(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

Journal of South American Earth Sciences 35 (2012) 27–37

Contents lists available at SciVerse ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

Hydraulic factors controlling the benthic invertebrate distribution within and among dunes of the Middle Paraná River (Argentina) and sampling techniques

Martín C.M. Blettler*, Mario L. Amsler, Inés Ezcurra de Drago

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

ARTICLE INFO

Article history:
Received 22 January 2011
Accepted 4 November 2011

Keywords:
Benthic invertebrates
Dunes geometry
Hydrodynamic bed conditions
Large rivers
Sampling techniques

ABSTRACT

Dunes are ubiquitous bed forms in river channels which deeply interact with the mean and turbulent flow dynamic. These interactions involve the intricate mechanisms governing the entrainment, transport, and deposition of bed sediment which are being studied since long time ago. However, the links between dunes and stream ecology, such as the benthic fauna distribution, was not yet investigated to the authors' knowledge. This study aims to optimize the benthic sampling techniques on bed forms, and links the different hydraulic characteristics prevailing on crests and troughs of dunes and the invertebrate distribution on the Middle Paraná River (Argentina). It was also possible to have an insight of the invertebrate distribution living in these bed areas (i.e. crests and troughs) as well as the influence of dunes location on the channel bed. A significant distinction of benthic distribution (densities) on dunes, as a consequence of their location on the bed and hydraulic conditions, was found. The overall results showed a clear preference by invertebrates for the dune with lower bed shear stresses. The study concluded that dunes could be considered as biotopes hydraulically differentiated and, consequently, with a stratified benthic distribution. Consequently, to discriminate bottom areas, by an appropriate selection of the hydraulic variables over the associated geometry of dunes, is an effective way to reduce the variance and to increase the accuracy of benthic samplings in large rivers.

1. Introduction

Dunes in alluvial rivers are an essential component of the current and sediment flow dynamics as they significantly influence both the nature of the flow mean and turbulent structure. Their crucial role on the entrainment, transport and deposition of bed particles is widely recognized. These reasons explain why dune dynamics has been a topic of intensive investigations in river engineering (Kennedy, 1977; Engel, 1981; Nelson et al., 1993; Best and Kostaschuk, 2002; Kostaschuk et al., 2004; Best, 2005), sedimentology (Kostaschuk and Villard, 1996; Williams et al., 2003; Carling et al., 2000a; Kostaschuck, 2000; Leclair and Bridge, 2001), morphology (Carling et al., 2000b; Parsons et al., 2005), as well as interdisciplinary disciplines (Coleman and Nikora, 2011).

The main characteristics of flow along a dune were derived essentially from laboratory experiments performed with increasing detailed since the pioneer study of Raudkivi (1963). They are: 1) accelerating flow over the dune stoss-side, 2) flow separation or deceleration after the dune crest on the lee side, 3) flow reattachment at 4–6 dune heights downstream, 4) a shear layer between the separated flow zone and streamwise flow above, which expands as it extends downstream, and 5) an internal boundary layer which grows from the reattachment beneath the wake zone along the stoss slope of the next dune downstream (Engel, 1981; Nelson et al., 1993; McLean et al., 1994; Best and Kostaschuk, 2002; see Fig. A1 in Appendix). Some of these features may not be present in natural rivers, e.g. the separation zone and the reattachment point (Ogink, 1989; Amsler and Schreider, 1992; Amsler and Gaudin, 1994). Moreover, superimposition of small dunes on the large bed forms is frequently recorded in large rivers like the Paraná (Amsler and Prendes, 2000).

The eventual relation of dune dynamics with the topics of river ecology is including into the 'eco-hydraulics' discipline. It involves research topics in the overlap between the hydro- morphological and ecological sciences (Hannah et al., 2004). Despite the increasing attention given to this new discipline it is still poorly explored (Zalewski and Robarts, 2003) perhaps due to the lack of proper accounting by ecologists of the role that hydraulics and morphology plays in ecological interactions (Kemp et al., 2000). Hydraulic engineers, in turn, began rather recently to investigate in detail certain topics closely related to biology of environments, e.g. the function of submerged vegetation in the flow resistance and

* Corresponding author. Tel.: +54 342 4511645; fax: +54 342 4511648.
E-mail address: martinblettler@hotmail.com (M.C.M. Blettler).

0895-9811/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jsames.2011.11.003

sedimentation (Stephan and Gutknecht, 2002). Regarding the specific incidence of alluvial dunes on the benthic distribution it is a subject insufficiently studied. One of the first contributions is due to Amsler et al. (2009) in the Middle Paraná River. Those authors concluded that dunes could be viewed as hydraulic biotopes (Wadeson, 1994) considering the benthic community distribution. However, the incidence of bottom hydraulics on the benthic distribution in large rivers claiming for more and deep investigations. In spite of this state of knowledge there exists a detailed description of the invertebrate community which inhabits the Paraná River (Marchese and Ezcurra de Drago, 1992; Ezcurra de Drago et al., 2004; Takeda and Fujita, 2004; between others).

Nevertheless the importance of the benthic sampling techniques, it is a topic poorly tested in large rivers with bed forms. Actually, discriminating bottom areas along dunes, which could influence the benthic distribution, would be an effective way to optimize sampling by reducing variance and increasing the accuracy of population estimates. To know the minimum number of samples needed in the different sectors of the dunes would be the desirable final purpose. The topic related with the frequency and methodology of sampling necessary for reliable assessments has been a matter of discussion in many papers (Somers et al., 1998; Doberstein et al., 2000; King and Richardson, 2002). By using a standard sampler the variation between samples will account for the invertebrate spatial distribution on the stream bed (Elliot, 1977). As the dispersion of many invertebrate species is frequently contagious, to take few samples will be statistically inaccurate. The simplest solution to this problem is to increase the samples number, something usually too costly in routine studies (Elliot, 1977). Actually, it is desirable to reduce the sampling efforts as much as possible without increasing the results uncertainty. The large spatial scales together with the presence of dunes of diverse hierarchy involve unavailable difficulties in the sampling techniques. For example, in deep areas the camber angle of the sampler (due to the flow drag) and the local bottom slope, may to reduce the collected sediment volume as much as to supply unreliable results. A morphological approach can help to decrease the inaccuracy generated by applying sampling without consider a morphodynamics point of view (Stevaux and Takeda, 2002). However, at a bed form scale the presence of dunes of diverse hierarchy involves unavailable difficulties in the sampling techniques. Therefore, a necessity exists for establishing the minimum number of samples that should be taken to achieve accurate results considering the natural community distribution and spatial scales involved when dunes are present.

Considering the above statements the objectives of this study were: 1) to estimate the minimum number of benthic samples (N minimum) in the different dune sectors of the main channel of the Middle Paraná River, 2) to look for a possible relationship between the benthic density and the sand amount of each sample caught at a given site, and 3) to relate bed hydraulic parameters estimated within (i.e. crest and trough) and among (i.e. thalweg and outside the thalweg) two dunes with the spatial distribution of the macroinvertebrates. This last purpose relies on the results of Amsler et al. (2009) which report that dunes influence the invertebrates' distribution primarily by differences in the bed hydraulic conditions. The authors have also discussed the possibility of considering the dunes as true hydraulic biotopes, following the definition introduced by Wadeson (1994).

2. Methods

2.1. Study area

The field measurements were performed at a cross section of the Middle Paraná River located upstream of Paraná city, Argentina (Fig. 1). The Paraná River is ranked ninth among the largest rivers of the world according to its mean annual discharge to the ocean (18,000 m^3 s^{-1}; Latrubesse, 2008). It has a sandy bed where fine and medium grain sizes prevail transported principally by saltation and suspension (Drago and Amsler, 1998; Alarcón et al., 2003). Two large dunes in the main channel were surveyed (see Fig. 1). One of them, dune 1 (31ó°41′59.3″ S; 60°30′34.3″ W), was 2.3 m height and 122 m length and had a slope angle on the lee side of 16° (Fig. 2A). The other one, dune 2 (31°42′14.3″ S; 60°30′39.1″ W), was 1.3 m height and 120 m length and had a slope angle on the lee side of 3°. Dune 2 was located just on the thalweg track (Fig. 2B). Both dunes had superimposed smaller dunes. These small dunes were present along the entire profile of dune 2, but they only appeared along its stoss-side up to the crest on dune 1.

2.2. Sampling

The survey was performed in October 2005 during a low water stage. The benthic samples were obtained at the crest and trough of each dune. Ten replicates were sampled at each sampling station with a clamshell bucket (trade mark: Tamura), i.e. a total of 40 samples were obtained. The bucket has a sampling area of 319 cm^2. Samples were fixed in 5% formaldehyde in the field and filtered with a 200 μm sieve. The invertebrates were hand-picked in the laboratory under a 10× stereoscopic microscope and stored in a 70% ethanol solution. All benthic organisms were counted and identified. For Turbellaria from Noreña (1995), Noreña et al., 2005; for Oligochaeta from Brinkhurst and Marchese (1992); and for Diptera Chironomidae from Trivinho-Strixino and Strixino (1995). For other taxa the determinations were made to genus and morphospecies.

Additional sediment samples for granulometric analysis (by dry sieving; Wenthword scale) and sediment organic matter content (ash-free dry matter method) were taken at each sampling station.

A key point to be considered in the sampling was the boat positioning. It was in order to assure the 10 samples be taken at each sampling station (i.e. at each crest and trough of the selected dune). A GPS equipment (Garmin GPS Personal Navigator) was used for this purpose (accuracy: ±10 m), complemented with checks of the corresponding depths with a Raytheon echo sounder at the moment of each sample attainment. Previously, the sampling procedure involved the record of the bed topography along longitudinal tracks aligned with the current direction defined by floats. The longitudinal bed profiles were used to select in situ the dunes to be studied. The position of each dune, as given by the GPS, was fixed. Finally the boat was positioned 50–100 m upstream the selected dune and left to drift with two buckets (one at each boat's sides) suspended and mounted at 1–2 m above the river bed. Thus, the samplers drag did not occur. When the boat was drifting above the selected dune crest (and trough), the buckets were let fall freely to the bottom, taking the respective samples. The corresponding positions were also recorded with the GPS. This last step was repeated ten times at each crest (trough) of the two selected dunes. Simultaneously with the benthic samples, the depth (m) and surface current velocity (m s^{-1}) were also recorded. Note in the inset of Fig. 1 that the width which encompasses the total sampling point's distribution on the crests (and the troughs) is a small fraction (2.5–3%) of the total cross section width (2000 m). In consequence, the possibility of pronounced transverse gradients of flow parameters and bed sediment texture in such a short distance is not relevant in large rivers like the Paraná (van den Berg and de Vries, 1979). The corollary is that the measured hydraulic and sediment parameters truly represent the local flow and substratum environments of each sampled dune where the benthic community lives. Note also that the transversal separation between dunes 1 and 2 is ≈21.5% of the total width, much larger than the referred 2.5–3%. In this case true possibilities exist of significant transverse hydraulic changes, as it is discussed below.

The following parameters were also measured: conductivity (μS cm^{-1}), pH and temperature (°C) with a HACH water checker; dissolved oxygen (mg l^{-1}) with a hand-held WTW series 300 probe and transparency as given by the Secchi disk (m).

2.3. Selection and treatment of the hydraulic variables

The classic hydraulic parameters cited above were used to calculate other flow variables based on well established hydrodynamics laws. Similar approaches were successfully applied in other previous studies (Growns and Davis, 1994; Wadeson and Rowntree, 1998; Brooks et al., 2005), i.e. the characterization of the hydraulics bottom habitats at each sampling point was estimated through direct measurements of the surface current velocity (U_{max}), the local depth (h), and an indirect estimate of the bottom roughness height (k_s). The U_{max} was measured by using an electrical propeller current meter. Those basic parameters provided the necessary inputs to calculate more complex hydraulic parameters such as the bed shear stress (τ_0), or its equivalent the shear velocity (U_*), and the mobility number (τ_*) (Table 1). The computation of the local bed shear stress (or U_*) at a given point in large rivers implies a difficult problem, since the local friction slope has to be estimated. It is well known that it varies at each point due to the three-dimensional character of natural rivers. The problem was solved by means of the equations and criteria detailed in the Appendix.

When examining the hydraulic parameters used in this study in the light of some basic principles of open channel hydraulics (see

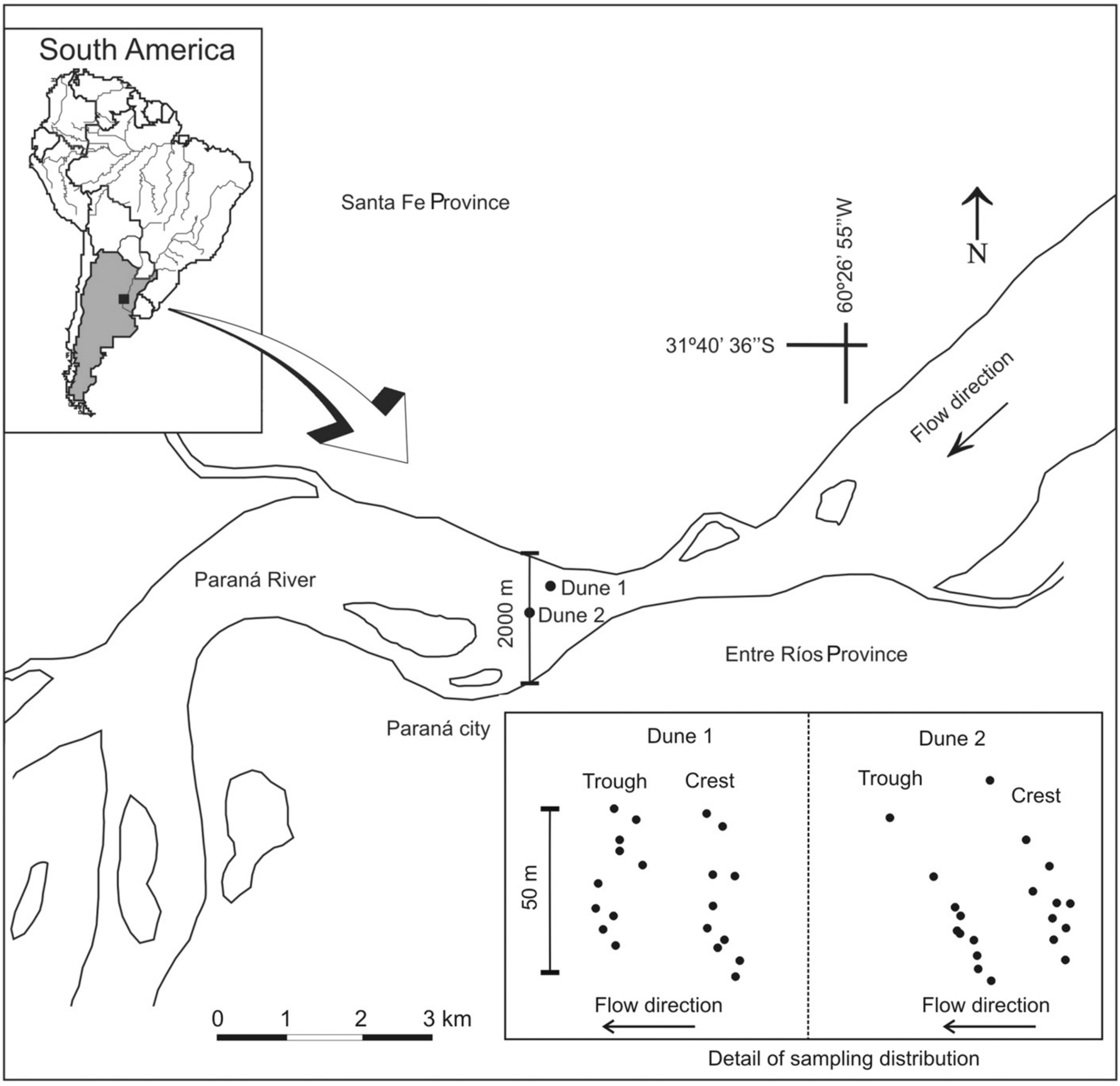


Fig. 1. Location and details of the sampling stations at the selected reach, in a plant view. See the position of each benthic sample in under inset.

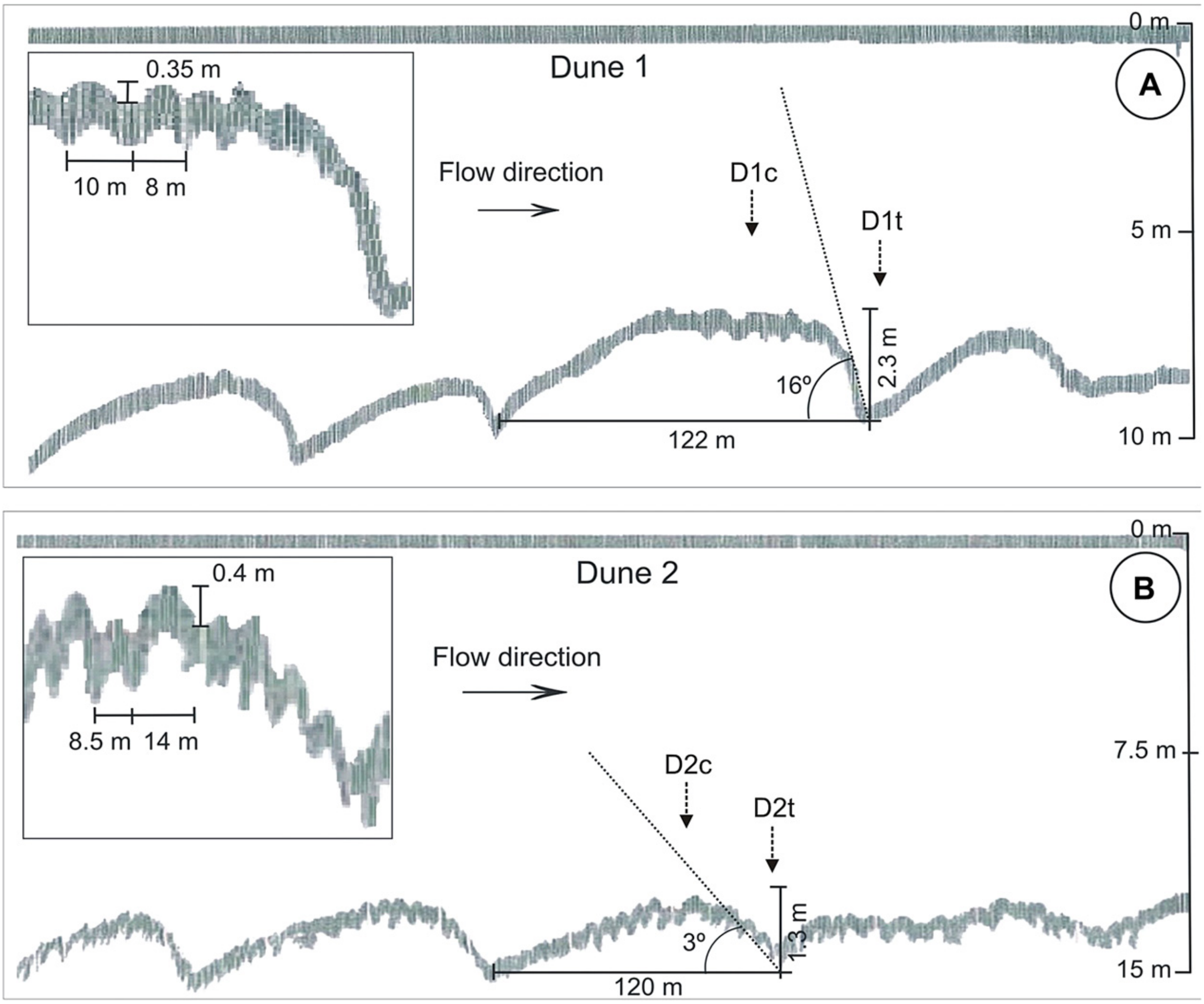


Fig. 2. Echo sounder charts showing the surveyed large dunes and the position of each sampling stations. A; dune 1. B; dune 2. The insets display details and overall mean dimensions of the superimposed small dunes. D1c = dune 1 crest; D1t = dune 1 trough; D2c = dune 2 crest; D2t = dune 2 trough.

some of the well known text books on this topic, e.g. Chow, 1959; Henderson, 1966), it is possible to show that the effects of depth and local friction slope are considered into the bed shear stress (and U_*). Respecting the mobility number, it is a hydraulic dimensionless variable involving the relationship between the flow tractive forces trying to move the bed particles and the particle weight which resist that movement, i.e. the passive force. Thus this number gives a measure of the transport intensity of the bottom sediment grains (Yalin, 1977). Taking into account that the median of the bed sediment size distribution (d_{50}) and τ_0 are included into τ_* (Table 1), this variable should be an important parameter to know the incidence of the bed sediment transport on the benthic community as was shown by Amsler et al. (2009), provided that its value be representative of the flow conditions surrounding the sampling point.

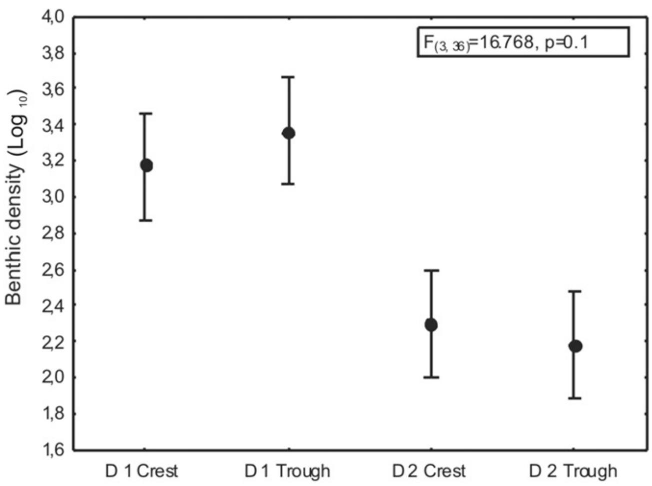


Fig. 3. ANOVA results (● = mean values; vertical bar = 95% confidence).

See List of Symbols at the end of de manuscript for the meaning of the symbols.

Although some authors (Statzner and Higler, 1986; Statzner et al., 1988; and Carling, 1992) also suggest to estimate other hydraulic variables such as the Froude (F_r) and Reynolds numbers (R_e) and the hydraulic radius (R) in benthic studies, these parameters were not considered in this study. That is because they describe the gross of the flow characteristics at a given cross section or vertical and, consequently, they say little about the local flow conditions close to the bed at a given point (see Amsler et al., 2009).

2.4. Statistical analysis

The organisms were identified and counted in order to calculate the diversity Shannon index (H).

Table 1
Summary of the hydraulic variables measured or computed in the study.

Name	Symbol	Units	Formula	Description
Surface current velocity	U_{max}	m s^{-1}	Direct measurement	Velocity measured at water surface.
Shear velocity	U_*	m s^{-1}	$U_* = \frac{U_{max}}{5.6\log_{10}\frac{h}{ks}+8.15}$	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 tractive and passive forces acting on the bed particles.
Bottom roughness height	k_s	m	Indirect measurement	Total roughness height at the sampling point.

The non-normal distribution of the benthic density data were logarithmically transformed [$\log_{10}(x+1)$] and tested for normality (Shapiro and Wilk, 1965) and homogeneity of variance (F_{max}; Sokal and Rohlf, 1981). The minimum number of samples was computed according to Wetzel and Likens (1991):

$$N_{min} = \frac{S^2}{\bar{x}(0.1)}$$

where: S^2: variance of the samples; $\bar{x}$: arithmetic mean of the samples; 0.1: selected average error of 10%.

The quantitative relationship between the sand weight of samples and the species density was analyzed through Pearson correlations. An ANOVA one-way (significant differences $= p < 0.05$) was used to determine significant differences between arithmetic means of benthic density at each sampling station. Post-hoc Fisher's LSD tests were used to explore differences among treatments in the ANOVA. Principal Components Analysis (PCA) of the physical variables was applied to summarize the total variation of data and identify major environmental gradients. Physical variables were also logarithmically transformed [$\log_{10}(x+1)$]. Community structure was analyzed using Canonical Correspondence Analysis (CCA). A program Multi-Variate Statistical Package (MVSP) version 3.1 (Kovach, 2002), was used.

3. Results

A total of 16 benthic species and morphospecies were identified. The taxonomic groups were Turbellaria, Nematoda, Oligochaeta, Collembola, Diptera Chironomidae and Ceratopogonidae, Mollusca Bivalvia. The total densities of benthic invertebrates considering individual collected sampler varied between 0 and 11,656 ind m^{-2}.The mean density for sampling stations ranged from 3884 ind m^{-2} (trough of the dune 1) to 226 ind m^{-2} (trough of dune 2; Table 2). The dune 1 (outside the thalweg) showed the highest mean density value (3092 ind m^{-2}) against 231 ind m^{-2} in the dune 2 (on the thalweg track). The variance of the density and, consequently, the N minimum were higher in dune 2 (Table 2). Only one (0.6–0.9) replicate should be sufficient in the dune 1 whereas a minimum of four (3.3–3.7) replicates are necessary in dune 2 for a reliable sampling of benthic community (average error = 10%).

The diversity Shannon index (H) ranged from 0.18 to 0.44 in the crest of the dune 1 and trough of the dune 2, respectively (Table 3). In dune 1 the species richness was generally higher and lower the evenness and diversity.

Respecting the sand amount caught by the clamshell bucket, the results are disparate. The trough of the dune 1 reveal the only significant relationship between invertebrate density and sand weight ($r = 0.81$, $p = 0.01$; Table 4).

The hydraulic and substratum variables measured along dune profiles are showed in Table 5. The strongest bed flow conditions as quantified by the mobility number, clearly occurred on dune 2. Table 5 shows that the difference in the transport intensity between each dune trough is larger than those between crest and trough of a given dune. It is particularly evidenced in dune 2 which is closely related with an apparent absence of separation due to very low angle of its lee side (Fig. 2B). Note that, despite of the highest flow conditions, the grain sand diameters are not so different in dune 2 (in the thalweg track), respecting those in dune 1.

According to the ANOVA results, a significant distinction between the mean densities of the sampled dunes was revealed, whereas the variations between the corresponding crest and troughs were no significant ($F_{(3.36)} = 16.7$, $p = 0.1$). The LSD Fisher post-hoc test verified this statement.

The first axis of the Principal Component Analysis (PCA) explained 61.6% of the physical variations, the second axis explained 28.6% and both axes together explained 90.2% of them. The dunes remained separated ratifying that the total physical variation was higher among the dunes than within them (i.e. between crests and troughs; Table 6, see case scores). Dune 2 was characterized by higher values of bed hydraulic variables, current velocity and depth (axis 1). On the contrary, dune 1 showed the lowest values of hydraulic variables (Table 6, see eigenvectors; and Fig. 4).

Canonical correspondence analysis (CCA) clearly showed a preference by benthic invertebrates for the dune with the least strong hydraulic conditions (U_{max}, τ_0 and τ_*; Fig. 5). The first two axes of CCA explained 75.3% of the total variance and scores of axis 1 explained 44.8% of the variance (eigenvalue = 0.005). Thus, CCA axis 1 separated the sampling sites according to a gradient. One end of this gradient is represented by sites with strong hydraulic conditions and the other end by sites with the opposite conditions (higher silt and organic matter content).

Table 2
Descriptive statitistics of macroinvertebrate density and computation results of minimum number of samples.

Sampling station	N	Density (ind m^{-2})			Variance [$\log_{10}(x+1)$]	N minimum [$\log_{10}(x+1)$]
		Mean	Minimum	Maximum		
Dune 1 Crest	10	2300.2	372	7812	0.200282	0.6
Dune 1 Trough	10	3884.3	217	11656	0.299314	0.9
Dune 1	20	3092.2	217	11656	0.246867	0.7
Dune 2 Crest	10	235.6	0	744	0.705810	3.7
Dune 2 Trough	10	226.3	0	713	0.669130	3.3
Dune 2	20	231	0	744	0.651362	3.2
Dune 1 + Dune 2	40	1661.6	0	11656	0.842677	3.2

Table 3
Shannon index (H), evenness and species richness in each sampling station.

Shannon's index	Diversity	Evenness	Species richness
Dune 1 crest	0.18	0.211	7
Dune 1 trough	0.20	0.199	10
Dune 2 crest	0.33	0.552	4
Dune 2 trough	0.44	0.487	8

Table 4
Pearson correlations between sand weight (gr) caught in each sample and macroinvertebrate density (ind m^{-2}).

Sampling station	Mean sand weight (gr)	*r*	*p*
Dune 1	487	0.51	**0.04**
Dune 2	315	0.07	0.8
Dune 1 crest	444	−0.03	0.93
Dune 1 trough	530	0.81	**0.01**
Dune 2 crest	260	0.46	0.3
Dune 2 trough	364	−0.27	0.5

Table 6
PCA results from scores and correlations of environmental variables for the first two principal axes.

PCA case scores		
Cases	Axis 1	Axis 2
Dune 1 crest	−0.07	−0.04
Dune 1 trough	−0.05	−0.05
Dune 2 crest	0.05	0.04
Dune 2 trough	0.07	−0.03
PCA eigenvectors		
Variables	Axis 1	Axis 2
Maximum current velocity	**0.13**	0.03
Depth	**0.80**	**−0.29**
Bed shear stress	**0.14**	**0.50**
Particle median diameter	0	0
Mobility number	**0.43**	**0.70**
Organic matter	**0.13**	0.01
Sand	−0.01	0.01
Silt	**0.01**	**−0.05**
Clay	**0.34**	**−0.41**
Conductivity	0.00	0.00
pH	0.00	0.00
Dissolved oxygen	0.00	0.00
Transparency	0.00	0.00

4. Discussion

The benthic assemblage of the active bed of the main channel of the Paraná River was dominated by the species *Narapa bonettoi* (Oligochaeta), *Myoretronectes paranaensis* and *Itaspiella parana* (Turbellaria), and *Tobrilus* sp (Nematoda). This was similar to the finding of other studies conducted in the Paraná River (Ezcurra de Drago, 1980; Ezcurra de Drago et al., 2004; Marchese and Ezcurra de Drago, 1992; Marchese et al., 2002, 2005; Montanholi-Martins and Takeda, 1999; Takeda and Fujita, 2004).

Estimation of benthic invertebrate population at large spatial scales is a difficult task due to the high variability in density and the costs involved in the samples processing and taxonomic analysis (e.g. Downing, 1979). To discriminate bottom areas, with their related alluvial bed forms and associated hydraulic variables, seems to be an effective way to reduce the density variance. Thus, it would be possible to get reliable benthic population estimates minimizing the number of replicates needed to achieve the specified objectives. The results of the N minimum analysis clearly showed how variable this number can be according to the different bottom places (dunes) and the varied bed hydraulic conditions. With an average error of 10%, in the dune 2 (on the thalweg and with small superimposed dunes) it is necessary to obtain a minimum of four samples (replicates) per sampling station, whereas in the dune 1 (outside the thalweg) only one sample should be sufficient (Table 2). It is remarkable that an error of 10% is a fairly good accuracy considering that Elliot (1977) suggests an average error of 20% as optimal in benthic studies. The results presented herein show the importance to know, as thorough as possible, the location of the sampling station, since the replicates number and the average error could be reduced significantly. In this sense, Stevaux and Takeda (2002) opened this interesting perspective in terms of benthic sampling following a morphological criterion, something that was not considered before in large rivers. Thus, these authors discerned between stable and unstable bed areas, laterally shifting at the channel (channel scale dynamics). In a few words, a refinement in the discrimination of the sampled places on or between dunes (channel and bed form scale, respectively) would lead to a reduction of the sampling efforts (and the corresponding cost) in benthic studies, particularly at large spatial scales. Sampling programs of benthic bioassessment, in example, would benefit from these preliminary results. It is important to stand out that the 'historical' number of samples taken in previous benthic studies performed in the Paraná River, without a proper consideration of bed forms, were always three (e.g. Ezcurra de Drago, 1980; Marchese and Ezcurra de Drago, 1992; between others), which is a close approach to the most general results obtained herein (see Table 2: dune 1 + dune 2).

The question about the existence of an eventual relationship between the sand amount of each sample and the benthic density had not a conclusive answer. As the bucket is not completely watertight, a certain quantity of the sampled sand could be washed out when the sampler is lifted up to the surface. Moreover, the bed irregularities (size and shape of the small superimposed dunes) could influence the sand amount caught by the bucket. Thus, a positive correlation between the sand weight of each sample and the corresponding benthic densities would be an evidence of an eventual incidence of the above factors. By applying the log Pearson analysis, a significant but poor correlation between sand and benthic density was obtained only on the trough of the dune 1 ($r = 0.81$; $p = 0.01$; Table 4). Although this result is inconclusive, it suggest that further studies of this kind would be advisable to decide if the sand amount of each sample should be consider as an additional parameter in invertebrate

Table 5
Hydraulic and substratum variables measured and computed in the study.

	Max. velocity (m s^{-2})	Depth (m)	Bed roughness (m)	Shear velocity (m s^{-1})	Shear stress (kg m^{-2})	d_{50} (m)	Mobility number
D 1 crest	1.29	7.3	0.125	0.070	0.499	0.00037	0.807
D 1 trough	1.29	9.6	0.025	0.047	0.23	0.00035	0.399
D 2 crest	1.44	12.1	0.18	0.076	0.589	0.0003	1.190
D 2 trough	1.44	13.4	0.14	0.064	0.42	0.00027	0.943

Water temperature: 22.3 °C.

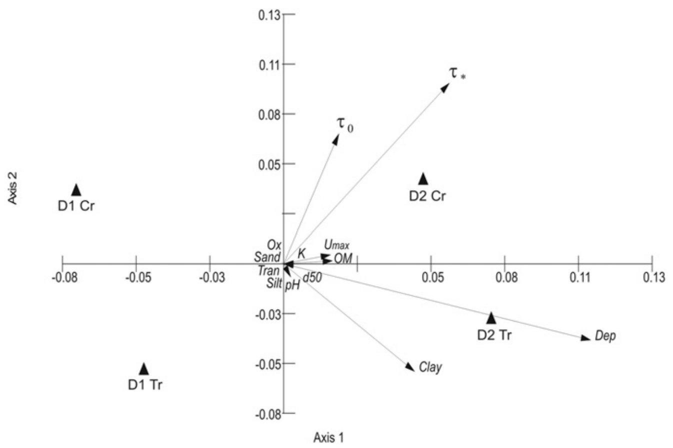


Fig. 4. Plot of scores distribution along principal component analysis (PCA) axis according to the physical (hydraulics and substratum) variables recorded in the studies dunes (considering crest and trough of each dune). D1 Cr = crest of dune 1; D1 Tr = trough of dune 1; D2 Cr = crest of dune 2; D2 Tr = trough of dune 2; Dep = depth; K = conductivity; OM = organic matter; Ox = dissolved oxygen; Tran = transparency (see List of symbols for the meaning of the other symbols).

sampling methodologies. Viewing the results, it was estimated a minimum sand amount of 250 g for each sample in order to minimize the associated errors until definite conclusions be available.

Regarding the invertebrate distribution, to the author's knowledge the study of Amsler et al. (2009) is the first dealing with the relationships between bed hydraulic variables measured on dunes in large rivers and the benthic fauna distribution. These authors described successfully this relationship on three areas (stoss-side, crest and trough) of dunes in the Middle Paraná River. This study data show that there are distinctive hydraulic biotopes (according to Wadeson's 1994 definition) with differentiable morphologic and hydraulic conditions (Figs. 3 and 4), given rise to a clearly stratified benthic distribution in the central strip (active bed of the channel) of the Middle Paraná River channel (Figs. 3 and 5). The CCA outputs show a clear invertebrate preference for places with less strong hydraulic conditions, such as those prevailing on dune 1. Note in Tables 2 and 5 that the highest densities occurred on dune 1, i.e. the hydraulic biotope with the smallest

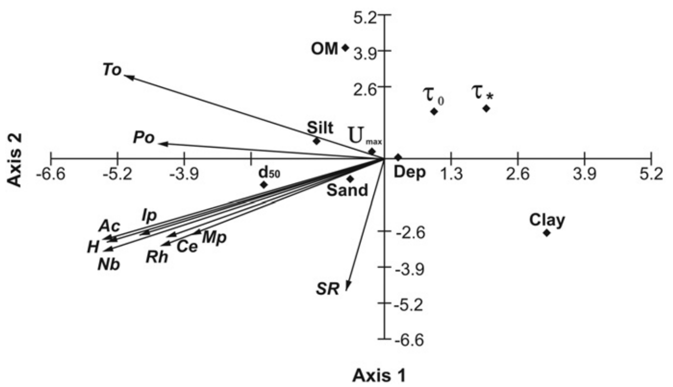


Fig. 5. Plot of physical (hydraulics and substratum) variables and sites along the first two axes of a canonical correspondence analysis (CCA) of aquatic invertebrate data collected on the Paraná river at the studied dunes (considering together crest and trough of each dune). To = *Tobrilus* sp I; Po = *Potamocaris* sp I; Ip = *Itaspiella parana*; Ac = *Hydracarina* sp. I; Nb = *Narapa bonettoi*; Rh = *Rhyacodrilus* sp I; Ce = Ceratopogonidae sp. I; Mp = *Myoretronectes paranaensis*; H = diversity index and SR = richness (see Fig. 4 for the other symbols).

values of τ_0 (U_*) and τ_*. In brief, dune 2 located in the thalweg region is subjected to larger bed shear stresses than dune 1 outside that region. As a consequence, considerably lower densities of benthic invertebrates were recorded in the thalweg dune irrespective location along it. Another sampling during a different month of the year (spring) with nearly the same river stages showed similar results but with different density magnitudes which can be attributed to the reproductive cycle of the dominant benthic species (Amsler et al., 2009). Takeda et al. (2001) and Stevaux and Takeda (2002) suggest that morphological stability of the river bed should be used to explain distribution of a very similar benthic assemblage in the active channel of the Upper Paraná River. The thalweg track is a morphologically less stable area due to the stronger hydraulic stresses. Consequently, the results of this study agree and complement those of the Upper Paraná, i.e. the natural dynamic of the thalweg shifting in the cross section (because of changes in hydrologic and hydraulic conditions) would control the invertebrate distribution in both Upper and Middle Paraná River.

At a minor scale, the highest densities of the benthic fauna were recorded in the trough region of dune 1 (Fig. 3, Table 2) compared with those in the crest, though the difference was not statistically significant. The lower values of the bed shear stresses in the trough respecting those in the crest, would account for the species preference of places where hydraulic conditions are not so hard.

Regarding, the largest evenness values and the lowest richness recorded on dune 2 (Table 3), they would be related with the stronger bed flow conditions occurring there (Table 5). This stressful hydraulic environment could reduce the number of species living at that place and also restrict the density of the dominant species (*N. bonettoi*). It infers that *N. bonettoi* would not support high turbulence levels.

The destruction of benthic organism due to increasing collisions between near bed sand particles it is a possibility closely related with the high values of τ_*, the variable which drives the amount of sand transported near the bottom. Blettler et al. (2008) advanced the following alternative hypothesis to this idea: i) benthic fauna begins to move down into the interstitial substratum spaces; ii) sweep of the benthic organisms, putting them into suspension due to the strong bed flow conditions (drift); and iii) all the previous hypothetical facts acting simultaneously. Nevertheless, little is known so far about the benthic macroinvertebrates behavior in the central strip of large rivers and the intimate processes driving their strategies to resist the hydraulic variables variation.

A morphologic analysis of each dune revealed that the number and height of the small superimposed dunes are larger in dune 2 than in dune 1 (Fig. 2). This remarkable feature could be linked with the benthic density variability, which is smaller in dune 1 (Table 2). Note that the stronger hydraulic variables in dune 2 imply that turbulent fluctuations near the bottom are more violent than in dune 1, something intricately related with the bed roughness, i.e. the small superimposed dunes in this case (Amsler and Schreider, 1992; Nezu and Nakagawa, 1993). However, the real significance of this last type of micro-dunes on the benthic fauna is unknown for the moment. It is still not possible to measure precisely the shear stresses variation along these small dunes in a large river (10 m depht or more) and to take the corresponding benthic replicates. Thus, it is a topic for future studies, as was suggested by Best (2005).

5. Conclusions

i .To know the proper number of benthic replicates samples (N minimum), a crucial issue if consistent and reliable results (i.e. with an acceptable error) are intended to be obtained, it is necessary: a) to know in detail the bed morphologic features; and b) to achieve an appropriate representation of the bottom flow conditions around the sampling point (a very difficult task in large rivers). In this study this requirement was met by designing a proper field methodology. This implied the identification of the bed morphologic structures combining echo sounding and satellite technology (GPS).

ii. Depending of the location, only a few samples are necessary to obtain a reliable representation of the benthic fauna (see Discussion), closely associated with the local flow features near the bed. Though it involved some assumptions concerning to the type of flow surrounding the sampling point, they normally may be approached at large spatial scales as was the case of this study (see Appendix).

iii. Two different hydraulic biotopes (dunes 1 and 2) with distinctive invertebrate characteristics could be identified in the central strip of the Paraná River, where benthic densities vary principally according to the dune location in the main channel. It was found that differences in their hydraulic conditions have an important role on the spatial distribution of the invertebrates.

iv. The results of this study should be added to those previously reported by the authors from measurements in the same cross section, hydrological conditions but different season. Together, they would be fairly representative of the influence of dunes on the benthic fauna of the Paraná River active channel. However, the authors acknowledge that several avenues of future research are necessary to further the understanding about the precise role of bed dunes on invertebrates and its ecological implications.

Acknowledgements

We thank Esteban Creus, Ambrosio Regner, Eduardo Lordi, and Ulises Molet for field and laboratory assistance. We are particularly grateful to Prof. Edmundo Drago and Lic. Aldo Paira for suggestions about the topic of this paper. This investigation was supported with financial assistance of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina), grant No 6209. The authors are deeply grateful to the reviewers for their ideas which undoubtedly improved this manuscript.

Appendix

Schematic model of a fluvial sandy dune.

A general fluvial dune could be represented as in Fig. A1.

Estimation of the bed shear stress from the Clauser's equation and the surface current velocity.

Clauser (1956) showed that the vertical velocity distribution in a turbulent boundary layer without wake component could be described by the following general equation:

$$\frac{U}{U_*} = 5.6\log\frac{U_* y}{\nu} + A - \frac{\Delta U}{U_*} \tag{a1}$$

where, y, distance from the bottom corresponding to the velocity U; ν, kinematic viscosity of the fluid; A, a constant equal to 4.9 according to Clauser; U_*, shear velocity (see Table 1); and $\Delta U/U_*$, the reduction velocity function due to the bed roughness. Clauser also showed that this function is given by the general expression:

$$\frac{\Delta U}{U_*} = 5.6\log\frac{U_* k}{\nu} + D \tag{a2}$$

for rough beds and constant pressure gradients. Hence, k is a roughness representative height and D is a constant varying according to the types and configuration of bed roughness.

If Eqs. (a1) and (a2) are combined with $A = 4.9$ and $D = -3.25$, it is possible to obtain:

$$\frac{U}{U_*} = 5.6\log\frac{y}{k_s} + 8.15 \tag{a3}$$

where $k_s \cong k$, the classical sand roughness height. Theoretically, measuring $U_{\max}$, the depth h and approaching k_s at a given vertical, a reliable value of the shear velocity, U_*, could be estimated by:

$$U_* = \frac{U_{\max}}{5.6\log_{10}\frac{h}{k_s} + 8.15} \tag{a4}$$

provided that the velocity profile at the verticals is fully logarithmic, i.e. without a wake component. As is well known this type of profiles occur along the stoss-sides and crests of dunes where pressure gradients are normally gradual and low, especially when dunes are large and have small steepnesses (Smith and McLean, 1977; Trento et al., 1990; Nelson et al., 1993). In brief, the Eqs. (a3) and (a4) in a natural river should give comparables results if the previous conditions are fulfilled.

Based on this theoretical background, Trento et al. (1990) showed that Eq. (a1) describes fairly well detailed velocity profiles carefully measured over large dunes in the Paraná River, under a diversity of flow conditions. Moreover, Amsler and Schreider (1992) analyzed the same profiles and showed that the constant D in Eq. (a2) differs only 15% in average from the theoretical value (−3.25) corresponding to the sand grain roughness straight line, given by Clauser. In the analysis the authors used the average height of the small superimposed dunes

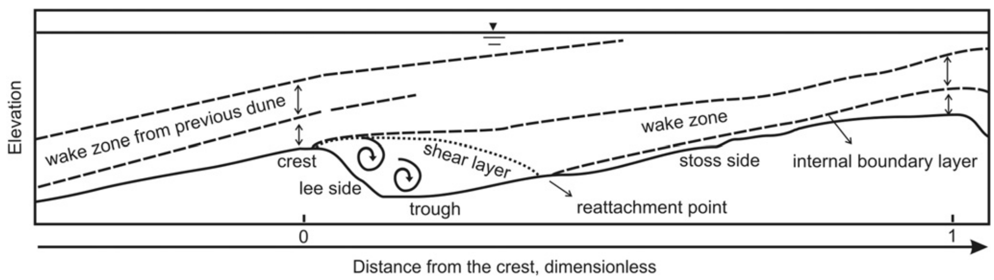
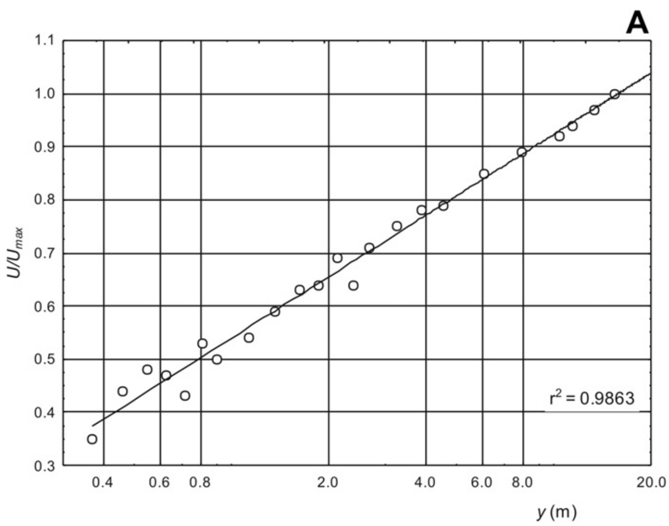


Fig. A1. Schematic flow over a dune showing the developing internal boundary layer and the developing wake zone (modified from Holmes and Garcia, 2008).

surrounding each measured velocity profile to approximate the k value in Eq. (a2). But Eq. (a3) is possible to apply when a sufficient number of point velocities, U, are known at distances, y, from the bottom. Then, the U_* values obtained from the slope of the regression line fitted to the pair $U - \log y$ data should not differ greatly with those estimated from Eq. (a4). The best procedure based on Eq. (a3) is the classical recommended in literature (see Schlichting, 1979) and as such is used when detailed observed point velocity vertical profiles are available (e.g. Kostaschuk et al., 2004).

In order to verify the above statement in a sand bed river like the Paraná, 19 of the velocity profiles used by Trento et al. (1990) measured on dune crests were used herein. These data were obtained 20 km upstream of the sampling area on dunes with similar characteristics like dunes 1 and 2 analyzed in this paper (located also in the thalweg track and outside of it). Two examples of these profiles are shown in Fig. A2 (and Table A1), represented in semi-logarithmic coordinates and dimensionless ordinates.



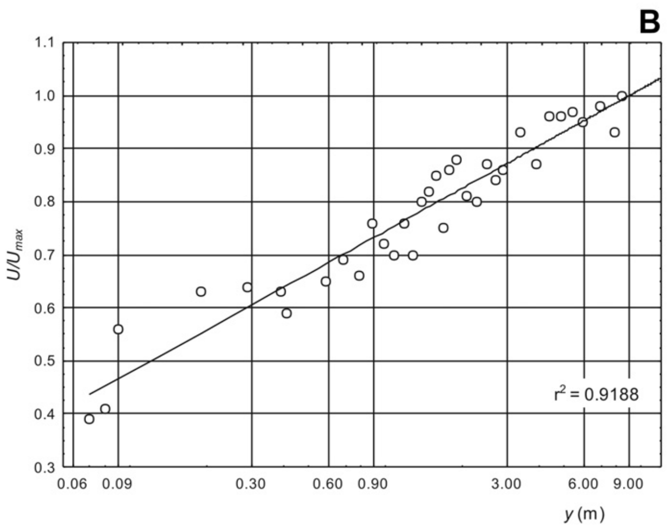


Fig. A2. Examples of the 19 velocity profiles presented in Table A2 measured on the stoss-side of large dunes in the Paraná River (Trento et al., 1990; Amsler and Schreider, 1992). A, B: profiles with the highest and lowest determination coefficients (r^2), respectively.

Table A1
Point data of profiles A and B of Fig. A2. Note: distances y are referred to the "virtual origin" (or "hydraulic bottom") fixed using the method suggested by Perry and Joubert (1963) (see Amsler et al., 2009).

Profile A (*thalweg*)		Profile B (outside the *thalweg*)	
$y - 0.75^*H_{sd}$	U/U_{max}	$y - 0.75^*H_{sd}$	U/U_{max}
0.37	0.35	0.07	0.39
0.46	0.44	0.08	0.41
0.55	0.48	0.09	0.56
0.63	0.47	0.19	0.63
0.72	0.43	0.29	0.64
0.81	0.53	0.39	0.63
0.9	0.5	0.41	0.59
1.13	0.54	0.59	0.65
1.37	0.59	0.69	0.69
1.62	0.63	0.79	0.66
1.87	0.64	0.89	0.76
2.13	0.69	0.99	0.72
2.4	0.64	1.09	0.7
2.67	0.71	1.19	0.76
3.26	0.75	1.29	0.7
3.88	0.78	1.39	0.8
4.56	0.79	1.49	0.82
6.09	0.85	1.59	0.85
7.98	0.89	1.69	0.75
10.4	0.92	1.79	0.86
11.41	0.94	1.89	0.88
13.37	0.97	2.09	0.81
15.38	1	2.29	0.8
		2.49	0.87
		2.69	0.84
		2.89	0.86
		3.39	0.93
		3.89	0.87
		4.39	0.96
		4.89	0.96
		5.39	0.97
		5.89	0.95
		6.89	0.98
		7.89	0.93
		8.39	1
$U_{max} = 1.85$ m s^{-1}		$U_{max} = 1.26$ m s^{-1}	
$r^2 = 0.9863$		$r^2 = 0.9188$	
Height superimposed small dunes = 0.17 m		Height superimposed small dunes = 0.145 m	

Using these velocities profiles U_* was estimated in two ways, through Eqs. (a3) and (a4). The results are presented in Table A2.

Table A2
Comparison of the τ_0 values obtained with Eqs. (a3) and (a1) from 19 velocity profiles measured on the stoss-side of large dunes in the Paraná River.

Profile	$\tau_0 = [kg/m^2]$		$\frac{\tau_{0eq.a4}}{\tau_{0eq.a3}}$	$h[m]$	$U_{max}[m/s]$	r^2
	Eq. (a3, fit)	Eq. (a4)				
Profiles on the *thalweg* (A)						
A1	1.65	0.96	0.58	15.38	1.85	0.98
A2	1.17	0.8	0.68	14.13	1.64	0.98
A3	0.7	0.64	0.92	12.2	1.46	0.97
A4	1.02	0.74	0.72	12.14	1.56	0.98
A5	0.94	0.7	0.74	12.21	1.44	0.99
A6	0.47	0.7	1.48	13.27	1.46	0.98
A7	0.81	0.75	0.93	14.73	1.51	0.97
A8	0.31	0.44	1.42	13.11	1.2	0.97
A9	0.42	0.41	0.97	13.2	1.16	0.96
A10	0.64	0.64	1	12.1	1.45	0.95
Profiles outside the *thalweg* (B)						
B1	0.56	0.64	1.14	8.17	1.31	0.93
B2	0.72	0.89	1.24	8.17	1.5	0.94
B3	0.65	0.64	0.98	8.12	1.37	0.98
B4	0.44	0.62	1.4	9.07	1.43	0.97
B5	0.43	0.55	1.27	6.9	1.28	0.94
B6	0.37	0.5	1.37	8.4	1.26	0.92

(continued on next page)

Table A2 (*continued*)

Profile	$\tau_0 = [kg/m^2]$		$\frac{\tau_{0eq.a4}}{\tau_{0eq.a3}}$	$h[m]$	$U_{max}[m/s]$	r^2
	Eq. (a3, fit)	Eq. (a4)				
B7	0.67	0.53	0.79	9.01	1.38	0.94
B8	0.39	0.44	1.13	5.89	1.17	0.95
B9	0.47	0.46	0.99	8.15	1.16	0.96

Roughness height, $k_s \cong$ average height of the superimposed small dune, H_d.

Fig. A3 was built with Table A2 and the data shows that the 63% of the τ_0 ratios (i.e. 12 points) are between 1.3–0.7 and the total points are between 1.4 and 0.5. Therefore, to estimate the bed shear stress acting on the stoss-side of dunes from Eq. (a4) is a reasonable approximation to the values obtained using the complete velocity profile (Eq. a3). However, the implicit assumption in this approach about the existence of fully logarithmic velocity profiles upstream of dune crests does not comply on the trough areas. Along these zones of dunes the flow is perturbed due to strong and positive pressure gradients (with or without flow separation). Consequently, the conditions under which Eqs. (a1)–(a3) were derived do not comply. It is well known (see van Rijn, 1993; Nelson et al., 1993) that the velocities reduce sharply near the bottom on these dune places since the depth increases abruptly as a consequence of larger lee face angles (the reduction includes the possibility of reverse flow in the case of flow separation).

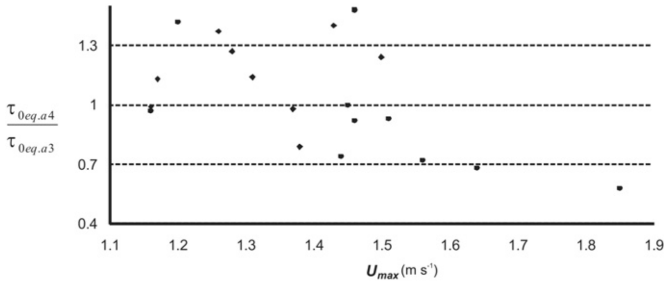


Fig. A3. Results of the comparison between τ_0 values obtained with the Eqs (a3) and (a4): $\tau_{0eq.\ a4}/\tau_{0eq.\ a3}$ ratios against U_{max} (see Table A2).

It is required considerably more complex models than the simple one represented by Eq. (a1) (or (a3)) to describe the flow features in these zones (Garcia, 2008; Lyn, 2008). Anyway, the resulting bed shear stresses may be considerably lower in the trough regions than on the dune crests. Direct measurements of these stresses are extremely scarce in literature and generally come from laboratory experiments. Amsler et al. (2009) used the shear stresses calculated from laboratory experiments to gain approximate quantitative information along the lee side of natural dunes when flow separation was present. Without separation, these authors designed a procedure based in the movement of the small superimposed dunes to estimate the bed shear stresses along the dune troughs. The same criteria were applied herein.

References

Alarcón, J.J., Szupiany, R., Montagnini, M.D., Gaudin, H., Prendes, H.H., Amsler, M., 2003. Evaluación del transporte de sedimentos en el tramo medio del río Paraná. Proceedings of the Primer Simposio Regional sobre Hidráulica de Ríos. Ezeiza, Argentina (CD).

Amsler, M., Schreider, M., 1992. Aspectos hidráulicos de la superposición de formas de fondo en el río Paraná (Argentina). In: Proceedings of the XV Congreso Latinoamericano de Hidráulica, Sociedad Colombiana de Ingenieros, 3. Asociación Internacional de Investigaciones Hidráulicas, Cartagena, Colombia, pp. 39–48.

Amsler, M., Gaudin, H., 1994. Influencia de la superimposición de dunas e el transporte de la carga de fondo en el río Paraná. In: Proceedings of the XV Congreso Nacional del Agua. La Plata, Argentina.

Amsler, M., Prendes, H., 2000. Transporte de sedimentos y procesos fluviales asociados. In: Paoli, C., Schreider, M. (Eds.), El río Paraná en su tramo medio. Contribución al conocimiento y prácticas ingenieriles en un gran río de llanura. Tomo, vol. 1. Centro de Publicaciones, Universidad Nacional del Litoral, Santa Fe, Argentina, pp. 233–306.

Amsler, M., Blettler, M., 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 Research doi: 10.1029/2008WR007537.

Best, J.L., Kostaschuk, R.A., 2002. An experimental study of turbulent flow over a low-angle dune. Journal of Geophysical Research doi: 10.1029/2000JC000294.

Best, J.L., 2005. The fluid dynamics of river dunes: a review and some future research directions. Journal of Geophysical Research, Earth Surface doi:10.1029/2004JF000218.

Blettler, M., Amsler, L., Ezcurra de Drago, I., Marchese, M., 2008. Effects of stream hydraulics and other environmental variables on density of *Narapa bonettoi* (Oligochaeta) in the Paraná River system. River Research and Applications 24, 1124–1140.

Brinkhurst, R.O., Marchese, M.R., 1992. Guide to the Freshwater Aquatic Oligochaeta of South and Central America. Asociación Ciencias naturales del Litoral, Santo Tomé, Argentina. Colección CLIMAX No 6pp. 1–179.

Brooks, A.J., Haeusler, T., Reinfelds, I., Williams, S., 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. Freshwater Biology 50, 331–344.

Carling, P.A., 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. Freshwater Biology 28, 273–284.

Carling, P.A., Williams, J.J., Gölz, E., Kelsey, A.D., 2000a. The morphodynamics of fluvial sand dunes in the River Rhine near Mainz, Germany, part II: hydrodynamics and sediment transport. Sedimentology 47, 253–278.

Carling, P.A., Gölz, E., Orr, H.G., Radecki-Pawlik, A., 2000b. The morphodynamics of fluvial sand dunes in the River Rhine near Mainz, Germany, Part I: sedimentology and morphology. Sedimentology 47, 227–252.

Chow, V.T., 1959. Open-channel Hydraulics. McGraw Hill, Kogakusha, Ltd, Tokio, Japan, p. 680.

Clauser, F.H., 1956. The turbulent boundary layer. Advances in Applied Mechanics 4, 1–51.

Coleman, S., Nikora, V.I., 2011. Fluvial dunes: initiation, characterization, flow structure. Earth Surface Processes and Landforms vol. 36, 39–57.

Doberstein, C.P., Karr, J.R., Conquest, L.L., 2000. The effect of fixed-count subsampling on macroinvertebrate biomonitoring in small streams. Freshwater Biology 44, 355–371.

Downing, J.A., 1979. Aggregation, transformation, and design of sampling programs. Journal of the Fisheries Research Board of Canada 36, 1454–1463.

Drago, E.C., Amsler, M., 1998. Bed sediment characteristics in the Paraná and Paraguay rivers. Water International 23, 174–183.

Elliot, J.M., 1977. Statistical Analysis of Samples of Benthic Invertebrates. Scientific Publication no 25, second ed. Freshwater Biological Association, p. 157.

Engel, P., 1981. Length of flow separation over dunes. Journal of Hydraulic Engineering – ASCE 107, 1133–1143.

Ezcurra de Drago, I., 1980. Campaña limnológica Keratella I en el río Paraná Medio. Complejo bentónico del río y ambientes leníticos asociados. Ecología 4, 89–101.

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.

Garcia, M.H., 2008. Sediment transport and morphodynamics. In: Garcia, M.H. (Ed.), Sedimentation Engineering, pp. 21–163, ASCE Manuals and Reports on Engineering Practice no 110, Reston, USA, p. 1132.

Growns, I.O., Davis, J.A., 1994. Longitudinal changes in near-bed flows and macroinvertebrate communities in a Western Australian stream. Journal of the North American Benthological Society 13, 417–438.

Hannah, D.M., Wood, P.J., Sadler, J.P., 2004. Ecohydrology and hydroecology: a 'new paradigm'? Hydrological Processes 18, 3439–3445.

Henderson, F.M., 1966. Open Channel Flow. Mac Millan Publishing Co. Inc, New York, United States, p. 522.

Holmes, J.R., Garcia, M.H., 2008. Flow over bedforms in a large sand-bed river: a field investigation. Journal of Hydraulic Research 46, 322–333.

Kemp, J.L., Harper, D.M., Crosa, G.A., 2000. The habitat-scale ecohydraulics of rivers. Ecological Engineering 16, 17–29.

Kennedy, J.F., 1977. Hydraulic relations for alluvial streams. In: Vanoni, V.A. (Ed.), Sedimentation Engineering. ASCE, New York, pp. 114–154. no 54.

King, R.S., Richardson, C.J., 2002. Evaluating subsampling approaches and macroinvertebrate taxonomic resolution for wetland bioassessment. Journal of the North American Benthological Society 21, 150–171.

Kostaschuck, R., 2000. A field study of turbulence and sediment dynamics over subaqueous dunes with flow separation. Sedimentology 47, 519–531.

Kostaschuck, R.A., Villard, P.V., 1996. Flow and sediment transport over large subaqueous dunes: Fraser River, Canada. Sedimentology 43, 849–863.

Kostaschuk, R.A., Villard, P.W., Best, J., 2004. Measuring velocity and shear stress over dunes with an acoustic Doppler profiler. Journal of Hydraulic Engineering 130, 932–936.

Kovach, K., 2002. Multivariate Statistical Package (MVSP 3.1). Kovach Computing Services, Wales, UK.

Latrubesse, E., 2008. Patterns of anabranching channels: the ultimate end-member adjustment of mega rivers. Geomorphology 101, 130–145.

Leclair, S.F., Bridge, J.S., 2001. Quantitative interpretation of sedimentary structures formed by river dunes. Journal of Sedimentary Research 71, 713–716.
Lyn, D.A., 2008. Turbulence models for sediment transport engineering. In: Garcia, M.H. (Ed.), Sedimentation Engineering. ASCE, Reston, USA, pp. 763–825. Manuals and Reports on Engineering Practice No 110p. 1132.
Marchese, M., Ezcurra de Drago, I., 1992. Benthos of the lotic environmets in the Middle Paraná River system: transverse zonation. Hydrobiologia 237, 1–13.
Marchese, M., Ezcurra de Drago, I., Drago, E., 2002. Benthic macroinvertebrates and physical Habitat relationship in the Paraná flood-plain system. In: McCalin, M. (Ed.), The Ecohydrology of South American Rivers and Wetlands, 7. IAHS Special Publication, pp. 111–132.
Marchese, M., Wantzen, M., Ezcurra de Drago, I., 2005. Benthic invertebrate assemblages and species diversity patterns of the Upper Paraguay River. River Research and Applications 21, 485–499.
McLean, S.R., Nelson, J.M., Wolfe, S.R., 1994. Turbulence structure over two-dimensional bedforms: implications for sediment transport. Journal of Geophysical Research 99, 729–747.
Montanholi-Martins, M.C., Takeda, A.M., 1999. Communities of benthic Oligochaetes in relation to sediment structure in the Upper Paraná River, Brazil. Studies of Neotropical Fauna and Environment 34, 52–58.
Nelson, J.M., McLean, S.R., Wolfe, S.R., 1993. Mean flow and turbulence over two-dimensional bedforms. Water Resource Research 29, 3935–3953.
Nezu, I., Nakagawa, H., 1993. Turbulence in Open Channel Flows. IAHR Monograph Series. Balkema, A.A, Rotterdam, The Netherlands, p. 177.
Noreña, C., 1995. Studies on the Systematic and ecology of Turbellaria (Plathyhelminthes) on the flood plain of the Paraná (Argentina). Part II: taxonomy and ecology of the Turbellaria. Arch. Hydrob. Suppl. 107, 211–262.
Noreña, C., Damborenea, C., Brusa, F., 2005. New freshwater interstitial Otoplanidae (Platyhelminthes: Proseriata) from the Paraná and Uruguay rivers, South America. Journal of Natural History 39, 1457–1468.
Ogink, H.J., 1989. Hydraulic Roughness of Single and Compound Bed Forms. Delft Hydraulics. Part XI Report on model investigations M2017, Delft, The Netherlands.
Parsons, D.R., Best, J.L., Orfeo, O., Hardy, R.J., Kostaschuk, R., Lane, S.N., 2005. Morphology and flow fields of three-dimensional dunes, Rio Paraná, Argentina: results from simultaneous multibeam echo sounding and acoustic Doppler current profiling. Journal of Geophysical Research doi:10.1029/2004JF000231.
Perry, A.E., Joubert, P.N., 1963. Rough-wall boundary layers in adverse pressure gradients. Journal of Fluid Mechanics 17, 193–211.
Raudkivi, A.J., 1963. Study of sediment ripple formation. Journal of Hydraulic Engineering – ASCE 89, 15–33.
Schlichting, H., 1979. Boundary-layer Theory. McGraw-Hill Book Co, New York, USA, p. 817.
Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.
Smith, J.D., McLean, S.R., 1977. Spatially avenged flow over a wavy surface. Journal of Geophysical Research 82, 1735–1746.
Sokal, R.R., Rohlf, F.J., 1981. Biometry, second ed. Freeman and Company, San Francisco, p. 859.
Somers, K.M., Reid, R.A., David, S.M., 1998. Rapid biological assessments: how many animals are enough? Journal of the North American Benthological Society 17, 348–358.
Statzner, B., Higler, B., 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 16, 127–139.
Statzner, B., Gore, J.A., Resh, V.H., 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7, 307–360.
Stephan, U., Gutknecht, D., 2002. Hydraulic resistance of submerged flexible vegetation. Journal of Hydrology 269, 27–43.
Stevaux, J., Takeda, A., 2002. Geomorphological Processes Related to Density and Variety of Zoobenthic Community of the Upper Paraná River (Brazil), vol. 129. Zeistschrift Für Geomorphology, Berlin. 109–129.
Takeda, A.M., Fujita, D.S., 2004. Benthic invertebrates. In: Thomaz, S.M., Agostinho, A.A., Hanh, N.S. (Eds.), The Upper Paraná River and Its Floodplain: Physical Aspect, Ecology and Conservation. Backhuys Publ, Leiden, The Netherlands, pp. 191–208.
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 & Varela, 1983 of the Upper Paraná River, Brazil. Hydrobiologia 463, 241–248.
Trento, A., Amsler, M., Pujol, A., 1990. Perfiles observados de velocidad en un tramo del río Paraná -Análisis teórico. In: Proceedings of the XIV Congreso Latinoamericano de Hidráulica, 3. Div. Reg. Latin. de la Asoc. Int. De Inv. Hidráulicas, Montevideo, Uruguay, pp. 1109–1121.
Trivinho-Strixino, S., Strixino, G., 1995. Larvas de Chironomidae (Diptera) do Estado de SâoPaulo – Guia de identificacão e diagnose dos gêneros. Universidade Federal de São Carlos, PPG-ERN, São Carlos, Brasil. 1–229.
van den Berg, J., de Vries, M., 1979. Principles of River Engineering. Pitman Publishing Ltd, London, England, p. 509.
van Rijn, L., 1993. Principles of Sediment Transport in Rivers, Estuaries and Coastal Seas. Aqua Publications, Amsterdam, The Netherlands, p. 614.
Wadeson, R.A., 1994. A geomorphological approach to the identification and classification of instream flow environment. Southern African Journal of Aquatic Sciences 20, 38–61.
Wadeson, R.A., Rowntree, K.M., 1998. Application of the hydraulic biotype concept to the classification of instream habitats. Aquatic Ecosystem Health 1, 143–157.
Wetzel, R.G., Likens, G.E., 1991. Limnological Analyses, second ed. Springer-Verlag, New York, USA, p. 391.
Williams, J.J., Bell, P.S., Thorne, P., 2003. Field measurements of flow fields and sediment transport above mobile bed forms. Journal of Geophysical Research doi:10.1029/2002JC001336.
Yalin, M.S., 1977. Mechanics of Sediment Transport, second ed. Pergamon Press, Oxford, UK, p. 298.
Zalewski, M., Robarts, R., 2003. Ecohydrology: a new paradigm for integrated water resources management. SIL News 40, 1–5.

Nomenclature

d_{50}: Particle median diameter
F_r: Froude number
g: Gravity acceleration
h: Depth
k_s: Substrate total roughness height
R: Hydraulic radius
R_e: Reynolds number
S: Friction slope
U: Flow velocity at a distance, y, from the bed
U_{max}: Maximum velocity at a given vertical
U_*: Shear velocity
ρ: Water density
γ_s: Specific weight of sediment
γ_w: Specific weight of water
τ_0: Bed shear stress
τ_*: Mobility number
υ: Fluid kinematic viscosity