *C. Caspia* (proper to river banks) and a predominance of *N. bonettoi* was found at SC, typical species from the active bed assemblage.

5. Conclusions

(i) The invertebrates in a meander of the Lower Paraguay River develop into two typical assemblages, also recorded along the Paraná River. One of them located on the active bed (thalweg included) and characterized by higher density values and r-strategist species ("active bed assemblage"). The other one inhabits the banks, with lower density and high diversity values, richness and evenness ("bank assemblage").

(ii) Considering the longitudinal benthic distribution along the thalweg track of the meander bend, the scour hole is a hostile area for the active bed assemblage, affecting benthic organisms' chances of colonization and settlement.

(iii) In the Paraguay and Paraná rivers, *N. bonettoi* density and shear stress (τ_0) relate according to a bell-shaped curve. It is speculated herein that in the Paraguay River the hydraulic stress is high enough so as not to allow sedimentation of fine particles but not that much so as to bring on the *N. bonettoi* drift (or damage it). On the other hand, in the Paraná River the shear stress would be simply too high to allow optimal colonization by the species.

(iv) Considering the diverse fauna found in the meander, associated with heterogeneous flow and morphology, a possible reduction in channel complexity (e.g. artificial channel rectifications) would have direct effects on ecosystem properties making density and diversity of riverine invertebrates go down. The challenge is now to integrate this type of information into river management and rehabilitation.

(v) The overall conclusion of this paper, that morpho-hydraulic features and biotopes are related, is an important step forward in river ecohydrology. With further development of this concept, river management techniques can improve and river rehabilitation projects can be designed with greater confidence and clear, testable aims.

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