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# A river's liver – microbial processes within the hyporheic zone of a large lowland river

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**Abstract.** Little is known on microbial activities in the sediments of large lowland rivers despite of their potentially high influence on biogeochemical budgets. Based on field measurements in a variety of sedimentary habitats typical for a large lowland river (Elbe, Germany), we present results on the abundance and production of sedimentary bacteria, the potential activity of a set of extracellular enzymes, and potential nitrification and denitrification rates. A diving bell was used to access the sediments in the central river channel, enabling us to sample down to 1 m sediment depth. Depth gradients of all measures of microbial activity were controlled by sediment structure, hydraulic conditions, as well as by the supply with organic carbon and nitrogen. Microbial heterotrophic activity was tightly coupled with the availability of carbon and nitrogen, whereas chemolithotrophic activity (nitrification rate) was related to the available surface area of particles. In the central bed of the river, bacterial production and extracellular enzyme activity remained high down to the deepest sediment layers investigated. Due to the large inner surface area and their connectivity with the surface water, the shifting sediments in the central channel of the river were microbially highly active There, vertically integrated bacterial production amounted to 0.95 g C $m^{-3}$ $h^{-1}$, which was 2.9 to 5.5 times higher than in the nearshore habitats. We conclude that carbon and nitrogen cycling in the river is controlled by the live sediments of the central river channel, which thus represent a ''liver function'' in the river's metabolism.

## Introduction

Large rivers with a relatively diverse morphological structure have the potential of high microbial activity and thus of an intense turnover of organic matter and inorganic solutes. It can be deducted from the analysis of biogeochemical budgets that river networks remove 37–76% of the total N-input mainly via denitrification, with a high proportion being removed in the high order sections of the rivers (Seitzinger et al. 2002). Large rivers are therefore important for the biogeochemical budgets of catchments (Behrendt and Opitz 1999; Seitzinger et al. 2002), even if the water depth-related retention decreases along a river continuum (Allan 1995; Alexander et al. 2000). Large rivers also process high amounts of organic carbon (Fischer et al. 2002) and thus play a pivotal

role in the carbon biogeochemistry of estuarine and coastal regions of the sea (Moran et al. 1999; Raymond and Bauer 2001). However, it is largely unknown how this metabolism is related to specific morphological structures present in rivers less impacted by human alterations.

In streams, these microbial processes occur to a large extent in the hyporheic zone (Pusch et al. 1998; Storey et al. 1999; Fischer and Pusch 2001). Microbially mediated chemical dynamics in the hyporheic zone exert control on materials cycles in the active channel and associated riparian vegetation (Stanford and Ward 1993). Availability of substrates and of terminal electron acceptors is the major determinant of microbial activity (e.g. Hedin et al. 1998). Therefore, gradients of physico-chemical conditions should lead to a spatial separation of the energy-yielding microbial processes. These gradients occur in different spatial scales – e.g. in a decimeter scale in a sediment profile, and in a micrometer-scale within the biofilm. By this, the intrinsic heterogeneity of sediments and the heterogeneity of the sedimentary biofilm allow the parallel existence of seemingly antagonistic processes, for example denitrification (anaerobic) and nitrification (aerobic) (Hedin et al. 1998; Storey et al. 1999; Gieseke et al. 2001). This functional diversity on a spatial scale can be enhanced in rivers by the temporal variability of hyporheic flow paths (Brunke and Gonser 1997; Hinkle et al. 2001), and by circadian variation in oxygen and nutrient concentration of the surface water that is transported into the hyporheic zone (Kaplan and Bott 1989). Large rivers are often characterized by frequent turnover of sediment structures by bedload transport (e.g. Elliott and Brookes 1997; Carling et al. 2000; Sauer and Schmidt 2001). Consequently, geomorphological and hydrodynamic features also influence the spatial characteristics of biogeochemical gradients in the sediments (Vervier et al. 1993; Fischer et al. 2003; Wilczek et al. 2004).

Despite the obvious importance for biogeochemical budgets, there still exists great uncertainty about the functioning of the turnover of matter in large rivers, and the role of the hyporheic zone, because of the relatively small ratio of sediment surface to the discharge of the river. General concepts of river ecology emphasize the importance of the hyporheic zone for ecosystem functioning (e.g. Ward 1989; Townsend 1996), but microbial activities in the sediments of large lowland rivers are widely unknown. This gap between theoretical significance and lack of sound data is due to a variety of technical problems researchers face in large rivers. Few data exist on the general level of microbial activity there, and even less on potential differences in various sediment types (habitats) on the river bottom, which would enable ecologists to define hot spots of microbial activity. This information is needed to broaden our view on ecosystem functioning of large rivers, and to evaluate the impact of river engineering or river restoration measures on in situ microbial metabolism (Dahm et al. 1998; Ward et al. 2001).

Hence, our study aimed at the following questions: (i) What are the levels of microbial activity to be found in various types of sediments in a lowland river? (ii) What is the vertical extension of the microbially active hyporheic

zone in a large lowland river? (iii) Which factors control microbial activity in the hyporheic zone, and how do available electron donors and terminal electron acceptors influence microbial activity in different types of river sediments? (iv) What are the implications for the functioning of large-river ecosystems?

## Material and methods

### *Study sites and sampling procedure*

Samples were taken in October 2001 at two sites of the 8th order lowland river Elbe in Germany: (i) downstream of Dresden around river km 426.5 (51°03′ N, 13°40′ E, = German Elbe km 61.5) and (ii) upstream of the city of Coswig around river km 598 (51°51′ N, 12°28′ E, = German Elbe km 232.5) (Figure 1, Table 1). Two habitats were sampled at each site, the center of the riverbed within the main river channel, and the nearshore area of the river. At each habitat, three replicate locations were sampled (distance between locations 100 m each) with the exception of the nearshore zone at Dresden, where only one location could be sampled. Samples from the river channel were taken using a diving bell (base area 6 $m^2$) run by the Office of Water and Navigation Magdeburg. The diving bell was operated with the internal air pressure being increased according to the water depth where the sediments were investigated. Samples from the nearshore zone in Dresden were collected on the right bank that was artificially reinforced by large stone embankment. Further downstream, the banks of the Elbe are in long sections protected by stone groynes (wing-dams, 20–30 m long) perpendicular to the flow direction in a distance of about 100 m from each other (Figure 1). The nearshore sediments in the flow-reduced areas between groynes (Brunke et al. 2002) were sampled at Coswig. The central riverbed in Dresden consisted of a framework of coarse sediments (gravel and stones) filled by sand, whereas at Coswig it consisted of homogenous coarse sands. It was more heterogenous between the groynes, where it consisted of a matrix of coarse gravel and also contained sand and fine organic components (Table 2).

*Table 1.* Discharge characteristics (daily means, observation time 1991–2000) of the Elbe River at the sampling sites Dresden and Coswig.

| | Dresden[a] ($m^3$/s) | Coswig[b] ($m^3$/s) |
|---|---|---|
| Minimum discharge | 89.1 | 87.5 |
| Mean annual minimum discharge | 109 | 126 |
| Mean discharge | 307 | 331 |
| Mean annual maximum discharge | 1320 | 1250 |
| Maximum discharge | 1740 | 1940 |
| Discharge in October 2001 | 210 | 250 |

[a]Gauging station Dresden, German Elbe km 59.
[b]gauging station Lutherstadt-Wittenberg, German Elbe km 214.

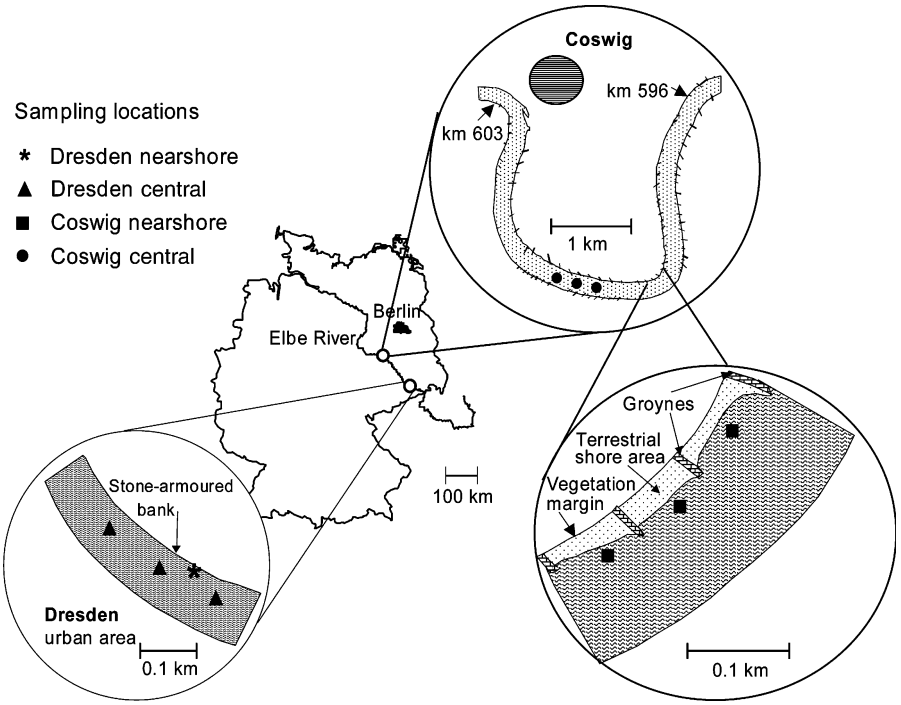


*Figure 1.* Location of the study sites: Map of Germany showing the river Elbe, and details of the investigated river reaches and sampling locations.

*Table 2.* Sediment characteristics and channel morphometry of the sampling sites Dresden and Coswig (mean ± sd, $n = 3$).

| | Dresden | | Coswig | |
|---|---|---|---|---|
| | Central riverbed | Nearshore riverbed[a] | Central riverbed | Nearshore riverbed |
| d10 (mm) | 1.1 ± 0.4 | 0.6 | 0.82 ± 0.34 | 0.59 ± 0.07 |
| d50 (mm) | 13.6 ± 3.2 | 44.0 | 2.4 ± 0.9 | 3.4 ± 0.9 |
| d60 (mm) | 19.0 ± 3.2 | 47.6 | 2.9 ± 1.0 | 4.4 ± 1.0 |
| $S_o$ | 0.24 ± 0.04 | 0.11 | 0.53 ± 0.06 | 0.37 ± 0.04 |
| Fraction < 5 mm (%) | 35 | 17 | 88 | 68 |
| Water depth (m) | 2–3 | 0.5 | 2–3 | 0.5–1.2 |
| Total channel width (m) (width of nearshore area) | 120 (30) | | 120 (60) | |

[a]Dresden nearshore, $n = 1$.
$S_o$ = sorting coefficient $(d10/d60)^{0.5}$. Nearshore areas consisted of stone embankments in Dresden and of flow-reduced areas between groynes in Coswig.

At each location, piezometers (steel pipes, internal diameter 5 cm) with perforations (diameter 5 mm) were inserted into the sediment down to four depth layers (0–5, 20–25, 50–55, 100–105 cm). In the following, these depth levels are described as 5, 25, 55 and 105 cm depth. For the collection of sediment, 10 l of interstital water were extracted with a hand pump after discarding the first two liters (Bou and Rouch 1967; Brunke and Fischer 1999). The particulate fraction passing a 90 μm mesh net is referred to in the following as mobile fine interstitial particles (MFIP) and was analyzed separately in order to examine its role as substrate and colonization site. The fraction $>90$ μm was collected as sediment samples. Subsamples were taken from each layer in order to determine bacterial abundance, production, potential denitrification and nitrification rates, and the activity of four extracellular enzymes ($\beta$-glucosidase, phosphatase, leucine-aminopeptidase, exo-1,4-$\beta$-glucanase). Samples were immediately stored on ice until being processed in the laboratory within 48 h. Additionally, loss on ignition, carbon, and nitrogen content were determined from the sediment samples. The latter variables were also determined for the MFIP. Thus, results on sediment characteristics refer to the $<5$ mm fraction at all sampling sites independent of their overall sediment characteristics, which facilitates comparisons. Additionally, some of the results were extrapolated on a river bottom area unit considering the differing particle compositions, as described in the calculations section.

Hyporheic water was collected immediately after the sediment samples were taken, by inserting a submersible electric pump into the piezometer. In these samples, chlorophyll a and physicochemical variables were analyzed. Water chemistry was not measured in 5 cm sediment depth, because in this depth uncontrolled mixing with pelagic water can occur during the sampling procedure. Samples from river water were collected from the center of the river flow.

### *Chemical analyses*

Nitrate, nitrite, sulfate, and chloride were analyzed using a ion chromatograph (Shimadzu) equipped with suppressor technique to reduce background conductivity. Ammonium concentrations were determined spectrophotometrically (Hach DR/2000, Loveland, Colorado, USA) modified for small sample volumes according to the German standard methods (DEW 1985). Phosphate was measured spectrophotometrically according to the German standard methods (DEW 1985). The results are given for $NO_3$-N, $NO_2$-N, $NH_4$-N, $PO_4$-P, or $SO_4$-S. At Coswig, oxygen content of the interstitial water was measured *in situ* using an aluminum-coated oxygen microsensor (Microx TX Microoptode, PreSens, Germany) with a spatial resolution of 1 cm. In each sediment depth, six replicated measurements were performed in steps of 5 cm in the mid-river habitat and of 1 cm in the nearshore habitat.

*Sediment composition*

Sediments (10 l) were taken from each location, dried, and sieved through a standard set of sieves comprising mesh sizes from 63 μm through 63 mm in order to examine the particle size distribution and the sorting coefficient ($S_o$ = d10/d60)$^{0.5}$ of the sediments.

Total particulate organic matter (POM) was determined as loss on ignition. Subsamples of 15–25 g wet weight were dried to constant weight at 105 °C, and subsequently combusted for 6 h at 550 °C in order to determine POM as ash-free dry mass. Particulate organic carbon (POC) and nitrogen (PON) content were determined using a CNS Analyser (Vario EL, Elementar Analysensysteme GmbH). About 50 g of the dried sediment samples were ground with an analytical ball mill (Pulverisette 6, Fritsch) for 15 min. Triplicate subsamples were filled into cylindrical silver foil capsules (9 mm height, 5 mm diameter; Lüdi AG, Flawil, Switzerland) for analysis. Inorganic carbon was removed with 1 M HCl. The calibration curve was established using acetanilide. Hot ethanol (90%, 78 °C) was used for the extraction of phytopigments. Extraction was applied for 12 h at room temperature in the dark. The clear ethanol-pigment-mixture was used to determine chlorophyll *a* and phaeopigments with a spectrophotometer (UV-2401 PC, Shimadzu) according to the German standard methods (DEW 1985).

*Bacterial production*

Subsamples of 1 cm$^3$ sediment were taken from each depth and weighed into precombusted 10 ml centrifuge vials containing 4 ml of fresh, filtered (0.2 μm pore size) river water. The vials were then kept at 4 °C until the experiment, which was started within 36 h after sampling. Bacterial production was measured using the leucine-incorporation method (Kirchman 1993) modified for use in river sediments (Fischer and Pusch 1999). We used L-[U−$^{14}$C]-leucine (Amersham Ltd., specific activity 11.4 GBq/mmol) diluted with cold L-leucine to a specific activity of 148 Bq/nmol leucine, and incubated the samples in vials at 20 °C with gentle shaking. For each habitat, six controls (two for each depth layer) were fixed with 3.2% formaldehyde (final concentration) immediately at the start of the incubation. Bacterial carbon production was calculated from leucine incorporation assuming 7.3 mol% leucine in total protein, and a carbon/protein ratio of 0.86 (Simon and Azam 1989). Measurements at the various sediment depths were integrated in order to calculate total bacterial production in the uppermost 1 m sediment layer.

*Bacterial abundance*

Subsamples for bacterial cell counts were taken from the supernatant of the incubated samples, after a 10 min sonication step and rigorous vortexing. They

were diluted with a sterile-filtered aqueous solution of 3.5% formaldehyde, 0.85% NaCl, and 1 mM pyrophosphate. Bacteria were stained using 4′,6-diamidino-2-phenylindol (DAPI) (Porter and Feig 1980) at a final concentration of 10 mg/l. After 40 min. of dark incubation, bacteria were filtered onto black polycarbonate filters (Nuclepore, pore size 0.2 μm) and mounted on slides using anti fading solution (AF1, Citifluor, London). At least 200 bacteria within at least 10 microscopic fields were counted by epifluorescence microscopy (Nikon FXA Microscope, HBO 100 W, Ex 330–380, DM 400, BA 400, immersion objective CF N DIC Plan Achromate 100×). Bacterial biomass was estimated using the abundance data from the Elbe sediments, and cell volumes determined in a comparable lowland river (Spree, Germany; Fischer et al. 2002). Turnover times of bacterial carbon were then calculated as biomass/production.

*Denitrification potential*

The acetylene ($C_2H_2$) block method (Sørensen 1978; Seitzinger et al. 1993) was used to determine the potential denitrification rate. The $C_2H_2$ block method is based on the linear accumulation of $N_2O$ during incubation of sediments with $C_2H_2$ added in order to inhibit the bacterial reduction of $N_2O$ to $N_2$. Assays were initiated within 36 h after sampling. About 10 to 20 g wet sediment samples were filled into 250 ml bottles sealed by rubber plugs. Headspace was replaced by $N_2$ for 20 min; 50 ml of $N_2$-saturated, sterile filtered river water with $KNO_3$ (1 mM) and glucose (1 mM) as carbon source was then added with a syringe in order to provide optimal conditions for denitrification. After 30 min of preincubation on a shaker (150 rpm, 25 °C), 10 ml $N_2$- and $C_2H_2$-saturated site water was injected to each sample. The first $N_2O$ analysis was carried out 30 min after $C_2H_2$ injection. Samples were incubated for 5 h on a shaker at 23 °C and $N_2O$ was analyzed using a gas chromatograph (Shimadzu GC-17A) equipped with a $^{63}Ni$ electron capture detector (oven temperature 50 °C, detector temperature 300 °C, nitrogen carrier gas flow 30 ml $min^{-1}$). $N_2O$ concentrations in the samples were calculated from the measured headspace concentration (Dahlke and Remde 1998). All values for denitrification rates are given in $N_2O$-N. Because the production of $N_2O$ was found to be linear, denitrification rates were estimated by the amount of $N_2O$ after preincubation and after 5 h incubation.

*Nitrification potential*

Potential nitrification rates were obtained by the measurement of the accumulation of nitrite in subsamples containing $KClO_3$ inhibiting the oxidation of nitrite (Belser and Mays 1980; Wolff and Remde 1998). Assays were initiated within 36 h after sampling. About 30 to 40 g wet weighed sediment samples were filled into 50 ml tubes and covered with 20 ml buffer (0.33 mM $MgSO_4$,

0.18 mM $CaCl_2 \cdot 3H_2O$, 8.5 mM NaCl, 0.01 M phosphate buffer, pH 7.6) and 1 ml $KClO_3$ (3 mM). After 30 min of preincubation on a shaker (200 rotations $min^{-1}$, 25 °C), 1 ml $NH_4Cl$ (3.7 mM) was added and the first subsample for nitrite measurement was taken. The second subsample was taken after 4 h, and nitrite was detected as described above. Preinvestigations showed that the incubation period of 4 h was within the linear phase of nitrite accumulation.

*Extracellular enzyme activities*

The action of extracellular enzymes usually marks the first step in the microbial degradation of organic compounds. It can limit the rate of substrate uptake by microorganisms, and consequently their growth (Chrost 1991). Because extracellular enzymes are substrate-specific, the measurement of EEA provides insight into the specific functional profile of microbial communities (Sinsabaugh and Linkins 1988). Fluorogenic substrate analogues (methylcumarinylamid (MCA)-substrates and methylumbelliferyl (MUF)-substrates, Sigma) were used to measure the potential extracellular enzyme activities ($V_{max}$) of leucine aminopeptidase, $\beta$-glucosidase, exo-1,4-$\beta$-glucanase and phosphatase (Hoppe 1993; Marxsen et al. 1998). These enzymes were chosen because they hydrolyse the major organic constituents (proteins, carbohydrates and organophosphoric esters) of allochthonous and autochthonous origin. Three replicates and two controls of each sediment sample were prepared using 3 g of wet sediment and 8 ml of filtered (0.2 μm) river water. After boiling the controls for 30 min, 1 ml of the substrate analogue (saturation concentration) was added to replicates and controls. The samples were incubated for 1–2 h at 22 °C in the dark under continuous shaking, and killed by boiling for 5 min. When cooled down to room temperature, 1 ml of 0.1 M alkaline glycine buffer (pH 10.5) was added. To samples used for measuring phosphatase activity, the glycine buffer was added before boiling. After centrifugation (5 min at $4000 \times g$), hydrolysis of the substrate analogue was measured by determining the fluorescence of the supernatant (Shimadzu RF-5001 PC spectrofluorometer, 1.5 nm slit, 360 nm (MCA) or 365 nm (MUF) excitation, 440 nm (MCA) or 450 nm (MUF) emission). Standard MCA (7-amino-4-methyl-coumarin) solutions and standard MUF (4-methyl-umbelliferone) solutions were used for calibration.

*Calculations and statistical analyses*

Spearman rank correlations were used to reveal relationships between bacterial variables and environmental factors. Data were then $\log_{10}$ transformed, and two-factor analysis of variance was used to test for possible effects of habitat and sediment depth on hyporheic water chemistry, particulate organic matter, and bacterial activity. Multiple comparisons were made with Tukey's HSD

test. Analyses were performed with the software SPSS (release 9.0, SPSS Inc.). Curve fittings and regression calculations were made using Origin 6.1 (Microcal Software Inc.).

In order to relate the measured bacterial activity to in-situ conditions, the particle size distribution of *in-situ* sediments was considered. Because significant proportions of the total sediment had particles sizes $>5$ mm that could not be sampled with the piezometers (Table 2), we first calculated the surface area of all particle sizes, assuming spherical shapes and using the radius of the arithmetic mean in each size class. We set this area as 1, and subtracted the proportion of surface area that was provided by particles $>5$ mm. Thus, the maximal factor 1 would indicate that all sediments were smaller than 0.5 mm. The resulting factors were 0.88 for Coswig central riverbed, 0.72 for Coswig nearshore riverbed, 0.43 for Dresden central riverbed and 0.18 for Dresden nearshore sediments.

## Results

### *Sediment characteristics*

Clear vertical gradients of the measured variables existed in the sediments at most locations, showing marked differences between the various habitats (Tables 3 and 4). In deep sediment layers, nitrate concentration generally decreased with sediment depth. No consistent trend was found for ammonium concentrations. Nitrate concentrations in the sediment pore water were significantly higher at Dresden than at Coswig, whereas ammonium concentrations were particularly high (up to 630 $\mu g\ l^{-1}$) in the interstitial zone at Coswig (Tables 3 and 4). Here, ammonium concentrations exceeded those of the water column by far. In Dresden, ammonium concentrations in the pore water were lower than in the water column. In contrast, nitrate concentration was lower in the pore water than in the water column at most locations (Table 3). At the Coswig midriver habitat, molecular oxygen decreased linearly down to 40 cm sediment depth. No molecular oxygen was found below this depth. In the nearshore habitats however, molecular oxygen was depleted already at depths between 5 and 10 cm (Figure 2).

POM contents were higher in nearshore than in mid-river areas, and decreased significantly with sediment depth (Table 3). The amount of mobile fine interstitial particles (MFIP) showed no consistent trend with sediment depth. However, MFIP concentrations were significantly higher at the Dresden site than at Coswig (Table 4). There were also significant interactions between sediment depth and habitat, as MFIP concentrations decreased with sediment depth nearshore at Coswig, and increased at the other locations. The proportion of carbon as well as of nitrogen in these particles decreased significantly with increasing sediment depth. C:N ratios increased slightly with sediment depth, and C:N ratios were higher between the groynes nearshore at

*Table 3*. Characteristics of particulate organic matter and water chemistry at the sites Dresden and Coswig (mean ± sd, $n = 3$), itemized for sediment depths and habitats.

| Site | Depth (cm) | POM (% dry mass) | MFIP (mg $l^{-1}$) | MFIP-C(%) | MFIP-N(%) | MFIP-C:N | Chl *a* (μg $l^{-1}$) | $NH_4$-N (μg $l^{-1}$) | $NO_3$-N (mg $l^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| Coswig surface water | – | | | | | | 12.6 | 15 | 4.09 |
| Coswig central riverbed | 5 | 0.46 ± 0.09 | 69 ± 23 | 6.4 ± 1.0 | 0.74 ± 0.14 | 10.1 ± 0.3 | | | |
| | 25 | 0.45 ± 0.04 | 89 ± 23 | 6.3 ± 0.3 | 0.85 ± 0.10 | 8.7 ± 0.8 | 45.3 ± 12.8 | 158 ± 185 | 2.28 ± 1.67 |
| | 55 | 0.36 ± 0.12 | 273 ± 225 | 4.1 ± 1.7 | 0.43 ± 0.18 | 11.1 ± 0.5 | 18.4 ± 7.3 | 290 ± 297 | 0.31 ± 0.31 |
| | 105 | 0.28 ± 0.08 | 3485 ± 5418 | 2.5 ± 0.8 | 0.25 ± 0.08 | 11.9 ± 2.5 | 3.5 ± 2.5 | 379 ± 298 | 0.06 ± 0.07 |
| Coswig nearshore area | 5 | 0.91 ± 0.09 | 1129 ± 295 | 5.6 ± 0.1 | 0.57 ± 0.04 | 11.5 ± 0.9 | | | |
| | 25 | 0.54 ± 0.21 | 692 ± 293 | 6.7 ± 2.7 | 0.56 ± 0.16 | 13.6 ± 1.4 | 6.8 ± 7.2 | 14 ± 16 | 0.65 ± 1.03 |
| | 55 | 0.44 ± 0.26 | 321 ± 215 | 5.9 ± 3.2 | 0.46 ± 0.18 | 14.4 ± 2.3 | 0.4 ± 0.4 | 43 ± 34 | 0.63 ± 1.10 |
| | 105 | 0.68 ± 0.39 | 302 ± 65 | 7.1 ± 2.7 | 0.46 ± 0.21 | 18.9 ± 4.5 | −0.2 ± 0.5 | 151 ± 67 | 0.10 ± 0.17 |
| Dresden surface water | – | | | | | | 18.2 | 64 | 3.92 |
| Dresden central riverbed | 5 | 0.67 ± 0.10 | 918 ± 456 | 6.9 ± 1.4 | 0.83 ± 0.20 | 9.8 ± 0.4 | | | |
| | 25 | 0.66 ± 0.27 | 1727 ± 2004 | 7.2 ± 2.4 | 0.78 ± 0.37 | 11.5 ± 2.6 | 10.8 ± 8.6 | 23 ± 11 | 3.38 ± 0.29 |
| | 55 | 0.72 ± 0.16 | 1955 ± 1039 | 5.8 ± 1.1 | 0.58 ± 0.12 | 11.8 ± 1.0 | 5.1 ± 9.6 | 22 ± 14 | 2.83 ± 0.13 |
| | 105 | 0.56 ± 0.08 | 4098 ± 3421 | 2.7 ± 0.8 | 0.26 ± 0.10 | 12.5 ± 1.1 | −0.3 ± 1.7 | 17 ± 4 | 1.98 ± 0.61 |
| Dresden nearshore area | 5 | 3.43 | 849 | 5.7 | 0.59 | 11.2 | | | |
| | 25 | 1.19 | 3086 | 5.4 | 0.59 | 10.7 | 25.6 | 57 | 4.05 |
| | 55 | 0.63 | 3732 | 2.9 | 0.31 | 10.7 | 10.8 | 24 | 7.18 |
| | 90 | 0.48 | 2472 | 1.5 | 0.18 | 10.2 | −0.7 | 23 | n.d. |

POM = particulate organic matter; MFIP = mobile fine interstitial particles; chl *a* = chlorophyll *a*; n.d. = not determined.

*Table 4*. Results of two-factor analysis of variance for particulate organic matter and water chemistry testing the effect of habitat and sediment depth.

| Factors | POM (df; *F*; *p*) | MFIP (df; *F*; *p*) | MFIP-C (df; *F*; *p*) | MFIP-N (df; *F*; *p*) | MFIP-C:N (df; *F*; *p*) | Chl *a* (df; *F*; *p*) | $NH_4$-N (df; *F*; *p*) | $NO_3$-N (df; *F*; *p*) |
|---|---|---|---|---|---|---|---|---|
| Habitat | 3; 16; $<0.001$ | 3; 15; $<0.001$ | 3; 3.4; $<0.05$ | 3; 1.3; 0.30 | 3; 12; $<0.001$ | 3; 8.0; $<0.01$ | 3; 5.2; $<0.01$ | 3; 15; $<0.001$ |
| Depth | 3; 15; $<0.001$ | 3; 1.7; 0.19 | 3; 9.2; $<0.001$ | 3; 12; $<0.001$ | 3; 3.3; $<0.05$ | 2; 13; $<0.001$ | 2; 0.56; 0.58 | 2; 12; 0.001 |
| Depth × habitat | 9; 4.9; $<0.01$ | 9; 2.6; $<0.05$ | 9; 2.0; 0.09 | 9; 1.2; 0.36 | 9; 1.4; 0.25 | 6; 1.3; 0.32 | 6; 0.39; 0.88 | 6; 2.7; $<0.05$ |

POM = particulate organic matter, MFIP = mobile fine interstitial particles, chl *a* = chlorophyll *a*.

Coswig than in the other habitats (Tables 3 and 4; all comparisons specified here were confirmed by Tukey's post-hoc tests, $p<0.01$). The trends for the biochemical composition of POM were similar to those described for MFIP, i. e. carbon and nitrogen content significantly decreased with sediment depth (data not shown, $p<0.01$).

### *Microbial activity rates*

Mean bacterial abundance in the uppermost mid-river sediment layer was up to $1.4 \times 10^9$ cm$^{-3}$ at Dresden, but only $4.7 \times 10^8$ cm$^{-3}$ at Coswig. Bacterial abundance decreased significantly with sediment depth, but still reached $1.4 \times 10^8$ cm$^{-3}$ at 105 cm sediment depth as a mean of all locations. Bacterial

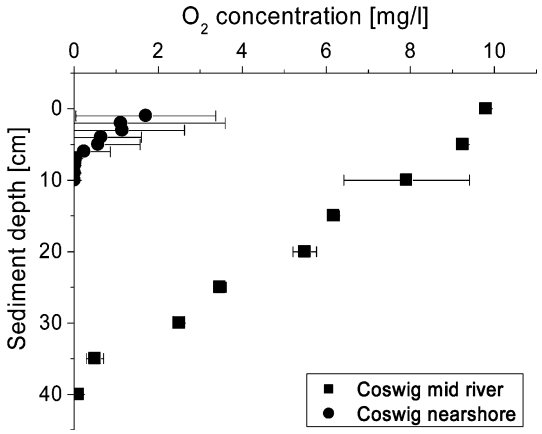


*Figure 2*. Dissolved oxygen concentrations in nearshore and mid-river sediments. Arithmetic means and standard deviations of 3 (mid-river) and 15 (nearshore) depth profiles.

production showed the same pattern as abundance, with rates of up to 2.5 μg C $cm^{-3}$ $h^{-1}$ in the uppermost sediment layer at Dresden (Tables 5 and 6). Turnover times of bacterial carbon resulting from these data were 7.9 ± 1.9 h in the 5 cm sediment layer. Turnover times increased towards deeper sediment layers (df = 3, $F = 9.7$, $p < 0.001$), where they were highly variable.

Leucine aminopeptidase, a peptide degrading enzyme, and alkaline phosphatase, a phosphomonoester-degrading enzyme, showed the highest activities at all sampling locations (mean values: 134 nmol MCA $cm^{-3}$ sediment $h^{-1}$ and 71 nmol MUF $cm^{-3}$, respectively). Activity of β-glucosidase (mean: 16 nmol MUF $cm^{-3}$ sediment $h^{-1}$), which degrades disaccharides, was higher than that of the polysaccharide-degrading exo-1,4-β-glucanase (mean: 4.9 nmol MUF $cm^{-3}$ sediment $h^{-1}$; determined in Coswig only). As for the other variables of bacterial activity, the activity of extracellular enzymes decreased significantly with increasing sediment depth (Tukey's post-hoc tests, $p < 0.01$) (Tables 5 and 6).

Potential nitrification rates reached 97 ng $NO_2$-N $cm^{-3}$ $h^{-1}$ at Dresden and 3.0 ng $NO_2$-N $cm^{-3}$ $h^{-1}$ at Coswig. Nitrification thus was significantly higher at Dresden than at Coswig, and strongly decreased with increasing sediment depth at all habitats (Tukey's post-hoc tests, $p < 0.01$). Potential denitrification rate also decreased significantly with sediment depth. Highest rates were measured in the nearshore habitats (Dresden, 16.8 μg $N_2O$-N $cm^{-3}$ $h^{-1}$ and Coswig, 5.7 μg $N_2O$-N $cm^{-3}$ $h^{-1}$). Rates at the midstream locations were 2–3 μg $N_2O$-N $cm^{-3}$ $h^{-1}$ in the uppermost sediment layer (Tables 5 and 6).

### *Patterns and controls of microbial activity*

Spatial patterns were similar for many microbiological variables. Bacterial abundance, production, activity of four extracellular enzymes, and denitrification rate significantly correlated with each other. Generally, these measures of bacterial activity correlated significantly with amount and quality of organic matter and with nitrate concentration, but not with MFIP concentrations (Table 7), indicating the tight coupling of heterotrophic processes with organic matter supply. Potential nitrification rate showed a different pattern than the other microbial variables, as it correlated with MFIP concentration, but not with organic matter. Potential nitrification rate had a negative correlation with ammonium concentration and a positive correlation with nitrate concentration (Table 7).

For most biotic variables, the variation between sediment depths was of higher statistical significance than that between habitats (Table 6). This decrease of microbial activity with sediment depth approached an exponential fit in the Coswig nearshore riverbed, whereas it was close to a linear fit in the Coswig central riverbed (Figure 3). In particular, the habitats differed in the slope of the decrease in microbial activity over the upper 25 cm of sediment. Bacterial activity (relative means of bacterial abundance,

*Table 5.* Bacterial abundance and activity at the sampling sites Dresden and Coswig (means ± sd, $n = 3$), itemized for sampling stations and sediment depths.

| | Depth | Abundance ($10^8$ cells $\sqrt{cm^{-3}\,h^{-1}}$) | Production (µg C $\sqrt{cm^{-3}\,h^{-1}}$) | Phosphatase (nmol MUF $\sqrt{cm^{-3}\,h^{-1}}$) | β-Glucosidase (nmol MUF $\sqrt{cm^{-3}\,h^{-1}}$) | Leucine aminopeptidase (nmol MCA $\sqrt{cm^{-3}\,h^{-1}}$) | $\sqrt{\text{Exo}-1,4-\beta}$-glucanase (nmol MUF $\sqrt{cm^{-3}\,h^{-1}}$) | Nitrification rate (ng $NO_2$-N $cm^{-3}\,h^{-1}$) | Denitrification rate (µg $N_2O$-N $cm^{-3}\,h^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| Coswig central riverbed | 5 | 4.69 ± 0.38 | 1.74 ± 0.15 | 59.91 ± 3.01 | 8.81 ± 1.42 | 123.77 ± 12.40 | 2.39 ± 0.38 | 3.00 ± 1.35 | 2.69 ± 2.79 |
| | 25 | 4.76 ± 0.43 | 1.59 ± 0.28 | 58.32 ± 2.92 | 7.66 ± 0.94 | 123.57 ± 13.09 | 2.07 ± 0.23 | 1.26 ± 0.38 | 1.33 ± 0.78 |
| | 55 | 3.19 ± 0.66 | 1.11 ± 0.29 | 36.41 ± 6.15 | 4.56 ± 0.53 | 70.80 ± 3.78 | 1.26 ± 0.09 | 1.05 ± 0.63 | 0.65 ± 0.18 |
| | 105 | 1.27 ± 0.90 | 0.32 ± 0.28 | 5.18 ± 5.07 | 1.30 ± 1.22 | 17.21 ± 15.78 | 0.21 ± 0.30 | 0.27 ± 0.70 | 0.24 ± 0.04 |
| Coswig nearshore area | 5 | 8.11 ± 2.48 | 2.19 ± 0.77 | 91.70 ± 24.89 | 22.61 ± 10.17 | 157.27 ± 19.19 | 4.93 ± 1.83 | 2.87 ± 0.35 | 5.70 ± 1.71 |
| | 25 | 3.15 ± 0.78 | 0.62 ± 0.19 | 37.40 ± 11.68 | 6.01 ± 1.87 | 63.53 ± 9.73 | 1.37 ± 0.33 | 2.00 ± 0.66 | 0.64 ± 0.16 |
| | 55 | 1.91 ± 1.13 | 0.24 ± 0.25 | 29.50 ± 22.96 | 3.99 ± 3.40 | 43.79 ± 28.16 | 0.52 ± 0.88 | 0.31 ± 0.43 | 0.24 ± 0.29 |
| | 105 | 1.62 ± 1.20 | 0.20 ± 0.27 | 23.56 ± 15.70 | 3.21 ± 2.82 | 32.87 ± 23.14 | 0.68 ± 0.66 | 0.92 ± 0.45 | 0.37 ± 0.48 |
| Dresden central riverbed | 5 | 9.59 ± 1.95 | 2.41 ± 0.45 | 59.86 ± 7.76 | 12.72 ± 4.05 | 136.25 ± 6.96 | | 58.90 ± 13.96 | 2.33 ± 1.04 |
| | 25 | 6.73 ± 1.30 | 1.33 ± 0.16 | 40.02 ± 10.82 | 6.01 ± 0.73 | 90.54 ± 28.16 | | 38.54 ± 14.74 | 0.60 ± 0.34 |
| | 55 | 4.23 ± 0.86 | 0.49 ± 0.14 | 30.90 ± 3.48 | 2.47 ± 0.83 | 106.58 ± 25.80 | | 15.54 ± 6.17 | 0.068 ± 0.031 |
| | 105 | 1.43 ± 0.84 | 0.07 ± 0.34 | 4.09 ± 3.72 | 0.87 ± 0.47 | 49.08 ± 23.05 | | 4.10 ± 0.25 | 0.018 ± 0.005 |
| Dresden nearshore area | 5 | 13.8 | 2.52 | 75.88 | 30.20 | 84.37 | | 97.34 | 16.84 |
| | 25 | 6.09 | 1.81 | 45.07 | 9.00 | 86.62 | | 49.34 | 2.61 |
| | 55 | 2.88 | 0.67 | 29.65 | 5.35 | 64.22 | | 20.59 | 1.43 |
| | 90 | 0.78 | 0.11 | 13.36 | 0.83 | 43.87 | | 5.26 | 0.084 |

*Table 6*. Results of two-factor analysis of variance for bacterial activity testing the effect of habitat and sediment depth.

| Factors | Abundance (df; *F*; *p*) | Production (df; *F*; *p*) | $\beta$-Glucosidase activity (df; *F*; *p*) | Leucine-amino-peptidase activity (df; *F*; *p*) | Nitrification (df; *F*; *p*) | Denitrification potential (df; *F*; *p*) |
|---|---|---|---|---|---|---|
| Habitat | 3; 2.0; 0.14 | 3;3.2; $<0.05$ | 3; 1.9; 0.16 | 3; 1.9; 0.17 | 3; 170; $<0.001$ | 3; 6.2; $<0.01$ |
| Depth | 3; 23; $<0.001$ | 3; 55; $<0.001$ | 3; 33; $<0.001$ | 3; 13; $<0.001$ | 3; 75; $<0.001$ | 3; 29; $<0.001$ |
| Depth× habitat | 9; 0.9; 0.57 | 9; 2.8 $<0.05$ | 9; 1.3; 0.28 | 9; 1.9; 0.10 | 9; 20; $<0.001$ | 9; 1.8; 0.13 |

production, and enzyme activity) was only 5% lower in 25 cm sediment depth than in 5 cm sediment depth. In contrast, bacterial activity in 25 cm depth was 65% lower than in 5 cm depth at Coswig nearshore riverbed. An intermediate decrease of 39% was found in Dresden (mean for both habitats). A similar pattern, but a stronger decrease with sediment depth was determined for denitrification.

Correction for particle size distribution was used to integrate bacterial production over 1 m sediment depth. The integrated bacterial production was highest in the central streambed at Coswig. It ranged from 0.17 g C $m^{-3}$ $h^{-1}$ in the nearshore sediments in Dresden to 0.95 g C $m^{-3}$ $h^{-1}$ in the Coswig central streambed. Intermediate values of 0.33 and 0.32 g C $m^{-3}$ $h^{-1}$ were calculated for the nearshore sediments at Coswig and in the central streambed at Dresden, respectively.

*Table 7*. Spearman rank correlation coefficients between bacterial variables and environmental factors.

| Environmental factor | *n* | Bacterial production | $\beta$-glucosidase activity | Leucine amino-peptidase activity | Denitrification rate | Nitrification rate |
|---|---|---|---|---|---|---|
| MFIP | 40 | n.s. | n.s. | n.s. | n.s. | 0.47** |
| MFIP-C percentage | 40 | 0.42** | 0.53*** | 0.46** | 0.32* | n.s. |
| MFIP-N percentage | 40 | 0.62*** | 0.66*** | 0.66*** | 0.49** | n.s. |
| MFIP C:N ratio | 40 | −0.56*** | −0.42** | −0.58*** | −0.43** | n.s. |
| Chlorophyll *a* | 28 | 0.72*** | 0.60** | 0.47* | 0.63*** | n.s. |
| POC $>90$ µm | 40 | 0.48** | 0.62*** | 0.34* | 0.54*** | n.s. |
| PON $>90$ µm | 40 | 0.62*** | 0.69*** | 0.49** | 0.69*** | n.s. |
| $NO_3$-N | 30 | 0.49** | 0.46** | 0.64*** | 0.39* | 0.69*** |
| $NH_4$-N | 30 | n.s. | n.s. | n.s. | n.s. | −0.61*** |

Levels of significance are *$p<0.05$, **$p<0.01$, ***$p<0.001$, n.s = not significant at a 0.05% level.

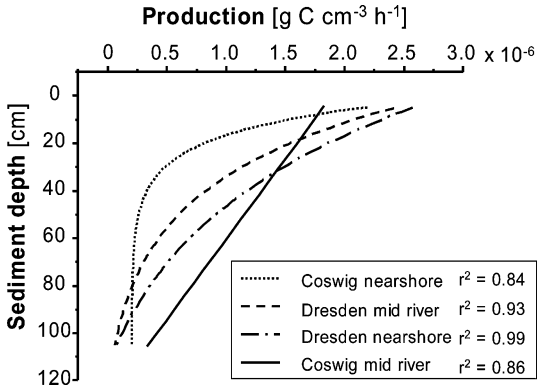


*Figure 3*. Bacterial production in samples of particles sizes < 5 mm, vertically interpolated over 1 m sediment depth. $n = 12$ at each of the four sampling stations, besides Dresden river bank, were $n = 4$. Data shown in Table 5.

## Discussion

Our findings demonstrate that an extended, microbially active hyporheic zone exists in the Elbe River. We found high rates of microbial activity stretching down to 1 m sediment depth at the mid-river habitat in Coswig. Results of bacterial production measurements revealed that bacterial activity in the uppermost sediment layer can reach the same order of magnitude as in a 6th order lowland river (Fischer et al. 2002), and was considerably higher than in most studies of small streams (e.g. Marxsen 2001). The relative activity of the four extracellular enzymes – leucine aminopeptidase > alkaline phosphatase > $\beta$-glucosidase > exo-1,4-$\beta$-glucanase – suggested that a high proportion of organic matter were proteins mainly derived from algae, and was typical for benthic epilithic biofilms in running waters (Chappell and Goulder 1994; Romaní and Marxsen 2002). Despite their potentially high activities, studies on extracellular enzymes in benthic and hyporheic sediments of running waters are particularly rare (Marxsen and Fiebig 1993; Sinsabaugh and Findlay 1995). The absolute rates of $\beta$-glucosidase activity were in the range of those found in a small, unpolluted stream (Marxsen and Fiebig 1993), for the other enzymes comparable data do not exist. Comparisons with potential nitrification and denitrification rates with those reported from other running waters are problematic because of a variety of methods used. Potential denitrification rates in Elbe sediments exceeded those measured in other running waters (e.g. García-Ruiz et al. 1998; Sheibley et al. 2003), probably because of high nitrate concentrations in the Elbe River and in the adjacent ground water, and because of the fact that we measured denitrification under optimized conditions here (Richardson et al. 2004). Published rates of nitrification cover a similar order of magnitude as in the Elbe River (e.g. Sheibley et al. 2003).

At each location, all bacterial variables measured showed a depth gradient in their activity. These gradients generally corresponded with gradients in organic matter and oxygen concentration. Although deficiency of oxygen is generally assumed to limit many microbiological processes in sediments, it has recently been found that the availability of labile organic matter limits bacterial heterotrophic activity in various aquatic ecosystems irrespective of oxygen concentration (Kristensen et al. 1995; Bastviken et al. 2001), and that a close interplay between both electron acceptors and donors exist in hyporheic environments (Hedin et al. 1998). At the Coswig mid-river and nearshore habitats, we measured high potential microbial activity in deeper sediment layers lacking molecular oxygen (Figures 2 and 3). This indicates that substrate rather than oxygen availability regulates microbial activity in the hyporheic zone of the Elbe River.

The potential for various microbial processes covaried tightly in the Elbe sediments, even if these processes seem to functionally exclude each other. For example, nitrification and denitrification both peaked in the upper sediment layer, and were highly correlated to each other when Dresden and Coswig samples were analyzed separately. This correlation can be attributed to the heterogeneity of the sediments that offers micro-niches for a high diversity of microbial processes occurring in close proximity to each other. Most bacteria capable of respiratory denitrification are facultative anaerobes that use molecular oxygen as electron acceptor under aerobic conditions (Tiedje 1988). Many bacteria can even perform aerobic denitrification within their natural habitat (Patureau et al. 2000). This metabolic flexibility would help these bacteria to cope with the varying availability of molecular oxygen in river sediments. Also, the spatial micro-heterogeneity and the metabolic flexibility contribute largely to the high rate of microbial metabolism found in these sediments.

However, the dynamics of nitrification rates differed from the other variables in the correlation matrix (Table 7). This can be traced back to significant differences in the hyporheic nitrification rates between Dresden and Coswig. Although there was a highly significant decrease in nitrification rates with increasing sediment depth, this decrease was not correlated with variables describing organic matter, because of the chemolithotrophic nature of the nitrification process. In contrast, organic carbon can even inhibit nitrification, in particular at high C:N ratios. It is argued that under these conditions heterotrophic bacteria would compete for $NH_4^+$, thus reducing the availability of $NH_4^+$ for nitrifying bacteria (Strauss and Lamberti 2000). However, availability of oxygen was probably most important for nitrification. This would explain the sharp decrease of potential nitrification rates with depth particularly in the Coswig mid-river sediments, where concentrations of $NH_4$-N were relatively high and organic carbon content was low. Surface area of fine interstitial particles (MFIP) seemed to influence nitrification rate, which was not the case for the other bacterial variables (Table 6). Thus, nitrifying bacteria may be imported into the hyporheic zone via MFIP. Additionally, the (mostly

negatively loaded) surfaces of MFIP are probably important because they provide binding places for reduced nitrogen ions, as for $NH4^{+}$. In Dresden, the concentration of these MFIP was higher than in Coswig, especially in the microbially active upper sediment layers. Consequently, nitrification rates were higher in Dresden, which lead to depletion in dissolved ammonium and accumulation of nitrate in the pore water.

Bacterial activity in the deeper sediments was particularly high at sites with significant sediment turnover. In the central river bed, a uniform grain size distribution of coarse sand and fine gravel provides vast surface areas for the colonization by bacteria, and large interstitial spaces enable import of matter from the overlying water via turbulent dispersion (Rutherford et al. 1993). Intense perfusion by pumping mechanisms and frequent turnover of sediment structures by bedload transport occurs in these regions (e.g. Carling et al. 2000; Sauer and Schmidt 2001; Fischer et al. 2003). These mechanisms will eventually expose bacteria from deeper layers to changing environmental conditions. Our study shows that the bacterial community can cope with these changing conditions. It therefore seems that the activity in this spatially extended zone is closely related to hydrodynamics and sediment movement, as shown before for a smaller (6th order) lowland river (Fischer et al. 2003).

The spatial extension of microbial processes in river sediments often depends on hyporheic water flow that carries nutrients and terminal electron acceptors to the biofilms (Brunke and Gonser 1997; Brunke and Fischer 1999; Battin 2000). As an example, nitrification rates depend on the flux of oxygen from the water column into the sediment interstices. Denitrification and other heterotrophic processes depend on the supply with organic matter along similar flow paths (Baker et al. 1999; Sobczak et al. 2003; Lefebvre et al. 2004). Low activity rates in deep sediment layers thus are either caused by reduced connectivity with the water column or by long hyporheic flow paths during which the substances that fuel microbial metabolism are stripped off the interstitial water. The result of both is reduced substrate supply in these deep sediment layers. Our results corroborate these hypotheses. In nearshore habitats dominated by sedimentation processes, activity was high in the uppermost sediment layer, and sharply decreased towards deeper sediments. Vertical exchange between sediment pore water and the water column is restricted in these sedimentation zones, leading to reduced microbial activity in deeper sediments. In the central river bed, with its more pronounced vertical connectivity, activity was not as high in the uppermost layer as in the sedimentation zones. The depth-integrated activity, however, was 2.9 fold higher than in the adjacent nearshore habitats. The shifting sediments of a free-flowing river, the ecosystem's compartment where several biochemical reactions run at high rates, thus represent a ''liver function'' in the river's metabolism (Figure 4). These sediments are well connected to the flowing water column via rapid vertical hydrological exchange. In natural lowland rivers, vast areas of the riverbed are covered with these unstable shifting sediment structures (Church 2002), which should exhibit intense hyporheic metabolism.

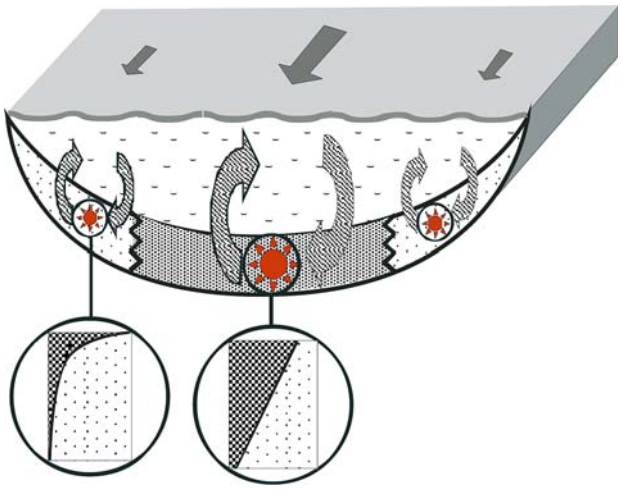

*Figure 4*. Schematic representation of the ecological functioning of central river sediments as a 'river's liver'. The shifting sediments on the central river bottom of a free-flowing lowland river are well connected to the flowing water column via rapid vertical hydrological exchange. Hence, particulate and dissolved organic matter is constantly transfered into the sediments, where it is partially retained. Thus, the sediments are oxygenated down to a larger depth, and well supplied by organic matter. This enables microorganisms to run their biochemical reactions at high rates down to a considerable sediment depth. In contrast, the nearshore sediments are only badly connected with the water column, and exhibit a much lower microbial activity in deeper sediments. The vertical integration of the activities within the central sediments results in a significant total effect on ecosystem metabolism. This intense hyporheic metabolism thus represents a "liver function" in the river's metabolism.

We used our production data in order to estimate theoretical carbon turnover lengths (Webster and Meyer 1997) by comparison of carbon transport with respiration, including bacterial growth with 30% efficiency (Benner et al. 1988). Such calculations only provide rough estimates due to uncertainties concerning bacterial production measurements and growth efficiency (Bastviken et al. 2003), but are scarce for large rivers. Based on the concentration of total organic carbon in the flowing water of 10 g C $m^{-3}$ during sampling time (Wilczek et al. in press), the mean discharge of the Elbe (Table 1), and the vertical profiles of bacterial production (Table 2), total amounts of 113 and 256 g C $h^{-1}$ were turned over per meter river profile length at Dresden and Coswig, respectively. From that, theoretical carbon turnover lengths can be estimated of about 100 km at Dresden, but only 50 km at the Coswig site with its highly active river bed (Figure 3). The short spiralling length at Coswig underlines the important role that unconsolidated, hydrologically well connected sediments can play in carbon turnover even in large rivers. A comparison with data compiled by Webster and Meyer (1997) shows that the carbon turnover length estimated for the Elbe is an order of magnitude shorter than would be expected by a regression of discharge versus turnover length for

a set of 26 streams and rivers from various biomes. This is probably caused by a high proportion of autochthonous, easily degradable organic material (Wilczek et al. in press) as well as by the high interstitial surface area and high retention efficiency in the sediments of the Elbe. Calculations on the turnover of organic nitrogen result in uptake lengths in the same order of magnitude than turnover lengths for organic carbon. However, uptake lengths for nitrogen are probably highly underestimated by such calculations, because the laboratory methods used included nitrate and carbon amendments and aimed to compare habitats rather than provide actual ambient rates (Richardson et al. 2004).

Hence, our findings indicate that it is probably this metabolic activity in the sediments of the central river channel that caused the marked dynamics of carbon and nitrogen compounds in lowland river sections, reported by balancing studies (Alexander et al. 2000; Raymond and Bauer 2001; Seitzinger et al. 2002). In recent concepts of river ecology, the importance of the hyporheic zone as an influential factor on surface water conditions is restricted to lower stream orders (reviewed by Ward et al. 2001). The riverine productivity model (RPP; Thorp and Delong 2002) deals specifically with sources of organic carbon in constrained reaches of larger rivers and is well applicable to the Elbe, but it does not localize the degradation of organic matter. Our findings may not only complement the RPP, but also shed new light on the predictions of the River Continuum Concept (Vannote et al. 1980) concerning the longitudinal mass balance in river networks. For that purpose, it would be valuable to know under which conditions this 'river's liver' would be able to counterbalance net exports of carbon, nitrogen and phosphorus from low order streams via uptake, transformation, and release of transported matter (Fisher et al. 1998; Kaplan and Newbold 2003). The metabolic functionality of streambed sediments is impacted by human alterations in river flow or morphology reducing lateral and vertical connectivity (Dahm et al. 1998). In the case of the Elbe and of other large rivers, the role of groynes and other engineering measures on riverine microbial processes is just beginning to be recognized.

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## References


Alexander R.B., Smith R.A. and Schwarz G.E. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. Nature 403: 758–761.

Allan J.D. 1995. Stream Ecology. Structure and Function of Running Waters. Chapman & Hall, London.

Baker M.A., Dahm C. and Valett H.M. 1999. Acetate retention and metabolism in the hyporheic zone of a mountain stream. Limnol. Oceanogr. 44: 1530–1539.

Bastviken D., Ejlertsson J. and Tranvik L. 2001. Similar bacterial growth on dissolved organic matter in anoxic and oxic lake water. Aquat. Microb. Ecol. 24: 41–49.

Bastviken D., Olsson M. and Tranvik L. 2003. Simultaneous measurements of bacterial production and organic carbon mineralization in oxic and anoxic lake sediments. Microb. Ecol. 46: 73–82.

Battin T.J. 2000. Hydrodynamics is a major determinant of streambed biofilm activity: from the sediment to the reach scale. Limnol. Oceanogr. 45: 1308–1319.

Behrendt H. and Opitz D. 1999. Retention of nutrients in river systems: dependence on specific runoff and hydraulic load. Hydrobiologia 410: 111–122.

Belser L.W. and Mays E.L. 1980. Specific inhibition of nitrite oxidation by chlorate and its use in assessing nitrification in soil and sediments. Appl. Environ. Microbiol. 39: 505–510.

Benner R., Lay J., K'nees E. and Hodson R.E. 1988. Carbon conversion efficiency for bacterial growth on lignocellulose: implications for detritus-based food webs. Limnol. Oceanogr. 33: 1514–1526.

Bou C. and Rouch R. 1967. Un nouveau champ de recherches sur la faune aquatique souterraine. Comptes Rendus Académie des Sciences Paris 265: 369–370.

Brunke M. and Fischer H. 1999. Hyporheic bacteria – relationships to environmental gradients and invertebrates in a prealpine stream. Arch. Hydrobiol. 146: 189–217.

Brunke M. and Gonser T. 1997. The ecological significance of exchange processes between rivers and groundwaters. Freshwat. Biol. 377: 1–33.

Brunke M., Sukhodolov A., Fischer H., Wilczek S., Engelhardt C. and Pusch M. 2002. Benthic and hyporheic habitats of a large lowland river (Elbe, Germany): influence of river engineering. Verh. Internat. Verein. Limnol. 28: 153–156.

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

Chappell K.R. and Goulder R. 1994. Seasonal variation of epilithic extracellular enzyme activity in three diverse headstreams. Arch. Hydrobiol. 130: 195–214.

Chrost R.J. 1991. Environmental control of the synthesis and activity of aquatic microbial ectoenzymes. In: Chrost R.J. (ed), Microbial Enzymes in Aquatic Environments. Springer, New York, pp. 42–50.

Church M. 2002. Geomorphic thresholds in riverine landscapes. Freshwat. Biol. 47: 541–558.

Dahlke S. and Remde A. 1998. Denitrifikation. In: Vereinigung für Allgemeine und Angewandte Mikrobiologie (VAAM) (ed), Mikrobiologische Charakterisierung aquatischer Sedimente: Methodensammlung. R. Oldenbourg Verlag, München, pp. 122–140.

Dahm C.N., Grimm N.B., Marmonier P., Valett H.M. and Vervier P. 1998. Nutrient dynamics at the interface between surface waters and groundwaters. Freshwat. Biol. 40: 427–451.

DEW 1985. Deutsche Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung. Verlag Chemie, Weinheim.

Elliott A.H. and Brooks N.H. 1997. Transfer of nonsorbing solutes to a streambed with bed forms: theory. Water Resour. Res. 33: 123–136.

Fischer H. and Pusch M. 1999. Use of the [$^{14}$C]leucine incorporation technique to measure bacterial production in river sediments and the epiphyton. Appl. Environ. Microbiol. 65: 4411–4418.

Fischer H. and Pusch M. 2001. Comparison of bacterial production in sediments, epiphyton, and the pelagic zone of a lowland river. Freshwat. Biol. 46: 1335–1348.

Fischer H., Sukhodolov A., Wilczek S. and Engelhardt C. 2003. Effects of flow dynamics and sediment movement on microbial activity in a lowland river. River Res. Appl. 19: 473–482.

Fischer H., Wanner S.C. and Pusch M. 2002. Bacterial abundance and production in river sediments as related to the biochemical composition of particulate organic matter (POM). Biogeochemistry 61: 37–55.

Fisher S.G., Grimm N.B., Marti E., Holmes R.M. and Jones J.B. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. Ecosystems 1: 19–34.

García-Ruiz R., Pattinson S.N. and Whitton B.A. 1998. Denitrification in river sediments: relationship between process rate and properties of water and sediment. Freshwat. Biol. 39: 467–476.

Gieseke A., Purkhold U., Wagner M., Amann R. and Schramm A. 2001. Community structure and activity dynamics of nitrifying bacteria in a phosphate-removing biofilm. Appl. Environ. Microbiol. 67: 1351–1362.

Hedin L.O., von Fischer J.C., Ostrom N.E., Kennedy B.P., Brown M.G. and Robertson G.P. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. Ecology 79: 684–703.

Hinkle S.R., Duff J.H., Triska F.J., Laenen A., Gates E.B., Bencala K.E., Wentz D.A. and Silva S.R. 2001. Linking hyporheic flow and nitrogen cycling near the Willamette River - a large river in Oregon, USA. J. Hydrol. 244: 157–180.

Hoppe H.-G. 1993. Use of fluorogenic model substrates for extracellular enzyme activity (EEA) measurement of bacteria. In: Kemp P.F., Sherr B.F. and Sherr E.B. (eds), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, pp. 423–431.

Kaplan L.A. and Bott T.L. 1989. Diel fluctuations in bacterial activity on streambed substrata during vernal algal blooms: Effects of temperature, water chemistry, and habitat. Limnol. Oceanogr. 34: 718–733.

Kaplan L.A. and Newbold J.D. 2003. The role of monomers in stream ecosystem metabolism. In: Findlay S.E.G. and Sinsabaugh R.L. (eds), Aquatic Ecosystems. Interactivity of Dissolved Organic Matter. Academic Press, San Diego, pp. 97–119.

Kirchman D.L. 1993. Leucine incorporation as a measure of biomass production by heterotrophic bacteria. In: Kemp P.F., Sherr B.F. and Sherr E.B. (eds), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, pp. 509–512.

Kristensen E., Ahmed S.I. and Devol A.H. 1995. Aerobic and anaerobic decomposition of organic matter in marine sediment: which is fastest? Limnol. Oceanogr. 40: 1430–1437.

Lefebvre S., Marmonier P. and Pinay G. 2004. Stream regulation and nitrogen dynamics in sediment interstices: comparison of natural and straightened sectors of a third-order stream. River Res. Applic. 20: 499–512.

Marxsen J. 2001. Bacterial production in different streambed habitats of an upland stream: sandy versus coarse gravelly sediments. Arch. Hydrobiol. 152: 543–565.

Marxsen J. and Fiebig D.M. 1993. Use of perfused cores for evaluating extracellular enzyme-activity in stream-bed sediments. FEMS Microbiol. Ecol. 13: 1–11.

Marxsen J., Tippmann P., Heininger P., Preuß G. and Remde A. 1998. Enzymaktivität. In: Vereinigung für Allgemeine und Angewandte Mikrobiologie (VAAM) (ed), Mikrobiologische Charakterisierung aquatischer Sedimente: Methodensammlung. R. Oldenbourg Verlag, München, pp. 87–114.

Moran M.A., Sheldon W.M.Jr and Sheldon J.E. 1999. Biodegradation of riverine dissolved organic carbon in five estuaries of the southeastern United States. Estuaries 22: 55–64.

Patureau D., Zumstein E., Delgenes J.P. and Moletta R. 2000. Aerobic denitrifiers from diverse natural and managed ecosystems. Microb. Ecol. 39: 145–152.

Porter K.G. and Feig Y.S. 1980. The use of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. 25: 943–948.

Pusch M., Fiebig D., Brettar I., Eisenmann H., Ellis B.K., Kaplan L.A., Lock M.A., Naegeli M.W. and Traunspurger W. 1998. The role of micro-organisms in the ecological connectivity of running waters. Freshwat. Biol. 40: 453–495.

Raymond P.A. and Bauer J.E. 2001. Riverine export of aged terrestrial organic matter to the North Atlantic Ocean. Nature 409: 497–500.

Richardson W.B., Strauss E.A., Bartsch L.A., Monroe E.M., Cavanaugh J.C., Vingum L. and Soballe D.M. 2004. Denitrification in the Upper Mississippi River: rates, controls, and contribution to nitrate flux. Can. J. Fish. Aquat. Sci. 61: 1102–1112.

Romaní A. and Marxsen J. 2002. Extracellular enzymatic activities in epilithic biofilms of the Breitenbach: microhabitat differences. Arch. Hydrobiol. 155: 541–555.

Rutherford J.C., Latimer G.J. and Smith R.K. 1993. Bedform mobility and benthic oxygen uptake. Wat. Res. 27: 1545–1558.

Sauer W. and Schmidt A. 2001. Die Bedeutung suspendierten Sandes für die Sohlhöhenentwicklung der Elbe. Wasserwirtschaft 91: 443–449.

Seitzinger S.P., Nielsen L.P., Caffrey J. and Christensen P.B. 1993. Denitrification measurements in aquatic sediments: a comparison of three methods. Biogeochemistry 23: 147–167.

Seitzinger S.P., Styles R.V., Boyer E.W., Alexander R.B., Gillen B., Howarth R.W., Mayer B. and van Breemen N. 2002. Nitrogen retention in rivers: model development and application to watersheds in the northeastern USA. Biogeochemistry 57(58): 99–237.

Sheibley R.W., Duff J.H., Jackman A.P. and Triska F.J. 2003. Inorganic nitrogen transformations in the bed of the Shingobee River, Minnesota: Integrating hydrologic and biological processes using sediment perfusion cores. Limnol. Oceanogr. 48: 1129–1140.

Simon M. and Azam F. 1989. Protein content and protein synthesis rates of planktonic marine bacteria. Mar. Ecol. Prog. Ser. 51: 201–213.

Sinsabaugh R.L. and Findlay S. 1995. Microbial production, enzyme activity, and carbon turnover in surface sediments of the Hudson River Estuary. Microbial Ecol. 30: 127–141.

Sinsabaugh R.L. and Linkins A.E. 1988. Exoenzyme activity associated with lotic epilithon. Freshwat. Biol. 20: 249–261.

Sobczak W.V., Findlay S. and Dye S. 2003. Relationships between DOC bioavailability and nitrate removal in a mountain stream: an experimental approach. Biogeochemistry 62: 309–327.

Sørensen J. 1978. Denitrification rates in a marine sediment as measured by the acetylene inhibition technique. Appl. Environ. Microbiol. 36: 139–143.

Stanford J.A. and Ward J.V. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. J. N. Am. Benthol. Soc. 12: 48–60.

Storey R.G., Fulthorpe R.R. and Williams D.D. 1999. Perspectives and predictions on the microbial ecology of the hyporheic zone. Freshwat. Biol. 41: 119–130.

Strauss E.A. and Lamberti G.A. 2000. Regulation of nitrification in aquatic sediments by organic carbon. Limnol. Oceanogr. 45: 1854–1859.

Thorp J.H. and Delong M.D. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543–550.

Tiedje J.M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In: Zehnder A.J.M. (ed), Biology of anaerobic bacteria. Wiley, New York, pp. 179–244.

Townsend C.R. 1996. Concepts in river ecology: pattern and process in the catchment hierarchy. Arch. Hydrobiol. Suppl. 113(Large Rivers 10): 3–21.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. and Cushing C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Vervier P., Dobson M. and Pinay G. 1993. Role of interaction zones between surface and ground waters in DOC transport and processing: considerations for river restoration. Freshwat. Biol. 29: 275–284.

Ward J.V. 1989. The four-dimensional nature of lotic ecosystems. J. N. Am. Benthol. Soc. 8: 2–8.

Ward J.V., Tockner K., Uehlinger U. and Malard F. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. Regul. Rivers: Res. Manage. 17: 311–323.

Webster J.R. and Meyer J.L. 1997. Organic matter budgets for streams: a synthesis. J. N. Am. Benthol. Soc. 16: 141–161.

Wilczek S., Fischer H., Brunke M. and Pusch M.T. 2004. Microbial activity within a subaqueous dune in a large lowland river (Elbe, Germany). Aquat. Microb. Ecol. 36: 83–97.

Wilczek S., Fischer H. and Pusch M.T. in press. Regulation and seasonal dynamics of extracellular enzyme activities in the sediments of a large lowland river. Microb. Ecol. (in press).

Wolff C. and Remde A. 1998. Autotrophe Nitrifikation. In: Vereinigung für Allgemeine und Angewandte Mikrobiologie (ed), Mikrobiologische Charakterisierung aquatischer Sedimente: Methodensammlung. R. Oldenbourg Verlag, München, pp. 156–170.