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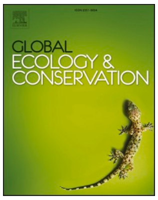

Habitat preferences and trophic interactions of the benthic invertebrate communities inhabiting depositional and erosional banks of a meander from Danube Delta (Romania)

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ABSTRACT

River restoration and biodiversity conservation programs require an in-depth knowledge of the influence that sediment composition and hydraulic stress have on invertebrate fauna composition and spatial distribution, as well as on nutrients cycling and food webs' structure and functionality. Compared to low-order streams, the traditional focus of river ecology, the knowledge of these ecosystem properties of the meanders developed along large, lowland watercourses, is currently insufficient. The present study assessed the ecological preferences and the trophic interactions of the benthic invertebrate communities inhabiting erosional and depositional banks developed within a meander of the River Danube flowing through its delta (Danube Delta, Romania). The invertebrates from two mesohabitats, the concave (i.e. erosional) and convex (i.e. depositional) banks developed in the apex region of the meander were sampled quantitatively and qualitatively, along with sediment samples for assessing the grain-size characteristics and hydrodynamic parameters (i.e., critical shear stress, the Reynolds number, the critical velocity and Shields parameter). For assessing their mesohabitat preferences, quantitative samples were taken from both banks, whereas for inferring the trophic interactions, stable isotopes of δ^{15}N and δ^{13}C were measured from qualitative samples, comprising both invertebrates and basal resources. The results showed that increased siltation with fine sediments in the depositional bank led to a community dominated by chironomids, oligochaetes and bivalves, whereas the opposite bank comprised crayfish, caddis fly larvae and amphipods with a preference for coarser sediments. The δ^{13}C of most consumers revealed that the dominant forms of carbon entries in the analysed food webs were photosynthetic based, whereas certain snails, chironomids and basal resources from the depositional bank were ^{13}C depleted (δ^{13}C: −35 to −39 ‰). Such low ratios for δ^{13}C (mean < −35 ‰) reflected the potential of carbon entry through the base of depositional food web as a result of methane oxidation at sediment-water interface (i.e. chemosynthesis), induced by the fine sediments deposition that could have favoured the methane production. Grazing methane-oxidising bacteria in the depositional meander bank could have provided the primary consumers with up to 50 % and the omnivores and predatory invertebrates with up to 30 % of their carbon, which could represent an important subsidy from an additional, chemosynthetic source. The impact of a supplementary carbon input was further reflected in increasing depositional food

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web basal niche diversity, which led to distinct trophic niches and lower interspecific competition of consumers compared to the erosional bank of the meander.

1. Introduction

The meanders comprise regular sinuous curves of large rivers, especially in the lowlands. Their hydrological, hydraulic and geomorphological features have a long history of research (Batalla et al., 2004; Harmar et al., 2005; Blettler et al., 2012). Moreover, their specific geomorphological features, such as bank structure, riffle-pools successions and apex zone (Fig. 1) were well delimited by physical geography (Tiron Duţu et al., 2014, 2019). Still, within an ecohydrological context, the linking between such morphological structures and invertebrate fauna composition and spatial distribution were mainly conducted in smaller order streams, which were traditionally the main focus of river ecology (Mérigoux and Dolédec, 2004; Dolédec et al., 2007). The reasons are multiple and could be a combination of more difficult sampling conditions compared to lower-order streams and the lack of attention that was paid to these interdisciplinary approaches (Blettler et al., 2012; Garcia et al., 2012). As such, despite a number of pioneering studies that focused on these aspects (Blettler et al., 2008, 2012; Amsler et al., 2009), the ecological preferences of aquatic fauna for various mesohabitats that develop in the meanders of large rivers still lacks behind the knowledge gathered from lower-order streams.

Proper implementation of practical aspects of environmental management and biodiversity conservation programs require an in-depth knowledge of the influence that sediments composition and hydraulic stress have on invertebrate fauna composition and spatial

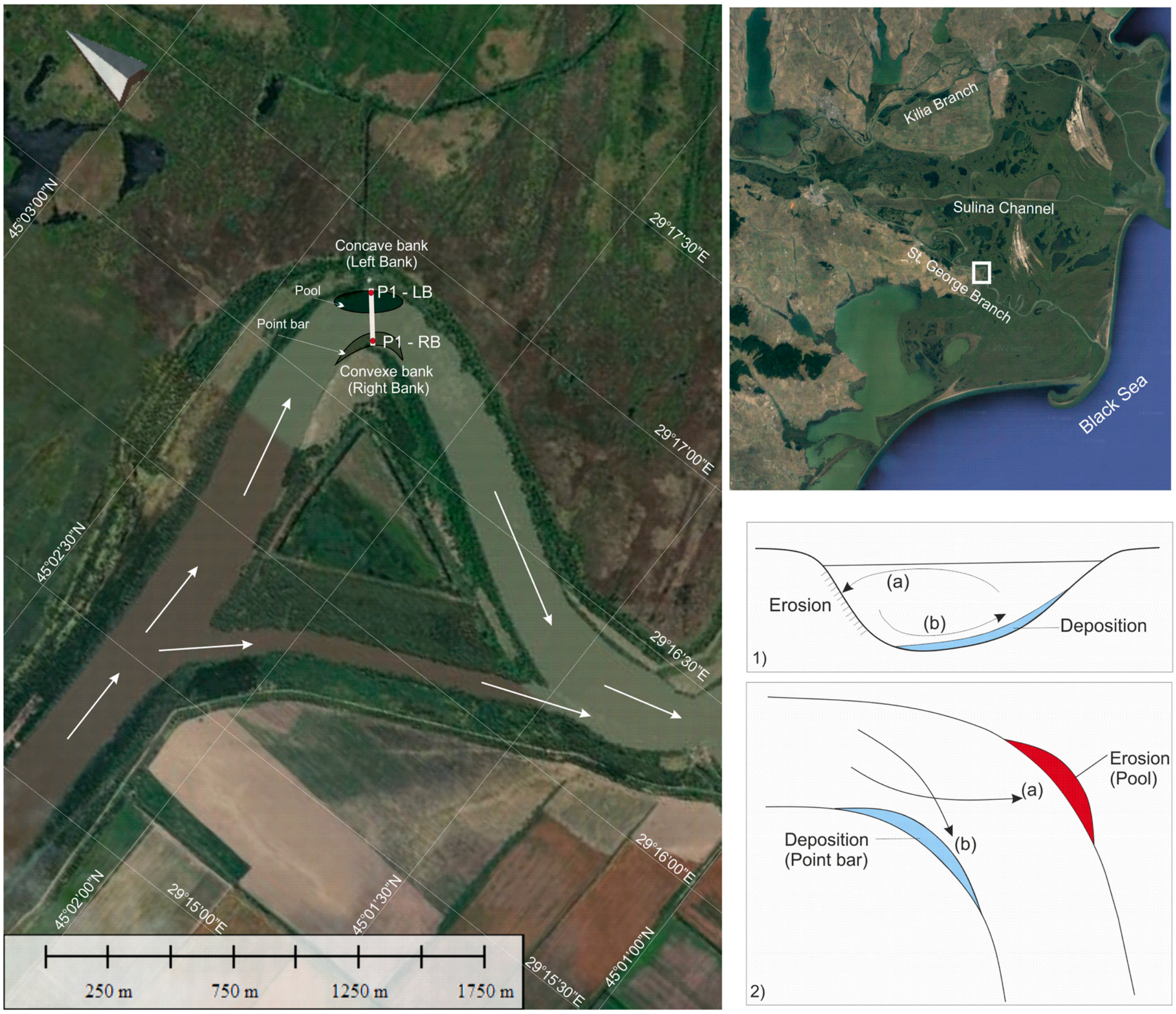

Fig. 1. Study area, the Dunavăţ de Sus meander, with the location of the sampling points in the apex zone. Schematic view of meander and cross-section pattern (1) and (2): (a) surface fast current, (b) slow bottom current (after Reineck and Singh, 1973).

distribution, as well as on nutrients cycling and food webs' structure and functionality. Examples include river restoration programs or specially protected areas such as meanders (see Thorp, 1992; Blettler et al., 2012) that need sound ecohydrological models and a thorough knowledge of such ecosystem components to start from.

Within meanders, a hotspot of erosional-depositional processes is the apex zone (Hooke, 1986, 2004; Bravard et al., 1999; Biedenharn et al., 2000; Kesel, 2003). The morphology of a meander apex zone (Fig. 1) is characterised by depth asymmetry (Blettler et al., 2012; Garcia et al., 2012), usually comprising an accumulation area (on the convex bank) and an erosive area located on the concave bank (Reineck and Singh, 1973; Bravard and Petit, 1997). As such, the depositional bank of a meander is usually characterised by increased fine sediment (i.e. silt and clay) ratios, as opposed to the erosional banks that comprise coarser sediments (Bridge, 2003; Tiron and Provansal, 2010).

The benthic invertebrates are known to be patchily distributed within river beds, mostly as a consequence of the local conditions of the substrate (Beisel et al., 2000; Rempel et al., 2000). The size of sediment particles, the hydraulic stress and the availability of basal resources (i.e. leaves, woody debris, fine detritus, epilithon) comprise three main drivers that condition the diversity and spatial distribution of benthic invertebrates in rivers (Jones et al., 2012; Buendia et al., 2014; Pacioglu and Moldovan, 2016). It is also suspected that the deposition of fine sediments in riverbeds decreases the availability of basal resources for consumers (Doretto et al., 2017). The burial of leaves in the riverbed via fine sediments deposition reduced their availability, further altering the growth rate of invertebrates (Danger et al., 2012). However, the synergic interactions among fine sediments deposition and the availability of basal resources for benthic invertebrates were rarely addressed in river ecology (see Doretto et al., 2016, 2017).

Another far-reaching implication of fine sediments deposition is related to nutrients cycling (Jones and Mulholland, 1998; Schalchli, 1992). The river sectors with coarse sediment structure were considered to have a sufficiently high concentration of dissolved oxygen to prevent methanogenesis (i.e. the production of methane by bacteria, Trimmer et al., 2012). However, high percentages of silt and clay that clog the gravel interstices, usually associated with increasingly fine organic matter deposition, hamper the water and dissolved oxygen flows, leading in the end to hypoxic or anoxic conditions that favour the occurrence of methanogenesis within sediments (Jones and Mulholland, 1998; Grey, 2016). Evidence suggests that methane plays an important role as a source of energy for aquatic food webs (Trimmer et al., 2009, 2010). The carbon fixation via chemosynthesis, besides photosynthesis, is a well-known process that takes place in many types of aquatic ecosystems (Whiticar, 1996). The reliance of consumers on chemosynthetic-derived carbon varies from 100 % in deep sea vents (MacAvoy et al., 2002) to 50–60 % for lake-dwelling zooplankton and chironomids (Jones et al., 1999), 30 % for stream caddis flies larvae (Trimmer et al., 2010) and 15 % for fish (Ravinet et al., 2010).

1.1. *Working hypotheses*

The Danube is the second-longest river in Europe, with a total length of 2860 km, and a total mean annual discharge of 6500 $m^3 s^{-1}$. The discharge of suspended sediment in the Black Sea is about 25–30 × 10^6 $t\,y^{-1}$ (Panin and Jipa, 2002) through the largest deltaic system in Europe, the Danube Delta (Fig. 1). The sediment discharge decreased during XX century as a consequence of damming (Iron Gates I and Iron Gates II in 1970's, see Panin, 2003), whereas the water discharge increased, mostly associated to climatic changes and marsh reduction. The southernmost branch of the Danube Delta, the St. George branch (Fig. 1), starts from 108 km upstream the Black Sea and carries about 21 % of the Danube sediment discharge (Jugaru Tiron et al., 2009). During 1984–1988, several free meanders were modified in order to improve navigation by cutoffs, reducing the total length of the St. George branch to 32 km from 108 km. The meanders' cutoffs by navigational canals since 1984–1988 (Fig. 1) produced the redistribution of river flow velocities and liquid and solid discharges in the St. George branch (Pojar et al., 2021).

First, we wanted to assess the ecological preferences of invertebrates inhabiting two opposite banks of a meander from Danube Delta (Fig. 1). As mentioned above, the relation among benthic invertebrates, sediment-size and hydraulic forces is understudied in the meanders developed within large rivers. In order to fill this knowledge gap, an apex zone of a meander affected by a cutoff was chosen because the opposite river banks from this particular area comprise active erosional versus depositional sites, with contrasting sediment compositions and hydraulic forces. Our study area, the cutoff of the Dunavăţ de Sus meander (Fig. 1) showed an increased dynamic activity of the apex zone after 1990 (Tiron Dutu et al., 2014). The chosen sites in the current survey comprised two mesohabitats that were surveyed for several years (Tiron Duţu et al., 2014) and that described the concave bank as erosional, whereas the inner, convex bank as depositional (Fig. 1). We hypothesised that the quantified invertebrate species and communities will show different mesohabitat preferences, reflected in their specific and overall abundances. This was followed by a discussion on their ecological preferences for depositional versus erosional mesohabitats and how the construction of cutoff navigation channels influenced the structure and spatial distribution of benthic invertebrates in both mesohabitats.

Second, we hypothesised that within the depositional meander bank, due the increased ratios of fine particles (i.e. clay and silt), the availability of basal resources for consumers was diminished (Jones et al., 2012; Doretto et al., 2017) and paralleled by occurrence of methanogenesis that modified the energy and nutrients fluxes through the local food web. The water of the Danube flowing within its delta is supersaturated with carbon dioxide and methane (Cole et al., 2007; Durisch-Kaiser et al., 2011). The Danube Delta was proved recently to be an important source of methane (Canning et al., 2021; Maier et al., 2021), with calculated emission rates to the atmosphere of 0.43 ± 0.53 mol m^2 yr^1, comparable to other wetlands distributed worldwide (Stanley et al., 2016). Benthic remineralisation of deposited organic biomass, along with input of incoming water from the river main stem into floodplains were showed to be the main factors driving the methane gas release from Danube Delta habitats (Pavel et al., 2009; Durisch-Kaiser et al., 2011; Tong et al., 2012). The assessment of the fine sediments impact on such ecosystem properties are virtually lacking in large rivers. The current survey is one of the few that tested the impact of fine sediments deposition on the availability of basal resources for consumers, trophic interactions of invertebrates and food webs topology, with the aid of stable isotopes of $\delta^{15}N$ and $\delta^{13}C$. We expected that as a result of fine sediments intrusion, the depositional mesohabitat to comprise species that will show signs of both chemo- and photosynthetic carbon reliance. In turn, the food web from the erosional meander bank, which is characterised by coarser sediments and higher local water velocities, was expected to be mainly based on the classic photosynthetic carbon entry pathway.

2. Materials and methods

2.1. Study area

The study area is located in the Danube Delta, on the former Dunavăţ de Sus free meander located between KM 58–54 (distance from the river mouth) of the St. George distributary (Fig. 1). Its wavelength is 1.93, radius of curvature is 425 m, and the sinuosity is 1.91 (Tiron Duţu et al., 2014). Biological, hydro-morphological and sedimentological measurements were performed in September 2020.

2.2. Hydrological and sedimentological measurements

The morphological and hydrological data were acquired with a powered boat-mounted acoustic Doppler current profiler (ADCP, RiverRay 600 kHz, manufactured by Teledyne). Reported water depths are expressed in local values. Bottom sediment samples were collected with a grab sampler, on the opposite banks (i.e. right bank and left bank of the cross-section) of the meander from the apex zone (Fig. 1). Three sediment replicates were taken from both meander banks and the grain-size composition was determined by diffractometry. The percentages of sand, silt and clay, as well as the average diameter of particles were calculated for both meander banks (Table 1). For technical approaches about the grain size analyses see Duţu et al. (2018).

The sediment initiation is mainly expressed as critical water velocity and critical shear stress (Buffington, 1999). The critical velocity method correlates the sediment initiation to an average flow velocity through a resistance law, whereas the critical shear stress method correlates the initiation to a bed shear stress. The Shields diagram empirically calculates the distribution of the dimensionless critical shear stress (i.e. the dimensionless shear stress required for the initiation of motion) as a function of a particular form of the particle Reynolds number, or Reynolds number related to the particle (Shields, 1936). The measured hydrodynamic parameters for each apex bend were the critical shear stress, the Reynolds number, the critical velocity and Shields diagram were calculated for each meander bank (Table 1).

2.3. Benthic invertebrates sampling and stable isotope analyses of $\delta^{13}C$ and $\delta^{15}N$

Five quantitative samples from each meander bank were collected with van Veen grab (mouth surface 420 cm^2). 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 (Pacioglu et al., 2022). The samples were preserved with a mixed solution of Rose Bengal and buffered formaldehyde 4 %. In the laboratory, the samples were sorted, and the 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 (individuals/m^2) estimated. Moreover, qualitative gut content analyses were carried for each taxa (excepting for the leaches), at 40 x magnification with the dissecting microscope for crayfish (Pacioglu et al., 2019) and at 400 x magnification, with the high power microscope, for the remaining taxa (Fukumori et al., 2016).

Invertebrates and basal resources were collected in the field with a hand net, as well as by hand and classified to taxonomic groups in place. The detritus was passed through 2 stacked sieves (1-mm and 250 μm-mesh size) and appropriate mass for woody debris (particles > 1 cm), coarse particulate organic matter (hereafter CPOM, particles 1 mm - 1 cm, comprising decayed reed leaves) and fine particulate organic matter (hereafter FPOM, particles > 250 μm, but < 1 mm) were selected. Cuttings were taken from fresh reed leaves (Phragmites sp.) along with their associated epiphytes, which were separated using established protocols (Pacioglu et al., 2019), and the resulting suspension were filtered through glass-fibre filter papers (GF/F Whatman). Samples were dried in an oven (60 °C, 48 h) and homogenised ($n = 3$ for each type). Stable carbon and nitrogen isotope analyses was done using a Flash 2000 elemental analyser coupled via a ConFlo IV interface to a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific). The reported stable carbon and nitrogen isotope values are expressed as δ (‰) relative to the international reference standards Vienna PeeDee Belemnite and atmospheric nitrogen, respectively. An internal reference material (i.e. casein) was measured in duplicate every ten samples revealing an imprecision (± 1 SD) ≤ 0.06 ‰ for both δ^{13}C and δ^{15}N.

Table 1

Sediment (i.e. percentages of sand, silt, clay and median distribution of size-classes, D50), water depth, as well as hydrologic (i.e. water velocity) and hydraulic (i.e. critical shear stress and velocity, Reynolds number and Shields' entrainment function) parameters of the erosional and depositional meander banks, respectively, from the apex region. In bold are parameters that differed significantly ($p < 0.05$, M.-W. tests) between meander banks.

Mesohabitat type	Sand %	Silt %	Clay %	D50 (mm)	Depth (m)	Water velocity (m/s)	Tcr (N/m^2)	Re^*_c	u* (m/s)	Shields
Depositional bank	**12.19**	**67.15**	**20.67**	**0.014**	**5.8**	0.4	0.08	0.35	0.03	11.04
Erosional bank	**99.82**	**0.14**	**0.04**	**0.178**	**8.2**	0.8	3.98	5.41	0.04	1.27

2.4. Statistical analyses

The sediment-grain size classes and species richness, as well as density of each taxa and total mean density of invertebrates (individuals/m^2) were pairwise compared between meander banks with Mann-Whitney (hereafter M.-W.) non-parametric tests ($p < 0.05$). Moreover, potential preferences of taxa for any of the meander banks was illustrated with non-metric Multidimensional Scaling (nMDS) ordination, based on Bray-Curtis distances, to visualise differences in taxonomic composition. One-way ANOSIM (analysis of similarity) randomisation test, based too on the Bray-Curtis similarity coefficients, was used afterwards to test for differences in community structure between meander banks. All analyses were undertaken in PAST software version 4.08.

The δ^{13}C of basal resources types and primary consumers (as indicated by qualitative gut content analyses and literature review) were compared with M.-W. tests ($p < 0.05$). When the δ^{13}C of both consumers and their food were low (i.e. < -35 ‰), they were considered potentially derived from chemosynthesis (see Introduction). In such food webs, the relative contributions of C via chemo- and photosynthetic pathways for consumers were estimated using the Bayesian isotope mixing model IsoWeb (Kadoya et al., 2012). This model requires the a priori estimation of trophic links, which were inferred from qualitative gut content analyses (see Section 2.3.) and in cases where such method was inapplicable (i.e. leeches) it was estimated from scientific literature. IsoWeb has the advantage of estimating dietary contributions for all consumers within a food web, based on δ^{13}C and δ^{15}N data and a topological description of the food web given a priori (Giraldo et al., 2017). The trophic enrichment factors were 0.8 for carbon and 3.4 for nitrogen (Post, 2002; Saigo et al., 2015; Fukumori et al., 2016). The IsoWeb model was run 106 chain length, burn-ins 500.000, and thin number 500 for three parallel Markov Chain Monte Carlo chains (Giraldo et al., 2017). The relative contribution of C from both chemo- and photosynthesis for non-primary consumers (i.e. omnivores and predators) was determined by calculating the relative dietary contribution of each source to primary consumers according to IsoWeb output, followed by their multiplication by the associated relative contribution to non-primary consumers' diet (see Fukumori et al., 2016). The cannibalistic loops were also included in the model, where applicable.

The trophic structure of the invertebrate communities was described for each meander bank using the metrics of Layman et al. (2007). These community-based metrics use the δ^{13}C and δ^{15}N of consumers to describe the niche and trophic structure of the community, providing information on the trophic diversity and redundancy within food webs (Abrantes et al., 2014). A Bayesian approach that distributes the sampling errors of the means estimated for species within a community and that generates *a posteriori* distribution of the estimates of these metrics was applied. Thus, six community metrics were calculated with Stable Isotope Bayesian Ellipses package in R (SIBER; Jackson et al., 2011): δ^{13}C range and δ^{15}N range (i.e. variety of resources exploited by consumers), the mean distance to centroid (i.e. trophic diversity within food webs), the mean and the standard nearest neighbour distance (i.e. density and clustering within the assemblage) and the total area of convex (i.e. total amount of niche space occupied within a food web).

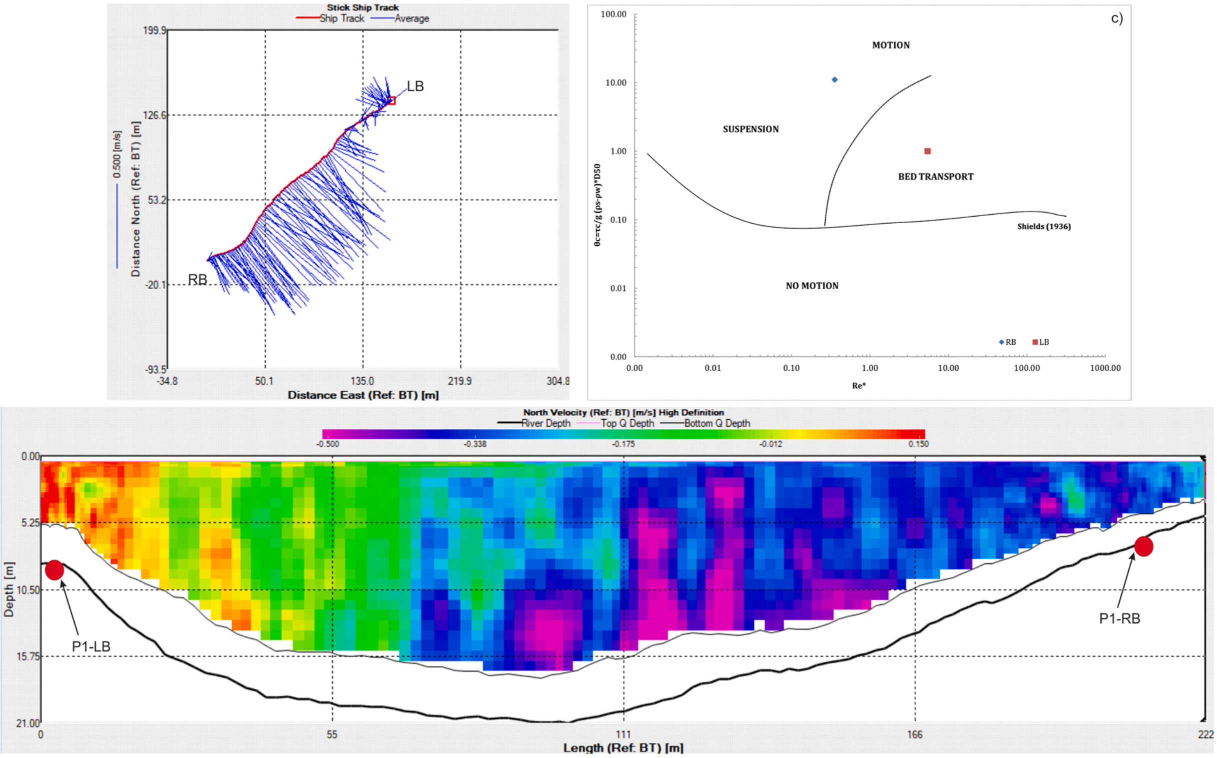

Fig. 2. Bathymetry and distribution of local velocity magnitude (North) within the investigated cross-section, with the exemplification of the turbulent flow on the concave bank. The Shields diagram for sediment initiation shows the condition of transport of the sediments on both opposite banks of the meander apex zone.

3. Results

3.1. Hydro- sedimentary processes

The sampling was performed during the average to high autumn waters; the measured liquid flow at the location of the study area was 1020 $m^3\ s^{-1}$. Grain-size analyses showed the predominance of fine fractions (i.e., silt and clay) on the right (depositional) bank (with a mean value of 0.014 mm) and medium/ fine sand on the left (erosional) bank (mean value of 0.178 mm), very well sorted on the right and very poorly sorted on the left bank (Table 1). Higher velocity values are located in the centre area and near to the left bank (Fir. 2a and 2b). Reversed currents (turbulent flows) were observed in the concave bank of the meander (Fig. 2a), as a result of the bank physiography and meander amplitude (meaning the maximum distance from the down-valley axis to the sinuous axis of a loop) that usually characterises this type of geomorphological structure (Reineck and Singh, 1973; Tiron, 2010). The water velocity measured alongside both banks was heterogeneous, higher next to the concave bank and much lower next to the opposite bank (Table 1). The erosional character of the concave bank was reflected also in the values of the hydraulic parameters, such as high values critical velocity (u*), critical particle Reynolds number (Re*, i.e. higher values on transitional to turbulent flow regime) and critical shear stress (Tcr) (Table 1). The erosional regime of the concave versus the depositional, convex bank is clearly showed by the Shields diagram (Fig. 2c).

3.2. Invertebrate fauna composition

Twelve invertebrate species were consistently well represented in both meander banks (Fig. 3, Table 2). The nMDS ordination showed that the communities formed two distinct clusters, but with weighted averages values of most taxa lying in-between (Fig. 2, stress value = 0.02). The one-way ANOSIM test showed that the communities were different in both mesohabitats ($R = 0.98$, $p < 0.01$). The crayfish *Pontastacus leptodactylus*, the amphipod *Dikerogammarus villosus* and the caddisfly *Hydropsyche bulgaromanorum* were found in significantly higher densities in the erosional meander bank, whereas other species showed opposite preferences (Fig. 3, Table 2). The species richness was rather similar between opposite meander banks, excepting the mussel *Unio pictorum* and the amphipod *Chelicorophium curvispinum* that were found only in the depositional mesohabitat (Table 2). The total density of invertebrates was significantly higher in the depositional area, mainly driven by two to three time higher abundances of oligochaetes, chironomids and of the clam *Corbicula fluminea* (Fig. 3, Table 2). The snails *Lithoglyphus naticoides, Viviparus viviparus*, the mayfly Caenis sp., the dragonfly *Ischnura elegans* and the leach *Erpobdella octoculata* had similar densities in both mesohabitats (Table 2).

3.3. Trophic interactions

The stable isotopes biplots (Fig. 4) of $\delta^{15}N$ and $\delta^{13}C$ revealed different signals for basal resources and consumers within the food webs from both banks. In the depositional bank, several consumers were depleted in terms of $\delta^{13}C$ values compared to their putative food (Fig. 4A). The snails *L. naticoides* and *V. viviparus* had a mean value of $\delta^{13}C$ significantly lower than the epiphytic algae ($p < 0.01$, M.-W. tests), but similar to reed fresh leaves. A similar depletion for the $\delta^{13}C$ values ($p < 0.05$, M.-W. tests) was observed for chironomids compared to FPOM and epiphythic algae, but similar to reed fresh leaves and woody debris or for the clam *C. fluminea* relative to FPOM (Fig. 4A). Overall, $\delta^{13}C$ values for these invertebrates were 2.3–5.8 ‰ lower than those of other invertebrates and their putative food sources (Fig. 4A). The overall $\delta^{13}C$ range for the food web in the erosional bank was much narrower (−32 up to −21 ‰) compared to the depositional mesohabitat (Fig. 4B). Primary consumers, like the chironomids, oligochaetes, the snails *V. viviparus*

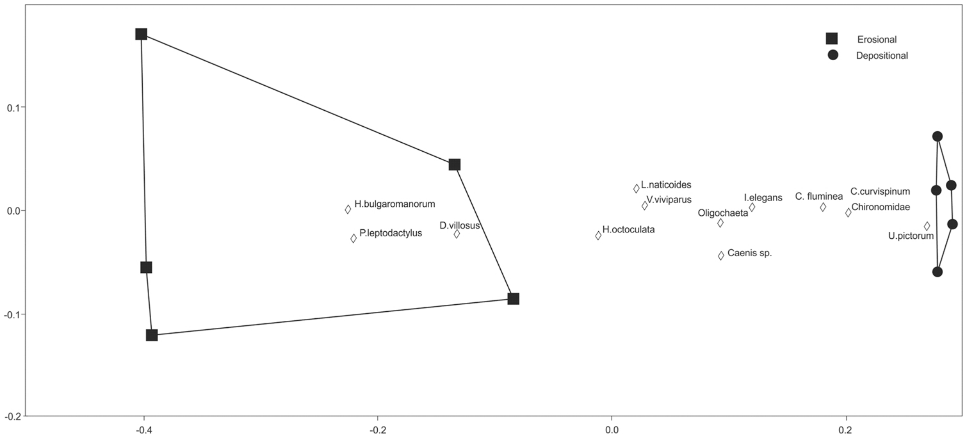

Fig. 3. nMDS plots derived from Bray–Curtis similarity coefficients based on taxa abundances for the erosional and depositional meander banks. The weighted averages of taxa were overlaid on the plot, along with convex hulls, to emphasise better the ordination patterns**.** The abbreviations of scientific names are given in Table 2.

Table 2

Mean and standard deviations of taxonomic richness, species and total density (measured as number of individuals/m^2) in the erosional and depositional bank of the meander. Taxa in bold present significant differences ($p < 0.05$, Mann-Whitney tests) between meander's banks.

River bank	*I. elegans*	*Caenis sp.*	*L. naticoides*	*V. viviparus*	*E. octoculata*	***P. leptodactylus***	***D. villosus***	**Oligochaeta**	***C. curvispinum***	***H. bulgaromanorum***	***C. fluminea***	**Chironomidae**	***U. pictorum***	**Total**	Species richness
Erosional	4.4 ± 3.6	21.1 ± 19.6	20.2 ± 8.4	27.0 ± 3.2	4.8 ± 2.3	5.0 ± 2.8	38.2 ± 14.1	61.5 ± 26	0	15.3 ± 2.9	39.9 ± 0.25.9	36.5 ± 21.8	0	332.1 ± 125.6	11.2 ± 0.7
Depositional	11. ± 9.2	37.6 ± 23.5	24.2 ± 6.8	33.8 ± 8.3	3.9 ± 2.2	0.7 ± 0.9	9.7 ± 8.1	123.0 ± 15	177 ± 21.6	1.5 ± 3	135.2 ± 34.2	194.6 ± 10	7.6 ± 7	759.9 ± 73.8	10.4 ± 0.5

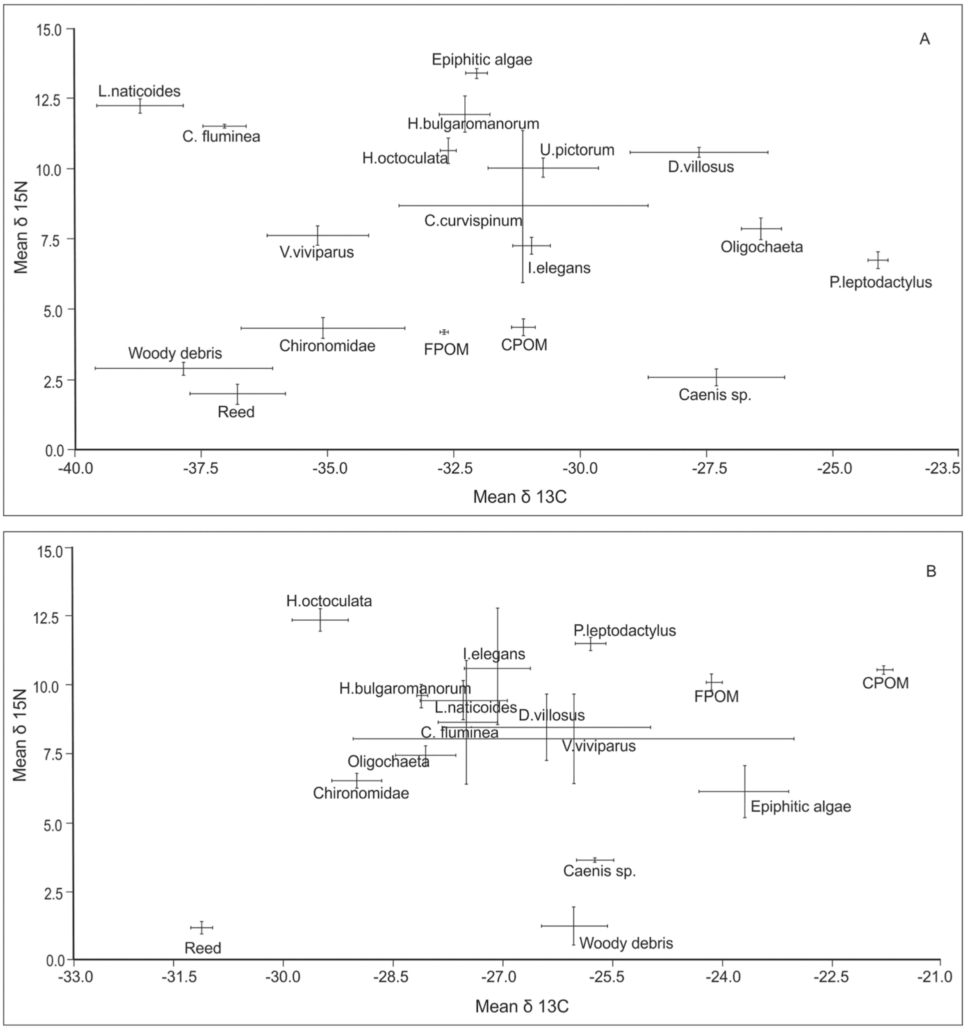

Fig. 4. Biplots (means ± standard deviation) of δ^{15}N and δ^{13}C in invertebrates and basal resources in the depositional (A) and erosional (B) banks of the meander. The abbreviation of scientific names are given in Table 2.

and *L. naticoides* and the mayfly *Caenis* sp. showed also depletion of δ^{13}C values compared to their putative food sources (i.e. epiphytic algae, FPOM and CPOM, Fig. 4B).

The primary consumers from the depositional bank (Fig. 4A) assimilated the C from chemo- and photosynthesis in equal percentages from basal resources, whereas the predators and omnivores assimilated about 30–40 % of C via the former pathway (Table 3).

The community-wide metrics reflected important aspects of the trophic structure of communities inhabiting the opposite banks of the meander (Fig. 5). The convex hull area, the δ^{13}C range, the mean distance to centroid, and the mean nearest neighbour distance (Fig. 5A, C, D, and E), respectively, had higher values in the depositional compared to the erosional bank, whereas the δ^{15}N range and standard deviation of the mean nearest neighbour distance showed similar values (Fig. 5B and F).

4. Discussion

4.1. *Ecological preferences of invertebrates for erosional versus depositional meander banks*

The knowledge of mesohabitat preferences by benthic invertebrates in the meanders developed along large rivers lacks behind the one accumulated from lower-order streams (Blettler et al., 2008). The current survey partially aimed the evaluation of mesohabitat preferences of benthic invertebrates for two contrasting meander banks, one depositional and one erosional (Table 1). Moreover, the shear stress in the concave mesohabitat was higher compared to the opposite bank, generating lateral bank erosion (Fig. 1, Table 1) and coarser sediment composition (Bathurst et al., 1979; Parker et al., 2011; Carling, 1995). The continuous collisions between suspended sediments in the apex zones of meanders are detrimental for certain invertebrates inhabiting these areas (Carling, 1995; Blettler et al., 2008), potentially explaining their significantly lower density in the erosional mesohabitat compared to the opposite bend (Fig. 3,

Table 3
Relative contribution (in %) of chemo- and photosynthetic C to consumers biomasses from the depositional meander bank.

Type of C production in the depositional bank	*U. pictorum*	Chironimidae	*C. fluminea*	Oligochaeta	*C. curvispinum*	Caenis sp.	*L. naticoides*	*V. viviparus*	*P. leptodactylus*	*D. villosus*	*I. elegans*	*H. bulgaromanorum*	*E. octoculata*
Chemosynthesis	0	58	0	0	0	49	48	52	32	39	39	36	39
Photosynthesis	100	41	100	100	100	51	51	47	68	61	61	64	61

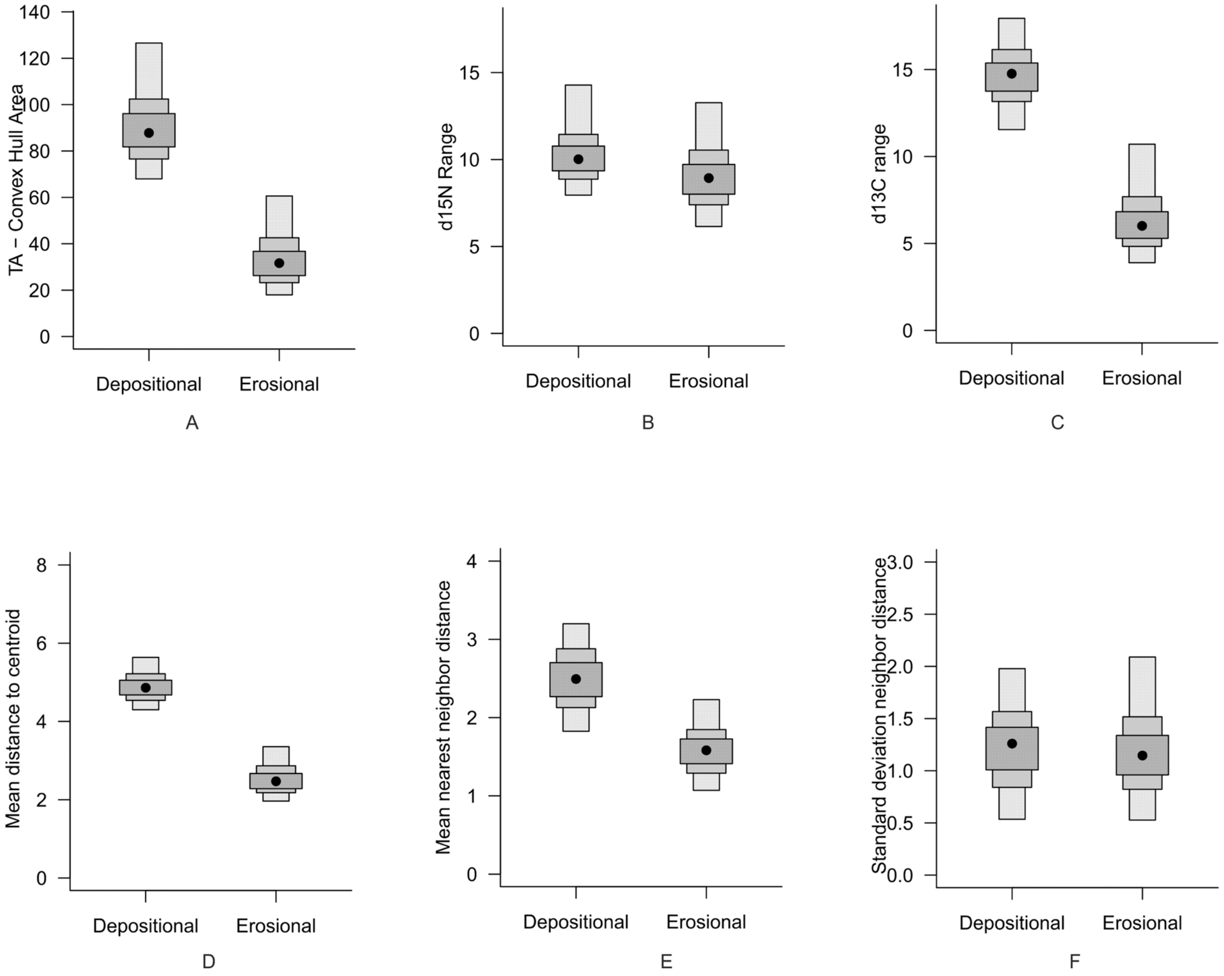

Fig. 5. The mean (black dots) and 25 %, 75 % and 95 % credibility intervals of the convex hull area (A), the $\delta^{15}N$ and $\delta^{13}C$ range (B and C), the mean distance to centroid (4D), as well as the mean and standard deviation of the mean nearest neighbour distance (E and F) of the invertebrate communities inhabiting the depositional and the erosional meander banks (*sensu* Layman et al., 2007).

Table 2). The invertebrate community with higher densities within the erosional bank of the meander comprised species known to prefer areas with lower silt and clay fractions and higher water velocity (Garcia et al., 2012). Crayfish such as *P. leptodactylus* are sensitive to silt deposition in slow-flowing lowland rivers; increased clay and silt fractions within river sediments were showed to be responsible for the permanent loss of crayfish populations (Maceda-Veiga et al., 2013; Reynolds et al., 2013). The caddisfly *H. bulgaromanorum* is considered a typical dweller of River Danube, but avoiding the banks characterised by high percentages of silt and clay and preferring higher water velocities compared to other conspecifics appurtenant to the same genus (Krno et al., 2018). Also, the killer shrimp *D. villosus* prefers coarse substrates (van Riel et al., 2006) and avoids mud and sandy habitats (Platvoet et al., 2009). In turn, the oligochaetes, the chironomids, the amphipod *C. curvispinum,* and the bivalves *C. fluminea* and *U. pictorum* showed the highest densities in the opposed meander bend (Fig. 2, Table 2). These taxa are known to occur in fine-sized substrates in large rivers (van den Brink et al., 1993; Norf et al., 2010), including the Danube Delta (Rîşnoveanu and Vădineanu, 2003; Pacioglu et al., 2022). The meanders sectors of the St. George branch that are characterised by increased percentages of silt and clay also retain larger quantities of organic matter compared to sectors with coarser sediment composition (Tiron Duţu et al., 2019), which is another crucial environmental factor that drives the ecological preferences of these taxa (Marchese et al., 2002; Blettler et al., 2012, 2016). The clam *C. fluminea* and the mussel *U. pictorum* are common dwellers within silted sediments of the Danube Delta floodplains (Shikhova and Mitrofanova, 2019), preferring mesohabitats with increased fine sediments ratios and organic content (Belanger et al., 1985; Ilarri et al., 2021).

The Danube Delta is a natural reserve, harbouring a large number of animal species that unfortunately was affected by human interventions over the past century (Zinevici and Parpală, 2006; Gâştescu, 2009). The cutoff channels interventions undertaken along St. George arm did not take into account that environmental issues will be induced by the changes in sediment and water fluxes within the meanders (Stoica et al., 2012; Habersack et al., 2016; Pavel et al., 2017; Vasiliu et al, 2021). Since we lack historic fauna census from this area, we cannot properly assess the environmental impact following the cutoff interventions. The redistribution of water through cutoff channels and meanders led to uneven changes in fine sediments circulation along St. George branch (Habersack et al., 2016). Meanders are generally considered as efficient fine sediments storage locations. However, the meanders from St. George arm were found to be affected differently by cutoff channels, with upstream units acting overall as efficient depositional areas for fine sediments, whereas the downstream units (including the meander surveyed in the current study) as rather erosional (Duţu et al., 2018). However, the preliminary results from the current survey showed that there were invertebrates with preferences for depositional and erosional meander banks and that were potentially affected by the increased redistribution of water and sediment fluxes following the human interventions. For example, the construction of cutoff channels in the lower Mississippi River (Thorp, 1992) has influenced sediment and organic input and diminished the amount of habitats available for benthic invertebrates in meanders. The results of the current survey could prove beneficial for future river restoration and biodiversity conservation programs within Danube Delta.

4.2. Trophic interactions in erosional versus depositional meander banks: potential role and consequences of methane-derived carbon for local food webs

Whereas the contribution of chemosynthesis to local aquatic food webs has a long history of research, spanning the last 40 years, the typical habitats where such additional carbon entries were highlighted were mainly the marine vents and lakes (see Grey, 2016). The types of habitats where the influence of chemosynthesis on consumers' diet and food webs' structure and functionality was quantified expended to free-flowing low-order streams only during the last decade (Trimmer et al., 2009), as well as in estuaries (Brankovits et al., 2017). Despite the acknowledgment of high quantities of methane released in atmosphere by deltas worldwide, little advance was made concerning the influence of chemosynthesis on aquatic food webs in such habitats (Grey, 2016; Cazzanelli et al., 2021). Despite their high frequency and large surfaces, the meanders of the Danube Delta comprise one component of a complex of highly interconnected water bodies, where the eutrophication is the norm (Zinevici and Parpală, 2006; Gâştescu, 2009), which promotes considerable production of phytoplankton, epiphytic algae and macrophytes (Sangiorgio et al., 2010; Florescu et al., 2022). For these reasons, the meanders within the Danube Delta are known to be reliant to a high degree on autochthonous production via photosynthesis (Sârbu, 2003). This fact was also confirmed by the results from the current survey, where several taxa (e.g., the snails *L. naticoides* and *V. viviparus*), reliant on epiphytic algae in the erosional meander bend and that were δ^{13}C depleted by 0–3 ‰ is not a surprise (Fig. 4B). However, several taxa dwelling in the depositional bend (Fig. 4A) were δ^{13}C depleted relative to other invertebrates and their putative food sources, indicating substantial reliance on dietary source with significantly lower δ^{13}C values. Such low δ^{13}C values (< -35 ‰) were attributed to typical microbiological processes, such as the methanogenesis, which occur within river banks and are known to affect the δ^{13}C of basal resources (Kankaala et al., 2006; McNeely et al., 2006; Trimmer et al., 2009, 2012). In our case, the snails *L. naticoides* and *V. viviparus* seem to have switched their food preferences from epiphytic algae in erosional banks to fresh reed leaves in the opposite bend, and the chironomids from epiphytic algae and FPOM to woody debris (Fig. 4A and B, Table 3). An advanced explanation in previous studies was that such consumers (i.e. those inhabiting the depositional meander bend) are feeding on the readily available carbon, which may have resulted from more active methane oxidation sites within the microbial biofilms developed on woody debris and fresh reed leaves and less from the photosynthetic pathway (Trimmer et al., 2009, 2012). Hence, the potential of chemoautotrophic derived carbon as part of the diet of several taxa dwelling within the depositional meander bend cannot be excluded. Several types of bacteria implied in the N cycle were found to produce depleted δ^{13}C values relative to CO_2 (of around -35 ‰, see Sakata et al., 2008; Grey, 2016), indistinguishable from the ones of fresh reed leaves and woody debris partially buried within the sediment from the depositional bends of the meander (Fig. 4A). If to consider the C origin from these basal resources as methane-derived, the output of the IsoWeb model (Table 3) indicated that these primary consumers inhabiting the depositional bank may have obtained in average about 50 % of their carbon subsidy via methane oxidation on basal sources such as fresh reed leaves for snails and woody debris for chironomids and the mayfly Caenis sp. These taxa are abundant in this meander bank (Fig. 3, Table 2), observation also supported by previous investigations (Pavel et al., 2017). On the same rationale, the invertebrate predators and omnivores derived about a third of their energy via chemosynthesis pathway in the depositional bank (Table 3), leading to the conclusion that an important proportion of the biomass available to species feeding higher in the food web may actually be derived from methane. Previous studies indicated that primary consumers, such as caddisfly and chironomids larvae build about a third and up to 70 % of their biomass, respectively, from methane derived C (Ings et al., 2012; Grey, 2016), whereas mobile top predators such as fish, for up to 15 % (MacAvoy et al., 2002). These findings, corroborated with high emission rates of methane recorded previously in this area (Canning et al., 2021; Maier et al., 2021), lead to the conclusion that the methane oxidising bacteria could represent an important food source for several consumers within the depositional meander bank.

A potential discrepancy was observed between the clam *C. fluminea* and FPOM with respect to the δ^{13}C signal in the isotopic biplot (Fig. 4B). Previous studies showed that the relative *C. japonica*, a common dweller in estuaries, despite reliant on FPOM as a consequence of their feeding strategy, embed also chemosynthetic bacteria as part of their diet (Yamanaka et al., 2013). This way, although the δ^{13}C signal of FPOM indicates the photosynthetic based original material for this type of basal resource (Fig. 4B), by the time this food item is consumed, it may become enriched with chemosynthetic bacteria, leading to a significantly lower δ^{13}C value of the clam (Doi et al., 2005).

The potential dual (i.e. photosynthesis and chemosynthesis) energy input via basal resources in the depositional meander bend led to important changes in food webs topology (Fig. 5). The δ^{13}C range, which is the distance between the most enriched and most depleted δ^{13}C taxa, when increased (Fig. 5C), is expected to be related to multiple basal resources inputs (Layman et al., 2007), leading to niche diversifications at the food web base (Doi et al., 2006; Parreira de Castro et al., 2016; Grey, 2016). This usually leads to an increase of the total amount of niche space occupied (i.e. convex hull area, Fig. 5A) and of the average degree of trophic diversity (i.e. the mean distance to centroid, Fig. 5D), but to lower trophic redundancy (i.e. the mean nearest neighbour distance, Fig. 5E) (Layman et al., 2007; Pacioglu et al., 2021). The potential explanations for these variations of the community-wide metrics between meander banks are, however, intimately related to the multiple effects induced by siltation on benthic communities. The overall impact of colmation with fine sediments on benthic food webs remains largely unknown (Jones et al., 2012). The classic changes in taxonomic composition of river benthic communities associated with increased colmation by fine sediments (and sometimes with shear stress) were unfortunately little extended towards unravelling the effects on trophic interactions and food webs structure (but see Yule et al., 2010). Increased deposition rates of silt and clay fractions were observed to limit the access of benthic invertebrates to basal food sources, such as CPOM, FPOM, woody debris and algae (Doretto et al., 2016, 2017). One of the advanced hypotheses regarding the effects induced by siltation on benthic assemblages was that the observed changes in species composition should also be paralleled by changes in their diet, given the lower or lack of availability for certain types of basal resources in the depositional areas or rivers (Jones et al., 2012). In the only study that we are aware of that quantified the effects of siltation on trophic interactions at community level (Yule et al., 2010), it was discovered that certain basal resources, following the river bed colmation, were no longer contributing to the food webs. As such, benthic algae were replaced by bacterial mats, inducing strong bottom-up effects along the food webs, such as the disappearance of scrapers and decrease in fish body-size that relied, as part of their diet, on bacterial mats (Yule et al., 2010). The variations of the community-based indices (Fig. 5) may be potentially explained by a lower access of certain primary consumers to basal resources and potential diet switch. Whilst the invertebrate community from the erosional bank consumed basal resources that come unaltered in terms of their δ^{13}C range, certain primary consumers from the opposite bend may have had limited access to certain basal resources. Therefore, the potential supplementary carbon via chemosynthesis from woody debris could have resulted from the synergic action of reduced available space in sediment for consumers and consequent anoxic conditions that favoured in situ methanogenesis (see Frossard et al., 2015). In comparison to δ^{13}C data of macrophytes analysed from various types of aquatic ecosystems (typically > -30 ‰, Finlay and Kendall, 2008), but in accordance to values recorded from rivers where methanogenesis does occur (Trimmer et al., 2009; Ings et al., 2012), the values for fresh reed leaves from the depositional meander bank were substantially more depleted (means of -36 ‰, Fig. 4A). Potential sites for methane oxidising bacteria on macrophytes were proven to be the rhizosphere for Ranunculus sp. in chalk streams (Sanders et al., 2007) or within the aerenchyma for Sphagnum sp. (Raghoebarsing et al., 2005).

The overall low species evenness distribution of trophic niches within both communities, corroborated with similar δ^{15}N range (Fig. 5B), indicates that the bottom-up effects through the food webs were somehow buffered by the primary consumers. This was reflected in a similar number of trophic levels for both communities and overall even distribution of trophic niches in both mesohabitats (0.5–1.5, Fig. 5F, see Layman et al., 2007), which indicates that the top consumers from the depositional bank, such as the leach *E. octoculata*, the amphipod *D. villosus* and the dragonfly larvae *I. elegans*, despite up to a third of chemosynthetic C reliance via animal consumption (Fig. 4 and Table 3) did not change their mean trophic position within food webs.

The current study is one of the few that assessed the impact of fine sediment deposition on the availability of basal resources to consumers and that emphasised the far-reaching consequences it has on invertebrate communities, by adding a supplementary basal energy input (i.e. chemosynthesis based C) to the local food webs. Moreover, the influence of bottom-up mechanisms through supplementary basal input on food webs' structure and topography were only sketched so far in theory, but rarely tested in nature (Careddu et al., 2015; Laigle et al., 2018). The interplay between photo- and chemosynthesis as important drivers in energy and nutrients transfer through aquatic food webs that were traditionally regarded as entirely photosynthetic-based was recently reconsidered (Åström et al., 2019; Günthel et al., 2020). The findings of the current survey will prove useful for future research programs undertaken within deltas that should cover a wider array of mesohabitats, with contrasting sediment composition and hydrological conditions, leading further to a better understanding of the interplay between the photo- and chemosynthesis processes within aquatic ecosystems.

5. Conclusions

The current study showed that antagonistic processes that take place in nature, such as erosion versus deposition of fine sediments acting on the opposite banks of a meander, have multifaceted impacts on the invertebrate communities dwelling in such mesohabitats. The current survey focused on the apex zone of a meander from Danube Delta because the opposite banks, one erosional and one depositional, comprise an excellent location for testing the influence of sediment-size and hydraulic forces on habitat preferences of invertebrate, as well as their influence on the structure and topography of local food webs and nutrients cycling. Such aspects were understudied in large rivers, mainly as a consequence of sampling and physical access difficulties, as opposed to lower-order streams that were the traditional focus in river ecology. It was showed that as a consequence of lower hydraulic stress and fine sediment infilling in the depositional bank, certain invertebrates (such as chironomids larvae, oligochaetes, amphipods and bivalves) rather preferred this mesohabitat, as opposed to common species of crayfish, caddisflies and killer shrimp, which preferred the coarser sediments and higher hydraulic stress, prevalent in the erosional bank. The smaller grain-size from the depositional meander bend potentially led to local anoxic conditions, which could have favoured the microbial-mediated methane production. Furthermore, the methane was incorporated by methane oxidising bacteria biofilm that colonised fresh reed leaves and partially buried woody debris, important food sources for certain primary consumers. As opposed to the erosional bank dwelling invertebrate community, which showed typical signs of a photosynthetic based food web, the chemosynthesis could be responsible for up to a half of the carbon incorporated in the biomass of snails and chironomids and about a third of omnivores and predatory invertebrates inhabiting the opposite banks. This additional basal energy input lessened the impact of structural bottom-up forces through the depositional food web, by channelising the chemosynthetic flow via basal resources and diet switch for certain primary consumers. In consequence, their trophic niches became distinct, accompanied by a widening of the network base. The current study is one of the few that tested the influence of erosional versus depositional processes on the availability of basal resources for consumers, nutrients cycling in aquatic habitats and the bottom-up effects of food webs structure and topography in large rivers.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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