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The influence of hydrology and sediment grain-size on the spatial distribution of macroinvertebrate communities in two submerged dunes from the Danube Delta (Romania)

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ABSTRACT

The influence of hydrology and sediment grain-size on the spatial distribution of macroinvertebrate communities in two submerged dunes from the Danube Delta (Romania)

The present study focused on the ecological preferences of benthic macroinvertebrates regarding water flow and sediment characteristics in two submerged dunes from Danube Delta (Romania). Three hydraulic microhabitats, the stoss, trough and crest areas were sampled, along with measurements of water hydraulics, hydrology, sediment grain-size, and organic content. The results showed that the slope angles between stoss-crest and crest-trough areas are crucial in modulating local flows, sediment structure, organic content, macroinvertebrate communities, and taxonomic richness and density. As such, the stoss microhabitats are considered zones with the highest turbulence, hence driving low taxonomic richness and density compared to crest and trough microhabitats. When local environmental conditions in trough microhabitats allow the accretion of fine and organically enriched sediments, the development of maximum density for certain macroinvertebrates groups is reached. However, the benthic assemblages did not show clear preferences for certain microhabitats, suggesting ubiquitous ecologic traits, crucial for the successful colonisation of dynamic habitats, such as the submerged dunes in large rivers. The results of this study offer a better understanding on the abiotic factors driving the spatial preferences, density, and diversity of benthic macroinvertebrates in these understudied hydrogeomorphological units from large rivers.

Key words: macroinvertebrates; submerged dunes; stoss, crest, and trough; hydraulic microhabitats

RESUMEN

La influencia de la hidrología y el tamaño de grano de los sedimentos en la distribución espacial de las comunidades de macroinvertebrados en dos dunas sumergidas del Delta del Danubio (Rumanía)

El presente estudio se centró en las preferencias ecológicas de los macroinvertebrados bentónicos con respecto al flujo de agua y las características de los sedimentos en dos dunas sumergidas del delta del Danubio (Rumania). Se tomaron muestras en tres microhábitats hidráulicos (stoss, trough, crest), junto con mediciones de la hidráulica del agua, la hidrología, el tamaño de grano de los sedimentos y el contenido orgánico. Los resultados mostraron que las pendientes entre microhábitats son cruciales para modular los flujos de agua a nivel local, la estructura del sedimento, el contenido orgánico, las comunidades de macroinvertebrados y su riqueza y densidad taxonómica. Los microhábitats stoss se consideran zonas con la mayor turbulencia, lo que genera una baja densidad y riqueza taxonómica en comparación con los otros microhábitats. Cuando las condiciones locales permiten la acumulación de sedimentos finos y enriquecidos orgánicamente, se alcanza la máxima densidad para ciertos grupos de macroinvertebrados pero sin mostrar preferencias claras, lo que sugiere ubicuidad en los rasgos ecológicos cruciales para la colonización exitosa de hábitats dinámicos, como las dunas sumergidas en grandes ríos. Los resultados de este estudio ofrecen una mejor comprensión de los factores abióticos que determinan las preferencias espaciales, la densidad y la diversidad de los macroinvertebrados bentónicos en estas unidades hidrogeomorfológicas poco estudiadas de los grandes ríos.

Palabras clave: *macroinvertebrados, dunas sumergidas, stoss, crest, trough, microhábitats hidráulicos*

INTRODUCTION

Large rivers represent complex ecosystems, driven by multiple environmental processes that create dynamic and heterogeneous habitats (Hannah et al., 2004, Wantzen et al., 2014). The interplay between hydrological and geomorphological processes leads to the formation of peculiar habitats within large rivers, such as the submerged dunes (Poole, 2002). These hydrogeomorphologic units result from the combination of flow dynamics, sediment transport, and river bed structure (Carling et al., 2000, Duţu et al., 2018). Despite their ubiquity in large rivers, little is known about the benthic macroinvertebrate fauna inhabiting these habitats (Blettler et al., 2012a, Wantzen et al., 2014). The inherent sampling difficulty of these habitats represents one of the main reasons of their still unknown macroinvertebrate communities' structure and functionality compared to the river banks or floodplains, which were traditionally the main focus of such studies (Humpesch & Elliott, 1990). The submerged dunes are regarded as hydraulic microhabitats (*sensu* Amsler et al., 2009), where hydrodynamics and sediment grain-size play a crucial role in benthic fauna composition, diversity, and topographic preference (Marchese et al., 2005). The dominant type of sediments in submerged dunes is mostly represented by different fractions of sand (e.g., sand, silt, clay) (see Parsons et al., 2005). The small sediment grain-size of sandy habitats in large rivers and the associated organic content is crucial for the spatial distribution and density of taxa (Leitner et al., 2015).

The assessment of habitat preferences of benthic fauna in riffles, pools, and within these microhabitats in streams was the focus of much research (Herbst et al., 2018, Mathers & Wood, 2016). However, the number of scientific studies investigating the spatial distribution of benthic macroinvertebrates within submerged dunes (Wones & Larson, 1991), as well as their preference for microhabitats, such as the stoss, trough, and crest areas, in large rivers is limited (Amsler et al., 2009; Blettler et al., 2012b). Therefore, the spatial preferences for such microhabitats can vary significantly within and among dunes, given the limited number of explored sandy associated bedforms from an ecological perspective (Watzner et al., 2014).

Understanding how biological communities are assembled is one of the main goals of community ecology (Vilmi et al., 2021). One important conceptual model explaining communities' structure is the habitat filtering hypothesis (Poff, 1997). This concept relates the functional traits of species to habitat selective filtering forces occurring at hierarchical landscape scales (e.g., ranging from microhabitats to river basins). The abiotic environment limits the successful establishment of only a group of species with a specific set of traits (Smith et al., 2013). Hence, environmental filtering may be especially important in harsh and constantly disturbed environments and may limit the local communities to taxa with similar adaptive traits to the prevailing environmental conditions (Crespo-Pérez et al., 2020). Another related fundamental conceptual model in community ecology is beta diversity and identifying the mechanisms that explain this key component of biodiversity (Baselga, 2010). Most approaches decompose beta diversity into turnover and nestedness components (Gutiérrez-Cánovas et al., 2013). Examples include the understanding of species turnover along gradients in productivity and elevation (Andrew et al., 2012, Melo et al., 2009) or recolonisation of areas affected by glaciation (Baselga et al., 2012).

The current study aimed to relate the density and taxonomic richness of the macroinvertebrate communities with the hydrological variations, hydraulic stress, sediment grain-size, and organic content across three microhabitats (i.e., stoss, crest, and trough areas), in two submerged dunes with different angle slopes, from the Sulina Channel in the Danube Delta (Romania). We hypothesised that due to different angle slopes between stoss-crest (hereafter stoss side) and and crest-trough (hereafter lee side) sides, respectively, the hydraulics, hydrology, sediment grain-size, and organic content will differ among these microhabitats, conditioning the density and the taxonomic richness of the macroinvertebrate communities. Moreover, we hypothesised that given differences in the measured environmental parameters, this would exert a strong filtering effect (Poff, 1997) on invertebrate fauna, leading to specific communities for each microhabitat characterised by strong nestedness patterns (Gutiérrez-Cánovas et al., 2013).

MATERIALS AND METHODS

Study area

The survey was undertaken in September 2019 on the Sulina distributary, the middle branch of the Danube within its Delta (Fig. 1A). The branch starts from a bifurcation of the Tulcea distributary and transports about 20 % of the water flow and suspended sediment discharge of the River Danube (Tiron Duţu et al., 2019). Two submerged dunes were selected such that they differed in their angle slope between stoss and lee sides (see figures. 1B and 1C), but were of similar dimensions (i.e., length, height, water depth, position-

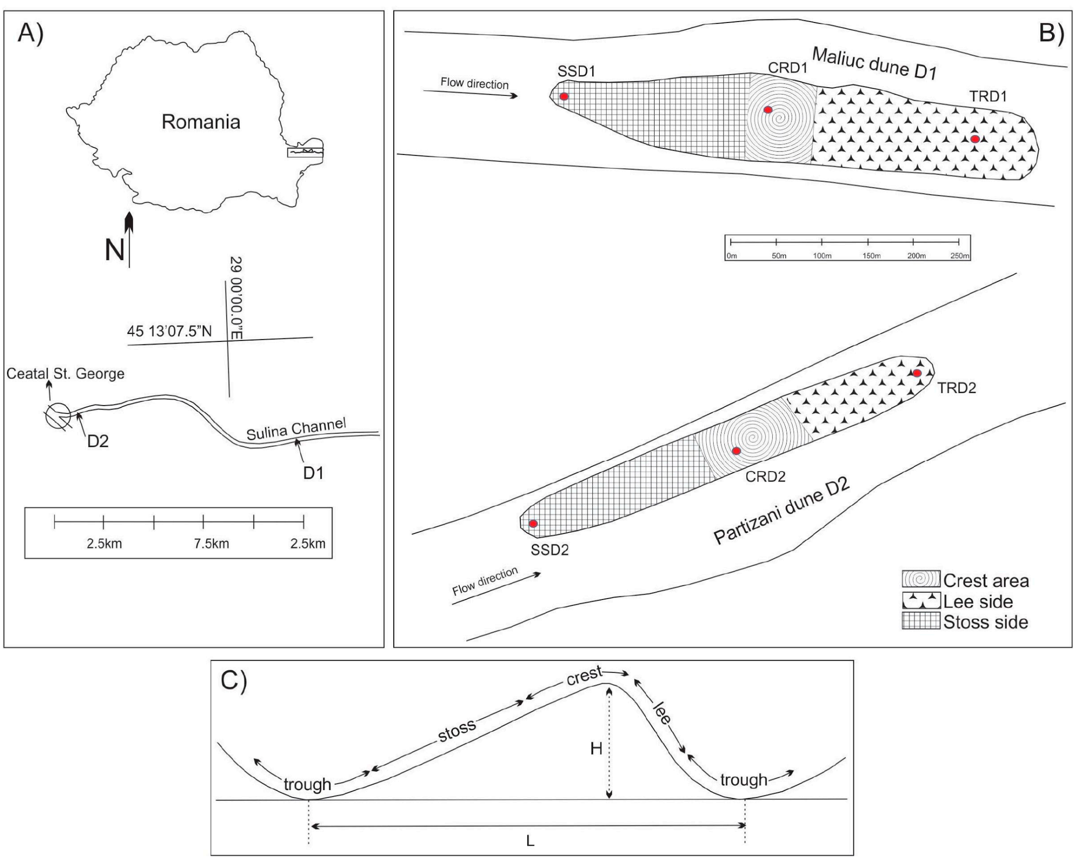

Figure 1. Location of the first (D1) and second (D2) sand dunes on the Sulina distributary (1A), as well as the delimitation of stoss and lee sides (1B). The specific location of microhabitats (i.e., stoss, crest and trough), as well as the height (H), length (L), and slope (β) of basic submerged dunes (after Bialik *et al.*, 2014) are given (1C). *Ubicación de la primera (D1) y segunda (D2) duna en la Sulina (1A), así como de la delimitación de microhábitats. Se muestra la ubicación específica de los microhábitats, así como de la altura (H), longitud (L) y pendiente (β) de las dunas sumergidas.*

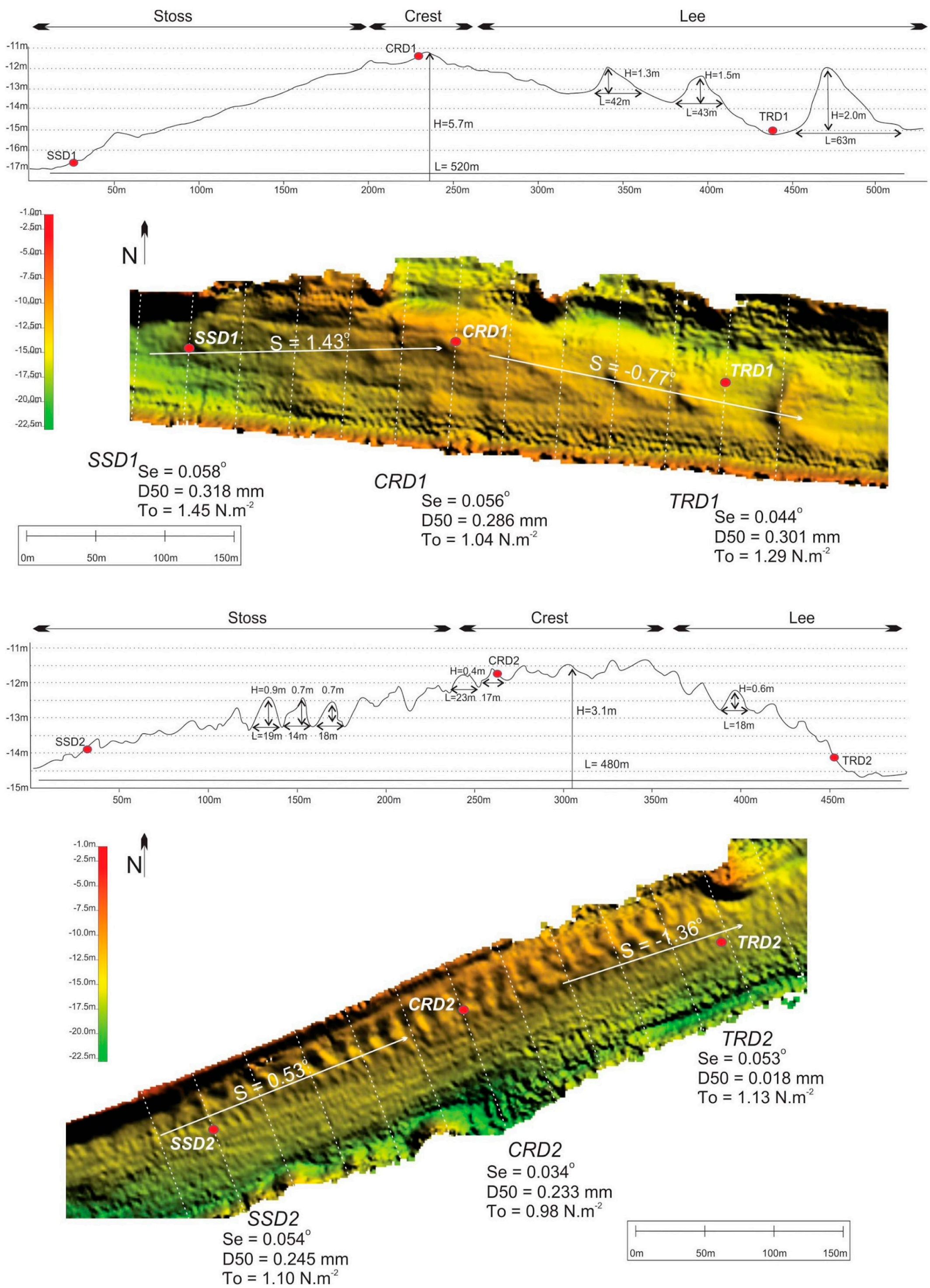

Figure 2. Morphodynamic and sedimentologic characteristics of the investigated dunes: Maliuc dune (D1, 2A) and Partizani dune (D2, 2B), as well as the positioning of sampling points in stoss (SSD), crest (CRD) and trough (TRD) microhabitats. *Características morfodinámicas y sedimentológicas de las dunas estudiadas: duna Maliuc (D1, 2A) y duna Partizani (D2, 2B), así como el lugar de los puntos de muestro en los microhábitats.*

ing along the water flow, and distance to river banks, see Tables 1 and 2), as well as the distance among sampled microhabitats (Fig. 2A and 2B). Both dunes were characterised by small secondary bedforms, such as small dunes and megaripples (Fig. 2A and 2B).

The research vessel R.V. ISTROS (NIRD GeoEcoMar) was used for measurements and sampling the selected sites. The sampling strategy followed the protocol of Blettler et al. (2012b). The positioning of the vessel was made by a GNSS, dual antenna, to provide heading to the MBES and working in RTK configuration (3-5 cm vertical and 2-3 cm horizontal accuracy). Once mapped, the morphology of the selected dunes was compared to their previous status, given the dynamic nature of these bedforms (Duţu et al., 2018). Afterwards, the GPS position of each microhabitat was fixed, and a boat was positioned above the desired sampling point (i.e., stoss, crests, and trough areas, see Fig. 1).

Bedforms mapping

Multibeam sonar bathymetry data were collected in the field (ELAC Nautik SeaBeam 1050D multibeam bathymetric system). The 180-kHz sounder contained 126 beams that were arrayed over an arc of 153°. The swath of riverbed covered on each survey line was typically eight to nine times the water depth. Navigation was by the Differential Global Positioning System, providing positional accuracy < 1 m. Sound velocity profiles through the water column were measured on each site, three times on each dune (i.e., stoss, crest, and trough areas) to reduce refraction errors. The acquired depth data were filtered, and erroneous values removed using the software packages HDP Post/FLEDERMAUS.

Hydrodynamics

Hydrodynamic data were measured using a powered boat-mounted acoustic Doppler current profiler (ADCP, RiverRay 600 kHz, manufactured by Teledyne). During the field campaign, 13 transverse ADCP profiles (40 m equidistance) were completed on each dune, to assure both an overall understanding of dunes' hydrodynamic characteristics and appropriateness of sampling conditions for each microhabitat at a local scale (Fig. 2A and 2B). The measured hydrodynamic parameters for each microhabitat were maximum water depth, specific stream power (ω), mean bed shear stress (τ_0), critical shear stress (T_{cr}), critical (u^*) and water velocity, water slope energy (S_e), and Reynolds number (R_e^*), according to Duţu et al. (2018) (see Table 1 for detailed definitions of each parameter). Shields' non-dimensional entrainment function (Shields, 1936) was calculated for an overall estimation of water dynamic for each dune. Heights (H) over length (L) ratios of both dunes were calculated to assess the equilibrium versus non-equilibrium stage of dunes' evolution (*sensu* Flemming, 2000).

Particle size analysis

Three sediment replicates were collected from each microhabitat with a van Veen grab. Only samples with a penetration of at least 10 cm and no evidence of disturbance (i.e., by washing) were accepted for processing, according to Bergen et al. (2001). Sediment grain-size analyses were undertaken in the laboratory by diffractometry using a granulometric laser analyser (Mastersizer, 2000E Ver.5.20 type, Malvern Instruments Ltd.-Malvern UK), and the percentage of size particles with a diameter between 0.10 µm and 1000 µm was assessed. Sediment samples were dispersed in 0.5 % sodium hexametaphosphate solution and particles larger than 1 mm separated by sieving (Shepard, 1954). The sediment texture (i.e., percentages of sand, silt, and clays) was expressed on the Udden-Wentworth logarithmic scale (Blair & McPherson, 1999) and the description of category types were according to Shepard (1954). The average diameter of particles (hereafter D_{50}), used as a surrogate for assessing macroinvertebrate fauna preference for sediment grain-size (Pacioglu & Moldovan, 2016), was calculated according to Wu et al. (2004). The percentage of total organic carbon (TOC) was determined using a titrimetric method by oxidising the carbon with $K_2Cr_2O_7$ and sulphuric acid. The excess was retitrated with Mohr salt, using diphenylamine as an indicator.

Table 1. Symbols and definitions of the sampled geomorphological units and of measured hydraulic, hydrologic and sediment variables. *Símbolos y definiciones de las unidades geomorfológicas muestreadas y de las variables hidráulicas, hidrológicas y sedimentarias.*

Name	Symbol	Units	Formula	Description
Depth	H	m	Computation of the ADCP	Water depth
Current velocity	V	m/s	Computation of the ADCP	Water speed
Bedform height	H	m	Direct measurement	The distance between the crest of the bedform and the river bed
Bedform length	L	m	Direct measurement	The distance between two successive troughs of a bedform
Stoss side of the bedform	-	-	-	The upstream-facing surface of a bedform, extending from a trough to the next crest downstream
Lee side of the bedform	-	-	-	The downstream-facing surface of a bedform, extending from a crest to the next trough downstream
Bedform crest	-	-	-	The region around the highest point on the bedform profile
Bedform trough	-	-	-	The region around the lowest point of the bedform profile
Water discharge	Q	m^3/s	Computation of the ADCP	The water volume rate of flow past a given cross section
Stream power	Ω	W/m	$\Omega = \rho \times g \times Q \times S$	The rate of energy dissipation against the bed and banks of the channel per unit length
Specific stream power	ω	W/m^2	$\omega = \Omega / B$	Total stream power per unit width
The bed mean shear stress	τ_0	N/m^2	$\tau_0 = \rho\ g\ R\ S$	The force per unit area the flow exerts on the bed
The critical shear stress	T*cr*	N/m^2	$Tcr = Ps / [(\rho s-\rho w)\cdot D]$	The magnitude of shear stress required to move a given particle
Shields' non-dimensional entrainment function	*θc*	-	$\theta c = \tau_0 / [g\cdot(\rho s-\rho w)\cdot D]^{-1}$	Define the incipient motion of a particle
The critical velocity	u*	m/s	$u^* = \sqrt{\tau_0/\rho}$	Defined as the critical velocity for initiation of motion and suspension of a particle
Reynolds number	Re*	-	$Re^* = (u^*.D)/\upsilon$	A dimensionless number used to categorize the fluids systems, to determine whether a fluid is in laminar or turbulent flow
Water slope energy	Se	^{0}	$Se = V^2n^2/R^{4/3}$	The slope of the water surface

Benthic fauna sampling

Besides sediment analyses, another four quantitative samples from each microhabitat were collected with van Veen grab (mouth surface 420 cm^2). Previous investigations concluded that four replicates per each microhabitat represented realistic estimations of macroinvertebrates' taxonomic richness and density within submerged dunes from large rivers (Amsler et al., 2009, Blettler et al., 2012b). The samples were washed on board through two sieves of 250 and 125 µm mesh size, respectively, to remove excessive sediment particles and concentrate the samples' volume. A mixed solution of Rose Bengal and buffered formaldehyde 4 % was used to preserve the samples until further processing. In the laboratory, the samples were sorted, and invertebrates were identified at the lowest possible taxonomical level, using both dissecting (Carl Zeiss SteREO Discovery V8) and high-power (Axiostar Carl Zeiss Axiostar and Series Transmitted-Light) microscopes. All organisms were counted following their taxonomic identification and their density (ind/m^2) estimated.

Statistical analysis

Principal components analysis (PCA) of the hydrological parameters, sediment grain-size, and organic content was used to identify major environmental gradients along microhabitats and dunes. Two-way PERMANOVA tests (1000 permutations) based on Bray-Curtis distances were employed to test if the benthic communities significantly differed between dunes and among microhabitats (i.e., stoss, crest, and trough areas of each dune). The macroinvertebrate communities were analysed using Non-metric Multidimensional Scaling (NMDS) ordination based on Bray-Curtis distances to visualise differences in taxonomic composition along both dunes. The SIMPER analysis was used afterwards to identify taxa responsible for any registered differences in fauna composition between dunes and among microhabitats within each dune, respectively.

Table 2. Mean values of median particle distribution (D50), maximum water depth, specific stream power (ω), mean bed shear stress (τ0), critical shear stress (Tcr), critical (u*) and water velocity, water slope energy (Se), Reynolds number (Re*), percentage of Total Organic Content (TOC), as well as the slope for stoss and lee sides, respectively, and maximum water depth of the first (D1) and second (D2) analysed submerged dunes. Measure units are provided in brackets. In bold, the average values significantly different according to the Kruskall-Wallis non-parametric test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). *Valores medios de la distribución media de partículas (D50), profundidad máxima del agua, potencia de corriente específica (ω), tensión media de cizallamiento (τ0), valor crítico de cizallamiento (Tcr), crítico (u*) y velocidad del agua, energía de la pendiente del agua (Se), número de Reynolds (Re*), porcentaje de Contenido Orgánico Total (TOC), así como las pendientes en las dunas, y la máxima profundidad del agua de la primera (D1) y segunda (D2) duna sumergida analizadas. Las unidades de medida están indicadas entre paréntesis. En negrita, los valores promedio significativamente diferentes de acuerdo con la prueba no paramétrica de Kruskall-Wallis (** p *< 0.05, *** p *< 0.01, **** p *< 0.001).*

Site	Max. depth (m)	D50 (mm)	ω (W/m^{-2})	τ_0 (N/m^2)	T_{cr}	Se (º)	u*	Re*	Velocity (m/s)	TOC (%)	Slope (º)
						D1					
SSD1	16.6	0.32	1.5	1.4	5.7	0.06	0.04	8.1	0.4	0.01	stoss = 1.43
CRD1	11.9	0.29	1.1	1	3.7	0.06	0.03	6.1	0.4	0.25	lee = -0.77
TRD1	14.7	0.3	1.2	1.3	4.8	0.04	0.03	7.2	0.5	0.11	
						D2					
SSD2	14.1	0.31	1.2	1.1	4.8	0.05	0.03	6.9	0.4	0.01	stoss = 0.53
CRD2	12.5	0.26	0.9	0.9	3.6	0.03	0.03	5.6	0.3	0.05	lee = -1.36
TRD2	14.4	**0.02***	1.1	1.1	0.4	0.05	0.03	0.5	0.4	**0.9***	

Invertebrates' density (ind/m^2), taxonomic richness, D50, and the organic content (TOC) were compared among microhabitats with nonparametric Kruskal–Wallis tests, followed by *post hoc* Mann–Whitney pairwise comparisons with Bonferroni corrections.

RESULTS

The H/L ratios were below 0.06 for both dunes (D1 = 0.01 and D2 = 0.006), suggesting that the studied bedforms were in a non-equilibrium stage (Ashley, 1990, Flemming, 2000). The steep stoss side of the first dune (D1) accelerated the sediment transport in the crestal area. Thus, the development of a sedimentary layer permits the accretion and creation of small secondary bedforms on the lee side (Fig. 2A). The second dune (D2) grew in amplitude and shortened the lee side by accretion on both the stoss and crestal areas, where small secondary bedforms developed H/L ratios approaching maximum steepness (H/L close to 0.05). On the second dune's crest area (D2), the small bedforms were attenuated and easily reshaped (H/L between 0.016 and 0.035, see Fig. 2B). The secondary bedforms influenced the bottom roughness, were strongly expressed on the dunes' crest, and decreased the tractive forces exerted on the bed (e.g., τ_0 is lower on the crest than on the lee and stoss sides, Tables 1 and 2). The estimation of entrainment forces using Shields' non-dimensional function (Shields, 1936) indicates that, over the crest of both dunes, the dynamic is slightly reduced (τ_0 = 1.04 N/m^2 on crest of D1 and 0.98 N/m^2 on crest of D2, Tables 1 and 2).

Most hydrologic, sediment, and hydraulic parameters were similar between the investigated dunes, excepting the Re*, $D_{50,}$ Tcr, and TOC (Table 2). Therefore, these parameters were entered in the PCA ordination (Fig. 3). The first axis of the PCA ordination explained 88.7 % of the total variation of the data set, whereas the second axis explained 11.1 % (Fig. 3). The stoss microhabitats of both dunes presented higher Re* and Tcr than the crest area; both parameters were below unit in the trough area of the second dune, whereas in the first dune they had similar values to the stoss (Fig. 3, Table 2). The D50 was negatively associated with the TOC; the former presented similar values in all microhabitats, except the trough of the second dune, which had a

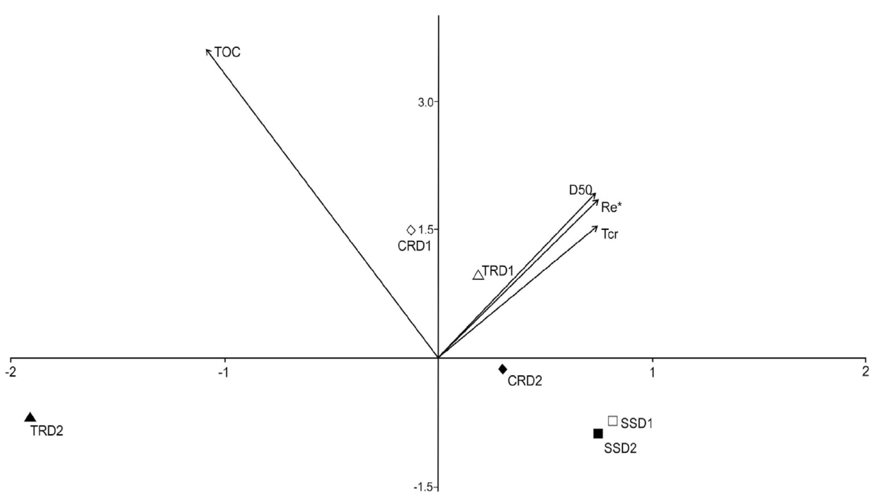

Figure 3. Principal Component Analysis ordination biplot explaining the variation of mean bed shear stress (τ0), median particle distribution (D50), Reynolds number (Re*) and the percentage of Total Organic Content (TOC) in stoss (SSD), crest (CRD) and trough (TRD) microhabitats in the first (D1) and second (D2) dunes. *Biplot del Análisis de Componentes Principales que explica la variación de los diferentes parámetros analizados en los microhábitats en la primera (D1) y segunda duna (D2).*

significantly higher percentage of fine sediments and associated organic content (Fig. 3, Table 2). A two-way PERMANOVA indicated significant differences in the structure of the macroinvertebrate communities between dunes ($F_{1, 12} = 22.5$, $p < 0.01$) and among microhabitats ($F_{5, 12} = 27.9$, $p < 0.001$), with no significant interactions between factors ($F_{5, 12} = 5.7$, $p > 0.05$). The nMDS ordination (stress value 0.1) suggested three major clusters: the invertebrate communities from the stoss area of the first and second dune and a third, comprising the trough and crest microhabitats of both dunes (Fig. 4). The SIMPER analysis showed that between dunes (all microhabitats clustered), the oligochaetes and the chironomids showed higher densities in the second dune (74 % cumulated dissimilarity, Tables 3 and 4). The comparisons in-between microhabitats within dunes revealed that the distinct clusters noticed in the nMDS ordination (Fig. 4) were driven by chironomids, oligochaetes, the amphipod *Chelicorophium curvispinum*, and the polychaete *Hypania invalida*; the latter taxa was not detected in the stoss area of both dunes and its density increased from crest to trough microhabitats (Tables 3 and 4). The comparison

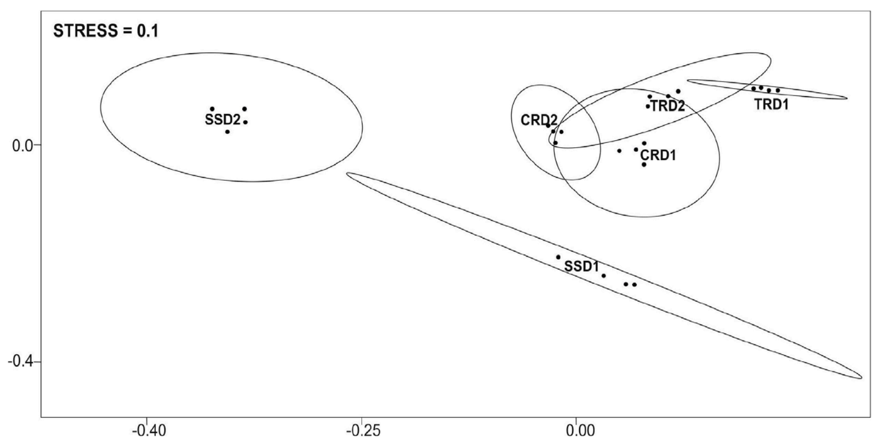

Figure 4. nMDS ordination of the macroinvertebrate communities in stoss (SSD), crest (CRD) and trough (TRD) microhabitats in the first (D1) and second (D2) dunes, along with 95 % confidence ellipses. *Análisis de ordenación nMDS de la comunidad de macroinvertebrados en los microhábitats en la primera (D1) y segunda duna (D2), junto con las elipses de confianza del 95 %.*

Table 3. Mean values of invertebrates' density (ind/ m2) and taxonomic richness in stoss (SSD), crest (CRD) and trough (TRD) microhabitats from the first (D1) and second (D2) dunes. *Valor medio de la densidad de invertebrados (ind/m2) y riqueza taxonómica, en los microhábitats estudiados.*

Dune	Microhabitat	*Unio pictorum*	*Dikerogammarus villosus*	*Acroloxus lacustris*	*Lithoglyphus naticoides*	*Corbicula fluminea*	*Chelicorophium curvispinum*	Bezzia sp.	Chironomidae	Oligochaeta haeta	*Hypania invalida*
D1	SSD1	0	0	0	0	0	16.8	0	9.9	31.5	0
D1	CRD1	0	27.8	0	0	37.7	0	6.9	160.6	203.6	22.6
D1	TRD1	0	23.8	0	0	0	444.9	38.8	139.7	434.4	45.2
D2	SSD2	3	0	9.4	13.4	0	0	0	0	0	0
D2	CRD2	7.8	0	16.4	11.2	161.2	176.1	6.8	45.7	235.4	13.6
D2	TRD2	0	0	0	0	0	785.1	0	359.8	888	233.7

in-between microhabitats across dunes revealed that the differences in communities' structure were driven by the same taxa as those within dunes, with higher densities in all microhabitats of the second dune (Tables 3 and 4). The snails *Acroloxus lacustris* and *Lithoglyphus naticoides* and the mussel *Unio pictorum* were present in the stoss and crest microhabitats of the second dune but absent in the trough area (Tables 3 and 4).

Taxonomic richness in the stoss area of both dunes was significantly smaller compared to both crest and trough microhabitats ($p < 0.008$ pairwise Mann–Whitney tests, Fig. 5A); in the second dune, the number of taxa was significantly higher in the crest area compared to the other two microhabitats ($p < 0.008$ pairwise Mann–Whitney tests, Fig. 5A). In both dunes, the macroinvertebrates' density was the lowest in the stoss side, intermediary in the crest area, and the highest in the trough ($p < 0.008$ pairwise Mann–Whitney tests, Fig. 5B, Table 3).

DISCUSSION

The dunes grow and migrate downstream as sediment is eroded from the lower stoss side and moves up towards crest areas and later down the lee side towards the trough (Flemming, 2000). The macroinvertebrate communities from the stoss area of both dunes were significantly less diverse (Fig. 5A) and less abundant than the other two microhabitats (Fig. 5B). Moreover, the Reynolds number and the critical shear stress were the highest in this area compared to crest microhabitats of both dunes (Fig. 3). This suggests that in the lower stoss side, the turbulence intensity reached its maximum, due to a series of mechanisms like the advection currents characteristic for turbulent flows (Kostaschuk, 2000, Wippermann, 1986). Previous findings showed that the lower stoss side of submerged dunes is exposed to maximum turbulence flows, which suspends sand particles (Kadota & Nezu, 1999), and decreases along the slope, due to convergent flows that

Table 4. Results (%) of the SIMPER analysis for taxa dissimilarity between the first (D1) and second (D2) dunes, as well as for the pairwise comparison among stoss (SSD), crest (CRD) and trough (TRD) microhabitats, respectively. *Resultados (%) del análisis SIMPER en taxones entre la primera (D2) y segunda (D2) duna, así como para la comparación entre pares de microhábitats.*

Microhabitats	Oligochaeta	Chironomidae	*Chelicorophium curvispinum*	*Corbicula fluminea*	*Hypania invalida*	*Unio pictorum*	*Lithoglyphus naticoides*
D1-D2	39.7	34.5	-	-	-	-	-
SSD1-CRD1	39.7	34.5	-	-	-	-	-
CRD1-TRD1	35.5	10.2	40.6	-	11	-	-
SSD1-TRD1	38.5	15.6	34.3	-	10.4	-	-
SSD2-CRD2	35.8	-	26.9	9.6	20.7	-	-
SSD2-TRD2	38.4	12.4	34.2	-	-	-	-
CRD2-TRD2	24.1	11.4	32.7	11.4	16.9	-	-
SSD1-SSD2	37.8	11.8	19	-	-	11.2	16.2
CRD1-TRD2	-	21.7	33.7	20.3	-	-	-
TRD1-TRD2	36	17.3	26.7	-	15	-	-

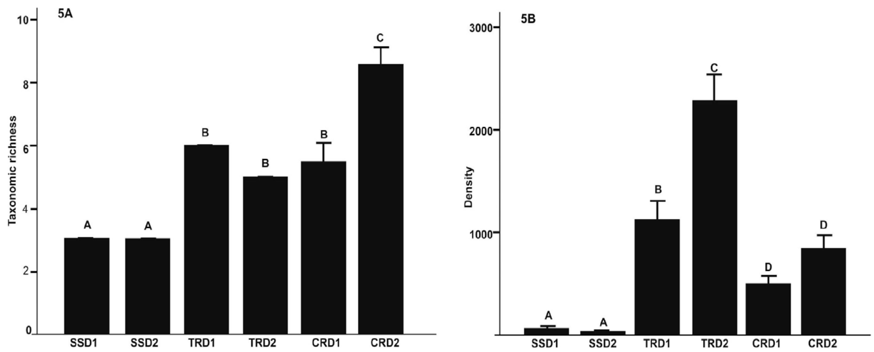

Figure 5. Mean (± 1SE) taxonomic richness (5A) and density (5B) of the macroinvertebrate communities in stoss (SSD), crest (CRD) and trough (TRD) microhabitats in the first (D1) and second (D2) dunes. Different letters indicate significant differences ($p < 0.008$) as a result of Mann-Whitney *post-hoc* pairwise comparisons. *Riqueza taxonómica media (± 1SE, 5A) y densidad (5B) de la comunidad de macroinvertebrados en los microhábitats de las dunas. Las letras diferentes indican diferencias significativas (*p *< 0.008) como resultado de la comparación por pares de Mann-Whitney* post-hoc.

control the internal accelerating boundary layer at the sediment interface (Nelson et al., 1993). The influence of the shear stress was found to prevail over other environmental parameters, such as the water velocity or sediment grain-size, in shaping the taxonomic composition of lotic macroinvertebrates (Jowett, 2000, Merigoux & Doledec, 2004, Quinn & Hickey, 1994). The hydraulic and biodiversity patterns from the current study concur with those previously noticed by Amsler et al. (2009) in two submerged dunes from Paraná River (Argentina), suggesting that higher species richness (Fig. 5B) and density (Fig. 5A) at the crest compared to stoss microhabitats is due to decreased turbulence up the stoss side of dunes. The high water speed lifts sediments in the lower stoss side of submerged dunes, making it a less hospitable place for life than the crest and trough microhabitats (Fig. 5A and 5B).

The highest densities of macroinvertebrates were observed in the trough microhabitat of both dunes (Fig. 5B). The trough area of D2 was characterised by the lowest values of the critical shear stress and Reynolds number, as well as by the finest sediment composition and the highest associated organic content from all sampled microhabitats (Fig. 3). The oligochaetes, the polychaete *H. invalida*, the chironomids, and the amphipod *C. curvispinum* showed the highest densities in this microhabitat (Table 3). All these taxa are known to occur in fine-sized, organically rich substrates in rivers and streams (Norf et al., 2010, Van den Brick et al., 1993;), hence their presence in large numbers in this microhabitat. The lower values recorded for Reynolds number and critical shear stress concur with the accumulation of fine, organically rich sediments in trough microhabitat of D2 (Fig. 3).

However, the macroinvertebrates' density in the trough microhabitat of D1 was significantly smaller than its counterpart from D2 (Fig. 5B). One possible explanation could be that the three times larger stoss side angle slope of D1 (1.43º) compared to D2 (0.53º) and the lower lee side counterslope angle (-0.77º) of D1 compared to D2 (-1.36º, see Fig. 2A and 2B) increased the chances for sediment suspension in the overlaying water flow for the former dune. We expected the trough area of D1 to have been equally exposed to high turbulences, similar to the upstream microhabitats, as observed previously by hydraulic investigations on submerged dunes (Kostaschuk, 2000). Moreover, the presence of large megaripples situated upstream the trough areas in submerged dunes (Hickin, 1995, van Rijn, 1984) usually increases the critical shear stress and Reynolds numbers, that in turn amplify the rate of suspended materials (Duţu et al., 2019, Drago & Amsler, 1998). This has important implications for the migration of invertebrates among microhabitats in submerged dunes (e.g., through induced drift, see Blettler et al., 2012b), providing a supplementary explanation for the significantly lower density of macroinvertebrates in the trough microhabitat of D1 compared to its counterpart from D2 (Fig. 5B).

In D1, the habitat filtering likely restricted the community from the stoss microhabitat to chironomids, oligochaetes, and the amphipod *C. curvispinum* (Fig. 4), explained by the potential to withstand higher hydraulic stress compared to other taxa. However, given that the chironomids and oligochaetes were not identified to a lower taxonomic level, they may comprise different species compared to those inhabiting downstream microhabitats with different hydraulic preferences. Chironomid species showed special adaptations to withstand strong hydraulic stress in submerged dunes in the River Paraná (Argentina) by ballasting their body through the ingestion of fine sediment grains within a dorsal bulge compared to species inhabiting other less stressful habitats (e.g., floodplains and meanders), which did not provide such special adaptations (Blettler et al., 2014). Oligochaetes inhabiting submerged dunes from River Paraná use ingested sand or attached particles to increase their specific weight (Marchese, 1984).

The findings of this survey match the general situation in which a reduced number of species inhabit chronically stressed habitats (Millán et al., 2011, Rapport et al., 1985). The Sulina branch of the Danube Delta has been significantly changed by human activities over the past 150 years, mainly through engineering works in the second half of the 19th century, when the channel was transformed for navigation (Stănica et al., 2007). The impact from navigation and sediment dredging on the benthic fauna from the Sulina branch was not studied. However, dredging activities in the Austrian sector of the River Danube showed up to 82 % decline in benthic invertebrates' biomass (Moog et al., 2018). Moreover, the turnover rates for the benthic assemblages were of approximately one year, associated with diminished taxonomic richness of the benthic community and dominated by ubiquitous, fast colonising, r-type strategist species (Fredette & French, 2004). The majority of macroinvertebrates inhabiting both dunes comprised ubiquitous, fast colonising, r-type strategist species (Norf et al., 2010, Van Riel & Van der Velde, 2006). By contrast, the snails *A. lacustris* and *L. naticoides*, as the mussel *U. pictorum* are slow dispersals and K-strategists (Kappes & Haase, 2012, Mouthon, 2007) and were present in low numbers in D2 (Table 3). Therefore, potential explanations for such distribution patterns are not straightforward in the light of the habitat filtering hypothesis (Poff, 1997). Previous investigations of the benthic macroinvertebrate communities from the Danube Delta revealed higher species richness in adjacent habitats, such as floodplains (Ignat et al., 1997, Rîșnoveanu, 1993) or meanders (Pavel et al., 2017), where hydraulic conditions are less harsh compared with the main stem of the river from the Sulina branch, where submerged dunes prevail (Duțu et al., 2018). The results of this survey support a scenario of fast turnover rates rather than nestedness patterns of beta diversity within (i.e., among microhabitats) the investigated submerged dunes, similar to those encountered in the Austrian sector of the River Danube following continuous dredging activities (Moog et al., 2018). Following other previous studies that tested the habitat filtering hypothesis in rivers (Leps et al., 2016, Li et al., 2015) and submerged dunes (Blettler et al., 2014), the current study indicates that the invertebrate communities inhabiting the investigated dunes probably depend on the species pool from adjacent habitats, such as the mid-channel or, in the case of the molluscs from the second dune, the macrophyte stands from the river banks.

The submerged dunes with low lee side angles (< 10°) represent common geomorphological features in large rivers (Cisneros et al., 2020). The contrasting morphology and slope angles of both investigated dunes suggest that they primarily influenced the hydraulic stress along these bedforms. Further, the interplay of local hydraulic factors, sediment grain-size, and intrinsic organic content represented important abiotic drivers of the taxonomic richness, composition, and density of the macroinvertebrate assemblages in stoss, crest, and trough microhabitats.

CONCLUSIONS

In the present study, we assessed the influence of environmental factors (i.e., hydraulics, hydrology, sediment grain-size, and organic content) in driving the topographic preference, taxonomic richness, and density of the benthic macroinvertebrate fauna in two submerged dunes. Our findings suggest that the benthic communities are dominated by ubiquitous taxa and differences in their density and diversity across the three main identified hydraulic microhabitats (i.e., stoss, crest, and trough) are driven by the synergic combination of the measured abiotic parameters. However, the preference of benthic macroinvertebrates for certain microhabitats was not clear, suggesting that the communities inhabiting the investigated dunes have their origin in proximal habitats, such as river banks or mid-channel. Moreover, the Sulina branch of the River Danube is exposed to a continuous stress induced by dredging works that induce frequent turnover rates for the benthic assemblages inhabiting submerged dunes. With this knowledge in mind, a larger number of submerged dunes should be more thoroughly studied in the future and cover a larger array of stoss and lee angle slopes to obtain a comprehensive understanding of the interplay among environmental factors and biodiversity of these understudied bedforms.

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