Sandy rivers: a review on general ecohydrological patterns of benthic invertebrate assemblages across continents

Karl M. Wantzen Professor[a], Martin C. M. Blettler Professor[b], Mercedes R. Marchese Professor[c], Mario L. Amsler Professor[de], Michel Bacchi Professor[f], Inés D. Ezcurra de Drago Professor[g] & Edmundo E. Drago Professor[h]

[a] UNESCO Chair for River Culture (Fleuve et Patrimoine), Interdisciplinary Research Center for Cities, Territories, Environment and Society (CITERES-CNRS UMR 7324), Université François Rabelais, Parc Grandmont, 37200 Tours, France

[b] Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:

[c] Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:

[d] Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina

[e] Facultad de Ingeniería y Ciencias Hídricas, Universidad Nacional del Litoral, Centro Internacional de Estudios de Grandes Ríos, C.C. 217 - 3000 Santa Fe, Argentina. E-mail:

[f] Interdisciplinary Research Center for Cities, Territories, Environment and Society (CITERES-CNRS UMR 7324), Université François Rabelais, Parc Grandmont, 37200 Tours, France. Email:

[g] Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:

[h] Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:
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Research paper

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KARL M. WANTZEN, *Professor, UNESCO Chair for River Culture (Fleuve et Patrimoine), Interdisciplinary Research Center for Cities, Territories, Environment and Society (CITERES-CNRS UMR 7324), Université François Rabelais, Parc Grandmont, 37200 Tours, France. Email:* karl.wantzen@univ-tours.fr *(author for correspondence)*

MARTIN C. M. BLETTLER, *Professor, Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:* martinblettler@hotmail.com

MERCEDES R. MARCHESE, *Professor, Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:* mmarchese@inali.unl.edu.ar

MARIO L. AMSLER, *Professor, Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina; Facultad de Ingeniería y Ciencias Hídricas, Universidad Nacional del Litoral, Centro Internacional de Estudios de Grandes Ríos, C.C. 217 – 3000 Santa Fe, Argentina. E-mail:* mamsler2003@yahoo.com.ar

MICHEL BACCHI, *Professor, Interdisciplinary Research Center for Cities, Territories, Environment and Society (CITERES-CNRS UMR 7324), Université François Rabelais, Parc Grandmont, 37200 Tours, France. Email:* michel.bacchi@sarl-rive.fr

INÉS D. EZCURRA DE DRAGO, *Professor, Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:* inesezcurra@arnet.com.ar

EDMUNDO E. DRAGO, *Professor, Instituto Nacional de Limnología (INALI; CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina. Email:* edmundodrago@arnet.com.ar

ABSTRACT

The middle and lower sections of most large rivers have fine-grained bed sediments, which may have a strong influence on the functional and taxonomical structure of benthic invertebrates. Based on results from several studies by the authors on the faunal assemblages and habitat structures of the Paraguay–Paraná River system (Brazil, Paraguay, Argentina), from European (Rhine, Loire) River systems, and data from the literature, this review identifies general patterns which appear to have a global character. On one hand, the invertebrate assemblages largely differed between the main channel (MC) and the corresponding floodplain habitats in different sections, and also the floodplain habitats along the river channel revealed great differences in their biodiversity. On the other hand, there was a remarkable homogeneity among the main-channel sections within and even between river systems. We consider physical habitat features as the crucial variables responsible for these patterns. In cross-sections from the MC towards the floodplain habitats, grain size, organic matter content and oxygen supply change dramatically, and different floodplain habitats along the same river system may have different successional stages even at small geographical distances. The sandy structure of potamal habitats (including underwater dunes), however, provides a set of habitat features characterized by continuously changing sediment structures with well-defined grain sizes, low organic matter contents and good oxygenation, which force a set of adaptations by the invertebrates that limits but stabilizes the diversity of invertebrates in these large river sections. A better understanding of the ecohydrological interactions between habitat dynamics and benthic invertebrates is needed to improve sustainable river ecosystem management. We discuss the non-recovery of large benthic invertebrate species in the lower section of large rivers after improvement of the water quality in the context of these ecohydrological features. Conclusions are drawn for river restoration.

Keywords: Benthic invertebrate assemblages; underwater sand dunes; Paraguay River; Paraná River; Loire River; ecohydraulics

1

1   Introduction

Large river systems are much more than just longitudinal channel networks. The complex driving forces and exchange processes acting across three spatial dimensions result in frequently changing connectivity conditions and in a highly heterogeneous habitat complex. As the most important consequence of the ever-shifting mosaic of habitats and ecotones, large rivers generally feature an outstandingly high biodiversity (Junk 1999, Ward *et al*. 1999, Jungwirth *et al*. 2002).

Sorting and diminishing grain size of sediment particles along the river continuum causes that the main channels (MCs) of most potamal sections of rivers have sandy sediments as dominant substrate spanning over very long distances. The sandy section is limited in its upper end by the contribution of coarse sediments deriving from passage of the river through mountainous landscapes or from tributaries adding gravel from their catchments, and at its lower end by the mud depositions caused by the back flooding through marine tides in the estuary. In spite of the fact that the sandy potamal sections generally cover far more than half of the river length, astonishingly little is known about their fauna, which plays an important role for the ecological functions of the river such as pelagic–benthic coupling, organic matter processing, nutrient spiraling and foodweb structure.

As the study of benthos in large rivers is difficult due to strong currents and great water depths, which require a great technical effort (Humpesch and Elliott 1990), most studies in large rivers were limited to the banks, which are often covered by artificial substrates in managed rivers. Benthic invertebrate patterns are noticeably less understood in large rivers than in smaller ones. Global comparisons of assemblages of functional groups and taxonomic units of benthic invertebrates have been made for many stream types of the world since many decades ago (Illies 1961), however global patterns of the distribution of the MC benthos of large rivers has been more recently analysed (Castella *et al*. 1991, Marchese and Ezcurra de Drago 1992, Resh *et al*. 1994, Dudgeon 1995, Nessimian *et al*. 1998, Tockner *et al*. 1998, Buffagni *et al*. 2000, Rempel *et al*. 2000, Malmqvist 2002, Gayraud *et al*. 2003). In the Neotropical region, benthic invertebrates assemblages of large rivers were mainly studied in the Paraná (Bonetto and Wais 1995, Marchese *et al*. 2002, Takeda and Fujita 2004, Ezcurra de Drago *et al*. 2007), Uruguay (Di Persia and Olazarri 1986) and in the Paraguay Rivers (Takeda *et al*. 2000, Barbosa *et al*. 2001, Ezcurra de Drago *et al*. 2004, Marchese *et al*. 2005, Wantzen *et al*. 2011, Blettler *et al*. 2012a).

Sand as a substrate for invertebrate colonization of running water systems is connoted with very different qualities. In the most classical view, sand is considered the least diversely colonized substrate with the lowest biomass of benthic organisms (Hynes 1970, Statzner and Higler 1986), especially in large habitats (Barton and Smith 1984). Sand entering a running water system in quantities above the natural range may cause severe damages to the local habitat structure, flora and fauna (Waters 1995, Wantzen 1997, 2006); they may also influence organic matter dynamics and distribution of pollutants (Nascimento *et al*. 2012). Natural or anthropogenic loss of bank stability may cause channel braiding in rivers flowing in sandy alluvia. The survival conditions for benthic invertebrates in braided rivers are very limited, as the sediment dynamics are too high for most true benthic invertebrates; these features have recently been reviewed (Wantzen and Mol 2013) and, therefore, are not further detailed here.

Sandy habitats harbouring a faunal colonization were earlier described in lentic or low-energy areas of aquatic ecosystems, being lakes (Pennak 1940) and river sections (Ruttner-Kolisko 1961). Organisms colonizing this habitat are known to be adapted to the mobile nature of the substrate. They live either by burrowing or mining inside the substrate (endopsammic), then their shape is often worm-like, with eyes and pairwise occurring organs being reduced, or they dwell on the sediment surface (epipsammic), which requires specific adaptations to cling to the highly mobile substrate, or use sand ingested or attached particles to increase their specific weight (e.g. in live specimens of *Narapa bonettoi* it was observed that sand grains were attached to the body, Marchese 1984). The high turnover rate of the sediment often requires an r-strategy to compensate population losses through sediment mobility by high reproduction rates.

In this review paper, we focus on the global patterns of benthic invertebrates in sandy sections of rivers, gathering insights mainly from studies of Neotropical and European rivers. The main questions dealt with are as follows:

- What are the driving forces for the distribution of benthic invertebrates in sandy sections of large rivers?
- Are there global patterns discernible and if so, how do these patterns interact with the transversal (MC–floodplain) distribution of the benthos?
- How does river management interfere with the fauna of sandy rivers?

2   What are the driving forces for the distribution of benthic invertebrates in sandy sections of large rivers?

The sediment composition of a given stretch of a river depends on the size of the eroded source material, hydraulic forces, and the distance from the sediment source. The general trend is a size reduction along this gradient due to erosion effects at the surface of the sediment particle during the transport (*downstream fining*), so that the lower sections of most rivers carry sandy sediments. However, tributary influence or the passage of rivers through a mountainous section or rocky outcrops may add new larger, scaled sediments. For example, the average sediment structure of the Upper Rhine downstream of Lake Constance is gradually reducing from the confluence with the Thur River (delivering coarse alpine sediments) downwards but the particle

size re-increases strongly when crossing the Rhenanian slate mountains in its middle section. After this passage, the sediment size continues to be reduced (Droege *et al*. 1992, Uehlinger *et al*. 2008, Frings 2011). Similarly, the Paraguay River at the Brazilian–Bolivian border encounters rocky outcrops approximately every 50 km (Wantzen *et al*. 2005), which however add little amounts of large-sized particles. Rather, the Andean tributaries to the Paraguay River contribute large amounts of sediments, including larger ones than that of the Paraguay main stem. This geological feature causes a slight increase in the Paraguay River above its confluence with the Paraná River, which shows the classical downstream fining of the sediment size (Drago and Amsler 1998).

Considering the functional ecology and the benthic invertebrate assemblages of potamal river sections, it seems to be important to analyse the relationships between the sandy bottom habitats of the active bed of the MC with other sediment structures in the bank zones and floodplain environments. Only in large rivers with long distance to the sediment source, a nearly exclusively sandy character of the bottom sediments develops, and even then there are interactions with the riparian zone, e.g. the vertical clay banks on the erosional sides of lowland rivers of old landscapes (Ezcurra de Drago *et al*. 2004, Marchese *et al*. 2005, Wantzen *et al*. 2005). Large woody debris (LWD) is of great importance for the benthic fauna, as it can harbor the manifold of biomass and diversity of the sandy substrates found in rivers (Benke *et al*. 1985, Wantzen and Junk 2006).

Interaction of channel morphology with hydrodynamics implies driving forces for benthic invertebrate assemblages. A study on the Paraguay River by Blettler *et al*. (2012a) analysed the variations in the spatial distribution pattern of benthic invertebrates along large meander bends on that river. The river flow is typically concentrated in the concave side of a meander bend. It induces the larger bed shear stresses on these areas and the consequent erosion, generating scour holes with a marked depth. Considering the longitudinal distribution of benthic organisms along the thalweg track of the meander bend, the meander scour hole is a hostile area for the benthic assemblages (Wantzen *et al*. 2005). The associated rise in the mobility number explains, in turn, the high level of suspended bed sediment recorded in that area (Constantine *et al*. 2009). Continuous collisions between suspended sand grains near the bottom could cause the damage or death of invertebrates inhabiting these areas (Blettler *et al*. 2008), which explains the low density recorded at the scour hole.

The most typical bed features of free-flowing sandy potamal river sections are the subaqueous sand dunes. Sand dunes have been studied since long time ago in alluvial rivers (see Garcia (2008) for review). Dune dimensions (height and length) at a given section change depending on flow (depth and velocity) and bed sediment characteristics. They are very variable with smaller superimposed dunes developing over the large ones. In the Rhine, dunes reach heights of one to one and a half

metres (Carling *et al*. 2000; Wilbers and Ten Brinke 2003); in the Middle Loire dune lengths of 4–6.5 m and heights of 10–35 cm were measured (Claude *et al*. 2012), whereas in the Paraná system, long-term flooding led to the formation of large migrating dunes, up to 6.5 m in height and ≈320 m in length (Amsler and García 1997). However, during low water stages, Parson *et al*. measured dunes of ≈1.2–2.5 m high and possessing a range of wavelengths from 45 to 85 m, yielding a range in the dune form index (or aspect ratio; height/wavelength) of ≈0.021–0.029.

Flow varies along a given dune profile. There are typically: (i) an accelerating flow over the dune stoss side; (ii) a flow separation or deceleration after the dune crest on the lee side; (iii) a flow reattachment region at 4–6 dune heights downstream; (iv) a shear layer between the separated flow zone and streamwise flow above, which expands as it extends downstream and (v) an internal boundary layer which grows from the reattachment beneath the wake zone along the stoss slope of the next dune downstream (McLean *et al*. 1994, Best and Kostaschuk 2002). Some of these features may not be present in large rivers like the Paraná and Paraguay, e.g. the separation zone and the reattachment point (Amsler and Schreider 1992). Moreover, other features like superimposition of small dunes on the large bed forms are frequently recorded in the Paraná River. These perturbations of flow due to dunes have associated variations in the field of bed shear stresses which imply disturbances of the hydraulic habitat at a micro-spatial scale.

First studies regarding the influence of alluvial dunes on the benthic distribution were performed by Amsler *et al*. (2009) and Blettler *et al*. (2012b) in the Middle Paraná River. These authors recorded the lower benthic densities at a section over dunes located in the thalweg region, which are subject to higher bed shear stresses and mobility numbers than dunes outside that region. It is remarkable that in spite of stronger hydraulic conditions were recorded on the thalweg track, dunes located on this section were smaller (1.7 m height and 175 m length, average) than those placed outside it (2.2 m height and 230 m length, average). In addition, differences in benthic densities were also found at microhabitat scales, i.e. within-dune scales. The highest densities were found in the dune troughs, where bed shear stresses were lowest, especially in larger dunes.

A study performed with a large number of benthic samples taken along the main rivers of the Paraná River basin showed the strong influence of the bed hydraulic conditions on benthic organisms (Blettler *et al*. 2008). The densities of *N. bonettoi* (the dominant species representative of the assemblage which inhabits the mobile sandy bed), were significantly related to hydraulic variables following a 'bell-shaped' tendency, i.e. there was an optimum range of these variables where the densities are the highest. For lower or larger values out of this range the densities tend to decrease. It is well known that these kinds of curves are usual in ecological theories (e.g. niche theory, intermediate disturbance hypothesis (Connell 1978)). Specifically, the Reynolds number had the highest correlation

with *N. bonettoi* density. *N. bonettoi* showed a preference for transitory values of turbulence and a moderate shear stress.

Large-scale analyses help to understand the factors that may override the findings that were made at the habitat patch scale. For this review, one of us (M.R. Marchese, original data) analysed a large data set of 49 sampling stations along the entire Paraguay–Paraná system from 16°2′ 60″ S to 57°30′ 35″ W and 34°36′ 36″ S to 58°22′ 11″ W applying canonical correspondence analysis (CCA, using the Multivariate Statistical Package (version 3.2 for Windows, Kovach Computing Services)) on $\log_{10}$ transformed abundance data of oligochaetes of the central strip. This analysis showed that the first two axes explained 32.67% of the variance and the species-environment correlations was 0.723 (Figure 1). The ordination obtained clearly showed a latitudinal gradient from Upper Paraguay to the Lower Paraguay River explained mainly by higher density of the dominant oligochaetes species (*N. bonettoi* and *Haplotaxis aedeochaeta*) and secondarily by *Bothrioneurum americanum* and *Dero righii)* in the Upper Paraguay. In general, a trend of decrease in density and richness from Upper Paraguay to Lower Paraná was found. The unique station with higher bottom organic matter and fine sediments in the Upper Paraguay was separated and represented by *Tubifex tubifex, Nais elinguis* and *Stephensoniana trivandrana.* The Middle and Lower Paraná River formed a unique group represented as the Paraguay River by the dominance of *N. bonettoi* and *H. aedeochaeta* and secondarily higher abundances of *Aulodrilus pigueti, Pristina acuminata* and *P. leidyi* than in the Paraguay River were recorded. These species were recorded mainly in sampling stations where the percentage of fine sediments increased.

Studies on this feature in Temperate Zone Rivers are rare; however the existing ones support the given statements (Table 1). Grain size in the Rhine River was as important for

the distribution as in the other sandy rivers studied here. In the coarser grained, southern section of the Upper Rhine, *Stylodrilus heringianus* dominated the oligochaetes by 62%; in the finer grained (partly sandy) northern section *Limnodrilus hoffmeisteri* by 54% (Schmelz and Schöll, unpublished manuscript). Once the sediments become purely sandy (above and below the Rhenanian slate mountains), the oligochaete fauna becomes less diverse and *Propappus volki* clearly dominates by 60–100% (Wantzen, Schmelz and Schöll, unpublished data).

3   Are there global patterns discernible and if so, how do these patterns interact with transversal (river MC–floodplain environments) distribution of benthos?

Studies on the Paraguay–Paraná River system in the past decades have shown that there is a global pattern along longitudinal axes of this ca. 3500 km long river corridor. In the sand-dominated habitats of the river MC and large anabranchs and large secondary channels, there is a benthic invertebrate community that is adapted to the survival in mobile sand and sand dunes. This assemblage is relatively stable along the entire corridor Paraguay–Paraná River system and along the different sections of the Paraná River (Figure 2 and see studies by Ezcurra de Drago *et al.* 2004, Marchese 1987, Marchese and Ezcurra de Drago 1992, Marchese *et al.* 2002, 2005, Suriani-Affonso *et al.* 2011, Varela *et al.* 1983).

In the longitudinal dimension of the Middle Paraná River, a decrease in density, biomass, species richness and diversity was clearly observed in the MC (Ezcurra de Drago *et al.* 2007; Figure 3). The psammophilous oligochaete, *N. bonettoi* is the most typical species of this assemblage, accompanied mainly by *H. aedeochaeta, Myoretronectes paranaensis, Potamocaris*
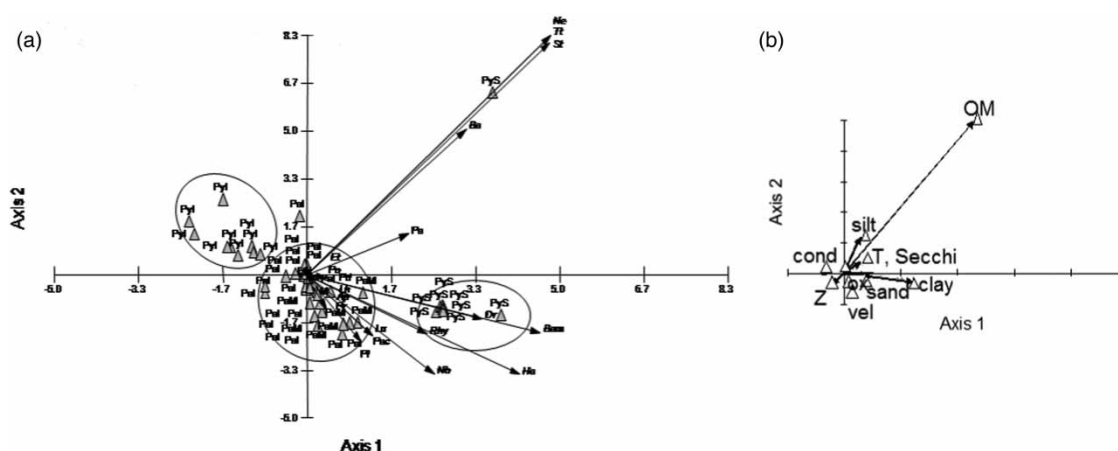
Figure 1   Ordination of the sampling sites and invertebrate data with environmental variables using CCA in the fluvial corridor Upper Paraguay–Lower Paraná River. PyS, Upper Paraguay River; PyI, Lower Paraguay; PaM, Middle Paraná River; PaI, Lower Paraná. (a) Ordination of sampling locations and the species density and (b) significant environmental variables are represented by arrows: clay percentage; silt percentage; sand percentage; OX, oxygen concentration; OM, organic matter; Vel, water velocity, pH; Z, depth; cond, conductivity. Abbreviations: AP, *A. pigueti*; Ba, *Brinkhurstia americana*; Bam, *Botrhioneurum americanum*; Dr, *D. righii*; Et, *Eiseniella tetraedra*; Ha, *H. aedeochaeta*; Lh, *L. hoffmeisteri*; Lu, *Limnodrilus udekemianus*; Nb, *N. bonettoi*; Ne, *N. elinguis*; Pa, *Pristina americana*; Pac, *P. acuminata*; Pd, *Paranadrilus descoleii* Pj, *Pristina jenkinae*; Pl, *Pristina leydii*; Po, *Pristina osborni*; Rhy, *Rhyacodrilus* sp.; St, *S. trivandrana*; Tt, *T. tubifex*.

Table 1 Synopsis on benthic invertebrate data from large, sandy rivers

| Continent	River system	Density and dominant taxa	Biomass	Source
North America	Athabasca	10,000–40,000 ind m^{-2} (Chironomids)	0.2 g m^{-2}	Barton and Lock (1979)
	Sand River with moving dunes (6 to 15 m high)	12,000–78,000 ind m^{-2} (two Chironomid spp.)	Very low biomass	Soluk (1985); Soluk and Clifford (1984)
South America	Paraguay–Paraná system	3600–49,600 ind m^{-2} in the straight–transitional sectors, and 700–6000 ind m^{-2} in floodplain lakes	Low	Ezcurra de Drago et al. (2004); Marchese (1981); Marchese and Ezcurra de Drago (1992); Marchese et al. (2005)
Northern Eurasia	Volga	100 ind m^{-2} (very small gammarids), and high density of Oligochaetes and Chironomids		Kontastinov (1979); Mordukhai-Boltovskoi (1979)
	Angara	14,000 ind m^{-2} (all taxa)	2.2 (g m^{-2})	Greeze (1953)
	Amur River	Lowest density	0.02–0.01 (g^{-2}) wet weight	Bogatov (1978)
Central Europe	Lower Rhine and sandy zones of Upper Rhine	>10,000 ind m^{-2} (small oligochaetes, e.g. P. volki)	Very low biomass	Wantzen (1992)
	Loire River	11,000–26,000 ind m^{-2} (MC sites), 12,000–18,000 ind m^{-2} (FWB)		Bacchi and Berton (2001)
East Asia	Ganges	High Amphipods density	Very low biomass	Dudgeon (1995)
Africa	Nile	High Chironomid density	Very low biomass	Monakov (1969)
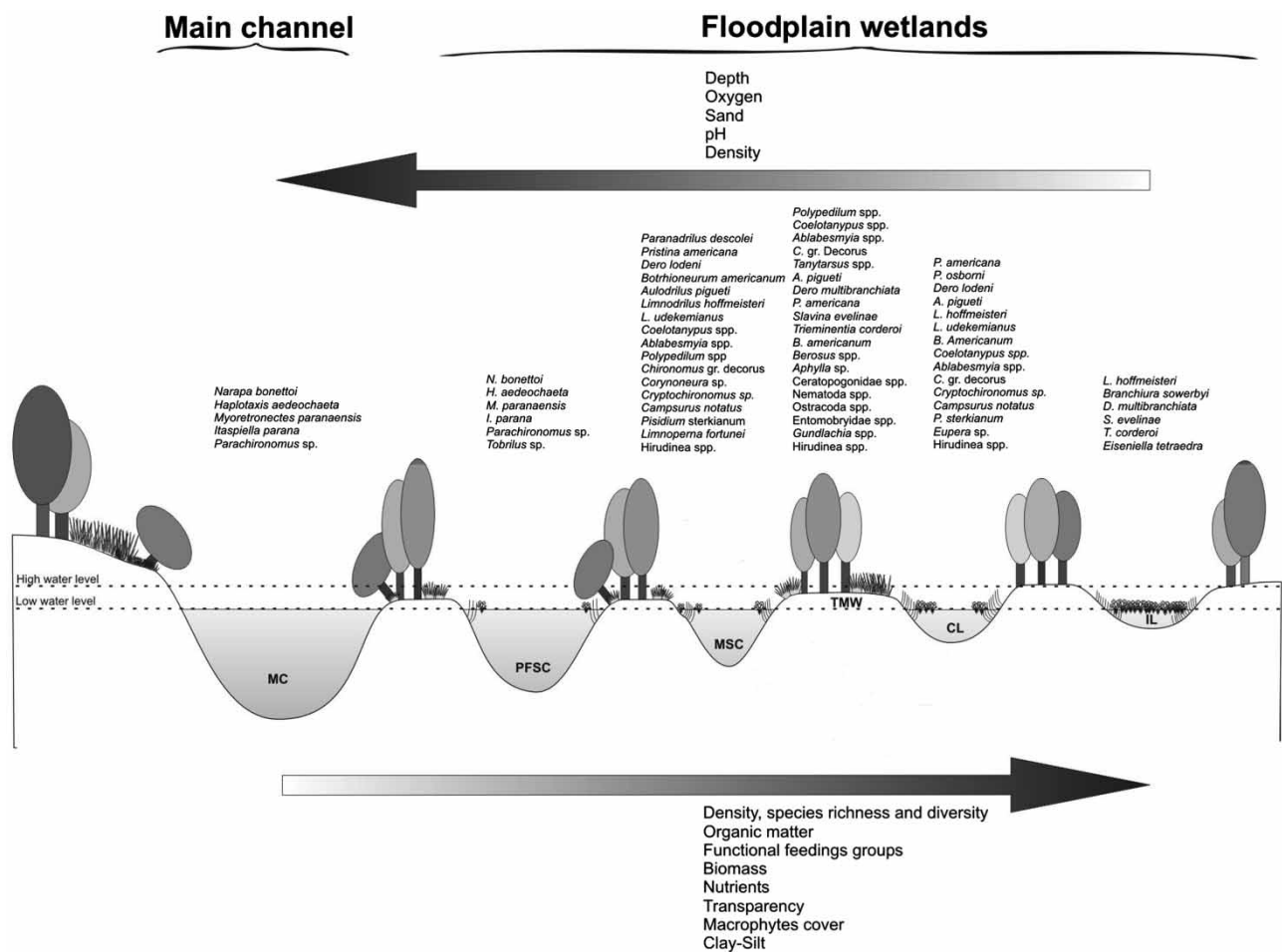
Figure 2 Transversal zonation of the most common benthic invertebrates of the Paraguay–Paraná River system Abbreviations: MC, main channel; PFSC, permanent flow secondary channel; MSC, major secondary channel; CL, connected lake; IL, isolated lake; TMW, temporal marginal wetland. The species included are the most frequent ones. Modified from: Ezcurra de Drago *et al*. (2007).

sp. and *Tobrilus* sp. and secondarily by *Lopescladius* sp., *Djalmabatista* sp. and *Parachironomus* sp. These are rheophilous species typically found in sandy and organic-matter-poor sediments of fast-flowing habitats (Blettler *et al*. 2008, Marchese *et al*. 2005, Ezcurra de Drago *et al*. 2007). The meandering sectors of the Paraguay River, including a large number of mesohabitats in an erosion–deposition pattern, caused a higher turnover of species (β diversity according Harrison *et al*. (1992)) and γ diversity than the straight sectors (Marchese *et al*. 2005).

On the other hand, there was a high diversity and a high species turnover in the transversal axis between MC central strip, the lateral river banks and the floodplain habitats (Figure 2, Marchese 1981, Marchese and Ezcurra de Drago 1992, Ezcurra de Drago *et al*. 2004, Marchese *et al*. 2005). Beta diversity was higher in the floodplain habitats than in the MC central strip, depending on the degree of connectivity of those environments and the hydrological phases of the rivers. Thus, the species turnover was higher in connected than isolated floodplain lakes. There
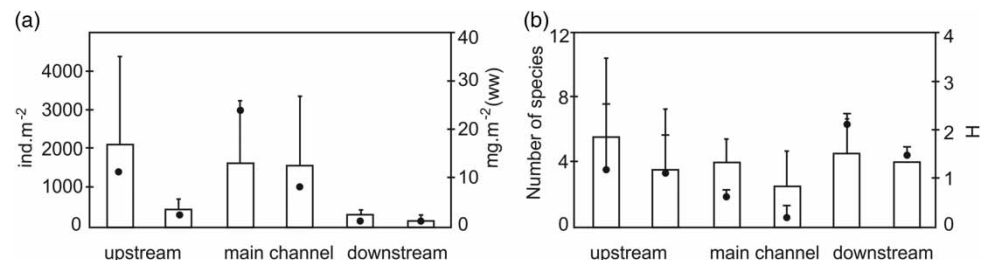
Figure 3 Distribution of benthic macroinvertebrates in the longitudinal dimension of the MC and permanent flown secondary channel of the Paraná (mean values and standard deviations, $n = 3$). (a, left graph): Density (ind m^{-2}, bars, left axis), biomass (wet weight; mg m^{-2}, line, right axis). (b, right graph): Number of species (bars, left axis), Shannon's diversity index (line, right axis). Modified from Ezcurra de Drago *et al*. (2007).

were two opposite gradients for habitat (stability of habitats and connectivity) that resulted in a higher diversity in the temporal marginal wetland habitats. A similar bell-shaped curve has been found for European rivers by Ward *et al.* (1999).

A very detailed study on the benthic invertebrate fauna of the Loire River (Bacchi and Berton 2001) revealed very similar results considering the biodiversity and density of benthic invertebrates. The study sites at the Middle Loire (La-Charité-sur-Loire and Bréhémont) revealed a similar pattern of habitats with a mobile central strip of the MC, presenting underwater sand dunes, and a series of lateral floodplain water bodies (FWB), most of which became entirely connected to the river and disturbed by the current during the flood season in winter and spring. Taking the number of 136 identified taxa as 100%, 89–96% of the taxa were found in the FWB, while 68–73% were found in the MC. After spring floods, an increase of taxon richness in FWB was observed due to a superposition of resident taxa and MC taxa that arrived there by drift. Only 3–10% of the taxa were exclusively found in the MC, while 27–31% were specific to the FWB. Annual average abundances, however, were quite similar between MC sites (11,000–26,000 ind m^{-2}) and FWB (12,000–18,000 ind m^{-2}). This pattern coincided with a turnover between a rather species-poor oligochaete-dominated faunal assemblage in the MC (78% Oligochaetes, 17% Chironomids, Shannon Index 0.67, equitability 0.29) and a species-rich, chironomid-dominated fauna of the FWB (26% Oligochaetes, 51% Chironomids, Shannon Index 1.34, equitability 0.40). Multivariate analyses confirmed the results found for the Paraguay–Paraná River system: concentrations of sand and organic matter, as well as hydraulic patterns such as Reynolds numbers were the most important descriptors for the habitat structures in the Loire River (data not shown).

Benthos sampling employing the diving chamber and large engineering drags in the MC of the Rhine River along a 700-km longitudinal transect revealed a nearly identical pattern. From the coarser to the finer sediment sections in two gradients (Northern to Southern Upper Rhine and, below the Rhenanian slate mountains, from the Middle to the Lower Rhine), large-bodied taxa (Ephemeroptera, Trichoptera and Amphipoda) decreased in diversity and density, whereas the density of few small-bodied, sand-adapted species increased. Sand dunes were dominated by the minute oligochaete *P. volki*, which occurred in very high densities of up to 40,000 ind m^{-2} (Wantzen 1992). In a literature survey we found a large body of support for this species-poor, high-abundance but low-biomass pattern of sand-dominated potamal sections of rivers worldwide (Table 1). There are biogeographic patterns that define which taxonomic group is dominating the faunal assemblages. While some Eurasian and Asian rivers seem to be dominated by sand-dwelling amphipods, most other rivers show the oligochaete – chironomid dominance pattern described above. The crucial environmental parameters decisive for these contrasting patterns are the homogeneity but high change rate of
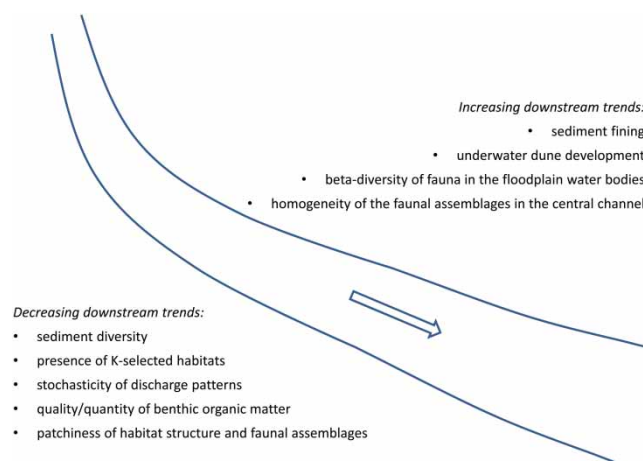

Figure 4 General trends of sediment-benthos-relationships along the river-floodplain continuum.

the habitat structure in the MC and the inverse patterns in the lateral habitats (floodplain environments).

Comparison of this feature in several sections of the river system (Upper Paraguay: Marchese *et al.* 2005; Lower Paraguay: Ezcurra de Drago *et al.* 2004; Paraná River: Marchese *et al.* 2002 and unpublished data) applying identical methods showed that: (i) this gradient was similar in different rivers, (ii) there was a low importance of water chemistry/oxygen content and salinity (oxygen concentrations were always sufficiently high and the water salinity low, both parameters are very important for the presence of *N. bonettoi* (Blettler *et al.* 2008)), (iii) grain size was the key factor to explain upstream–downstream benthic gradients and finally (iv) organic matter content was a secondary parameter to explain the distribution of these species (Figure 4).

4 How does river management interfere with the fauna of sandy rivers?

The management of sediments in rivers has so far been dealt with almost exclusively under the aspect of managing its physical aspects, i.e. avoidance of situations that bring along unwanted consequences for water use, urban planning or navigation. These situations were either lacking sediments causing unwanted erosion (hungry rivers), which require the addition or terrestrial transport of sediments from above the dam to the downstream site or excess of sediments that impede navigation and require dredging. Sediment management considering the well-functioning of the ecosystems, including maintenance of biodiversity and ecosystem services has yet rarely been an important issue of river management plans (with some exceptions of the introduction of gravellish spawning sites for salmon). The lessons learnt from hydrosystems such as the Paraguay–Paraná River system, which are still in a nearly natural state in large parts, can and should be integrated into management of strong and heavily modified river systems, as they are found in Central Europe and North America.

In many European Rivers, the originally known potamal fauna has vanished due to water pollution in the 1950–1970s and it has not recovered afterwards, even though the water quality has improved. Species known by the Rhine studies from the beginning of the twentieth century (Lauterborn 1916, 1917) have not recovered in the lower sections (Tittizer *et al*. 1991), e.g. the mayflies *Oligoneuriella rhenana, Palingenia longicauda, Potamanthus luteus,* the stoneflies *Brachyptera braueri, Oemopteryx neglecta, Leuctra fusca, Isoperla grammatica* and the caddis flies *Hydropsyche pellucidula, Tinodes waeneri, Potamophylax nigricornis*, to name a few. The reasons for the lack of re-establishment of these species are largely unknown. Several hypotheses can be developed on the grounds of sediment dynamics.

4.1   *Removal of the natural habitat structure and dynamics causes that stenoceous species still cannot recover*

This may apply to habitat specialists such as the large stonefly and caddis fly species. One of the most dramatic changes coming along with the regulation of rivers for navigation has been the removal of LWD (Sparks *et al*. 1998). This type of organic matter does not only deliver a substrate to cling on, but also offers food sources in the form of biofilms and trapped organic matter, including living drifting smaller organisms that will be preyed upon by large aquatic insect species. In a natural river, LWD also releases both food and large substrate particles to its downriver sections and may thereby enrich the fauna on sandy substrates. Moreover, LWD and the re-established woody vegetation strongly influence the sediment dynamics of rivers by provisioning of slow-flowing sections of small-sized sediments which would be highly mobile otherwise (Montgomery and Piegay 2003, Gurnell *et al*. 2005, Rodrigues *et al*. 2007), and K-selected habitats of a long residence time, which allow the occurrence of large-bodied, long-lived invertebrate taxa. In a study in Brazilian running water systems, large-bodied mayflies and dobson flies were found exclusively on substrates that had a sufficiently long residence time (Wantzen 2006). It can be anticipated that the re-establishment of natural sediment dynamics including the dynamics of LWD would considerably increase the biodiversity of the lower, sandy sections of impacted rivers. Due to the intensive use of these rivers for navigation, a complete restoration of the original situation will not be possible, but even a small improvement of the environmental quality could increase its biodiversity.

4.2   *Stabilization of naturally dynamic sediments and introduction of artificial habitats causes that stenoceous species still cannot recover*

River training also tends to stabilize underwater structures in rivers, rather than allowing their natural dynamics. Fixing sediment banks and reducing sediment movements can negatively affect the potamal fauna in several ways. There is a general effect of hydrodynamics on plankton (Van Den Brink *et al*. 1993), resulting in a potential reduction of food sources for filter-feeding organisms and micro-particle gatherers that use the sand dunes as filters for plankton, such as the small oligochaete species such as *N. bonettoi* and *P. volki*. Another impact is the reduction of the self-purification of the sediment filter, which acts as 'the river's liver' (Fischer *et al*. 2005), i.e. the interstitial pore space of fixed sediment structures tend to clog and does not fulfill its filtering function any more. As a result, organisms depending on freshly deposited organic matter and the following food chain members that they support will decrease.

In managed rivers worldwide, we find stabilized riverbanks using rip-rap, and locally groyne fields that stabilize river flow for navigation (Brunke *et al*. 2002). In terms of the native sand-bed fauna, this management has severe consequences, as it introduces permanent habitats that favour the occurrence of highly competitive invasive species. In the case of the Rhine and other European rivers, over the past years have experienced a roundabout of invasive species, mostly arriving via the Danube-Main-Channel, each of which being more competitive than the precedents (Bij de Vaate *et al*. 2002, van Riel *et al*. 2006, Uehlinger *et al*. 2008), currently accumulating in the voracious amphipod *Dikerogammarus villosus*, which is a strong intraguild and unselective predator (Dick *et al*. 2002, Hesselschwerdt *et al*. 2008, Piscart *et al*. 2010), and benthic gobiid fish, which are both piscivorous and invertivorous (Borcherding *et al*. 2011). Moreover, these invasive species provide a large potential of parasites and diseases for the native fauna, which is only scarcely known. We alert that further 'rip-rapping' of river banks, as it is currently seen in the Loire river, may have deleterious effects on the native invertebrate fauna by providing habitat of invasive predators and 'Trojan horses' carrying parasites, and by impeding the natural habitat dynamics. Similar effects are observed in tropical rivers, where the introduction of sheet piles has opened the expansion routes for invasive benthic organisms that depend on solid substrates, such as the golden mussel *Limnoperna fortunei* (Darrigran 2002, Ezcurra de Drago *et al*. 2004, Oliveira *et al*. 2011). In the Lower Paraná River (Upper Delta area), a series of road bridges built across the floodplain river caused alterations of the benthic fauna as a consequence of erosion under the bridges due to the turbulent flow, mainly at the pillars, that affects the surrounding bottom. However, the typical species assemblage related to mobile sandy substrates recolonized the habitat successfully in less than one year (Blettler and Marchese 2005).

Invasive species themselves may also directly change sediment structure. The invasion of *Chelicocorophium curvispinum*, a tube-spinning amphipod, changed the surface structure of solid and sandy substrates (van Riel *et al*. 2006) and limited the colonization of the hyporheic pore space below the 'carpet' of tubes (Wantzen 1992). The shells of invasive *Corbicula* clams change the substrate composition of rivers and lakes worldwide (Werner and Rothhaupt 2007), apart from the direct concurrence for

phytoplankton between invasive and native mussels settling in sandy sediments (Darrigran 2002).

5 Conclusions

This review has underlined the central role of grain size, sediment dynamics and of the connectivity between MC and floodplains for the composition of benthic invertebrates in the potamal of large rivers. The apparent homogeneity of low-diverse, highly specialized assemblages in the MC is in sharp contrast to the high β and γ diversity within and between the floodplain habitats along the river corridor. MC and floodplain faunae have reciprocal relationships, as floods contribute to MC organisms to the floodplain and vice versa (Figures 2 and 4). Sediment dynamics and composition are often strongly modified by river management, contributing to the decline or the non-recovery of native species even after the improvement of water quality. Challenging research questions in this context refer to the distance of hard-substrate stepping stones for both native and invasive species and the ecohydraulical preferences of these animal groups in order to adapt to river engineering towards an increased resilience of the original fauna. Providing enough space for rivers (Malavoi *et al.* 2003, Piegay and Hicks 2005, Florsheim *et al.* 2008), longitudinal and transversal connectivity (Ward *et al.* 1999) and sediment dynamics seem to be the most important elements of river management in order to support biodiversity and important ecosystem services such as water purification. In the context of densely populated river valleys, this goal is very difficult to achieve, therefore additional engineering efforts and wise operation of dams and weirs are needed to improve the biodiversity and the functionality of river ecosystems.

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