

The impact of significant input of fine sediment on benthic fauna at tributary junctions: a case study of the Bermejo-Paraguay River confluence, Argentina

Martín C. M. Blettler,^{1*} Mario L. Amsler,¹ Inés Ezcurra de Drago,¹ Luis A. Espinola,¹ Eliana Eberle,¹ Aldo Paira,¹ James L. Best,^{2,3,4,5} Daniel R. Parsons⁶ and Edmundo E. Drago¹

¹ Instituto Nacional de Limnología (INALI-CONICET-UNL), Ciudad Universitaria (3000), Santa Fe, Argentina

² Department of Geology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

³ Department of Geography and Geographic Information Science, University of Illinois at Urbana-Champaign, Urbana, IL 61801 USA

⁴ Department of Mechanical Science and Engineering, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

⁵ Ven Te Chow Hydrosystems Laboratory, University of Illinois at Urbana-Champaign, Urbana, IL 61801 USA

⁶ Department of Geography, University of Hull, Hull HU67RX, UK

ABSTRACT

This study examines the morphological features, suspended sediment inputs and hydraulic conditions within a large river in association with ecological patterns before and after a tributary confluence. In order to examine these effects, the macroinvertebrate distributions from three reaches of the Paraguay and Bermejo Rivers (Paraguay-Argentina) are investigated. The Bermejo River is a tributary that supplies significant quantities of fine sediment to the Paraguay River, primarily in suspension. Two reaches were examined on the Paraguay River, upstream and downstream of the Bermejo River junction, with the third study reach located on the Bermejo River, upstream of the confluence with the Paraguay River. The results provide clear evidence that a significantly increased loading of fine sediment at a river confluence has effects on the distribution and potential movement of benthic invertebrates in the lotic environment by representing physical barriers at affected sites. These effects may be important at both local and regional scales, and such increases in suspended sediment (especially associated with anthropogenic change) may thus pose a major threat to ecosystem integrity that has been historically underestimated. Copyright © 2014 John Wiley & Sons, Ltd.

INTRODUCTION

Sedimentation is widely acknowledged as one of the major causes of degradation to the ecological integrity of rivers (e.g. Cordone and Kelley, 1961; Hynes, 1970; Hogg and Norris, 1991; Wood and Armitage, 1997; Fossati *et al.*, 2001; Ehrhart *et al.*, 2002; Freeman and Schorr, 2004). Fine sediments have wide-ranging impacts on aquatic biota, both when in suspension and when deposited on the river bed, which have been described comprehensively in a number of reviews (Newcombe and MacDonald, 1991; Ryan, 1991; Waters, 1995 and Wood and Armitage, 1997). Research on the effect of fine sediment accumulation on macroinvertebrates has primarily been based on correlative fieldwork (Quinn & Hickey, 1990; Hogg and Norris, 1991; Death *et al.*, 2003; Kaller and Hartman, 2004; Chessman *et al.*, 2006) that has shown that the transport of fine particles in rivers can smother the benthic zone and community, clogging the interstitial spaces between substrate particles utilized by invertebrates as habitat and refuge. This phenomenon can significantly modify the colonization patterns of organisms and may lead to physical damage of the organism due to abrasion (Doeg and Koehn, 1994; Waters, 1995, Wood and Armitage, 1997).

Factors such as changes in bed sediment size, duration, intensity and frequency of sediment loading events and existing substrate composition may all influence the response of individuals and invertebrate communities to sedimentation (Crowe and Hay, 2004). Wood and Armitage (1997) report indirect ways by which fine sediment can also affect macroinvertebrates, including (i) the increasing spatial drift of macroinvertebrate populations as a result of sediment deposition or substrate instability (Culp *et al.*, 1986), (ii) sediment deposition on respiration structures affecting oxygen uptake or low oxygen concentrations being associated with fine sediment deposits (Waters, 1995) and (iii) reduction of the density of prey items (Peckarsky, 1984). Benthic fauna can also be affected indirectly, through changes in the availability or quality of food resources within the sediment. Therefore, when the streambed is degraded by fine sediment, there may be a tipping point where macroinvertebrate communities change and become less diverse. However, sedimentation affects particular species and assemblages differently. Ultimately, sediment-physical barrier for benthic fauna. Moreover, it is known that organisms with high dispersal potentials may be expected to overcome geographical barriers more readily than those with poor dispersal ability (Marchant *et al.*, 2006). In this sense,

the confluence of the Bermejo River (high suspended sediment load) with the larger Paraguay River (essentially a clearwater river) in northern Argentina represents an excellent opportunity to examine the effect of a point source input of fine sediment on benthic invertebrates. with taxa that are intolerant of fine sediment being replaced by those better adapted (e.g. burrowing taxa) to the presence of fine sediment deposits (Waters, 1995).

A localized input of large volume of fine sediment from a tributary river could be considered comparable with a sedimentation may result in changes to community composition, sediment barrier on the benthic fauna in a large river.

METHODOLOGY

Sampling site

The sampling sites were located upstream and downstream of the Bermejo River confluence (hereafter referred to as 'P.Up-reach' and 'P.Dw-reach', respectively), on two meander bends located on the Lower Paraguay River, both approximately 15 km from the Bermejo River junction (26° 47'70''S–58°17'30''W and 26°00'27''S–58°28'84''W, respectively). A third meander bend was examined, located on the Bermejo River ('B-reach') 2.5 km upstream from its confluence (26°52'69''S–58°23'83''W). The three meanders were selected as sample sites because of their complex morphology and hydraulic diversity, which aid cross-channel mixing of suspended sediments.

The meandering Lower Paraguay River drains a large alluvial floodplain, with the river being on average 575 m wide and 9 m deep (Drago, 1990), with a mean discharge of 4000 m³s⁻¹ (Giacosa *et al.*, 2000), a catchment of 133 000 km² and a length of 1800 km. The suspended sediment concentration of the Bermejo River is up to 40 g l⁻¹ during high water phases, showing an annual average of 6.5 g l⁻¹ (Drago and Amsler, 1988, Amsler and Drago, 2009). The importance of the Bermejo River extends far beyond its catchment, as most of the suspended sediment of the Middle Paraná River comes from the Bermejo, after being supplied by the Paraguay River. The Bermejo River also contributes to the lower section of the Paraguay and Middle Paraná Rivers with approximately 108 million tons of sediment per year (Drago and Amsler, 1988), which thus modifies the physical and chemical characteristics of both rivers.

In the present study, sampling and detailed measurements were collected in October 2007 during a low and relatively steady water stage ($Q = 1719 \text{ m}^3 \text{ s}^{-1}$) at three cross sections along each meander: one transect at the entrance to the bend, the second in the zone of maximum depth near the bend apex and the third at the bend exit (Figure 1). Sampling and measurements were made at five stations along each transect, three of them over the mobile bed (termed herein the 'central strip') and one at each river bank (left and right). Figure 1 also shows the longitudinal bathymetric profiles along each meander bend.

detailed biological, sedimentological and hydraulic records obtained before and after the confluence during 2007 and supplemented with historic results from 2001. The investigation specifically highlights the effects of a fine

The effect of the input of significant volumes of fine sediments on the distribution of benthic invertebrates downstream of the Bermejo–Paraguay confluence is quantitatively described in this paper. The study is based on

Sediment dynamics at the Bermejo–Paraguay confluence

The bed morphology of the Bermejo–Paraguay confluence is dominated by a tributary mouth bar that extends from the Bermejo River into the confluence, reflecting the dominance of the Bermejo River sediment load at this site. It is noticeable that a zone of central confluence scour, often characteristic of channel junctions with such planform configurations, is absent at this site. Measurements of flow within the confluence demonstrate that the water from the Bermejo River forms an underflow when it meets the Paraguay River and generates a flow that moves underneath that of the clearer mainstream water (Figure 2A and B; Parsons *et al.*, 2006; Best *et al.*, 2007). Although the main Bermejo River flow moves under that of the Paraguay River, distinct upwellings of denser fluid are common on the water surface (Figure 2B) and act against the local density gradient.

Flow measurements, water chemistry, bed sediments and benthic sampling

The boat position at the selected at-a-point sampling locations was attained using a Furuno GP-1650WF echo sounder (Furuno Electric Co. LTD, Nishinomiya city, Japan.) coupled to a Global Positioning System (GPS). The river bed topography was surveyed using the software package Fugawi Marine version 4.5 (Northport Systems Inc., 2007). The current velocity profiles were obtained using an electric propeller current metre, operated simultaneously with the

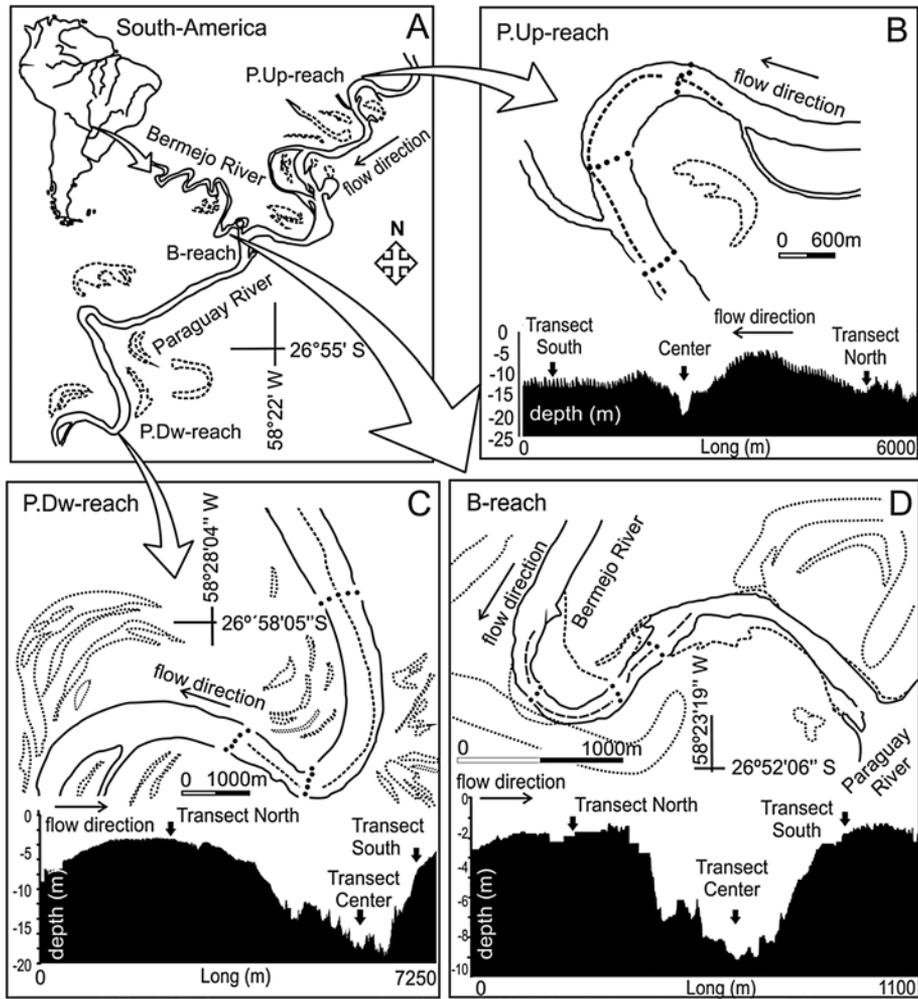


Figure 1. Plan view of the selected meanders with location and details of sampling stations. (A) Bermejo and Paraguay Rivers confluence and studied reaches. (B and C) Paraguay River upstream and downstream of the Bermejo River confluence, respectively. (D) Bermejo River. Longitudinal bathymetric profiles are included in B, C and D showing the position of the studied cross sections.

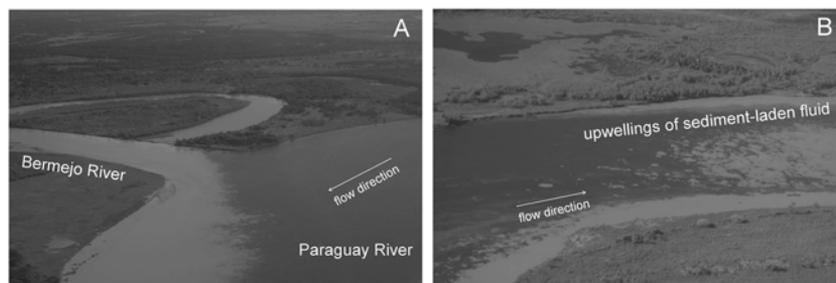


Figure 2. (A) Aerial image of the Paraguay-Bermejo River confluence. (B) Upwelling of the sediment-laden Bermejo fluid within the less-dense water of the Paraguay River.

collection of benthic samples. A total of 8–16 point velocities (depending on the local depth) were recorded in the water column at each vertical, with measurements more closely spaced in the first metre above the bed. Each point velocity was the average value over a 100-s measuring period.

Three benthic sample replicates were taken at each sampling station using a Tamura™ clamshell bucket, with

the samples being 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 10 \times stereoscopic microscope and stored in a 70% ethanol solution. All benthic taxa were identified and counted under the microscope. The determinations for each taxon were made at the species and morphospecies levels

(taxonomic species based wholly on morphological differences from related species). The literature used for taxonomic determinations is listed in Blettler *et al.* (2012a). Additional sediment samples for granulometric analysis (by dry sieving) and organic matter estimation (by ignition and subsequent ash-free dry matter weight; gC%) were collected at the same sites.

The following variables were recorded in order to characterize the water quality: transparency (Secchi disk; m), electric conductivity ($\mu\text{S cm}^{-1}$), pH, bed dissolved oxygen (mg l^{-1}), total alkalinity ($\text{mg l}^{-1} \text{CaCO}_3$), bicarbonate ($\text{CaCO}_3 \text{ mg l}^{-1}$), chloride (mg l^{-1}), total hardness ($\text{mg l}^{-1} \text{CaCO}_3$), calcium (mg l^{-1}), magnesium (mg l^{-1}), potassium (mg l^{-1}) and sodium (mg l^{-1}).

Selection and treatment of the hydraulic variables

The characterization of hydraulics near the bed at each sampling station was attained by direct measurements of the local velocity profiles, flow depth (h), bed sediment particle size mean size (d_{50}) and distribution, and an estimation of the bedform height at a given point. These parameters are the necessary inputs to compute hydraulic variables (see definitions in Table I) such as the bed shear stress (τ_0), or its equivalent the bed shear velocity (U_*), the sediment mobility number (τ_*) and the 'mobility-velocity number' ($\tau_* U$). $\tau_* U$ is a modification suggested by Yalin (1977) of the conceptually similar mobility number, but with the practical advantage that its estimation is simpler because it is based on the local mean velocity (U), instead of τ_0 for the estimation of τ_* (see Table I for definitions).

The methodological details concerning the calculation of these variables in a large river are given in Amsler *et al.* (2009) and specifically for the Paraguay River in Blettler *et al.* (2012a). Appendix A shows an example of a velocity profile measured during the present study, and then fitted to a logarithmic distribution considering the virtual origin following the *ad hoc* procedure advanced by Perry and Joubert (1963, Figure A1). The values of τ_0 were computed on the basis of the a slopes of the fitted curves (Kostaschuk *et al.*, 2004), and all r^2 values ranged between 0.8 and 0.99. It should be noted that all the hydraulic variables considered

herein have been shown to have ecological relevance for benthic invertebrates in large rivers by Blettler *et al.* (2008; 2012a, 2012b) and Amsler *et al.* (2009).

Statistical analysis

As the data of macroinvertebrate density were not normally distributed, they were logarithmically transformed [$\log_{10}(x + 1)$] and then checked for normality (Shapiro and Wilk, 1965) and homogeneity of variance (F_{\max} ; Sokal and Rohlf, 1981). As normality was verified after log transformation, a one-way analysis of variance (ANOVA) test was conducted (significance < 0.05) to determine the differences between the means of total benthic density, *Narapa bonettoi* density (the key species of the system; see succeeding text), between the main physical variables and between the individual meanders. The *post hoc* Fisher's test (multiple comparison test) was applied in all cases to identify where significant differences occurred between individual groups. In order to test spatial differences in benthic assemblage patterns, multivariate analyses were used.

The Canonical Analysis of Principal coordinates (CAP; Anderson, 2004) was applied to the dataset and 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). To achieve this, a Bray-Curtis similarity index (Bray and Curtis, 1957) and 999 permutations (Manly, 1997) were used. CAP was undertaken using the CAP software (Anderson, 2004). The MULTIV computer programme, version 2.4.2 (Pillar, 2006; available from <http://ecoqua.ecologia.ufrgs.br/ecoqua/MULTIV.html>), was then used to identify significant differences within the CAP results.

Invertebrate densities were modelled using linear models (McCullagh and Nelder, 1989). The explanatory variables tested were bed organic matter, percentage of bed sand, percentage suspended sand, percentage suspended fine sediments, water velocity, d_{50} grain size and shear stress. These variables were combined linearly and modelled

Table I. Summary of the hydraulic variables measured and computed in the study.

Name	Symbol	Units	Equation	Description
Current velocity	U	m s^{-1}	Direct measurement	Measured point velocity at each vertical profile
Depth	h	m	Direct measurement	Local depth
Shear velocity	U_*	m s^{-1}	$U_* = a/5.75$	An estimate of velocity gradient close to the riverbed
Shear stress	τ_0	kg m^{-2}	$\tau_0 = U_*^2 \rho$	Bed shear stress derived from shear velocity
Mobility number	τ_*	None	$\tau_* = \frac{1}{4} \frac{\tau_0}{\rho(\gamma_s - \gamma_w) d_{50}}$	Dimensionless relationship between active forces acting on the bed and particle mass
Mobility-velocity number	$\tau_* U$	None	$\tau_* U = \frac{1}{4} \frac{U \tau_0}{g \delta s - 1 \rho d_{50}}$	Version of τ_* using U instead of τ_0

a , regression slope coefficient of the relationship current velocity *versus* depth; ρ , water density; γ_s , specific weight of sediment; γ_w , specific weight of water; s , γ_s/γ_w ; g , gravity acceleration; d_{50} , median of the bed sediment size distribution.

expected values of the dependent variable. The models were fitted to the data from the three study reaches. To select the best model, Akaike information criterion (AIC; Burnham and Anderson, 1998) was employed. This criterion was used to find the most parsimonious model, following Richards (2005). According to Burnham and Anderson (1998), when the ratio is ≤ 40 , the AIC needs adjustment.

Thus, the AICc was calculated as follows:

$$AIC_c = AIC - \frac{2k}{n-k-1}$$

where n indicates the number of observations and k is the number of parameters in the model. As the AIC value is relative in scale, it was calculated as the difference between each model's AIC values and the minimum AIC value (Burnham and Anderson, 1998):

$$\Delta_i = AIC_i - \min AIC$$

where Δ_i is the difference between the model i and the best value of AIC, AIC_i is the AIC for the model i and $\min AIC$ is the minimum value for all models.

RESULTS

A total of 45 species and morphospecies were identified in the three meander reaches. The taxonomic groups found were Oligochaeta, Bivalvia, Turbellaria, Copepoda, Diptera (Chironomidae, Tanytopodinae and Ceratopogonidae), Nematoda, Hydrozoa and Acari. The main species assemblage found at each reach and sampling position are summarized in Table II.

Total invertebrate densities, considering all sampling stations (39), ranged from 0 (in the Bermejo River) to 96 786 ind. m⁻² (southern station located in the thalweg

track at site P.Up-reach). The mean densities on each transect and for each position in the channel, for both the active bed (thalweg included) and banks, are presented in Table III. This table also includes the densities of the Oligochaeta *N. bonettoi*, because this was the key species within the active bed assemblage (Blettler *et al.*, 2012a, 2012b) and the most abundant species recorded in the present study.

Values of sediment organic matter, percentage sand, flow depth, median particle sizes of sand, hydraulic variables and suspended sediment concentrations are shown in Table IV. Slightly higher flow velocities were recorded in the P.Dw-reach, with maximum values on the active bed stations. Note that it was not possible to estimate some hydraulic variables for the bank stations because the velocity profiles did not follow a logarithmic distribution.

The potential statistical differences in total benthic densities (and *N. bonettoi* density) between selected areas and along both bank stations of the P.Dw-reach were explored through ANOVA. The results indicate that there is a significant difference in total invertebrate and *N. bonettoi* densities between the reaches ($F_{(2,15)} = 25.5$, $p = 0.001$; and $F_{(2,15)} = 24.1$, $p = 0.001$, respectively; Figure 3A).

However, the left bank stations along the P.Dw-reach (downstream of the sediment input from the Bermejo that is on the right river bank) did not display a significant differences compared with right bank stations ($F_{(1,10)} = 0.01$, $p = 1.00$) as predicted.

We also examined data collected in November 2001 from a reach on the Paraguay River ($Q = 1595 \text{ m}^3 \text{ s}^{-1}$), upstream and downstream of the Bermejo confluence (see Ezcurra de Drago *et al.*, 2004). These data also indicated significant difference in total invertebrate and *N. bonettoi* densities between sampling stations downstream and upstream of the confluence ($F_{(2,6)} = 18.3$; $p = 0.002$ and $F_{(2,6)} = 12.8$; $p = 0.006$, respectively; Figure 3B). Station S7

Table II. Main species (and taxonomic groups) recorded at each river reach and sampling positions.

Reach position	Sampling position	Taxonomic group	Main species
P.Up-reach and P.Dw-reach ^a	'Active bed assemblage'	Oligochaeta	<i>Narapa bonettoi</i> , <i>Haplotaxis aedeochaeta</i>
		Turbellaria	<i>Myoretronectes paranaensis</i>
		Nematoda	<i>Tobrilus</i> sp. I
		Copepoda	<i>Potamocaris</i> sp. I
		Chironomidae	<i>Corynoneura</i> sp. I
B-reach ^b	'Active bed assemblage'	Chironomidae	<i>Aedokriptus</i> sp. I, <i>Cryptochironomus</i> sp. I, <i>Paralauterborniella</i> sp. I
P.Up-reach and P.Dw-reach	'Bank assemblage'	Bivalvia	<i>Limnoperna fortunei</i>
		Hydrozoa	<i>Cordylophora caspia</i>
		Oligochaeta	<i>Paranadrilus descolei</i> , <i>Pristina americana</i> , <i>Brinkhurstia americanus</i> , <i>Haplotaxis aedeochaeta</i>
B-reach ^b	'Bank assemblage'	Chironomidae	<i>Cryptochironomus</i> sp. I

Note that the active bed assemblage at the B-reach is completely different than that at the P.Up-reach and P.Dw-reach.

^a Low in density.

^b Extremely low density.

Table III. Mean benthic invertebrate densities for each transect and channel position.

Reach position	Sampling position	Mean benthic density (ind. m ⁻²)	Mean <i>N. bonettoi</i> density (ind. m ⁻²)
P.Up-reach	North	20 883	14 929
	Centre	5 636	4 749
	South	20 279	16 828
	Active bed	25 769	20 210
	Banks	4 633	107
P.Dw-reach	North	780	26
	Centre	466	8
	South	1 638	252
	Active bed	685	381
	Banks	45	24
B-reach	North	13	0
	Centre	221	0
	South	286	0
	Active bed	52	0
	Banks	468	0

Mean densities of *N. bonettoi* were included for comparative purposes.

Table IV. Ranges of physical variables.

Sampling reaches		Range of physical variables								
		sOM (gC%)	bSand (%)	Depth (m)	<i>U</i> (m s ⁻¹)	τ_0 (kg m ⁻²)	<i>d</i> ₅₀ (mm)	τ^*	$\tau^* U$	SS (mg l ⁻¹)
P.Up-reach	Active bed	0.1-0.2	96-98	9.8-12	0.4-0.5	0.04-0.06	0.21-0.26	0.1-0.16	45-55	45-60
	Banks	0.9-2.1	36-57	1.4-2.3	0.2-0.3	—	—	—	—	46-65
P.Dw-reach	Active bed	0.2-0.5	97-98	6.1-11	0.6-0.8	0.1-0.3	0.1-0.2	0.5-1.2	130-293	90-110
	Banks	0.7-1.7	20-81	1.3-2.8	0.1-0.4	—	0.04-0.1	—	—	85-183
B-reach	Active bed	0.2-0.7	73-96	3.1-7.6	0.3-0.7	0.01-0.18	0.07-0.2	0.05-0.5	47-166	479-506
	Banks	1.8-2.4	23-58	0.9-2.5	0.1-0.4	-	0.04-0.09	—	—	445-542

sOM, percentage of organic matter in the bed sediment; bSand, percentage of sand in the bed sediment; *d*₅₀, median of bed sediment distribution; SS, suspended sediment distribution.

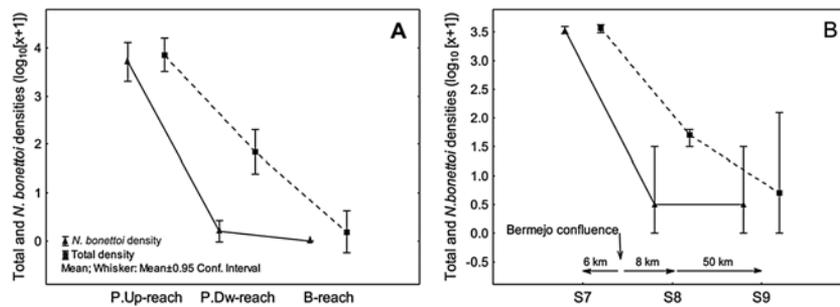


Figure 3. Whisker plot showing the logarithmic values of total and *N. bonettoi* densities at each selected reach, during the sampling campaigns in (A) 2007 and (B) 2001. S7: station upstream of Bermejo River confluence; S8 and S9: stations downstream of the confluence. The distance between each station downstream of the Bermejo-Paraguay junction is shown at the bottom of Figure 3B.

was located 5 km upstream of the Bermejo River confluence, whereas Stations S8 and S9 were located 8 and 50 km downstream, respectively (Figure 3B).

The water level stages at Pilcomayo Port, the nearest monitoring station to the sampling stations, are shown in Figure 4. The water levels cover the period up to 1 year

prior to sampling (2001 and 2007), with both campaigns being undertaken at low water stage in October and November for 2001 and 2007, respectively.

The analyses of fauna using CAP (Figure 5) indicate that the samples could be classified into three groups on the basis of each of the study reaches ($T = 1.577$, $p = 0.001$;

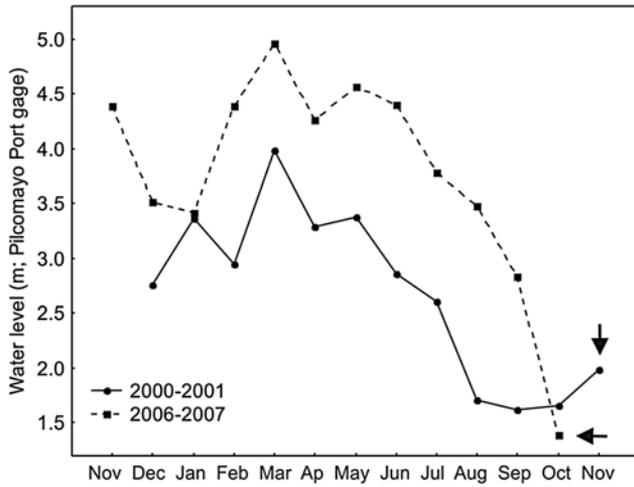


Figure 4. Water level stages at Pilcomayo Port. Note the levels shown 1 year before both sampling campaigns (2001 and 2007). Arrows show sampling dates.

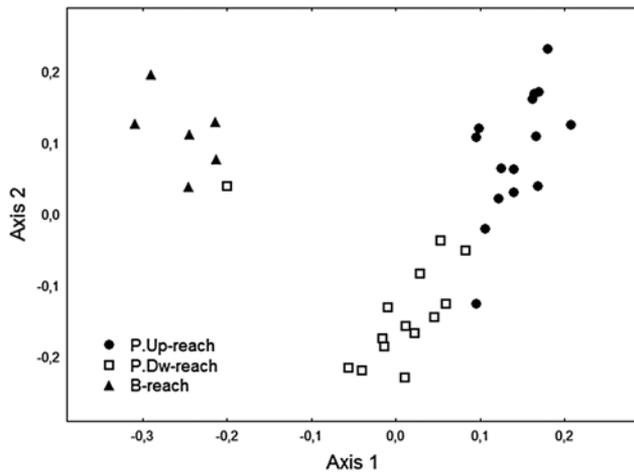


Figure 5. Ordination plot of the Canonical Analysis of Principal coordinates showing significant differences in the composition and relative abundance of benthic invertebrates at each selected meander (generated with the first two principal coordinate axes from the computed results).

$\Delta_1^2 = 0.896$; $p = 0.001$). In addition, the results of comparisons between each group (MULTIV; Pillar, 2006) confirm that the invertebrate communities from each reach

are statistically different from each other ($1 - 1 0$, $p = 0.001$; $1 0 - 1$, $p = 0.002$; $0 1 - 1$, $p = 0.001$).

The variables most significantly correlated with the invertebrate density were d_{50} ($p = 0.016$) and percentage suspended sand ($p = 0.054$). The models that accounted for most of the variance in the faunal density data were percentage of suspended sand and d_{50} within each of the reaches (Table V and Figure 6).

The results for chemical parameters (total alkalinity, bicarbonate, carbonate, chloride, total hardness, calcium, magnesium, potassium, silica, sodium, conductivity, pH and bed dissolved oxygen concentration; Figure 7) indicate that the B-reach always has the highest concentrations of the chemical parameters; P.Up-reach and P.Dw-reach share comparable concentrations for each chemical variable.

On the basis of the physical and ecological characteristics examined in this study, it is possible to create a schematic model illustrating the physical and ecological patterns, focusing on suspended sediment input, discharge and benthic invertebrate density, around the Bermejo-Paraguay confluence (Figure 8).

DISCUSSION

The typical assemblage of invertebrates adapted to the sand bed channels of the Paraná-Paraguay hydrosystem, termed the 'active bed assemblage' (Blettler *et al.*, 2012a), was recorded at the P.Up-reach. This finding corresponds with the physical and chemical parameters recorded previously on the river (Ezcurra de Drago *et al.*, 2004; Blettler *et al.*, 2008, 2012a). This assemblage inhabits the sandy bed along nearly 3500 km in the Paraguay-Paraná River hydrosystem (Marchese and Ezcurra de Drago, 1992; Takeda *et al.*, 2001; Takeda and Fujita, 2004; Marchese *et al.*, 2005; Ezcurra de Drago *et al.*, 2007). The Oligochaete *N. bonettoi* is clearly the dominant taxon within this assemblage (Table II) and keystone species of the system (e.g. Marchese, 1994), followed in abundance by *Myoretronectes paranaensis*, *Haplotaxis aedeochaeta*, *Tobrilus* sp. and *Potamocaris* sp. This assemblage persists well in association with the high-energy hydraulic bed conditions. The majority of fauna inhabit the mobile sandy

Table V. Model and number of parameters, value of Akaike information criterion (AIC), AIC adjusted (AICc), and the difference between the model i and the lowest value of AIC from (ΔAIC) .

Models	Number of parameters	AIC	AICc	$\Delta AICc$
LogDensity \sim sOM + bSand + sSand + sfS + U + d_{50} + τ^*	8	76.26	96.96	24.73
LogDensity \sim d_{50} + d_{50} :reach	4	67.62	72.23	0
LogDensity \sim sSand + sSand:reach	4	79.05	83.67	11.44
LogDensity \sim sSand * d_{50} :reach	6	65.88	76.06	3.83

sOM, bed organic matter; bSand, percentage sand in bed; sSand percentage of suspended sand; sfS, suspended fine sediments; U , water velocity; τ^* , shear stress.

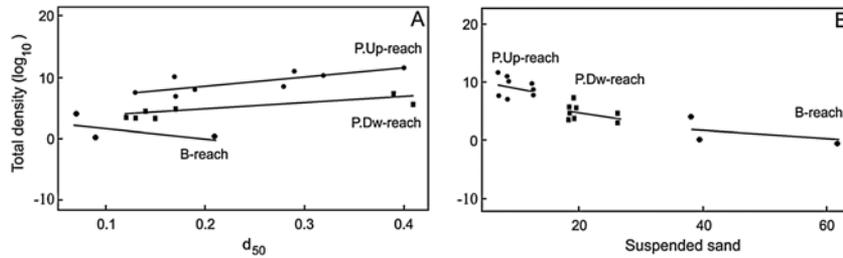


Figure 6. Multiple regression models showing the relationship between d_{50} and suspended sand with total invertebrate density at each sampling reach.

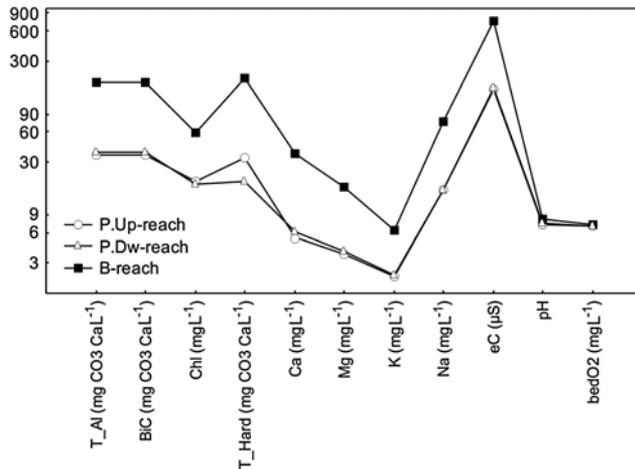


Figure 7. Chemical variables at each studied meander. T_Al, total alkalinity; BiC, bicarbonate; Chl, chloride; T_Hard, total hardness; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium; eC, electrical conductivity; bedO2, dissolved oxygen concentration near the bed.

bed, characterized by very low organic matter content (Table IV), and all taxa have relatively high reproduction rates (Marchese *et al.*, 2002).

The active bed assemblage at the P.Dw-reach comprised similar taxa to the active bed assemblage at P.Up-reach but was significantly impoverished in terms of both density and diversity with increasing volumes of suspended sand (Table III) despite the appropriate percentage of sand-sized sediment, d_{50} and bed hydraulic stresses recorded in the benthic zone (Table IV; Blettler *et al.*, 2008). The dominant species recorded in this reach were *N. bonettoi*, *Limnoperna fortunei*, *M. paranaensis*, *Corynoneura* sp. and *Limnodrilus udekemianus* (Table II). In marked contrast, this assemblage was not recorded in the active bed sites on the Bermejo River at the B-reach, where *Aedokriptus* sp. I, *Cryptochironomus* sp. I and *Paralauterborniella* sp. I are the dominant taxa (Table II). In addition to these taxa, during the 2001 campaign, *Ceratopogonidae* sp. I and *Polypedilum* sp. I were recorded on the Bermejo River. Although there are other rivers with higher suspended sediment loads than the Bermejo River around the world (e.g. see López-Tarazón *et al.*, 2009), the influence of this river extends far beyond its catchment, as most of the suspended sediment of the Paraná River

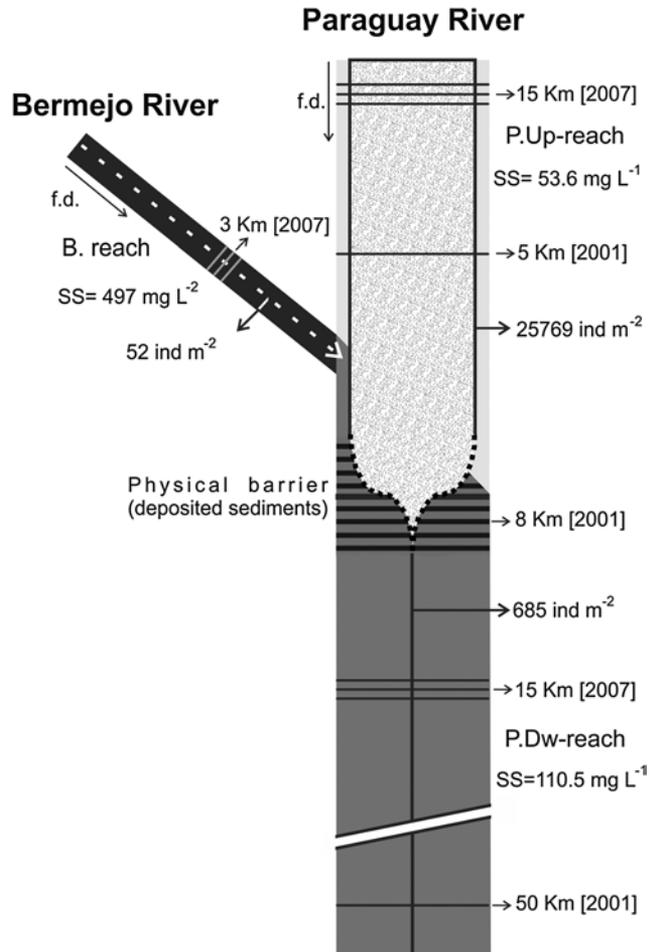


Figure 8. Schematic model showing the physical and ecological relationships upstream and downstream of the Bermejo-Paraguay confluence. Note the large differences in invertebrate densities and suspended sediments between reaches. The channel widths are proportional to the flow discharge of each river (Paraguay = $1719 \text{ m}^3 \text{ s}^{-1}$; and Bermejo = $340 \text{ m}^3 \text{ s}^{-1}$, approximately). SS, suspended sediments; f.d., flow direction.

catchment is derived from the Bermejo, after being delivered by the Paraguay River. The Bermejo River contributes approximately 108 million tons per year of sediment to the lower reaches of the Paraguay and Middle Paraná Rivers (Drago and Amsler, 1988). Their unusual fine sediment characteristics could explain the distinctive benthic assemblage inhabiting it.

The CAP results quantitatively confirm the aforementioned statement from an ecological perspective, demonstrating that there are clearly three different benthic groups, one at each of the meander sites (Figure 5). Despite the input of the Bermejo River, the P.Up-reach and P.Dw-reach have a relatively similar bed sediment composition and sand grain size distribution (Tables IV and V; Figure 6). It is widely acknowledged that the benthic habitat characteristics considerably affect the composition and distribution of many benthic taxa (e.g. Gurtz and Wallace, 1984; Rempel *et al.*, 2000; Takeda *et al.*, 2001; Amsler *et al.*, 2009). The direct association of taxa with the degree of substratum roughness and hydraulic characteristics has also been demonstrated in previous research (e.g. Fuller and Rand, 1990; Holomuzki and Messier, 1993; Quinn and Hickey, 1994; Hart *et al.*, 1996; Rempel *et al.*, 2000; Amsler *et al.*, 2009; Blettler *et al.*, 2012a, 2012b). In this study, d_{50} and percentage of sand in suspension were the best explanatory variables of benthic faunal distribution when all three reaches were considered (Figure 6), although the d_{50} values recorded at the P.Up-reach and P.Dw-reach were different. Whereas hydraulic stress was slightly higher at the P.Dw-reach, as witnessed by the higher flow velocities and bed shear stresses, the benthic sediments were similar in composition and grain size distribution (Table IV). The benthic assemblage recorded at the P.Dw-reach was different from its counterparts upstream (Figures 3A, 5 and 6). The minor hydraulic differences recorded are unlikely to be the main reason for the modification to the benthic assemblage downstream of the Bermejo River confluence. As a result, the massive increase of suspended sand downstream of the confluence has been interpreted as the main reason for change observed in the faunal community (Table IV and Figure 6B).

It has been well documented that sediment inputs, from different origins, greatly modify the assemblage structure and composition of benthic communities (e.g. Shaver *et al.*, 1997; Bond and Downes, 2003; Death *et al.*, 2003; Harrison *et al.*, 2007). As individuals succumb to the direct negative effects of increased sediment loads, changes occur in the abundance of individual species, which in turn change the community composition (e.g. Fossati *et al.*, 2001; Ehrhart *et al.*, 2002; Freeman and Schorr, 2004). However, in the present study, the effect of sediment delivery from the Bermejo River was not necessarily a direct consequence of the sedimentation phenomenon itself. Considering the dramatic increase of suspended sediment delivered by the Bermejo River, it is speculated that at least four factors may contribute to explain the effects of suspended/deposited fine sediment input on the benthic invertebrates.

First, the large sedimentological changes, which occur immediately downstream of the junction as the Bermejo River plume mixes across channel (Best *et al.*, in review),

are responsible for the modification and impoverishment of the benthic assemblage downstream of the confluence at 8 (2001 samples), 15 (2007 samples), and 50 km (2001 samples; Figures 3AB and 5). The sedimentary dynamics at the Bermejo–Paraguay junction probably represent a major physical barrier (1–2 km approximately). This barrier (comparable to a blockage) is formed by the input of sediment from the Bermejo River, with the bed below the fine sediment plume not being viable for invertebrate colonization or being difficult (depending of the water level stage), to pass by invertebrates. As a result, the assemblage downstream of the confluence is poorly represented despite the presence of appropriate physical and chemical conditions (e.g. sediment composition; Table IV and Figure 7). Second, for any invertebrates that were able to pass through this physical barrier, the colonization of the reach between the Paraguay–Bermejo and Paraguay–Paraná confluences (80 km approximately) would be a significant challenge. According to previous studies (Hydraulic Research Stations, 1972) and Figure 6, downstream of the Bermejo River junction, there is a fining of the sand size fraction, which reaches a median of approximately 0.170 mm. When the input of fine sediment from the Bermejo River to the Paraguay River increases (especially during flooding events), the average size of bed particles is reduced, and the interstices between the larger particles become filled with finer sediment (Kaufmann *et al.*, 2009). Both sampling campaigns (November 2001 and October 2007) were undertaken during low water stage (1.99 and 1.39 m at Pilcomayo Port, respectively; Figure 4). Therefore, d_{50} values recorded upstream and downstream to the confluence were not significantly different. Only a slight trend of fining sand grains was recorded in the P.Dw-reach. This feature is directly attributable to the reduced input of fine sediment from the Bermejo River, characteristic during low water stage (peak discharges and sediment yields from this river occur between January and March; Best *et al.*, in review). Considering all information together, the effect of the fining and coarsening of grain size (during low and high water stages, respectively) on organisms should not be treated like a ‘physical action reaction’ but rather as an ecological relationship with lag-periods between each parameter. This lag-period is due to the time required by organisms to colonize after substratum modification. Recolonization of available habitats takes longer when motile species are lacking from the community (Gjerløv *et al.*, 2003; Hutchens *et al.*, 2009), and this explain the reduced diversity in the reach from the Paraguay–Bermejo to the Paraguay River–Paraná River confluence. Therefore, the persistent fining and coarsening of the grain size, due to the temporal changes in grain size delivered during the Bermejo River hydrograph, would result in an extremely dynamic situation on the river bed, preventing or severely limiting colonization by invertebrates.

The third tentative explanation for the dramatic reduction in invertebrate density and composition at the Bermejo River confluence pertains to food availability. A reduction in phytoplankton quality may occur because of the effect of turbidity on algal growth (Parkhill and Gulliver, 2002). High levels of suspended sediment reduce light penetration and result in a reduction of algal growth (Quinn *et al.*, 1992, 1997). Downstream of the Bermejo River confluence, the phytoplankton community on the Paraguay is severely reduced (Zalocar de Domitrovic *et al.*, 2007), because of the sediment input and, as a consequence, a reduction in light penetration. This explanation is supported by the results of the Secchi disk measurements recorded in this study of 45 (P.Up-reach), 29 (P.Dw-reach) and only 10 cm (Bermejo). This highlights the clear reduction in water transparency downstream of the confluence. Additionally, Ezcurra de Drago *et al.* (2007) postulated that the basis of the food web and the main food item of *N. bonettoi* was the algae *Aulacoseira granulata* (Bacillariophyceae). This alga is an *r*-strategist species adapted to variations in turbulence. Although the present study did not survey the phytoplankton community, the results suggest that the

A. granulata population is markedly diminished downstream of the confluence, and this has negative consequences for *N. bonettoi* and the wider benthic assemblage.

Finally, the most speculative hypothesis is that the suspended fine sediment is continuously moving and in contact with the upper layers of the sand bed, constantly being deposited and eroded by the flow. This would probably cause the interstitial spaces of the substratum to clog (Packman *et al.*, 2000). Without interstitial pore spaces free of fine sediments, there would be limited habitat for the invertebrates of the active bed (Takeda *et al.*, 2001, Blettler *et al.*, 2008). In addition, the fine sediment particles may act as an abrasive if moving at high velocity. Unprotected fleshy body parts are particularly prone to damage (Newcombe and MacDonald, 1991). Moreover, physical damage by abrasion and the transport of fine particles, particularly clays and silts, can cause a build-up on organs, making respiration and feeding difficult and less efficient.

When the results recorded from 2007 are compared with those obtained in 2001, a similar pattern was observed (Figure 3A and B). The earlier survey confirms the strong influence of suspended sediment input from the Bermejo

River on the density and diversity of invertebrates. In addition, the 2001 results indicate that the impact extends at least 50 km downstream of the confluence (Figures 3B and 8).

The deposition of fine sediment on river beds is usually associated with profound changes to the chemical environment. Reduced interstitial flow through the substrate resulted in the establishment of steep gradients of oxygen and other dissolved substances (Pretty *et al.*, 2006). However, in the present study, the chemical variables were similar between the P-Up-reach and P-Dw-reach. Although

the concentrations of all chemical parameters were slightly higher at the B-reach, they are within the appropriate range of chemical water quality (Figure 7). In this sense, chemical characteristics by themselves cannot explain the ecological patterns and faunal distribution recorded. Optimal water quality was recorded during the 2007 sampling period, and water chemistry variables were in the normal range expected in this fluvial system (Depetris and Pasquini, 2007). However, the electric conductivity of water deserves special consideration because of the sensitivity of *N. bonettoi* (Marchese, 1994; Takeda *et al.*, 2001; Ezcurra de Drago *et al.*, 2004). Taking into account the optimal range of electric conductivity for *N. bonettoi* established by Blettler *et al.* (2008), and indirectly for the whole active bed assemblage, the conductivity of the Bermejo River is at the upper boundary of this range ($750 \mu\text{S cm}^{-1}$). However, the P-Up-reach and P-Dw-reach show an optimal conductivity for colonization and survival (157 and $163 \mu\text{S cm}^{-1}$, respectively) and thus is not a limiting factor.

CONCLUSIONS

This study shows that a significantly increased loading of fine sediment at a large river confluence, either in suspension or by deposition, has both direct and indirect effects on benthic invertebrates. This effect extends at least 50 km downstream of the source (Figure 8). Four hypotheses have been proposed to explain the impoverished invertebrate assemblage in the Paraguay River downstream the Bermejo River confluence: (i) the sediment input from the Bermejo River forms a physical barrier on the Paraguay River bed immediately downstream of the confluence, which makes colonization exceedingly difficult and/or a zone that is difficult to migrate through; (ii) if invertebrates were able to break through this physical barrier, the constant erosion and deposition of sediment on the bed of the Paraguay River (due to the naturally dynamic sediment input and discharge from the Bermejo River) may create a harsh environment that prevents colonization by most common invertebrates on the river; (iii) the reduction in light penetration, due to the high suspended sediments concentrations, reduces algal growth, a key food resource for invertebrates; and finally (iv) the suspended sediments are in continuous contact with the upper layers of the substratum, which may cause clogging of the interstitial spaces where invertebrates inhabit or it may have an abrasive effect. All of these hypotheses could act independently or in combination at any point in time.

Although quantifying the impacts of fine suspended sediment on invertebrates is fraught with difficulty, this study demonstrates the need to measure the effect of suspended sediment *per se* as well as the influence of sedimentation. The extent nature of the impact of fine sediment appears dependent upon the hydrological and

sedimentological context and specific invertebrate assemblage present. The present study suggests that consideration of the effects of fine sediment input on benthic invertebrates and its interaction with flow is important in the field of ecohydrology. Future research should consider both anthropogenic and natural sources of fine sediment input so that management techniques can be developed for large rivers and integrate into rehabilitation projects.

ACKNOWLEDGEMENTS

The authors are grateful to Dr Mercedes Marchese for making available previous sampling data (2001), E. Creus and A. Regner for field assistance and Dr Chichipeo Wilson for comments that improved the manuscript. We would like to express our sincere gratitude for all the valuable and constructive comments we have received from the expert reviewers. This research was supported with financial assistance of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina), grant PIP number 6209.

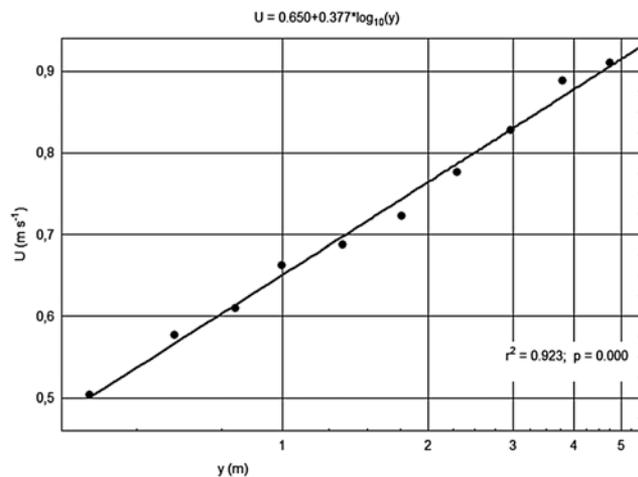


Figure A1. Example of a smoothed semi-log velocity profile at the P.Dw-reach (transect south, thalweg site). The y values were corrected accounting for the position of the virtual origin (see Perry and Joubert, 1963; Amsler *et al.*, 2009).

APPENDIX

Example of detailed velocity profile measured at the P.Dw-reach (transect South, thalweg site). Note the good fit of the data to the log function derived from the ‘law of the wall’ (Schlichting, 1979).

Table A1 shows the r^2 results of each adjusted velocity profile measured in this study.

REFERENCES

- Amsler ML, Drago, EC. 2009. A review of the suspended sediment budget at the confluence of the Paraná and Paraguay Rivers. *Hydrological Processes*. DOI: 10.1002/hyp.7390
- Amsler ML, Blettler, MCM, Ezcurra de Drago I. 2009. Influence of hydraulic conditions over dunes on the distribution of the benthic macroinvertebrates in a large sand bed river. *Water Resource and Research* 45. DOI: 10.1029/2008WR007537.
- Anderson MJ. 2004. *CAP: A FORTRAN Computer Program for Canonical Analysis of Principal Coordinates*. Department of Statistics, University of Auckland: New Zealand.
- Anderson MJ, Robinson J. 2003. Generalised discriminant analysis based on distances. *Australian and New Zealand Journal of Statistics* 45: 301–318.
- Anderson MJ, Willis TJ. 2003. Canonical Analysis of Principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84: 511–525.
- Best J, Parsons D, Amsler M, Kostachuck R, Lane S, Orfeo O. 2007. On the influence of density contrast between mixing flows at channel confluences: the Rio Bermejo and Rio Paraguay, Argentina. In Workshop on Morphodynamic Processes in Large Lowland Rivers, Santa Fe, Argentina.
- Blettler MCM, Amsler M, Ezcurra de Drago I, Marchese M. 2008. Effects of stream hydraulics and other environmental variables on density of benthic macroinvertebrates in the Paraná River system. *River Research and Application* 24: 1124–1140.
- Blettler MCM, Amsler M, Ezcurra de Drago I, Drago E, Paira A, Espinola L. 2012a. Hydrodynamic and morphologic effects on the benthic invertebrate ecology along a meander bend of a large river (Paraguay River, Argentina-Paraguay). *Ecological Engineering* 44: 233–243.
- Blettler M, Amsler L, Ezcurra I. 2012b. Sampling techniques of benthic invertebrates and spatial distribution on dunes at a section of the large Middle Paraná River (Argentina). *Journal of South American Earth Sciences* 35: 27–37.

Table A1. r^2 results of each adjusted velocity profile measured in this study.

Transects at each sampling area	Sampling station	P.Up-area (r^2)	P.Dw-area (r^2)	B-area (r^2)
North	CL	0.98	0.98	—
	CC	0.97	0.99	0.99
	CR	0.99	0.97	—
Centre	CL	0.99	0.94	—
	CC	0.93	0.8	0.9
	CR	0.98	0.98	—
South	CL	0.95	0.98	—
	CC	0.98	0.99	0.98
	CR	0.99	0.99	—

Maximum and minimum values = 0.99 and 0.8, respectively. CL, sampling vertical located next to the central one, on the left side; CC, sampling vertical located in the central position; CR, sampling vertical located next to the central one, on the right side (Figure 1B–D).

- Bond NR, Downes BJ. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology* 48: 455–465.
- Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monograph* 27: 325–349.
- Burnham KP, Anderson DR. 1998. *Model Selection and Inference: A Practical Information-Theoretical Approach*. Springer: New York, p 353.
- Chessman BC, Fryirs KA, Brierley GJ. 2006. Linking geomorphic character, behaviour and condition to fluvial biodiversity: implications for river management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 267–288.
- Cordone AJ, Kelley DW. 1961. The influences of inorganic sediment on the aquatic life of streams. *California Fish and Game* 47: 189–228.
- Crowe A, Hay J. 2004. Effects of fine sediment on river biota. Prepared for Motueka Integrated Catchment Management Programme. Cawthron Institute 98 Halifax Street East Private Bag 2. Nelson, New Zealand, pp. 35.
- Culp JM, Wrona FJ, Davies RW. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* 64: 1345–1351.
- Death RG, Baillie B, Franssen P. 2003. Effect of *Pinus radiata* logging on stream invertebrate communities in Hawke's Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 37: 507–520.
- Depetris PJ, Pasquini AI. 2007. The geochemistry of the Paraná River: an overview. In *The Middle Paraná River. Limnology of a Subtropical Wetland*, Iriondo MH, Paggi JC, Parma MJ (eds). Springer: Berlin, Heidelberg; 143–174.
- Doeg TJ, Koehn JD. 1994. Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *Regulated Rivers: Research and Management* 9: 263–278.
- Drago E. 1990. Geomorphology of large alluvial rivers: Lower Paraguay and Middle Paraná. *Interciencia* 15: 378–387.
- Drago EC, Amsler ML. 1988. Suspended sediment at a cross section of the Middle Paraná River: concentration, granulometry and influence of the main tributaries. Sediment Budgets (381–396). Proc. of the Porto Alegre Symposium, December 1988, IAHS Publ. N° 174.
- Ehrhart BJ, Shannon RD, Jarrett AR. 2002. Effects of construction site sedimentation basins on receiving stream ecosystems. *Transactions of the ASAE* 45: 675–680.
- Ezcurra de Drago I, Marchese M, Wantzen M. 2004. Benthos of a large neotropical river: spatial patterns and species assemblages in the Lower Paraguay and its floodplains. *Archiv für Hydrobiologie* 160: 347–374.
- Ezcurra de Drago I, Marchese M, Montalto L. 2007. Benthic invertebrates. In *The Middle Paraná River. Limnology of a Subtropical Wetland*, Iriondo MH, Paggi JC, Parma MJ (eds). Springer-Verlag Berlin: Germany; 251–274.
- Fossati O, Wasson JG, Hery C, Salinas G, Marin R. 2001. Impact of sediment releases on water chemistry and macroinvertebrate communities in clear water Andean streams (Bolivia). *Archiv für Hydrobiologie* 151: 33–50.
- Freeman PL, Schorr MS. 2004. Influence of watershed urbanization on fine sediment and macroinvertebrate assemblage characteristics in Tennessee Ridge and Valley Streams. *Journal of Freshwater Ecology* 19: 353–362.
- Fuller RL, Rand PS. 1990. Influence of substrate type on vulnerability of prey to predacious aquatic insects. *Journal of the North American Benthological Society* 9: 1–8.
- Giacosa RE, Paoli CU, Cacik P. 2000. Conocimiento del régimen hidrológico. In *El río Paraná en su tramo medio. Contribución al conocimiento y prácticas ingenieriles en un gran río de llanura*, Vol. 1, Paoli C, Schreider M (eds). Centro de Publicaciones, Universidad Nacional del Litoral, Santa Fe, Argentina; 301.
- Gjerlov C, Hildrew AG and Jones JL. 2003. Mobility of stream invertebrates in relation to disturbance and refugia: a test of habitat templet theory. *Journal of the North American Benthological Society* 22: 207–223.
- Gurtz ME, Wallace JB. 1984. Substrate-mediated response of stream invertebrates to disturbance. *Ecology* 65: 1556–1569.
- Harrison E, Norris R, Wilkinson S. 2007. The impact of fine sediment accumulation on benthic macroinvertebrates: implications for river management. In *Proceedings of the 5th Australian Stream Management Conference. Australian Rivers: Making a Difference*, Wilson AL, Dehaan RL, Watts RJ, Page KJ, Bowmer KH, Curtis A (eds). Charles Sturt University: Thurgoona, New South Wales; 139–144.
- Hart DD, Clark BD, Jasentuliyana A. 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography* 41: 297–308.
- Hogg ID, Norris RH. 1991. Effects of runoff and land clearing and urban development on the distribution and abundance of macroinvertebrates in pool areas of a river. *Australian Journal of Marine and Freshwater Research* 42: 507–518.
- Holomuzki JR, Messier SH. 1993. Habitat selection by the stream mayfly *Paraleptophlebia guttata*. *Journal of the North American Benthological Society* 12: 126–135.
- Hutchens JJ, Schuldt JA, Richards C, Johnson LB, Host GE, Breneman DH. 2009. Multi-scale mechanistic indicators of Midwestern USA stream macroinvertebrates. *Ecological Indicators* 9: 1138–1150.
- Hydraulic Research Station. 1972. River Paraguay study. Hydraulic studies and mathematical models of the river between Asunción and Confluencia. Report No. EX606, Wallingford, England.
- Hynes HBN. 1970. *The Ecology of Running Waters*. Liverpool University Press: Liverpool.
- Kaller MD, Hartman KJ. 2004. Evidence of a threshold level of fine sediment accumulation for altering benthic invertebrate communities. *Hydrobiologia* 518: 95–104.
- Kaufmann PR, Larsen DP, Faustini JM. 2009. Bed stability and sedimentation associated with human disturbances in Pacific Northwest streams. *Journal of the American Water Resources Association* 45: 434–459.
- Kostaschuk R, Villard P, Best JL. 2004. Measuring velocity and shear stress over dunes with acoustic Doppler profiler. *Journal of Hydraulic Engineering, ASCE* 130: 932–936.
- López-Tarazón JA, Batalla RJ, Vericat D, Francke T. 2009. Suspended sediment transport in a highly erodible catchment: the River Isábena (Southern Pyrenees). *Geomorphology* 109: 210–221.
- Manly BFJ. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd Edn. Chapman and Hall: London.
- Marchant R, Ryan D, Metzeling L. 2006. Regional and local species diversity patterns for lotic invertebrates across multiple drainage basins in Victoria. *Marine and Freshwater Research* 57: 675–684.
- Marchese MR. 1994. Population dynamics of *Narapa bonettoi* Righi and Varela, 1983 (Oligochaeta: Narapidae) from the main channel of the Middle Paraná River, Argentina. *Hydrobiologia* 278: 303–308.
- Marchese MR, Ezcurra de Drago I. 1992. Benthos of the lotic environments in the Middle Paraná River system: transverse zonation. *Hydrobiologia* 237: 1–13.
- Marchese MR, Ezcurra de Drago I, Drago E. 2002. Benthic macroinvertebrates and physical habitat relationship in the Paraná flood-plain system. *The Ecohydrology of South American Rivers and wetlands, IAHS Special Publication* 7: 111–132.
- Marchese MR, Wantzen M, Ezcurra de Drago I. 2005. Benthic invertebrate assemblages and species diversity patterns of the Upper Paraguay River. *River Research and Application* 21: 485–499.
- McCullagh P, Nelder JA. 1989. *Generalized Linear Models*, 2nd edn. Chapman & Hall: London; 532.
- Newcombe CP, MacDonald DD. 1991. Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management* 11: 72–82.
- Northport Systems Inc. 2007. Fugawi Marine ENC® 4.5. <http://www.fugawi.com>
- Packman AI, Brooks NH, Morgan JJ. 2000. A physicochemical model for colloid exchange between a stream and a sand streambed with bed forms. *Water Resources Research* 36: 2351–2361.
- Parkhill KL, Gulliver JS. 2002. Effect of inorganic sediment on whole stream productivity. *Hydrobiologia* 472: 5–17.
- Parsons DR, Best JL, Lane SN, Orfeo O, Kostaschuk R, Amsler ML, Hardy RJ. 2006. Sediment dynamics of a large river confluence with marked contrast of transport in suspension: the Bermejo and Paraguay Rivers (Argentina). IV Congreso Latinoamericano de Sedimentología – XI Reunión Argentina de Sedimentología. Bariloche, Argentina.
- Peckarsky BL. 1984. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology* 63: 1519–1530.
- Perry AE, Joubert PN. 1963. Rough-wall boundary layers in adverse pressure gradients. *Journal of Fluid Mechanics* 17: 193–211.

- Pillar VP. 2006. MULTIV, multivariate exploratory analysis, randomization testing and bootstrap resampling software. Available at: <http://ecoqua.ecologia.ufrgs.br/ecoqua/software.html>
- Pretty JL, Hildrew AG, Trimmer M. 2006. Nutrient dynamics in relation to surface-subsurface hydrological exchange in a groundwater fed chalk stream. *Journal of Hydrology* 330: 84-100.
- Quinn JM, Hickey CW. 1990. Magnitude of effects of substrate particle size, recent flooding and catchment development on benthic macroinvertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24: 411-427.
- Quinn JM, Hickey CW. 1994. Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. *Freshwater Biology* 32: 489-500.
- Quinn JM, Davies-Colley RJ, Hickey CW, Vickers ML, Ryan PA. 1992. Effects of clay discharges on streams 2. Benthic invertebrates. *Hydrobiologia* 248: 235-247.
- Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill country streams. *New Zealand Journal of Marine and Freshwater Research* 31: 579-597.
- Rempel LL, Richard JS, Healey MC. 2000. Macroinvertebrates community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology* 45: 57-73.
- Richards SA. 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86: 2805-2814.
- Ryan PA. 1991. Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* 25: 207-221.
- Schlichting H. 1979. *Boundary-Layer Theory*. McGraw-Hill Book Co.: New York, US; 817.
- Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591-611.
- Shaver ML, Shannon JP, Wilson KP, Benenati PL, Blinn DW. 1997. Effects of suspended sediment and desiccation on the benthic tailwater community in the Colorado River, USA. *Hydrobiologia* 357: 63-72.
- Sokal RR, Rohlf FJ. 1981. *Biometry*, 2nd ed. Freeman: San Francisco, US; 219.
- Takeda AM, Fujita DS. 2004. Benthic invertebrates. In *The Upper Paraná River and Its Floodplain: Physical Aspect, Ecology and Conservation*, Thomaz SM, Agostinho AA, Hanh NS (eds). Backhuys Publ: Leiden the Netherlands, 191-s208.
- Takeda A, Stevaux J, Fujita D. 2001. Effect of hydraulics, bed load grain size and water factors on habitat and abundance of *Narapa bonettoi* Righi and Varela, 1983 of the Upper Paraná River, Brazil. *Hydrobiologia* 463: 241-248.
- Waters TF. 1995. *Sediment in Streams: Sources, Biological Effects and Control*. American Fisheries Society: Bethesda, Md..
- Wood PJ, Armitage PD. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21: 203-217.
- Yalin MS. 1977. *Mechanics of Sediment Transport*, 2nd Edn. Pergamon Press: Oxford, England; 298.
- Zalocar de Domitrovic Y, Devercelli M, García de Emiliani M. 2007. Phytoplankton. In *The Middle Paraná River: Limnology of a Subtropical Wetland*, Iriondo MH, Paggi JC, Parma MJ (eds). Berlin-Heidelberg: Springer-Verlag, Berlin; 175-203.