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Influence of hydraulic conditions over dunes on the distribution of the benthic macroinvertebrates in a large sand bed river

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[1] This study aims to relate the flow structure over mobile dunes recorded on the channel bed of the Paraná River (Argentina) with the spatial distribution of the benthic macroinvertebrates. The following main conclusions have been obtained: (1) the dunes found in the active channel could be considered as hydraulic biotopes at a mesohabitat scale: the bed forms in the thalweg region are subjected to higher shear stresses with low benthic densities; (2) differences in benthic densities were also recorded at within-dunes microhabitat scales: the largest densities were found in the dune troughs where small bed shear stresses occur and minimum densities on the low stoss side of dunes where turbulent agitation near the bottom strongly disturb the bed particles; (3) superimposed dunes on larger dunes may be considered as another microhabitat of still smaller dimensions. Summarizing, multiscale approaches are needed if a comprehensive understanding linking hydrodynamics and morphodynamics processes with benthic ecology is intended.

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1. Introduction

[2] The term 'ecohydrology', including the subdiscipline of 'ecohydraulics', involves research topics in the overlap between the hydrological 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 absence lack of proper accounting by ecologists of the role that hydraulics 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 sedimentation [*Stephan and Gutknecht*, 2002] or the dampening of turbulence near the bottom of a river due to the periphyton fixed to the bed particles [*Godillot and Caussade*, 2001].

[3] Major efforts to merge these two approaches have been made in the field of macroinvertebrate ecology. There is strong evidence that the distribution of benthic macroinvertebrates is influenced to a great extent by the bed hydraulic conditions [*Statzner et al.*, 1988; *Carling*, 1992; *Lancaster and Hildrew*, 1993; *Robertson et al.*, 1995; *Rempel et al.*, 2000; *Blettler et al.*, 2008].

[4] An important contribution in this new field was the development of the 'hydraulic biotope' concept [*Wadeson*, 1994] defined as 'a spatially distinct instreamflow environment characterized by specific hydraulic attributes that provide the abiotic environment in which species assemblages or communities live'. The concept links 'functional habitats' from ecology [*Smith et al.*, 1991; *Harper et al.*, 1998] with 'flow biotopes' from geomorphology [*Padmore*, 1997]. On the basis of this definition, M. C. Blettler et al. (Influence of dunes geometry on macroinvertebrate distribution and sampling techniques in a section of the Middle Paraná River (Argentina), submitted to *River Research and Applications*, 2009) showed that the dunes of the active bed in the Middle Paraná River may be thought as hydraulic biotopes.

[5] The particular topic of dunes in alluvial streams has received a considerable amount of experimental and theoretical research along the past half century. Despite those efforts, a clear understanding of the interactions between these bed forms and the overlying turbulent flow in natural rivers is still far from completely developed. Field investigations are limited in number as well as in the specificity of measurements, because of inherent difficulties involved in obtaining detailed data on bed form-flow interactions within natural streams [*McLean and Smith*, 1979; *Grinvald and Nikora*, 1988; *Kostaschuk and Villard*, 1996; *Best*, 2005]. Recent advances due to the advent of new technologies in the measurements of rivers are not still enough. The subject implies an important challenge for river scientists since bed forms (such as dunes), are ubiquitous in alluvial natural channels and significantly influence the nature of the mean flow as well as its turbulent structure and, consequently, exert a strong control on the entrainment, transport, and deposition of sediment.

[6] Regarding to the incidence of alluvial dunes on the benthic distribution is a matter not well studied. To the authors knowledge, research made along dunes of small streams but in connection with bacterial activity yielding significant results [*Fischer et al.*, 2003], and the referred

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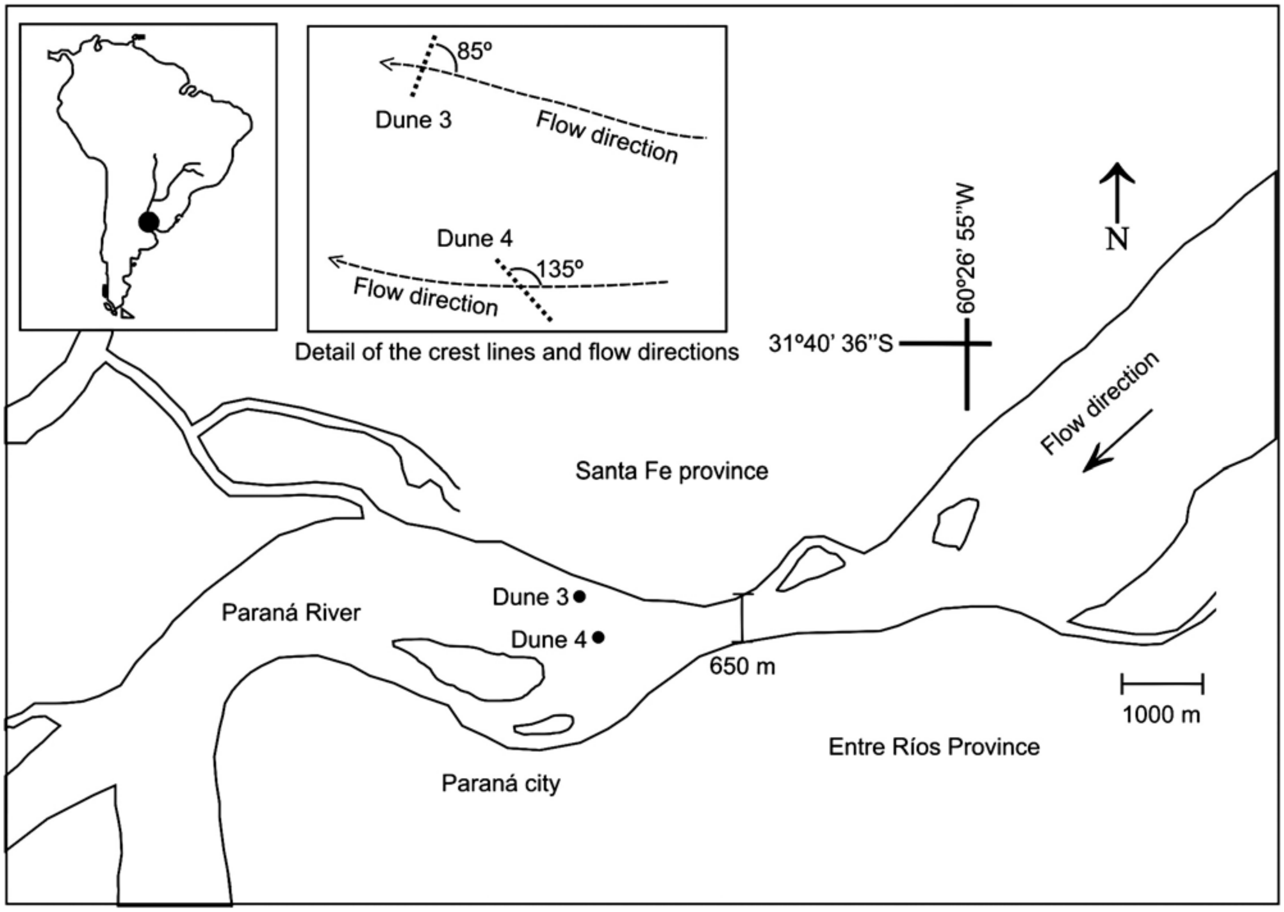

Figure 1. Location and details of the sampling stations.

study of Blettler et al. (submitted manuscript, 2009), would be the first on this topic. Some results of this last study are used herein to stress particular findings of both investigations.

[7] Taking account of the above rationale, this study aims to relate the structure of flow over the stoss side, crest and trough of mobile dunes recorded on the main channel of the Middle Paraná River, with the spatial distribution of the macroinvertebrate community living in those bed areas. If the occurrence of benthic functional habitats is correlated with hydraulic variables, it would be a strong evidence of the connection between these habitats and the bottom local flow dynamics. Moreover, it would further confirm that dunes should be viewed as hydraulic biotopes. This research is innovative since it involves detailed measurements of vertical velocity profiles which provided the bed flow characteristics over migrating dunes in a large river, and their influence on invertebrate distribution.

2. Methods

2.1. Study Area

[8] The field measurements were performed at a reach of the Middle Paraná River between Santa Fe and Paraná cities (Argentina). The Paraná River is the second largest in South America in catchment area (2.8×10^6 km^2), the third in mean discharge to the ocean (21000 m^3 s^{-1}), and the sixth in the world due to this discharge [*Schumm and Winkley*, 1994]. The region of the river studied has a sandy bed where fine and medium grain sizes prevail transported as bed (9%) and suspended loads (91% [*Drago and Amsler*, 1998; *Alarcón et al.*, 2003]). Two dunes selected in the referred reach were surveyed (Figure 1).

[9] Their main dimensions (Figure 2) were: height, 2.15 m (dune 3) and 2.2 m (dune 4); length, 230 m (dune 3) and 340 m (dune 4); mean lee slope angles (crest and trough), 5.5° (dune 3) and 13.5° (dune 4).

[10] Dunes were named 3 and 4 following the sequence of bed forms (1 and 2) surveyed at the same site in a preliminary study (Blettler et al., submitted manuscript, 2009). Dune 3 was located just on the thalweg track (31°41′55.8″ S; 60°30′46.8″ W) while dune 4 was out of that strip (31°42′15.5″ S; 60°30′39.3″ W). Both dunes were characterized by superimposition of small dunes over them.

2.2. Sampling

[11] The field survey was performed in August 2007 with a lower midwater level. The benthic samples were obtained at three sites (stoss side, crest and trough) of each dune. It should be noted that the samples taken at the stoss side (and named as such along the paper), were really obtained at the ‘low stoss side’ (or ‘upper stoss side’) of each dune. The reasons for selecting these sampling sites along the dune profiles are given in section 4.

[12] Following Blettler et al. (submitted manuscript, 2009), four samples (replicates) at each sampling station are necessary to get a reliable estimate of the benthic

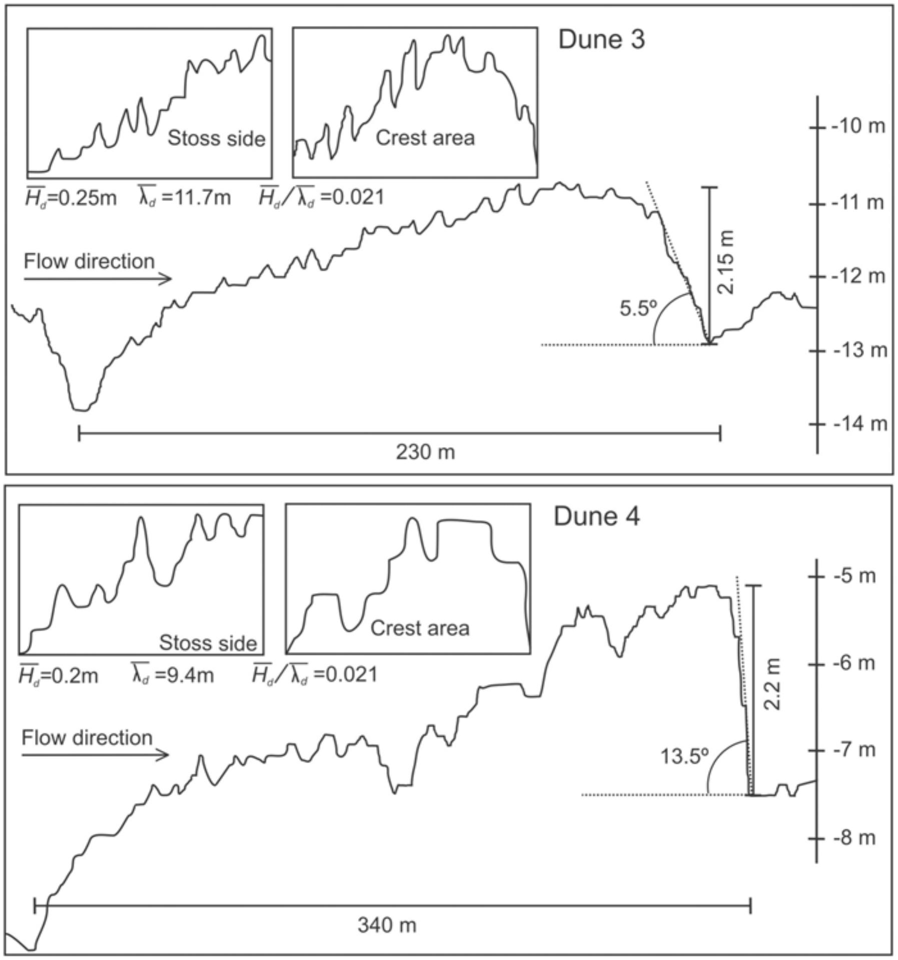

Figure 2. Surveyed dunes. Vertical scales on the right side illustrate the corresponding depths as measured from the water surface. Insets show details of the crest and stoss-side areas with overall mean dimensions of the small superimposed dunes.

population. Samples were taken with a bucket Tamura grab, filtered with a 200 μm sieve and fixed in 5% formaldehyde in the field. The invertebrates were hand-picked in the laboratory under a 10× stereoscopic microscope and stored in a 70% ethanol solution. All benthic taxa organisms were identified and counted in order to calculate density (ind m^{-2}), the diversity Shannon and Weanner index (H), evenness and species richness. The taxonomic determinations were made to species level (for Turbellaria from *Noreña* [1995] and *Noreña et al.* [2005]; for Oligochaeta from *Brinkhurst and Marchese* [1992]; and for Diptera Chironomidae from *Trivinho-Strixino and Strixino* [1995]). For other taxa the determinations were made to genus and morphospecies.

[13] Additional sediment samples for granulometric analysis (by dry sieving) and to obtain the organic matter content (by ignition and subsequent ash-free dry matter weight), were taken at the same sites.

[14] A key point in the sampling procedure was the vessel positioning in order to assure the four samples are taken at the stoss side, crest, and trough of the selected dunes (Figures 3a–3d). It was attained by using a Furuno GP-1650WF echo sounder coupled to a GPS and checking the corresponding coordinates and flow depths at the moment of each sample catch. Previously, details of the river bed topography were surveyed with the echo sounder along longitudinal tracks aligned with the current direction. The software package Fugawi Marine version 4.5 [*Northport Systems Inc.*, 2007] was used to know and process at real time the bed forms' morphology (Figure 3).

[15] Once the vessel anchored at each sampling point, measures of depth and current velocity profiles were obtained simultaneously with the benthic samples. Thus three velocity verticals were measured along the length of each selected dune by using an electrical propeller current meter. A total of 12–20 point velocities were recorded at the verticals, closer spaced in the first one meter from the bottom. Each point velocity was the average value of a 100s measuring interval (Figures 4a and 4b).

[16] The following parameters were also obtained: conductivity (μS cm^{-1}), pH and temperature (°C) with a HACH water checker; dissolved oxygen (mg l^{-1}) with a handheld WTW series 300 probe, and transparency as given by the Secchi disk (m). Float tracks were recorded to know the current direction.

2.3. Selection and Treatment of the Hydraulic Variables

[17] The characterization of the river hydraulics near the bottom at each sampling point was attained through direct

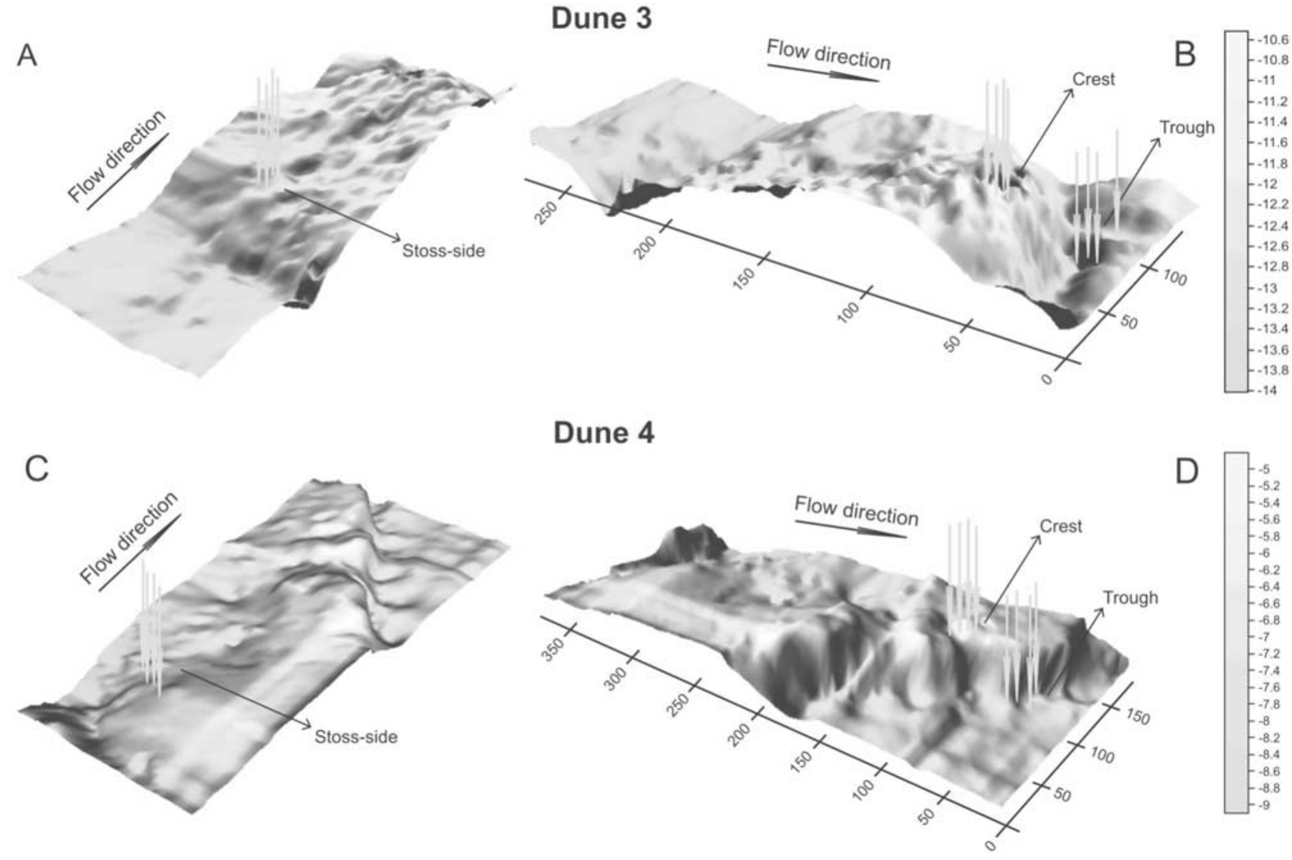

Figure 3. Three-dimensional graphs of the studied dunes with location of each benthic sample shown by arrows. Note: these graphs were built with the information recorded in longitudinal profiles closely spaced across each dune. (a) Dune 3, stoss side; (b) dune 3, crest and trough; (c) dune 4, stoss side; (d) dune 4, crest and trough.

measurements of the local velocity profiles, depths (h), median diameters of the bed sediment size distributions (d_{50}), dimensions of the small superimposed dunes (height and length) and lee slope angles of the dune. These parameters are the necessary inputs to calculate hydraulic variables such as the bed shear stress (τ_0) or its equivalent, the shear velocity (U_*), and the mobility number (τ_*), based on well established hydrodynamic laws. Regarding to τ_*, it is a widely known dimensionless variable in river sciences involving the relationship between the flow active forces trying to move the bed particles and the particle weight which resist that movement. Thus, this number gives a measure of the transport intensity of the bottom sediment grains [*Yalin*, 1977]. Considering that the median diameter (d_{50}) and τ_0 are included into τ_* (Table 1), this variable is an important parameter to know the incidence of the bed sediment transport on the benthic community in a given natural stream, provided that its value be representative of the flow conditions surrounding the sampling point.

[18] Some authors suggest also the use of other hydraulic variables such as the Froude (F_r) and Reynolds numbers (R_e) and the hydraulic radius (R) in eco-hydraulic studies related with the benthic fauna [*Statzner and Higler*, 1986; *Statzner et al.*, 1988; *Carling*, 1992]. These variables were not considered herein because of the following reasons: the Froude and Reynolds numbers describe by definition the gross flow characteristics at a given cross section or vertical and, as such, they say little about the local flow conditions close to the bed at a particular point. Following a similar reasoning, the hydraulic radius is another measure associated to the complete cross section of a channel, which equals the average depth when the width/depth ratio is great (say > 10), as it is in the majority of large rivers.

[19] The estimation in natural streams of local values of τ_0 (or U_*), the main flow variables of those cited above, is not an easy task. Usually, it can be approached through the well known relation [*van Rijn*, 1993]:

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

which can be expressed in the more handy form [*Kostaschuk et al.*, 2004]:

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

where, u: current point velocity at a distance, y, from the bottom, Z_0: $k_s/30$ for rough turbulent flow, k_s: roughness length, b: regression coefficient and, a: regression slope between measured point velocities and log y. Theoretically [*Schlichting*, 1979; *Yalin*, 1977], it was shown that equation (1) is valid with $a = 5.75U_*$, provided that turbulent, steady and uniform flow conditions along a plane bed are properly satisfied.

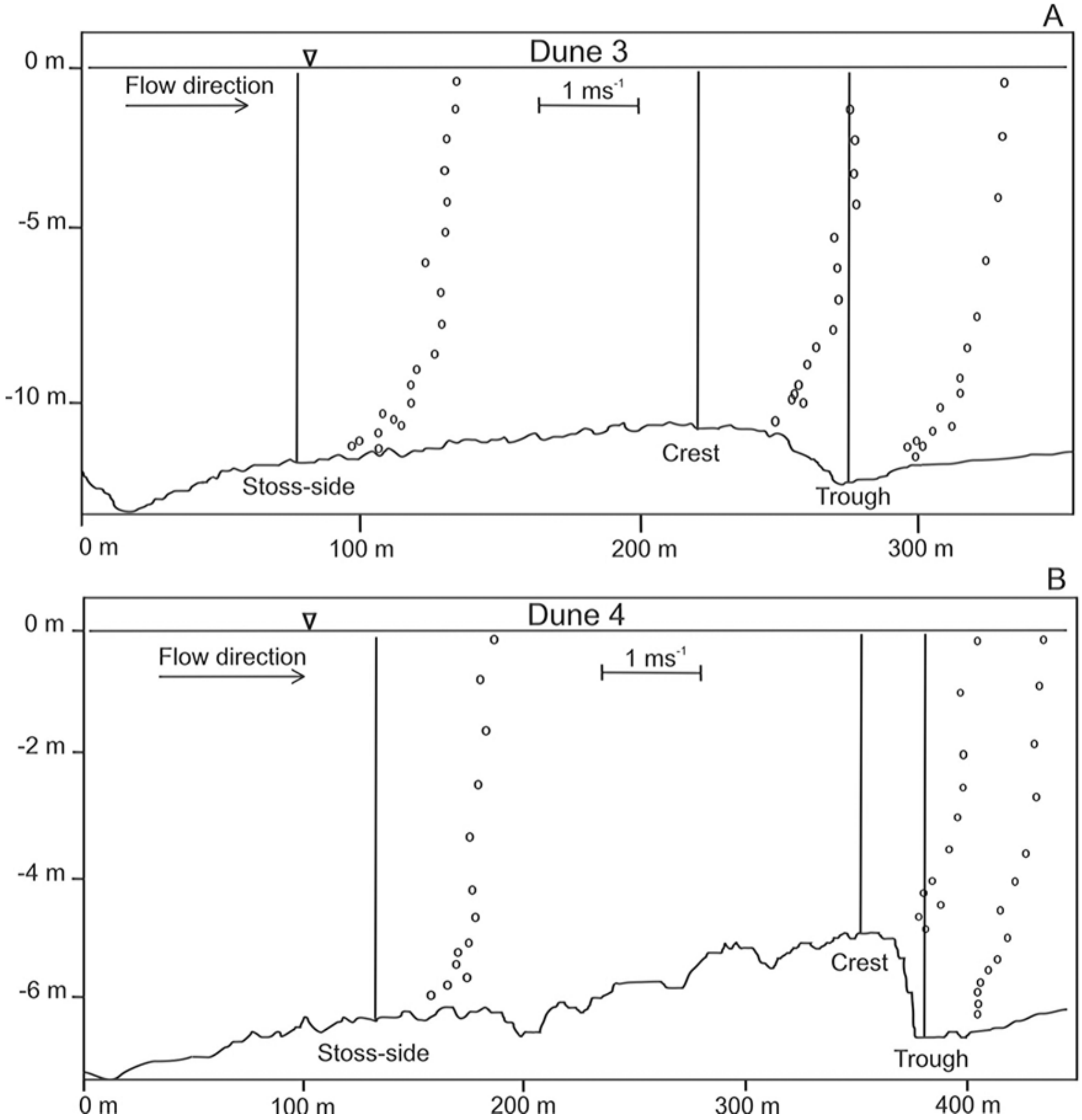

Figure 4. Velocity profiles measured along (a) dune 3 (thalweg) and (b) dune 4. Note the marked reduction of point velocities near the bottom on the trough of dune 4. Flow separation is expected at that site due to the relatively high slope of the lee side of that dune (see Figure 2b).

[20] Strictly speaking with an undulated bed, i.e., when dunes are present as on the bed of an alluvial stream, the flow may be perturbed in such a way as to question the application of the logarithmic approach to describe the local flow velocity profile. However, intensive investigations performed during the last decades, specifically based on laboratory experiments, proved that logarithmic expressions of equation (1) type would be still valid to describe the velocity profiles along the stoss side of dunes [see *Smith and McLean*, 1977; *Nelson et al.*, 1993] (among others).

Table 1. Summary of the Hydraulic Variables Measured or Computed in the Study[a]

Name	Symbol	Units	Formula	Description
Current velocity	U	m s^{-1}	direct measurement	Velocity measured at each point in the vertical profile.
Small superimposed dunes height	H_d	m	indirect measurement	Superimposed small dunes height around the sampling point.
Depths	h	m	direct measurement	Local depth.
Shear velocity	U_*	m s^{-1}	$U_* = a/5.75$	An estimate of turbulence intensity close to the bottom.
Shear stress	τ_0	kg m^{-2}	$\tau_0 = U_*^2\ \rho$	Bed shear stress derived from the shear velocity.
Mobility number	τ_*	none	$\tau_* = \frac{\tau_0}{(\gamma_s - \gamma_w)d_{50}}$	Dimensionless relationship between active and passive forces acting on the bed particles.

[a] Here a, regression slope from equation (2); ρ, water density; γ_s, specific weight of sediment; γ_w, specific weight of water.

Moreover, complete logarithmic velocity profiles are common on the nearly horizontal region of dune crests. The gradual variation of flow characteristics along the stoss side, particularly in large natural dunes, would contribute to maintain the approximate validity of using a logarithmic function to describe part or the entire local velocity profiles.

[21] In this respect, *Amsler and Schreider* [1986, 1992] and *Trento et al.* [1990] showed the validity of approaching the vertical velocity distribution by a semilog function such as equation (1) at a large stream like the Paraná River. These authors fitted successfully the general expression from which equation (1) is derived, to a large number of vertical velocity profiles measured in the main channel for a wide diversity of flow and bottom conditions. The most of these vertical profiles, however, were recorded on the crests or on the stoss sides of large sand dunes. However, problems arise when equation (1) is applied to estimate local bed shear in the lee side of dunes or in troughs. Along this part of the dune, the flow is perturbed due to the deformation of streamlines (with or without flow separation) in such a way that the conditions under which equation (1) was derived do not comply. It is well known [see *van Rijn*, 1993, Figure 5.2.11a; *Nelson et al.*, 1993] that the velocities reduce sharply near the bottom on these dune sites due to the rather sudden depth increment (the reduction includes the possibility of reverse flow in the case of flow separation). It is required considerably more complex models than the simple one represented by equation (1) to describe the flow features within these zones [*Garcia*, 2008; *Lyn*, 2008]. Anyway the consequences are bed shear stresses which may be considerably lower in the trough region than on the dune crest. Direct measurements of these stresses along the lee side and trough of dunes, are extremely scarce in literature and come from laboratory experiments. In field studies they are nonexistent. Thus, a procedure was designed to gain approximate quantitative information about the hydraulic conditions in the trough of dune 3 located in the thalweg region (the ratio of crest bed shear stress/trough bed shear stress was estimated). On the other hand a few laboratory data were used in dune 4 for the same purpose. The details are presented in Appendix A at the end of the paper.

[22] In order to apply equation (2), the simplified form of equation (1), it is further necessary to define the proper origin of the measured velocity profiles, the so-called ‘hydraulic bottom’ (or ‘virtual origin’), since the slope *a* and, thus, the τ_0 (or U_*) accuracy is deeply influenced by that origin [*Perry and Joubert*, 1963]. The location of the velocity profiles origin is particularly important in rough turbulent flows. For the case of the Paraná River, *Amsler and Schreider* [1992] showed that the small superimposed dunes (see Figure 2) act as roughness elements which make the gross flow behave as rough turbulent. From this starting point and depending on the relative submergence and geometry of the small superimposed dunes at a given site, the virtual origin can be located anywhere between the trough and crest of the small dunes. As there is no theoretical method to find that origin in rivers with a hierarchy of dunes, an ad hoc procedure advanced by *Perry and Joubert* [1963], was used herein.

[23] Essentially, it is a trial-and-error method which enables finding the hydraulic bottom as that corresponding to the best regression (highest r^2 coefficient) between the point velocities (U) and the distance from the bottom defined as log ($y \pm \Delta e$), being: Δe: a fraction of the roughness elements with a height *e*. In this case, the average small dunes height surrounding each vertical velocity profile defined the *e* value. The original data of the velocity profiles were smoothed with simple procedure (see Appendix A), before the determination of the virtual origin. The results of the *Perry and Joubert*’s [1963] method applied to the four velocity profiles where equation (2) was valid are presented in Table A1 of Appendix A.

[24] Finally, in Figures 5a–5d, the fitnesses of equation (1) to the measured velocity profiles on crest and stoss side of dunes 3 and 4 once defined the virtual origins are presented. On the basis of the slopes *a* of the fitted curves the bed shear stress, τ_0, values of Table 3 were computed (see later in the text).

2.4. Statistical Analysis

[25] In order to verify the normality of the benthic data, they were logarithmically transformed [$\log_{10}$ (x + 1)] and checked their normality within a strata [*Shapiro and Wilk*, 1965] and homogeneity of variance between strata (*F*max [*Sokal and Rohlf*, 1981]). As normality was not verified, nonparametric statistics was applied. Thus, a Mann-Whitney U Test was carried out (significance < 0.05) to determine differences between medians of benthic density between the two studied dunes.

[26] Principal Components Analysis (PCA) of the physical variables is a common analysis in ecology researches [see *McGarigal et al.*, 2000], and was used herein to summarize the total variation of data and identify major environmental gradients. A MultiVariate Statistical Package (MVSP), version 3.1 soft [*Kovach*, 2002] enabled all the computations.

3. Results

[27] Considering the sampling sites all together, only 8 species and morphospecies were identified: *Narapa bonettoi* and *Dero nivea* (Oligochaetes); *Myoretronectes paranaensis*, *Itaspiella parana* (Turbellaria); *Tobrilus* sp. (Nematoda); *Polypedilum* sp. and *Tanypodinae* sp. (Chironomids); and Acari sp.

[28] Total densities considering all the samples varied between 0 and 7020 ind m^{-2} with averages for sampling stations ranging between 0 ind m^{-2} (stoss side of dune 3) to 3383 ind m^{-2} (trough of dune 4). Densities recorded on dune 3 were lower than on dune 4. The diversity Shannon index ranged between 0 (stoss side of dune 3) and 0.95 (crest of dune 4; Table 2). The sediment organic matter, conductivity, pH, temperature, dissolved oxygen, and transparency values did not vary significantly between the dunes.

[29] The Mann-Whitney U Test ($p = 0.0001$) revealed a significant distinction between the median benthic densities (Table 2) of the sampled dunes. Figure 6 shows that benthic densities along dune 4 are clearly higher than along dune 3 with a remarkably high density in the trough of dune 4.

[30] The hydraulic and substratum variables measured along the dune profiles are presented in Table 3. The highest bed shear stresses occurred on dune 3 (thalweg).

[31] The first axis of the PCA, crosses the maximum data variation and explains 74.6% (eigenvalue = 3.73) of the physical variations while 16.2% the second axis (or

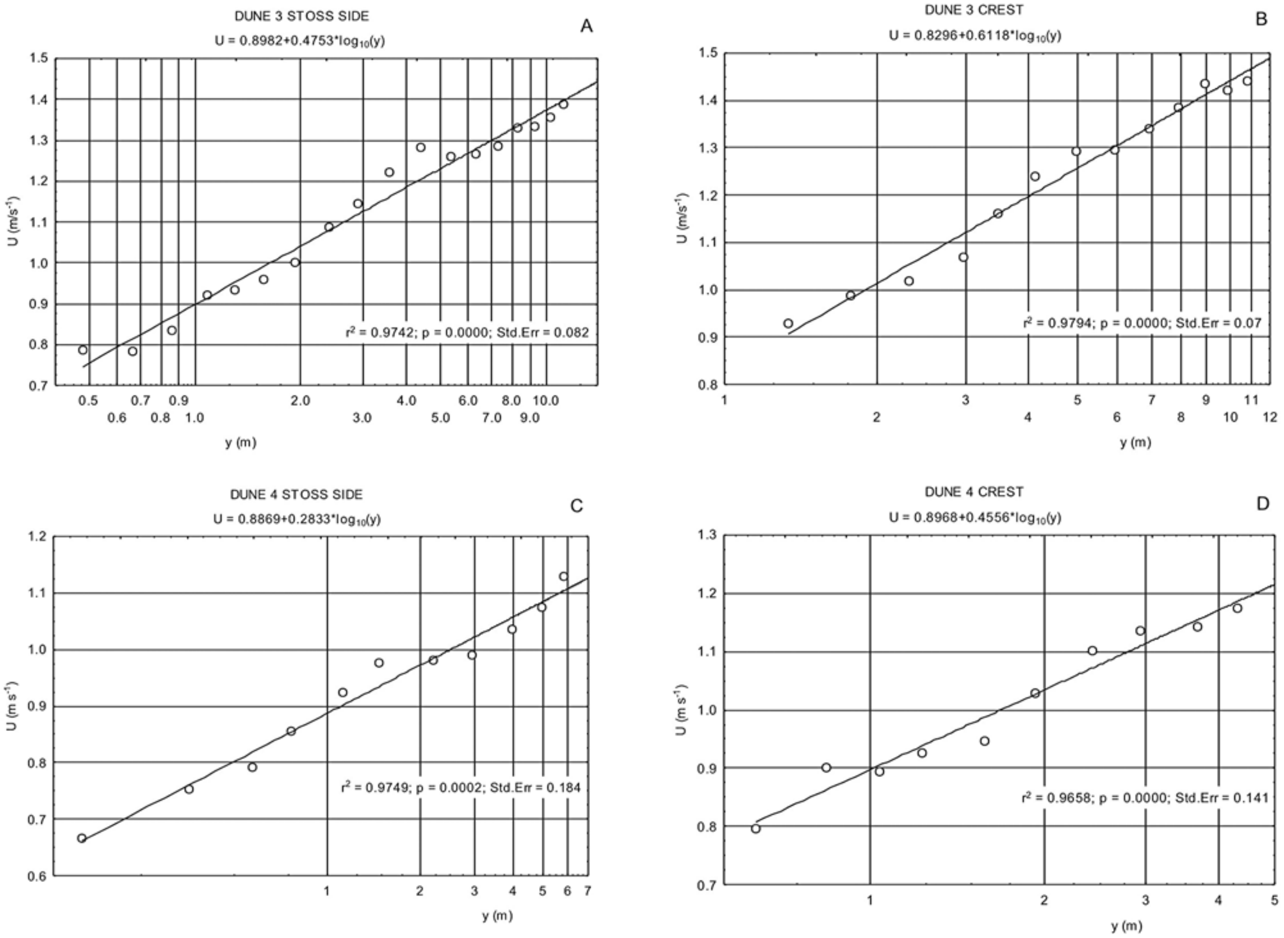

Figure 5. Semilog plots of the smoothed velocity profiles measured on crest and stoss side of dunes 3 and 4 showing the fitness of equation (A2). The *y* values were determined taking account of the virtual origin concept (see Appendix A).

orthogonal axis; eigenvalue = 0.81). Thus, both axes explain 90.9% of the whole variation. The dunes remained clearly separated suggesting a higher physical variation between them than along each of their profiles (Table 4 and Figure 7). The variables: current velocity, shear stress and mobility number are strongly associated with the axis 1, being depth the most significant variable inversely associated with the axis 2 (see PCA variables in Table 4). The axis 1 is positively correlated to the dune 3, especially with the crest (Table 4). On the other hand, axis 2 is positively related (and therefore correlated with) dune 4, where the hydraulic variables are less intensive. Specifically the trough of dune 4 is highest negatively correlated with axis 1. Note that the other variables related with the water quality were not included in this analysis because of their extremely low variability between and along the sampled dunes.

4. Discussion

[32] Typical benthic community living in the active bed of the Paraná main channel [*Marchese and Ezcurra de Drago*, 1992; *Takeda*, 1999; *Ezcurra de Drago et al.*, 2004; *Takeda and Fujita*, 2004; *Marchese et al.*, 2002, 2005], was recorded in this study. The community presented an assemblage composed principally of *Narapa bonettoi* (Oligochaeta), *Myoretronectes paranaensis and Itaspiella parana* (Turbellaria), and *Tobrilus* sp. (Nematoda).

[33] The Mann-Whitney U test results applied at mesohabitat scale showed a clear macroinvertebrate preference for dune 4 (located outside the thalweg region) where less strong hydraulic conditions prevail. Indeed, the highest densities occurred along this dune, i.e., the hydraulic biotope with the smaller values of U_* (or τ_0) and τ_*. On the contrary, along dune 3 (in the thalweg) where these hydraulic variables are larger, the lowest benthic densities were recorded with a minimum of 0 organisms on the upper

Table 2. Results of Shannon's Diversity Index H, Evenness, and Species Richness at Each Sampling Point

	Mean Benthic Density (ind. m^2)	Index H	Evenness	Species Richness
Dune 3 stoss side	0	0	0	0
Dune 3 crest	146	1.3	0.8	5
Dune 3 trough	175	0.76	0.55	4
Dune 4 stoss side	751	0.85	0.77	3
Dune 4 crest	1297	0.95	0.59	5
Dune 4 trough	3383	0.47	0.43	3

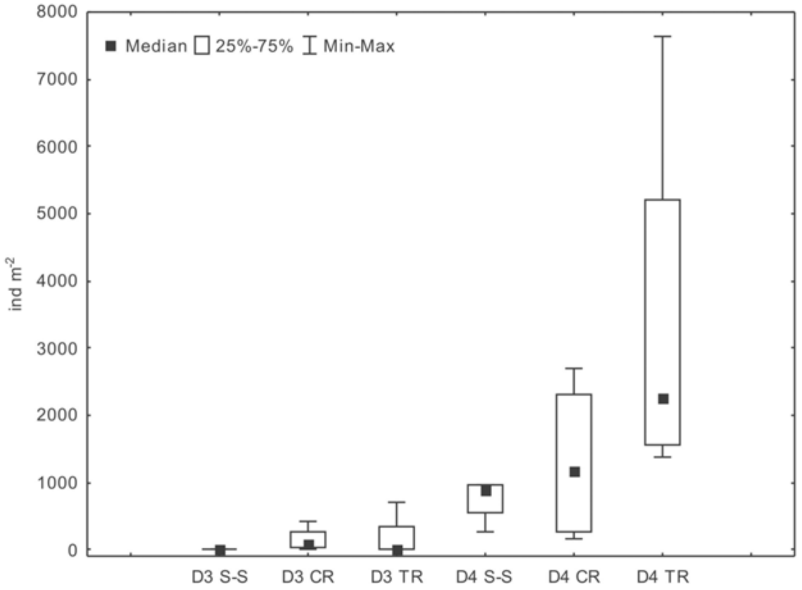

Figure 6. Box plot of the median of density distribution at each sampling point. D3, dune 3; D4, dune 4; S-S, stoss side; CR, crest; TR, trough of dune.

stoss side (Tables 2 and 3 and Figures 3 and 4). Considering only the hydraulic factor, the previous results agree with those reported by *Orth and Maughan* [1983], in a woodland stream in North America, *Rempel et al.* [2000] in the Fraser River, and *Brooks et al.* [2005], in the Kangaroo River (New South Wales).

[34] Moreover, the results at a mesohabitat scale of the current investigation (sampling date: August 2007) were compared with those reported by Blettler et al. (submitted manuscript, 2009) from a similar study performed on two dunes located nearly at the same site as dune 3 and 4, but sampled on October 2005. The principal hydraulic variables of the recent study were recalculated with the same methodology used at that time. When the hydraulic results were compared, it was possible to note that the flow and sediment variables were similar in both samplings. However, the benthic densities were larger on the dunes surveyed in 2005 (Tables 5 and 6).

[35] This interesting fact would have an explanation based on the abundance of the dominant species in the central channel, *Narapa bonettoi* (Table 5), and on its seasonal biological cycle. *N. bonettoi* is dominant and often the only benthic species present in the main channel of the Middle Paraná River [*Bertoldi de Pomar et al.*, 1986; *Marchese*, 1987; *Marchese and Ezcurra de Drago*, 1992]. This species clearly prevails in dunes 1 and 4 but does not in dunes 2 and 3 where the hydraulic conditions are stronger (Table 5). Regarding the seasonal patterns in the abundance of these organisms, *Marchese* [1994] showed that they are more abundant during spring and summer due to their reproductive strategy: mature specimens predominate in September resulting in a larger reproductive activity in the subsequent months. Thus this biological factor would explain the differences in the absolute value of densities (larger in October 2005) found in both samplings, in spite of the similar hydraulic conditions. The influence of the hydraulic variables persists, however, since the smallest densities verified in the thalweg region in the two cases with the referred minimum in dune 3 where the hydraulic forces were so large as to prevent *N. bonettoi* to be dominant.

[36] As a final remark concerning this comparison, the overall results inspection at mesohabitat scale as shown in Table 6, reveals the existence of significant and distinct

Table 3. Hydraulic and Bed Sediment Variables[a]

	Maximum Velocity (m s^{-1})	Mean Velocity (m s^{-1})	Depth (m)	Height of Small Dunes (m)	Shear Velocity (m s^{-1})	Shear Stress (kg m^{-2})	d_{50} (mm)	σ_g	Mobility Number
Dune 1 crest	1.29	1.1	7.3	0.125	-	-	0.37	-	-
Dune 1 trough	1.29	1.1	9.6	0.025	-	-	0.35	-	-
Dune 2 crest	1.44	1.24	12.1	0.18	-	-	0.3	-	-
Dune 2 trough	1.44	1.24	13.4	0.14	-	-	0.27	-	-
Dune 3 stoss side	1.4	1.2	12.4	0.17	0.082	0.7	0.33	1.45	1.27
Dune 3 crest	1.5	1.3	11	0.22	0.106	1.15	0.33	1.36	2.1
Dune 3 trough	1.4	1.2	12.8	0.2	0.079	0.64	0.33	1.36	1.15
Dune 4 stoss side	1.2	1	7.2	0.2	0.05	0.25	0.285	1.29	0.53
Dune 4 crest	1.2	1	5.1	0.2	0.079	0.64	0.38	1.35	1.02
Dune 4 trough	1.1	0.9	7.3	0	0.05	0.25	0.3	1.3	0.5

[a] Here d_{50}, median and σ_g, geometric standard deviation of sediment size distribution. Water temperature,15.8°C.

Table 4. PCA Results of Environmental Variables for the First Two Principal Axes[a]

	Axis 1	Axis 2
PCA Case Scores		
Cases		
Dune 3 stoss side	0.48	−0.28
Dune 3 crest	1.16	0.06
Dune 3 trough	0.47	−0.24
Dune 4 stoss side	−0.64	0.23
Dune 4 crest	−0.27	0.66
Dune 4 trough	−1.20	−0.42
PCA Variable Loading		
Variables		
Maximum current velocity ($v_{\max}$)	0.510	−0.149
Depth (*Dep*)	0.362	−0.743
Bed shear stress (*Shs*)	0.483	0.159
Small dunes height (*Hsd*)	0.361	0.628
Mobility number (*MoN*)	0.495	0.083

[a] See text for detailed explanations.

hydraulic biotopes with different hydraulic and morphologic geometries (Figures 2 and 3). Consequently, the apparent homogeneous central strip of the Paraná River main channel (a large-scale habitat due to its dimensions), presents a very stratified benthic distribution.

[37] *Boyero* [2005] shows that variation in functional composition also occurs at such small scales as pools, riffles, and even within-riffle scales. In this regard, the incidence of flow dynamics features on invertebrate community at within-dune scale (stoss side, crest, and trough) in large rivers, could be thought as a microhabitat scale analysis. To have an insight at this level, however, requires certain knowledge about the hydraulic features of these dune microhabitats as a previous step to find their influence, if any, on the organisms living there. The main flow characteristics along a dune profile were known essentially through laboratory experiments. Those prevailing along the lee side of a dune were yet briefly described in the paper in connection with the validity of equation (1) and in Appendix A.

[38] The study of flow pattern along the stoss side has received the bulk of the attention since the pioneer paper of *Raudkivi* [1963]. Precisely this author showed experimentally that the mean bed shear stress is low in the flow separation zone and high near the crest of the bed form. Moreover, Raudkivi called attention to the zone of the reattachment point in the upper part of the stoss side at 5 to 8 bed form heights downstream from the crest. In that region, where the separation line or interface reaches the sand surface again, turbulent agitation is high in spite of the low value of bed shear stresses.

[39] These early findings were further verified or put in due context later on by a number of investigators through more sophisticated laboratory experiments, numerical modeling as well as field measurements [*McLean and Smith*, 1986; *Nelson and Smith*, 1989; *Nelson et al.*, 1993; *Kadota and Nezu*, 1999; *Kostaschuk*, 2000] (among others). Refined theories of turbulent flows above dunes are implicit in this research which includes the development of an accelerating boundary layer from the lower stoss side toward the crest and interacting with the wake region existing over it. These main flow features are generally accepted to develop along the stoss side of dunes with or without separation downstream of the crest, given the accumulated evidence. Some facts derived there of and of interest for this investigation, are summarized next:

[40] 1. The point of maximum shear stresses on the crest of bed forms in the Raudkivi's experiments, moves upstream when dune steepness (H/λ) is lower than 0.1 [*Nelson and Smith*, 1989] (here dune 3: $H/\lambda = 0.009$; dune 4: $H/\lambda = 0.007$) and with a rougher boundary of the stoss side, e.g., due to the existence of small superimposed dunes [*McLean and Smith*, 1986].

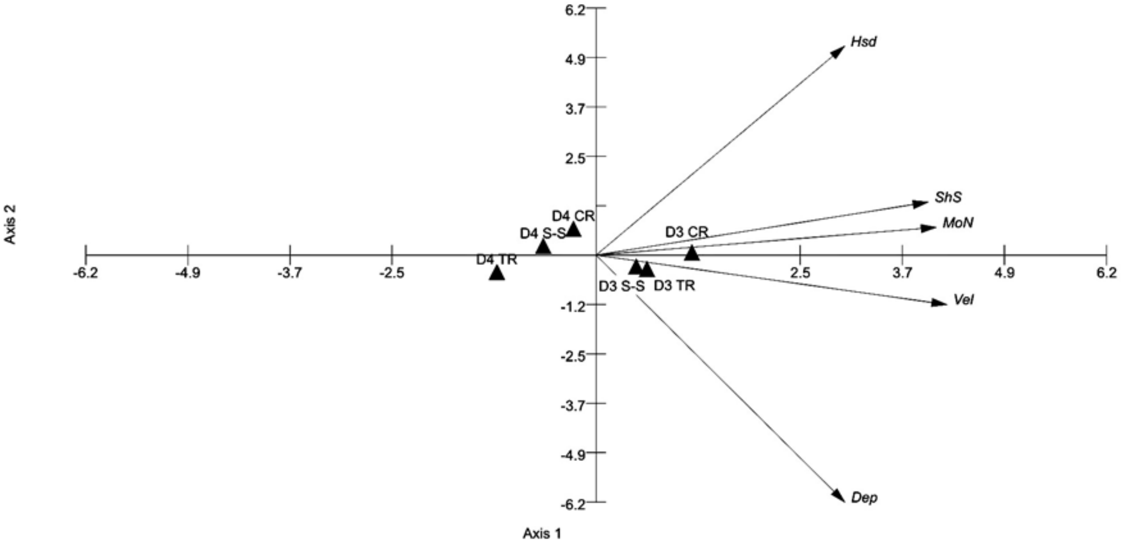

Figure 7. Plot of score distributions along principal component analysis (PCA) axes for the physical (hydraulics and substratum) variables recorded in the studied dunes (stoss side, crest, and trough area of each dune). D3 S-S, stoss side of dune 3; D3 CR, crest of dune 3; D3 TR, trough of dune 3; D4 S-S, stoss side of dune 4; D4 CR, crest of dune 4; D4 TR, trough of dune 4 (see Table 4 for score values).

Table 5. Results of the Survey Performed on Dunes 1 and 2 and on Dunes 3 and 4[a]

Sampling	Dune	Total *N. bonettoi* Density (ind. m^{-2})	Others Species Density (ind. m^{-2})	Total Species Density (ind. m^{-2})
Sampling I (spring 2005)	Dune 1 crest	2049	251	2300
	Dune 1 trough	3525	360	3885
	Dune 2 crest	177	59	236
	Dune 2 trough	149	77	226
Sampling II (winter 2007)	Dune 3 stoss side	0	0	0
	Dune 3 crest	29	117	146
	Dune 3 trough	0	175	175
	Dune 4 stoss side	400	351	751
	Dune 4 crest	780	517	1297
	Dune 4 trough	2915	468	3383

[a] Dunes 1 and 2, October 2005 (Blettler et al., submitted manuscript, 2009); dunes 3 and 4, August 2007 (present study). Note the dominance of *N. bonettoi*.

[41] 2. At some location in the low stoss region the turbulence intensity reaches its maximum due to a series of mechanisms such as the advection of turbulent flow from the wake zone down to the bed. Further downstream toward the crest the intensity decreases due to, essentially, the accelerating boundary layer effects [*Nelson et al.*, 1993]. This region of high turbulence agitation was measured on natural dunes by *Kostaschuk* [2000]. This author also argue that this turbulent pattern occur on large dunes with low leeside angles and no flow separation which are common in large rivers [*Kostaschuk and Villard*, 1996].

[42] 3. Recent advances in coherent flow structure's theory and instrumentation, revealed a complicated and refined structure of coherent vortices (kolk-boil vortices) generated just downstream of the separated vortices on the low stoss of laboratory dunes [*Kadota and Nezu*, 1999]. Those types of vortices would be responsible for sudden low-speed flow ascension from that region.

[43] 4. *Nelson et al.* [1993] suggest that due to the high turbulence intensity sediment flux will be maximum on the upper part of the stoss side. Moreover, *Kostaschuk* [2000] could relate the turbulent structures of this region with high concentrations of suspended sand in his measurement on the Fraser River dunes. The linking of these facts with the kolk-boil vortices studied by *Kadota and Nezu* [1999] is a logical corollary. Indeed, these vortices would be a mechanism to transport high sand concentrations from the bottom at the low stoss of dunes to the water surface, as was early suggested by *Jackson* [1976].

[44] While more investigation is undoubtedly absolutely needed to deepen an understanding of the intricate interactions between the different processes implicit in i to iv, it seems clear that the low stoss side of dunes is a region subjected to high turbulent agitation which affect strongly the bed sediment particles facilitating their suspension. This turbulent agitation not necessarily coexists with a high average shear stress since it would depend on the dune steepness and the stoss side roughness. The bed shear stresses at the crest maintain a relatively high value but with decreasing turbulence intensity near the bottom, due to the convergent flow which controls the development of an internal accelerating boundary layer. Note in dune 3 and 4 (Table 3) that the highest mean values of the bed shear stress were recorded over the crest. In these sites, the benthic densities are relatively larger than in the stoss sides (Tables 2 and 5 and Figure 6) in accordance with lower bed disturbances due to decreasing turbulent intensities and in spite of the highest shear stress values. Considering the nature of flow structure along a dune described above, the lowest benthic densities found in the low stoss sides of dune 3 and 4 in comparison to the other dune areas would have an explanation relying on the largest bed perturbation, given by the high turbulence intensity, occurring at those sites of the dune profiles. In a few words, further downstream near reattachment, there are large near-bed velocity (and pressure) fluctuations that actively pick up sediment from the bed making it a less inviting place to live.

[45] The highest densities of the benthic fauna were recorded in the trough region of both dunes (Table 2). The same is true for dunes 1 and 2 in the 2005 sampling (Table 5). The lower values of the bed shear stresses in these sites in comparison to those in the crest, would account for the species preference of these places which provide refuge and specific food resources. It is well know that the accumulation of organic matter downstream of dune crests is facilitated by the favorable flow conditions, especially when separation occurs. Thus, it would not be surprising the highest benthic densities in the troughs of dune 4 and 1, both outside of the thalweg region and where the probability of separation is high due to the relatively larger values of the lee side angles (see Figure 2). The value of this angle is a crucial parameter which controls the occurrence of flow separation given a turbulent boundary layer. Under this condition, *Rouse* [1950] states that with boundary inclinations less than about 4°, the flow may be completely free from separation. It would be the case of dune 3 (and also dune 2), with very low lee side angles and, thus, reduced

Table 6. Comparison of the Mean Benthic Densities Computed From the Results Presented in Table 5

	Mean Benthic Density
Sampling I spring 2005	
Dune 1 (outside thalweg)	3092
Dune 2 (thalweg)	231
Sampling II winter 2007	
Dune 3 (thalweg)	160
Dune 4 (outside thalweg)	2340

possibilities of detached recirculating near bed flow in the trough. The presence of small superimposed dunes migrating along the lee side of dune 3 and in its trough region (absent in dune 4), is a phenomenon difficult to explain with flow separation. This type of superimposition in the dune trough would be frequent in natural dunes [*Ogink*, 1988; *Amsler and Schreider*, 1992; *Amsler and Prendes*, 2000; *Best and Kostaschuk*, 2002] and a probable consequence of rather high bed shear stresses which increase the rate of suspended bed material in comparison to the bed load [*Amsler and Schreider*, 1999; *Sukhodolov et al.*, 2006]. The higher bed shear stresses and mobility numbers in the thalweg strip where dunes 3 (and 2) locates, explain the smaller trough benthic densities and differences with those in the crests compared with the respective values in dunes 4 (and 1) (Tables 2, 3, and 5).

[46] The significance of the small superimposed dunes (which cover the surface of both dunes, with the exception of the trough area in dune 4) on the benthic fauna is practically unknown. These small dunes are normal in natural dunes and specially in large rivers [*Ogink*, 1988; *Amsler and Schreider*, 1992; *Gabel*, 1993; *Carling et al.*, 2000; *Sukhodolov et al.*, 2006]. As noted by several investigators, they have different propagation velocities in comparison to those of the dunes [*Amsler and Gaudin*, 1994; *Nikora et al.*, 1997] and may exert a strong influence on bed load transport [*Amsler and Gaudin*, 1994; *Serra and Vionnet*, 2006] as well as on flow resistance since their existence generate an extra bottom roughness [*McLean and Smith*, 1986; *Ogink*, 1989; *Amsler and Schreider*, 1992]. In spite of these contributions, the dynamics of the small superimposed dunes is the topic in the alluvial bed forms field where, perhaps, more investigation is needed [*Best*, 2005; *Parsons et al.*, 2005]. Taking due account of this context, the superimposed dunes in benthic studies should be considered as another microhabitat within dune scale though yet smaller than those treated so far.

[47] It is likely that the smaller dunes that migrate on the backs of the larger dunes will induce separation even if the larger one does not. Figure 2 suggests more asymmetry in the smaller dunes than the larger ones. Sediment is picked up on the stoss of the dunes (downstream of reattachment) and is carried toward the crest or where there is a slope break where it is deposited because of flow separation. The sediment deposit near the slope break builds up until it becomes unstable and avalanches down the lee face of the dune where it is buried by subsequent avalanches. Sediment moves rapidly up the stoss to the crest, avalanches quickly to some point along the lee slope where it is buried until it is reeroded after the crest passes over. This has great consequence for macroinvertebrates living in the bed. The large dunes move very slowly and there is plenty of time for the benthic organisms themselves to migrate as the dune moves. The smaller dunes on the other hand move much more quickly, (10–20 m d^{-1} at midwater stage [*Amsler and Gaudin*, 1994]). This means that the entire volume of the small dune is mixed in less than 12 h. For the larger dunes it takes days or weeks. In the trough of dune 4, no small dunes are found because they are buried by the larger dune in the avalanching process. Thus the organisms in the trough of the separating dune have the benefit of low flow and a stable environment.

[48] It should be remarked that the findings presented above as a whole, agree with studies of macroinvertebrates communities (abundance, richness, evenness) performed in small streams which showed the influence of spatial scales in the results [*Downes et al.*, 1993; *Townsend et al.*, 1997; *Boyero and Bailey*, 2001; *Li et al.*, 2001; *Boyero*, 2003]. In short, multiscale studies would be essential in rivers if the identification of the habitat dimensions at which ecological patterns vary is intended.

[49] Little is known about the benthic macroinvertebrates reaction when exposed to the flow forces in large rivers, especially in those microhabitats more strongly perturbed. In this respect, Blettler et al. (submitted manuscript, 2009) suggested the following hypothesis to be explored: (1) benthic fauna begins to move down into the intersticial substratum spaces; (2) destruction of species individuals due to increasing collisions between near bed sand particles (a possibility closely related with high values of τ_*, the main variable which controls the amount of transported sand at a vertical of given depth and velocity); (3) the simultaneous occurrence of the previous facts.

[50] Another alternative hypothesis could be advanced herein; (4) the sweep and drift of the benthic organism putting them into suspension due to the high turbulent forces acting on the bed.

[51] Finally, it deserves to be noted that the bulk of flow features on dunes cited and used along this discussion are consequence of measurements and/or theoretical developments on two-dimensional dunes, i.e., a simplification of real dunes since three-dimensionality predominates in nature. Apparently 3D effects in dunes morphology influence significantly the bed flow structure [*Parsons et al.*, 2005], with special concern to the occurrence, location and intermittency of the separation zone. Note in Figures 1 and 3 that 3D effects would be of importance in dune 4 whose crest line is deviated by angle of 45° from the surface flow direction. Nevertheless, according to the agreement of the results obtained and discussed above with findings in carefully conducted experiments, such 3D effects would be of minor influence in this case, something attributable perhaps to the gentle boundary variations frequent in large sand bed rivers.

5. Conclusion

[52] A study was performed based on field measurements aims to link the diverse hydraulic conditions along sand dunes with the benthic fauna living in the active bed of the Paraná River. A number of conclusions may be drawn from the study:

[53] 1. The dunes of the central strip of the Paraná River behave as hydraulic biotopes (following the definition advanced by *Wadeson* [1994]) at a mesohabitat scale where benthic densities vary principally according to the dune location in the main channel.

[54] 2. At that scale, dunes located in the thalweg region are subjected to larger bed shear stresses and mobility numbers than dunes outside that region. As a consequence, considerably lower densities of benthic macroinvertebrates were recorded in the thalweg dunes. A previous sampling during a different month of the year with a similar river stage showed similar results but with different magnitudes

of density which can be attributed to the reproductive cycle of the dominant benthic species.

[55] 3. Differences in benthic densities were also found at microhabitat scales, i.e., within-dune scales. Hydraulic conditions varied between the crests, troughs and stoss sides of dunes. The highest densities were found in the dune troughs where bed shear stresses were lowest, especially when flow separation occurs (dunes outside the thalweg zone and relatively larger lee side angles). The lowest densities (including null densities) were recorded on the stoss side of dunes where other researchers suggest turbulent fluctuations are large, leading to greater disturbance of bed particles.

[56] 4. Small superimposed dunes were observed at all sampled locations on the dunes studied here, including within the trough regions of thalweg dunes. These small dunes may form smaller microhabitats which should be considered in future research.

[57] 5. It was showed herein that benthic macroinvertebrates distributions vary across spatial scales also in very large sand bed rivers. The study showed that a mesoscale (location of the dune) and a microscale (position on the dune) should be considered if a comprehensive understanding linking hydrodynamics and morphodynamics processes with benthic organisms is intended. A further smaller microhabitat (the position along the small superimposed dunes observed on the large dunes) introduce another hypothetical influence on benthic fauna still unknown. The importance of 3D effects of dunes morphology on the flow near the bed and the behavior of organisms facing hydraulic conditions increasingly harder, are additional factors justifying the necessity of further investigations.

Appendix A

A1. Estimation of the Bed Shear Stress in the Trough Region of Dunes 3 and 4

A1.1. Lee Side Without Flow Separation (Dune 3)

[58] The very low lee side angle of dune 3 (Figure 2) impedes the flow separation (see section 4), permitting the migration of the small superimposed dunes downstream along the lee face. Taking account of this fact a simple procedure was designed to derive an expression for the ratio between the shear stresses at the crest and trough of this type of dune. It is based on well known formulas of fluvial hydraulics which proved to yield reliable results in the Paraná River flow and sediment conditions. The first one is the bed load formula based in the dune displacement velocity [*Yalin*, 1977]:

$$g_{sf} = (1 - P)C_f H U_d \tag{A1}$$

where g_{sf}, bed load rate (L^2/T); P, porosity of bed material ($\approx$ 0.4 for natural sands); C_f, shape coefficient for dunes ($\approx$ 0.67 for natural dunes); H, dune height (L); U_d, dune displacement velocity (L/T). The other one is a general conceptual formula for bed load rate of the *Meyer-Peter and Muller* [1948] type:$\O k$

$$\O = k\left(\tau'_* - \tau_{*_c}\right)^n \tag{A2}$$

where Ø, dimensionless bed load parameter ($= g_{sf}/[(s-1)^{0.5} d_s^{1.5}\ g^{0.5}]$); τ'_*, dimensionless shear stress due to grain roughness ($= \tau'_0/[(\gamma_s - \gamma)d_s]$); τ_{*c}, critical dimensionless shear stress for initiation of motion ($= \tau_c/[(\gamma_s - \gamma)d_s]$); τ'_0, shear stress due to grain roughness (F/L^2); τ_c, critical value of shear stress for initiation of motion (F/L^2); k and n, dimensionless coefficients; s, specific gravity (γ_s/γ);γ_s, specific weight of sediment grains (F/L^3); γ, specific weight of water (F/L^3); d_s, size of bed particles (L); g, acceleration of gravity (L/T^2).

[59] Equating equations (A1) and (A2), and applying them to the small superimposed dunes located on the crest and trough of the larger dunes, results:

$$\frac{H_d U_d\rfloor_c}{H_d U_d\rfloor_t} = \left[\frac{\left(\tau'_* - \tau_{*_c}\right)_c}{\left(\tau'_* - \tau_{*_c}\right)_t}\right]^n \tag{A3}$$

where d, account for small dunes; c, t, account for crest and trough.

[60] Replacing ($\tau'_0 - \tau_c$) in (3) using the universal expression of *Engelund* [1967], which was yet successfully applied to predict the flow resistance in the Paraná River [*Amsler and Prendes*, 2000]:

$$\tau'_* - \tau_{*_c} = 0.3\tau_*^{1.5} \tag{A4}$$

where τ_*, dimensionless shear stress or mobility number ($\tau_0/[(\gamma_s - \gamma)d_s]$); τ_0, total bed shear stress (F/L^2), may be finally obtained:

$$\frac{\tau_0\rfloor_c}{\tau_0\rfloor_t} = \left[\frac{H_d U_d\rfloor_c}{H_d U_d\rfloor_t}\right]^{\frac{1}{1.5n}} \tag{A5}$$

It may be noted in equation (A5) that estimating the τ_0 value on the crest of the larger dune as was done in the paper and with information of the small dunes heights and their displacement velocities at the crest and trough of the large dune, it would be possible to approach a τ_0 value in the trough, provided that the n coefficient is known. Regarding to this coefficient, available developments [e.g., *Yalin*, 1977] have proved that bed load formulas derived from diverse theoretical approaches can be all expressed in the form of equation (A2) with an $n \approx 1.5$. This last value was adopted here, since it seems to be fairly reliable to predict the bed load in the Paraná River [*Amsler and Prendes*, 2000]. The ratio between the small dunes' velocities on the crest and trough represents a real problem since the dynamics of these dunes is practically unknown (see section 4). However, recent measurements performed in the Paraná River to clarify this topic on two large dunes located in the channel constriction upstream from the position of dunes 3 and 4, revealed a $U_{dc}/U_{dt} \approx 1.9$ (H. H. Prendes, personal communication). This value was used as a first tentative approach in equation (A5).

[61] Finally, with mean measured values of H_{dc} = 0.36 m and H_{dt} = 0.20 m, equation (A5) yield:

$$\frac{\tau_0\rfloor_c}{\tau_0\rfloor_t} = 1.8$$

As $\tau_0\rfloor_c$ = 1.15 kg m^{-2} then $\tau_0\rfloor_t$ = 0.64 kg m^{-2} (see Table 3).

Table A1. Laboratory Experiments Used to Compute the Bed Shear Stress in the Trough τ_{0t} of Dunes With a Flow Separation Region

	Dune Dimension					
Source	H (m)	λ (m)	Lee Side Angle	Froude Number	Surface Roughness	τ_c/τ_t
Delft Hydraulics [from *van Rijn*, 1993]	0.08	1.6	26°	0.29	sand grains[a]	~3.13
Fernandez et al. [2000]	0.025	0.574	51°	0.36	metal	3.0
Mattar [2002]	0.05	2.3	14°	0.13	metal with superimposed small dunes[b]	2.52

[a] Attached layer of sand gains with d_{50} = 1600 μm and d_{50} = 1900 μm.

[b] The small superimposed dunes were placed on the stoss side of the large dune and had the following dimensions: H_d = 0.005 m; λ_d = 0.12 m.

[62] The following more complex equation was also derived based on the same ideas as equation (A5), but using the bed load formula of *Engelund and Fredsøe* [1976], instead of equation (A2):

$$\tau_0\rfloor_t = (1650 d_{50})^{1-\frac{1}{kd}} 4.315^{\frac{1-kd}{3.647kd}} \tau_0\rfloor_c^{\frac{1}{kd}} \tag{A6}$$

where d_{50}, median diameter of the bed granulometric distribution and,

$$k_d = \left(H_d U_d\rfloor_c\right) / \left(H_d U_d\rfloor_t\right).$$

[63] The *Engelund and Fredsøe* [1976] formula predicts fairly well the bed load transport in the Paraná River [*Amsler and Prendes*, 2000]. Equation (A6) yields the same results as equation (A5) with d_{50} = 0.29 mm (obtained from bed material samples collected during the field measurements).

A1.2. Lee Side With Flow Separation (Dune 4)

[64] To approach a value of the shear stress in the trough of dunes when separation occurs, the above ratio of shear stresses was also estimated but from existing data. This information is extremely scarce in literature and yielded by laboratory studies performed with laboratory fixed dunes. A number of them are listed in Table A1.

[65] While the number of cases is quite a few, the geometric and flow conditions are fairly distinct. Nevertheless the ratios τ_{0c}/τ_{0t}, are not so different. Additionally in the experiments of *Mattar* [2002], geometrically similar dunes measured in the Paraná River ~20 km upstream of dune 4, were reproduced. Moreover, the prototype flow conditions resembled also those prevailing on dune 4 and the experiments met with the Froude similitude. Owing to these arguments the τ_{0c}/τ_{0t} ratio of the *Mattar* [2002] experiments was selected to estimate τ_{0t} in dune 4.

A2. Location of the Virtual Origin of the Measured Velocity Profiles on Dunes 3 and 4

[66] By examining a number of detailed velocity profiles measured in field at different flow conditions, *Amsler and Schreider* [1992] showed that the Paraná River has a hydrodynamically rough bed with the small superimposed dunes acting as the main roughness elements with heights in the order of, H_d, the height of the small dunes. These authors concluded that, any velocity profile measured in rivers like the Paraná, where superimposition of dunes prevails along the stoss side of larger dunes, should have a virtual origin (or hydraulic bottom) located at a certain fraction/multiple of H_d, being H_d a representative value of the small dunes height surrounding the profile position. It is well known that an incorrect location of the virtual origin may yield unreliable values of parameters derived from a given velocity profile (such as the bed shear stress [*Reynolds*, 1974]). In order to fix that fraction/multiple in a turbulent rough boundary layer with adverse pressure gradients, *Perry and Joubert* [1963] suggest a method which was adopted herein. It essentially consists in finding the logarithmic line (in a semilog plot) which best fits the observed point velocities, U, through successive regressions each with a different fraction of H_d correcting the original distances, y, from the bottom where velocities were measured. Implicitly the method assumes the validity of the classic logarithmic function to describe the velocity profile developed in a rough turbulent boundary layer [*Schlichting*, 1979]. Strictly speaking it would be valid in the lowest 15–20% of the profile.

[67] For the original velocity profiles measured on the crests and lower stoss sides of dunes 3 and 4, the existence of a break point indicating a deviation of the point data scatter from the semilog line as to suspect the influence of an upper wake region, was not noticeable. However, they were smoothed in order to depict a possible deviation from a complete logarithmic curve obscured by the original point scatter. The smoothing procedure implied the computation of moving averages of point velocities each including three point data. The resulting profiles confirmed the previous statement. Finally, the Perry and Joubert method was applied to the smoothed profile (Figures 5a–5d). The results are shown in Table A2. It is clearly seen in Table A2 the

Table A2. Results of the Perry and Joubert's Method Applied With the Four Velocity Profiles to Define the Virtual Origins[a]

	r^2	τ_0
	D3 Stoss Side	
U; y	0.9727	0.81
U; y − 1.25*Hd	0.9741	-
U; y − Hd	0.9742	0.7
U; y − 0.75*Hd	0.974	-
	D3 Crest	
U; y	0.9585	0.58
U; y + 5*Hd	0.979	-
U; y + 4*Hd	0.9794	1.15
U; y + 3*Hd	0.9784	-
	D4 Stoss Side	
U; y	0.96	0.4
U; y − 1.5*Hd	0.973	-
U; y − 1.25*Hd	0.975	0.25
U; y − Hd	0.9735	-
	D4 Crest	
U; y	0.9588	0.38
U; y + 2*Hd	0.9657	-
U; y + 1.6*Hd	0.966	0.64
U; y + 1.45*Hd	0.9657	-

[a] Four velocity profiles: crest and stoss side of dunes 3 and 4.

marked differences between the τ_0 values obtained applying the virtual origin concept and those computed ignoring it (U;y alternative).

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