Attermeyer, K., **Anlanger, C.**, **Weitere, M.**, **Kamjunke, N.**, **Brauns, M.** (2023):
Benthic metabolism and nutrient uptake vary with geomorphology and season in a lowland river
Freshw. Sci. **42** (1), 58 – 69

http://dx.doi.org/10.1086/723895

Geomorphology and season interactively determine benthic metabolism and nutrient uptake in a lowland river

Katrin Attermeyer[1,2], Christine Anlanger[1,3], Markus Weitere[1,4], Norbert Kamjunke[1,5], and Mario Brauns[1, 6]

[1]Helmholtz Centre for Environmental Research-UFZ, Department River Ecology, Brückstraße 3A, 39114 Magdeburg, Germany

E-mail addresses: [2]Present address: WasserCluster Lunz – Biologische Station, Dr Carl Kupelwieser Promenade 5, 3293 Lunz am See, Austria & University of Vienna, Department of Functional and Evolutionary Ecology, Djerassiplatz 1, 1030 Vienna, Austria, katrin.attermeyer@wcl.ac.at, https://orcid.org/0000-0002-6503-9497; [3]christine.anlanger@ufz.de, https://orcid.org/0000-0001-6666-422X; [4]markus.weitere@ufz.de, https://orcid.org/0000-0002-5259-2293; [5]norbert.kamjunke@ufz.de https://orcid.org/0000-0002-8016-5352; [6]mario.brauns@ufz.de, https://orcid.org/0000-0002-5012-9721

Received 22 December 2021; Accepted 26 September 2022; Published online XX Month 2022; Associate Editor, Robert Hall.

Freshwater Science, volume 42, number 1, March 2023. © 2023 The Society for Freshwater Science. All rights reserved. Published by The University of Chicago Press for the Society for Freshwater Science. https://doi.org/10.1086/XXXXXX

Abstract: Meandering rivers are characterized by geomorphic units like cut banks, point bars, and thalwegs. These units arise from interactions between hydrological and geomorphological forces. However, the individual contributions of geomorphic units to whole-river metabolism or nutrient processing are unclear because these quantifications are often done at larger spatial scales. We used closed recirculating chambers to measure benthic gross primary production (GPP), respiration (R), N uptake or release, and P uptake or release at bimonthly intervals over 1 y at different geomorphic units in the Mulde River, Germany. We compared GPP, R, and nutrient processing among a cut bank, a point bar, and the thalweg at a natural meander. We also compared the cut bank of this natural meander with a cut bank fixed by riprap at a human-altered meander. In the natural meander, GPP, R, and nutrient processing rates were higher at the point bar than the cut bank or thalweg. The reason probably is that larger sediment grain sizes provide a more stable substrate for microbial communities. A strong interaction between geomorphic units and time for GPP and NH_4^+ fluxes suggested that differences in nutrient processing rates among geomorphic units were restricted to specific times during the year. During the warmer summer months, we found differences between the three geomorphic units at the natural meander that were absent during the winter. Furthermore, in June and August 2017, R was 2 to 3× lower at the cut bank stabilized by riprap than at the natural cut bank. Our results demonstrate that rivers are composed of functionally distinct geomorphic units susceptible to human-induced hydromorphological degradation. However, strong interactions between space and time and large within-geomorphic unit variability suggest that local drivers influence ecosystem function, suggesting that we need additional research to resolve these drivers at the scales of geomorphic units.

Key words: cut bank, gross primary production, respiration, nutrient cycling, riprap, benthos, hydromorphological degradation

Rivers and their surrounding floodplains are highly productive ecosystems that provide essential ecosystem services (Tockner and Stanford 2002, Hotchkiss et al. 2015), yet understanding the controls of essential ecological processes on different spatial and temporal scales in streams and rivers remains a major challenge. Uncertainties in river metabolism estimates suggest that environmental factors may cause within-river variation in productivity (Tromboni et al. 2017, Reijo et al. 2018). This uncertainty can be attributed to spatial heterogeneity originating from habitats with different biological reactivity (Reijo et al. 2018). For example, submerged macrophytes can contribute substantially to whole-stream nutrient uptake in temperate (Riis et al. 2012, Peipoch et al. 2014) and tropical streams (Tromboni et al. 2017). In forested headwater streams, epilithic biofilms are strong drivers of nutrient cycling (Tank et al. 2018, Risse-Buhl et al. 2020b). However, most studies have focused on smaller streams, with only a few reporting on small-scale spatial heterogeneity of metabolism or nutrient processing in larger streams and rivers (Uehlinger 2006, Dodds et al. 2013, Hall et al. 2016).

Streams and rivers are physically heterogeneous environments consisting of various channel or geomorphic units (Bisson et al. 2017, Belletti et al. 2017). Geomorphic units form when hydraulic and morphodynamic processes create distinctive erosion and deposition patterns (Belletti et al. 2017). For example, geomorphic units such as riffles, runs, and pools are spatially distinct patches with homogenous water flow and substrate (Frissell et al. 1986, Belletti et al. 2017), which can exhibit distinct differences in benthic metabolism because of their different physical conditions such as grain size or flow velocity (Whitledge and Rabeni 2000). Meandering rivers are characterized by larger geomorphic units. Bends of meandering rivers have a shallow zone at the inner bank, called a point bar, with a gentle, lateral slope towards the channel center and scour holes outside the bend. The outer bend of the meander, called the cut bank, has steep banks exhibiting floodplain soils. The thalweg is the longitudinal line that connects the deepest positions along the riverbed. These geomorphic units show distinct environmental conditions, with shallow point bars characterized by the highest light availability and summer water temperatures (Fig. 1D, E).

Flow pattern changes across geomorphic units. The flow pattern in meander bends is characterized by a complex, helical flow pattern driven by centrifugal forces and large-scale pressure gradients (Leopold and Wolman 1960, Bathurst et al. 1979). At the point bar, flow is controlled by a shoaling effect, which directs the flow towards the channel center and increases water velocity at the outer bend (Hickin 1978, Dietrich and Smith 1983). However, small counter-rotating flow structures may reduce flow velocities close to the bank at the outer cut bank (Blanckaert and de Vriend 2003). A stronger curvature of the bend also leads to flow separation at point bars, which can provide a hydraulic dead zone that creates weak reverse flow near the bend apex (Ferguson et al. 2003).

Different environmental and flow conditions can modify the composition, metabolism, and nutrient processing of microbial biofilms (Risse-Buhl et al. 2017, 2020a, b). For example, Mori et al. (2017) detected higher heterotrophic respiration (R) in fine sediment (<5 mm) than in coarse sediment (>5 mm) in a gravel-bed river in Slovenia. Furthermore, other factors that vary by geomorphic unit, such as light, temperature, flow pattern, and grain size, control primary production (Uehlinger 2006, Tank et al. 2010). Accordingly, the physical and biotic characteristics of geomorphic units may result in large differences in metabolism and nutrient processing among units. Furthermore, metabolic changes in each of the geomorphic units can translate into metabolic changes on the reach scale. Where, when, and in which direction those changes occur has consequences for whole-ecosystem metabolism and nutrient fluxes and, therefore, has implications for river management and restoration efforts.

Engineers use training structures like riprap to prevent erosion (Strayer et al. 2012). These structures influence the diversity and composition of biological communities by altering flow patterns (Risse-Buhl et al. 2020a) and may affect ecosystem functioning. For example, Brabender et al. (2016) demonstrated that a shore engineered with ripraps had benthic secondary production rates 4× lower than an unmodified natural shore. We expect that engineered shores may experience other changes to ecosystem function, but we lack research on the influence of engineered shores on ecosystem metabolism and nutrient cycling. Method constraints also complicate studying the role of natural and human-modified geomorphic units on river functioning. For example, most geomorphic units are too short for conventional whole-reach approaches like the open-water diel oxygen technique (Marzolf et al. 1994, Young and Huryn 1998). Establishing benthic chambers combined with in-situ loggers may help us quantify ecosystem functioning at smaller-than-reach scales. Researchers have used these installations to successfully delineate sources of small-scale metabolism heterogeneity and nutrient uptake in streams and small rivers (Hensley and Cohen 2020, Irwin et al. 2020).

The aim of this study is to understand the variation of benthic metabolism and nutrient processing among geomorphic units and over 1 y in the meandering Mulde river in Germany. We hypothesized that 1) metabolism and nutrient processing would be highest at the point bar of a natural river reach because relatively stable environmental conditions and high light availability in shallow water at point bars allow for higher standing stocks of benthic biofilm and 2) metabolism and nutrient processing at the riprap would be higher than the natural cut bank because the cobbles at the riprap provide a more stable area for biofilm growth.

METHODS

We assessed how benthic metabolism and nutrient processing differ among natural geomorphic units and between a natural and human-altered cut bank in the Mulde River, Germany. We also assessed how these differences vary seasonally over 1 y. To test our first hypothesis, we compared benthic metabolism (gross primary production [GPP] and R), uptake, and release of NO_3^-, NH_4^+, and soluble reactive P [SRP] at a cut bank, a point bar, and the thalweg in a natural meander. We incubated sediments from each geomorphic unit in triplicate in enclosed, transparent chambers (Bott et al. 1978, Rüegg et al. 2015). Samplings and measurements were conducted bimonthly over 1 y. To test our second hypothesis, we compared the same metrics of benthic metabolism and nutrient uptake and release as described above between the natural cut bank and a riprap.

Experimental design

To test if metabolism and nutrient processing would be highest at the point bar of a natural river reach, we took samples for chamber measurements from 3 natural geomorphic units (a cut bank, a point bar, and the thalweg) at 1 natural meander. We tested for differences in metabolism (GPP and R), nutrient fluxes, and environmental parameters between the 3 geomorphic units at the natural meander with a repeated measure analysis of variance followed by Dunnett tests for post-hoc comparisons. We designated metabolism (GPP and R), and nutrient fluxes (NO_3^-, NH_4^+, and SRP) as dependent variables and the geomorphic units (levels are cut bank, point bar, thalweg) and time (levels are the sampling times) and their interaction as independent variables.

Furthermore, to test if metabolism and nutrient processing at the riprap would be higher than the natural cut bank, we additionally sampled a riprap at a human-altered meander. We tested for differences in metabolism and nutrient processing between cut banks at the natural and human-altered meander using a repeated measure analysis of variance with site, time, and their interaction as independent variables. All response variables were tested for homogeneity of variances and sphericity and model residuals were tested for normality using Shapiro-Wilk tests. Response variables that did not meet the normality requirement were transformed as sign(x)*log|x+1|. The α level was set to 0.01 to avoid type I errors due to the high number of tests. All statistical analyses were conducted with IBM® SPSS® Statistics (version 22; Chicago, Illinois).

Study area

We conducted our study at the lower Mulde River Germany, a 6th-order tributary of the Elbe River (Fig. 1). The lower Mulde River is a gravel bed river with long-term mean discharge and baseflow of 66.7 and 17.9 m^3/s, respectively, as measured between 1995 to 2017. The mean bed slope of the lower Mulde River is ~0.025%, resulting in highly dynamic hydromorphological processes. The studied meanders were situated within the nature protection site “Untere Mulde” and exhibited quasi-natural meandering river courses with a slight sinuosity of 1.3. However, ~75% of the shoreline is modified and largely stabilized by riprap to prevent lateral erosion, fixing the river width to ~40 to 60 m (Puhlman 1997). Floodplain soils consist of 1 to 4 m of high alluvial loam above glacial gravel.

The human-altered meander (lat 51°44'51"N, long 12°18'41"E) was ~2 km upstream of the natural meander (lat 51°46'12"N, long 12°17'46"E) (Table 1, Fig. 1). We chose the 2 meanders because of their close proximity to each other and similar meander characteristics. The meander of the natural and human-altered site had a radius of 170 and 270 m, a mean width of the 2 inflection points of 50 and 52 m, and a dimensionless bend curvature of 3.4 and 5.2, respectively. The natural meander had no bank stabilization, whereas the human-altered meander had a cut bank stabilized by a riprap installed in the 1980s (Fig. S1A, B). The cut banks at both meanders were steep and the water column is characterized by a heterogeneous flow pattern caused by local bank erosion and small embankments at the natural meander and increased bank roughness by the riprap structure at the human-altered meander.

Benthic metabolism and nutrient processing

We measured benthic GPP, R, and nutrient uptake and release (hereafter referred to as fluxes) by monitoring changes in DO concentrations with HOBO® optical DO sensors (Onset®, Bourne, Massachusetts) and measuring nutrients (NO_3^-, NH_4^+, and SRP) at the start and the end incubation periods in enclosed, transparent chambers (Bott et al. 1978, Rüegg et al. 2015). We followed Rüegg et al. (2015) and constructed benthic chambers from 10 to 15-mm transparent polycarbonate sheets (Fig. S1C, D). Chambers had rectangular dimensions (60 × 13 × 19 cm) and were sealed with polycarbonate lids positioned with steel clamps. We used underwater pumps (Mini-Red-Dragon 2500; Royal Exclusiv®, Cologne, Germany) to recirculate water within the chambers (pump rate = 0.78 L/s and flow velocity of 20 cm/s). We confirmed that chambers did not leak by quantifying salt-tracer diffusion rates for 23 h.

We measured benthic metabolism and nutrient fluxes bimonthly from June 2017 to April 2018. Exact sampling dates are given in Table S1 and the chamber incubations started between 9 and 10 am. We filled each of 3 chambers with samples of the dominant sand–gravel mixture present in each geomorphic unit to account for the variation within the respective geomorphic unit. We sampled the sediments at the natural cut bank and point bar at depths of 0.3 to 0.5 m with a 0.3-m long metal pipe cut into halves (gutter; see Fig. S1C, D). The round half-pipe allowed us to extract the bottom sediment without disturbing sediment composition and arrangement. The thalweg had a water depth of >2 m and current velocities of >1 m/s that precluded conventional sampling techniques and sampling by metal pipes. Instead, we collected the dominating coarse gravel from this geomorphic unit using a hand net (250-µm mesh) connected to a 3-m pole that we operated from a boat. This sampling technique efficiently collected thalweg sediments, but we acknowledge that the pole disturbed the natural arrangement of sediment layers.

The riprap was dominated by cobbles that were 15 to 20 cm long and 8 to 10 cm wide. We collected 3 to 5 cobbles at depths of 0.3 to 0.5 m/chamber. To compare the natural cut bank and the riprap, we used the total area of the cobbles but assumed a plane surface area for all other sediments for the calculations of rates/m^2. Consequently, we may have underestimated the surface area of the sediment at the natural cut bank and overestimated the surface area of the cobbles from the riprap. However, we tried to keep the surface areas of the cobbles within the range of the plane surface area. We filled 1 chamber with surface water only to correct for water column rates.

We placed all chambers from the meander on the river bottom at a water depth of 0.3 m to keep the chamber temperature at ambient conditions during incubation (Fig. S1D). Hence, light conditions were similar among the 3 geomorphic units during incubations in the light. Water temperatures in the chambers increased by 2°C during the first 2 h of deployment, probably because of heat produced by the pump. We therefore excluded the oxygen values of the first 2 h from our calculations (see below).

We operated chambers in a 4-h light phase and a 2-h dark phase. For the dark phase, we covered all chambers with a lightproof fabric that reduced light levels to below detection. We monitored the DO concentrations with HOBO® optical DO sensors (Onset®, Bourne, Massachusetts) set to measure at 1-min intervals. We collected NH_4-N, NO_3-N, and SRP concentration samples at the beginning and end of the 6-h deployment period. The nutrient processing rates included a light and a dark phase because it was impossible to open the chambers during the logging phase for subsampling. We analyzed the samples in the laboratory using national standard procedures described in Kamjunke et al. (2013).

Calculations of chamber metabolism and nutrient processing

First, we calculated the rate of net ecosystem production (NEP) and R (mg O_2 m^{-2} h^{-1}) from linear regressions of DO changes over time in the light (for NEP) and dark phase (for R) and the fluxes of nutrient changes from start to end of the incubation phase for each chamber as:

$$Flux = \frac{S \times V}{A}, \quad \text{(Eq. 1)}$$

where S is the slope of the linear regression (mg O_2 L^{-1} h^{-1}) or the change in nutrient concentration from start to end (µg nutrient L^{-1} h^{-1}), V is chamber volume (L), and A is area (m^2). We used the chamber volume and the plane surface area of substrata for the sites with sand–gravel mixture calculate areal hourly rates. For sites with cobbles, we used individual cobble area. Then, we calculated GPP by summing NEP and R. Subsequently, we converted the rates of oxygen to CO_2 by using 1.25 as a photosynthetic quotient for GPP and by using 1 as a respiratory quotient for R (Duarte and Agustí 1998, Berggren et al. 2012). We calculated the net NH_4^+, NO_3^-, and SRP uptake and release flux (µmol m^{-2} h^{-1}) based on the rate of change in nutrient concentrations from samples taken at the beginning and the end of the chamber deployment. Negative values indicate nutrient removal, whereas positive values indicate nutrient release. The fluxes for chambers containing benthic substrate are the sum of benthic and water column processes. We report benthic fluxes by subtracting values from the chamber containing water only from those with substrata.

Water column and biofilm measurements

We collected water column samples for dissolved organic C (DOC), particulate organic C, nutrients (NH_4-N, NO_3-N, and SRP), and chlorophyll *a* (Chl *a*) at the point bar and cut bank during each sampling campaign. We filtered DOC and nutrient samples through glass fiber filters (GF/F, nominal pore size 0.7 µm, Whatman, Maidstone, United Kingdom) and 0.2-µm polycarbonate filters (Nuclepore™, Whatman), respectively. We stored DOC samples at 4°C and analyzed samples via high-temperature oxidation with non-dispersive infrared detection within 24 h of collection (CEN-TC 1997). We analyzed the nutrients as described above for nutrient fluxes during incubation. We measured Chl *a* spectrophotometrically after direct extraction of the substrate in 96% ethanol from glass fiber filters (Whatman) (DIN 2019). In addition, we used the sediment samples from each chamber after deployment. We took approximately 100 g of sediment from each chamber and split this sediment for analyses of ash-free dry mass (AFDM), Chl *a* of benthic biofilms, and grain size distribution. The substrate for AFDM was sonicated for 15 min at 60% in a sonication bath (Sonorex Super DK 510-P; Bandelin Electronic GmbH & Co KG, Berlin, Germany). We analyzed AFDM by drying, weighing, combusting (5 h at 540°C), and reweighing the samples.

Grain size distribution

We dried the sediments from each chamber at 55°C for 24 h and sieved the sample through a 4-level sieving cascade (10–0.2 mm; Analysette 3 Pro; Fritsch International, Idar-Oberstein, Germany). We weighed each fraction and computed the mean grain size with the script “SANDY” (version 2.0; Gallon and Fournier 2013, Ruiz-Martínez et al. 2016) in MATLAB (version R2019b; MathWorks, Natick, Massachusetts).

RESULTS

Mulde River water chemistry

The chemical parameters in the water column of the 2 meanders in the Mulde River were similar (Table 1). Across all sites and times, the DOC concentration was 4.5 ± 1.1 mg/L (mean ±SD), and particulate organic C concentration was comparably high with 2.1 ± 2.7 mg/L. Furthermore, inorganic N was dominated by NO_3-N with an average of 3.3 ± 1.2 mg/L, and SRP accounted for ~30% of the total P with 31 ± 18 µg/L.

Differences in grain size and biofilm among natural geomorphic units

Mean grain size was 40 to 60% higher at the point bar compared with the cut bank and thalweg at the natural meander (Table S2, Fig. 2A). We found no difference in benthic Chl *a* among geomorphic units and times (Fig. 2B), whereas benthic AFDM differed strongly with time and among geomorphic units (Fig. 2C). The AFDM was highest in June and August 2017 at all 3 geomorphic units at the natural meander.

Differences in metabolism and nutrient fluxes among natural geomorphic units

Benthic metabolism and nutrient fluxes showed different patterns among geomorphic units at the natural meander (Table 2, Table S2, Figs 3, 4A, B). GPP differed with the interaction of unit and time. Post-hoc comparisons at different sampling times revealed strong differences among geomorphic units in June and October 2017 (Table S3). This pattern is reflected in pronounced seasonal changes of mean GPP, with the lowest GPP at the thalweg in December 2017 (3.1 ± 0.9 mg C m^{-2} h^{-1}) and the highest GPP at the cut bank in June 2017 (98.3 ± 8.6 mg C m^{-2} h^{-1}; Fig. 3). R differed strongly among geomorphic units and times, but we detected no interaction with time and unit. Mean R was lowest at the thalweg in March 2018 (–2.8 ± 3.2 mg C m^{-2} h^{-1}) and highest at the point bar in June 2017 (–60.7 ± 10.6 mg C m^{-2} h^{-1}; Fig. 3). R was highest for all natural geomorphic units in June 2017, August 2017, and April 2018, when the natural point bar was about 30 to 45% higher compared to the natural cut bank and thalweg (Fig. 3).

Nutrient fluxes switched between uptake and release in the different sampling months (Table 2, Fig. 4A–C). Fluxes of NH_4^+ related to the interaction between geomorphic units and times (Table S2), and, like GPP, post-hoc comparisons of sampling months revealed strong differences among geomorphic units in June and October 2017 (Table S3). In June 2017, the point bar had its highest NH_4^+ releases with –121.7 ± 24.7 µmol m^{-2} h^{-1}, which was 4× higher than the natural cut bank and 6× higher than thalweg (Table 2). In October, the thalweg showed the highest NH_4^+ uptake with 264.4 ± 32.5 µmol m^{-2} h^{-1}, which is 20% higher than the point bar and ~3× higher than the natural cut bank (Table 2). Fluxes of NO_3^- changed between uptake and release among geomorphic units and times but without an interaction between time and unit (Tables 2, S2). However, the SRP uptake fluxes differed with time but not among the different geomorphic units (Table S2, Fig. 4C). SRP fluxes showed uptake in all geomorphic units in August 2017 and the highest releases in October and December 2017 (Table 2).

Differences in grain size and biofilm between natural cut bank and riprap

Benthic AFDM and Chl *a* did not differ between natural cut bank and riprap or by time (Table S4). On average, benthic AFDM was 10.7 ± 18.0 µg/cm^2 at the natural cut bank and 71.8 ± 68.2 µg/cm^2 at the riprap and benthic Chl *a* was 0.11 ± 0.11 µg/cm^2 at the natural cut bank and 0.33 ± 0.50 µg/cm^2 at the riprap (Fig. 2A–C).

Differences in metabolism and nutrient fluxes between natural cut bank and riprap

The metabolism and nutrient fluxes at the riprap were much higher or lower than the natural cut bank at specific times (Table S4, Figs 3, 4A–C). For example, GPP was much higher at the natural cut bank than at the riprap in June 2017 (Table S5). For R, only time and geomorphic unit were important in explaining the variation, but we detected no interaction (Table S4). R was 2× as high at the natural cut bank compared with the riprap, while differences at other times of the year were less pronounced due to substantial variation within each structure (Table 2).

NH_4^+ fluxes only varied with time and not between natural cut bank and riprap (Table S4), whereas NO_3^- and SRP fluxes varied between natural cut bank and riprap only at specific times (Table S4). NO_3^- differed strongly between the natural cut bank and riprap in August 2017 and April 2018. SRP differed strongly between the units in June, August, October, and December 2017 (Table S5). During those months, the natural cut bank often showed opposite fluxes (in August 2017 for both nutrients) or fluxes 10 to 50× higher fluxes than the riprap (Table 2, Fig. 4A–C).

DISCUSSION

We expected systematic differences in benthic metabolism and nutrient fluxes among geomorphic units at a natural meander. However, benthic metabolism and nutrient processing varied greatly among the geomorphic units and sampling months. Contrary to our expectations, the riprap exhibited lower metabolic rates and nutrient fluxes than the natural cut bank. In our study, seasonal differences masked most of the spatial differences for benthic GGP, R and uptake or release of NH_4+, NO_3^-, and SRP. Hence, local factors influencing metabolism and nutrient dynamics, such as sediment structure, only act at times of high metabolic activities when water temperature does not limit microbial activities.

Time superimposes spatial differences in benthic metabolism and nutrient processing

The first hypothesis postulated strong differences in benthic metabolism and nutrient processing among geomorphic units at the investigated natural meander with the highest rates at the point bar. However, absolute differences in metabolic rates and nutrient fluxes were highest among the different time points and not among the different geomorphic units. The degree of differences in GPP and NH_4^+ fluxes among geomorphic units depended on the time of year. For example, GPP was higher in June at all geomorphic units. In addition, R peaked in June and August 2017 at all geomorphic units, with 10× higher R rates than in December 2017, when we detected the lowest rates. The strong seasonal variation with higher metabolic rates during the warmer summer months occurs also in the River Thur, a tributary of the upper Rhine, where about ½ of the variation of GPP and R was attributed to season (Uehlinger 2006). Following the classification system of river productivity by Savoy et al. (2019), the Mulde River shows the metabolic regime of a “summer peak river”. We can see that the benthic GPP of the Mulde River peaked in August; however, our measured GPP maxima might be conservative because we did not measure GPP every month. In the Saint John River in Canada, for example, benthic metabolism peaked mid-July (Irwin et al. 2020). Our study does not have a value for this time of year. Nevertheless, this metabolic regime has mostly been explained by a high light availability throughout the year due to little riparian shading, which is also true for our sites in the Mulde River.

R was one of the benthic activities that consistently differed among geomorphic units and was highest at the point bar. These rates support our first hypothesis that metabolism is highest at the point bar, a trend that may be explained by the larger average grain sizes at the point bar, which have proven to be more stable and favor algal growth (Hoyle et al. 2017). Increased riverbed roughness induced by larger grain sizes (Aberle and Nikora 2006) might also support the deposition and trapping of organic material at the riverbed and interstitial (Koiter et al. 2015, Ann et al. 2019). In comparison, grain sizes at the cut bank were much smaller and more dynamic because of the steep banks.

Potential factors explaining strong seasonal effects of benthic activities

The observed seasonal pattern suggests a temperature dependence of the benthic biofilm. This pattern has been described for metabolism and nutrient uptake in other streams and rivers (Demars et al. 2011, Bernhardt et al. 2018); however, mean annual water temperature was not a major driver regulating annual metabolism across US rivers (Bernhardt et al. 2022). Understanding how small-scale metabolic heterogeneity interacts with season is important, as small changes in each geomorphic unit can potentially influence metabolism on the reach-scale.

We point out that our comparisons among geomorphic units are biased because we placed chambers at similar water depths. We chose this installation because of environmental conditions in the thalweg, where water depths of >2 m and high flow velocities precluded a secure chamber placement. We acknowledge that this procedure has harmonized potential differences in light availability among geomorphic units. For example, thalweg samples were taken from water depths >2 m, where autotrophic production may be light limited, while light limitation can be excluded at the 2 shallow near-shore units. Light availability drives ecosystem metabolism and nutrient dynamics (Wagner et al. 2017, Bernhardt et al. 2018, 2022). Therefore, differences among geomorphic units may be more pronounced than our data suggested here.

Higher within-unit variation than among geomorphic units at the natural meander

Contrary to our expectations, the variation of the metabolic and nutrient fluxes within the defined geomorphic units was larger than between the geomorphic units. This might also explain the absence of strong differences in benthic metabolism and nutrient fluxes among geomorphic units. Other studies support the trend that the productivity of benthic microbial communities can vary substantially on a small scale (Fellows et al. 2009, Villamizar et al. 2014, Adams et al. 2016). For example, Adams et al. (2016) illustrate a large diel variation in R rates in seagrass ecosystems, implying a significant difference between daytime and nighttime R rates (Hotchkiss and Hall 2014, Rheuban et al. 2014). Furthermore, researchers studying waterholes of the Warrego River in Australia ascribed high variability on the temporal and spatial scale with more frequent disturbance events of the littoral zone, which potentially inhibited biofilm development (Fellows et al. 2009). Fine-scale heterogeneity can affect the metabolic processes and nutrient processing in large meandering rivers, similar to small streams (see Reijo et al. 2018). To date, most studies quantified metabolism or nutrient uptake and their drivers at just 1 or a few locations on the reach or whole-river scale (Schechner et al. 2021). Our results suggest that the small-scale heterogeneity of metabolism and nutrient fluxes can be substantial, highlighting the necessity to unravel small-scale processes and drivers to understand whole-system dynamics of rivers. We argue that more targeted studies are needed across different rivers and physical and chemical conditions to find the responsible drivers.

Riprap shows lower rates than natural cut bank

In contrast to our second hypothesis, areal metabolism and nutrient processing rates were lower at the riprap than at the natural cut bank. We attribute the low activities to the fewer fine particles at ripraps. Fine particles host a large diversity of microorganisms with relatively high activity levels (Mori et al. 2017). Consequently, our results suggest that fixing cut banks with riprap can reduce metabolism and nutrient fluxes, which complement a body of research that shows that riprap sections in rivers are less productive (Brabender et al. 2016) and have simplified food webs (Brauns et al. 2022). Despite the low sample size of our study, it adds to the growing understanding that river training for flood protection or navigation has substantial effects on ecosystem functioning.

We can only speculate to which extent our local results apply to other reaches of the Mulde River and other similarly sized rivers. However, comparisons with other meandering rivers are cautiously possible as our study covered microbial communities inhabiting a substrate spectrum from a sand–gravel mixture at the natural meander to cobbles at the riprap. Moreover, morphologies of other meander bends in the Mulde River or other similarly sized rivers are similar to those studied here (Bagnold 1960). However, we still lack studies comparing the metabolism or nutrient processing at human-altered versus natural meanders in rivers (Reid and Church 2015). To our knowledge, only 1 study reports and compares metabolic rates at human-altered sites with riprap to restored natural sites in a river (Kupilas et al. 2017). This study showed higher reach-scale metabolism for sites with high restoration efforts and, thus, more natural sediments in the 3rd-order, gravel-bed Ruhr River in Germany. However, the authors attribute this difference mostly to the abundance of macrophytes, a factor which is irrelevant to our chamber study (Kupilas et al. 2017). Hence, our data show that the investigated riprap can potentially reduce metabolism and nutrient retention of the whole river. However, we urgently need more research to assess the functional impacts of human modifications on ecosystems services (Elosegi et al. 2010).

Geomorphic units as functional process domains

There is increasing awareness that the physical template of rivers does not only determine biodiversity (Armitage and Pardo 1995, Beisel et al. 2000) but may also determine the magnitude and distribution of key riverine ecosystem functions such as benthic metabolism or nutrient processing (Irwin et al. 2020). For example, Valett et al. (2022) defined nutrient process domains for running waters based on the concept of riverine process domains (Montgomery 1999) and showed that certain river reaches can either act as sources or sinks of nutrients. Similarly, Scholl et al. (2021) attributed patterns of macroinvertebrate secondary production to geophysical properties, that is habitat types, in US rivers. We expand these findings and show that benthic metabolism and nutrient processing are already different at scales smaller than reach scale including human-modified geomorphic units such as riprap. Our results suggest that the interplay of nutrient release and uptake at the scale of geomorphic units may determine the overall uptake efficiency of a given reach. However, this functional role of geomorphic units as nutrient sources and sinks were governed by season, with higher metabolic activities associated with higher water temperatures during summer. To refine the functional role of geomorphic units for whole-reach or whole-river scales, future studies should consider fine-scaled measures of riverine ecosystem functions across different rivers and across seasons. This improved understanding of the variability at small spatial scales and underlying drivers will advance river science and inform management.

ACKNOWLEDGEMENTS

Author contributions: NK, MW, and MB contributed substantially to the study's conception; KA, NK, MB, and CA to data acquisition; and KA, CA, and MB to data analysis. KA, CA, and MB contributed substantially to drafting the manuscript, and all authors commented and approved the final submitted manuscript.

We want to thank Sven Bauth, Christin Siesing, Marcel Otte, Ines Locker, and Ute Link for their invaluable help with sampling, sample preparation, and processing. We are grateful to P. Portius and his team for technical support. We thank Heiko Schrenner and Georg Rast (World Wide Fund for Nature Germany) and Christiane Schulz-Zunkel for coordinating the project. We would like to thank the 2 anonymous reviewers and associate editor Robert Hall for their suggestions and comments. The project was funded by the Federal Ministry of Education and Research (Initiative for Sustainable Development FONA), the Federal Agency for Nature Conservation and the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety in Germany (grant number: FKZ 16LC1322B). The authors declare no conflicts of interest.

Data availability: The data that support the findings of this study are openly available in figshare at https://figshare.com/articles/dataset/dx_doi_org_10_6084_m9_figshare_6025748/6025748.

LITERATURE CITED

Aberle, J., and V. Nikora. 2006. Statistical properties of armored gravel bed surfaces. Water Resources Research 42:W11414.

Adams, M. P., A. J. Ferguson, P. S. Maxwell, B. A. Lawson, J. Samper-Villarreal, and K. R. O’Brien. 2016. Light history-dependent respiration explains the hysteresis in the daily ecosystem metabolism of seagrass. Hydrobiologia 766:75–88.

Ann, V., A. Freixa, A. Butturini, and A. M. Romaní. 2019. Interplay between sediment properties and stream flow conditions influences surface sediment organic matter and microbial biomass in a Mediterranean river. Hydrobiologia 828:199–212.

Armitage, P. D., I. Pardo, and A. Brown. 1995. Temporal constancy of faunal assemblages in 'mesohabitats' — application to management? Archiv für Hydrobiologie 133:367-387.

Bagnold, R. A. 1960. Some aspects of the shape of river meanders. Geological Survey Professional Paper 282-E. United States Government Printing Office, Washington, DC.

Bathurst, J. C., R. D. Hey, and C. R. Thorne. 1979. Secondary flow and shear stress at river bends. Journal of the Hydraulics Division 105:1277–1295.

Beisel, J. N., P. Usseglio-Polatera, and J.C. Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. In Assessing the ecological integrity of running waters (pp. 163-171). Springer, Dordrecht.

Belletti, B., M. Rinaldi, M. Bussettini, F. Comiti, A. M. Gurnell, L. Mao, L. Nardi, and P. Vezza. 2017. Characterising physical habitats and fluvial hydromorphology: A new system for the survey and classification of river geomorphic units. Geomorphology 283:143–157.

Berggren, M., J. F. Lapierre, and P. A. Del Giorgio. 2012. Magnitude and regulation of bacterioplankton respiratory quotient across freshwater environmental gradients. The ISME Journal 6:984–993.

Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. W. Harvey, M. Arroita, A. P. Appling, M. J. Cohen, W. H. McDowell, R. O. Hall Jr, J. S. Read, B. J. Roberts, E. G. Stets, and C. B. Yackulic. 2018. The metabolic regimes of flowing waters. Limnology and Oceanography 63:S99–S118.

Bernhardt, E. S., P. Savoy, M. J. Vlah, A. P. Appling, L. E. Koenig, R. O. Hall Jr, M. Arroita, J. R. Blaszczak, A. M. Carter, and M. Cohen. 2022. Light and flow regimes regulate the metabolism of rivers. Proceedings of the National Academy of Sciences 119:e2121976119.

Bisson, P.A., D. R. Montgomery, and J. M. Buffington. 2017. Valley segments, stream reaches, and channel units. In Methods in Stream Ecology, Volume 1 (pp. 21-47). Academic Press.

Blanckaert, K., and H. J. de Vriend. 2003. Nonlinear modeling of mean flow redistribution in curved open channels. Water Resources Research 39:1375.

Bott, T. L., J. T. Brock, C. E. Cushing, S. V. Gregory, D. King, and R. C. Petersen. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. Hydrobiologia 60:3–12.

Brabender, M., M. Weitere, C. Anlanger, and M. Brauns. 2016. Secondary production and richness of native and non-native macroinvertebrates are driven by human-altered shoreline morphology in a large river. Hydrobiologia 776:51–65.

Brauns, M., D. Kneis, M. Brabender, and M. Weitere. 2022. Habitat availability determines food chain length and interaction strength in food webs of a large lowland river. River Research and Applications 38:323–333.

CEN-TC (European Committee for Standardization-Technical Committee). 1997. EN 1484: Water analysis–Guidelines for the determination of total organic carbon (TOC) and dissolved organic carbon (DOC). European Committee for Standardization, Brussels, Belgium.

Demars, B. O. L., J. R. Manson, J. S. Olafsson, G. M. Gislason, R. Gudmundsdottir, G. U. Y. Woodward, J. Reiss, D. E. Pichler, J. J. Rasmussen, and N. Friberg. 2011. Temperature and the metabolic balance of streams. Freshwater Biology 56:1106–1121.

Dietrich, W. E., and J. D. Smith. 1983. Influence of the point bar on flow through curved channels. Water Resources Research 19:1173–1192.

DIN (German National Standards). 2019. DIN 38409-60:2019-12: German standard methods for the examination of water, waste water and sludge–Parameters characterizing effects and substances (group H) - Part 60: Spectrometric determination of the chlorophyll-a concentration in water (H 60).

Dodds, W. K., A. M. Veach, C. M. Ruffing, D. M. Larson, J. L. Fischer, and K. H. Costigan. 2013. Abiotic controls and temporal variability of river metabolism: Multiyear analyses of Mississippi and Chattahoochee river data. Freshwater Science 32:1073–1087.

Duarte, C. M., and S. Agustí. 1998. The CO_2 balance of unproductive aquatic ecosystems. Science 281:234–236.

Elosegi, A., J. Díez, and M. Mutz. 2010. Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. Hydrobiologia 657:199–215.

Fellows, C. S., S. E. Bunn, F. Sheldon, and N. J. Beard. 2009. Benthic metabolism in two turbid dryland rivers. Freshwater Biology 54:236–253.

Ferguson, R. I., D. R. Parsons, S. N. Lane, and R. J. Hardy. 2003. Flow in meander bends with recirculation at the inner bank. Water Resources Research 39:1322.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management 10:199–214.

Gallon, R. K., and J. Fournier. 2013. *G2Sd*: Grain-size statistics and description of sediment.

(Available from: https://cran.r-project.org/web/packages/G2Sd/index.html)

Hall Jr, R. O., J. L. Tank, M. A. Baker, E. J. Rosi-Marshall, and E. R. Hotchkiss. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems 19:73–86.

Hensley, R. T., and M. J. Cohen. 2020. Nitrate depletion dynamics and primary production in riverine benthic chambers. Freshwater Science 39:169–182.

Hickin, E. J. 1978. Mean flow structure in meanders of the Squamish River, British Columbia. Canadian Journal of Earth Sciences 15:1833–1849.

Hotchkiss, E. R., and R. O. Hall Jr. 2014. High rates of daytime respiration in three streams: Use of $\delta^{18}O_{O2}$ and O_2 to model diel ecosystem metabolism. Limnology and Oceanography 59:798–810.

Hotchkiss, E. R., R. O. Hall Jr, R. A. Sponseller, D. E. Butman, J. Klaminder, H. Laudon, M. Rosvall, and J. Karlsson. 2015. Sources of and processes controlling CO_2 emissions change with the size of streams and rivers. Nature Geoscience 8:696–699.

Hoyle, J. T., C. Kilroy, D. M. Hicks, and L. Brown. 2017. The influence of sediment mobility and channel geomorphology on periphyton abundance. Freshwater Biology 62:258–273.

Irwin, C. E., J. M. Culp, and A. G. Yates. 2020. Spatio-temporal variation of benthic metabolism in a large, regulated river. Canadian Water Resources Journal 45:144–157.

Kamjunke, N., O. Büttner, C. G. Jäger, H. Marcus, W. von Tümpling, S. Halbedel, H. Norf, M. Brauns, M. Baborowski, R. Wild, D. Borchardt, and M. Weitere. 2013. Biogeochemical patterns in a river network along a land use gradient. Environmental Monitoring and Assessment 185:9221–9236.

Koiter, A. J., P. N. Owens, E. L. Petticrew, and D. A. Lobb. 2015. The role of gravel channel beds on the particle size and organic matter selectivity of transported fine-grained sediment: Implications for sediment fingerprinting and biogeochemical flux research. Journal of Soils and Sediments 15:2174–2188.

Kupilas, B., D. Hering, A. W. Lorenz, C. Knuth, and B. Gücker. 2017. Hydromorphological restoration stimulates river ecosystem metabolism. Biogeosciences 14:1989–2002.

Leopold, L. B., and M. G. Wolman. 1960. River meanders. Geological Society of America Bulletin 71:769–793.

Marzolf, E. R., P. J. Mulholland, and A. D. Steinman. 1994. Improvements to the diurnal upstream–downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Sciences 51:1591–1599.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 35:397–410.

Mori, N., B. Debeljak, D. Kocman, and T. Simčič. 2017. Testing the influence of sediment granulometry on heterotrophic respiration with a new laboratory flow-through system. Journal of Soils and Sediments 17:1939–1947.

Peipoch, M., E. Gacia, A. Pastor, M. Ribot, J. L. Riera, F. Sabater, and E. Martí. 2014. Intrinsic and extrinsic drivers of autotrophic nitrogen cycling in stream ecosystems: Results from a translocation experiment. Limnology and Oceanography 59:1973–1986.

Puhlman, G. 1997. Wasserbau und Hochwasserschutz an der unteren Mulde–Historie–Status Quo–Perspektiven. Naturschutz im Land Sachsen Anhalt 34:38–46.

Reid, D., and M. Church. 2015. Geomorphic and ecological consequences of riprap placement in river systems. Journal of the American Water Resources Association 51:1043–1059.

Reijo, C. J., R. T. Hensley, and M. J. Cohen. 2018. Isolating stream metabolism and nitrate processing at point-scales, and controls on heterogeneity. Freshwater Science 37:238–250.

Rheuban, J. E., P. Berg, and K. J. McGlathery. 2014. Multiple timescale processes drive ecosystem metabolism in eelgrass (*Zostera marina*) meadows. Marine Ecology Progress Series 507:1–13.

Riis, T., W. K. Dodds, P. B. Kristensen, and A. J. Baisner. 2012. Nitrogen cycling and dynamics in a macrophyte-rich stream as determined by a release. Freshwater Biology 57:1579–1591.

Risse-Buhl, U., C. Anlanger, A. Chatzinotas, C. Noss, A. Lorke, and M. Weitere. 2020a. Near streambed flow shapes microbial guilds within and across trophic levels in fluvial biofilms. Limnology and Oceanography 65:2261–2277.

Risse-Buhl, U., C. Anlanger, K. Kalla, T. R. Neu, C. Noss, A. Lorke, and M. Weitere. 2017. The role of hydrodynamics in shaping the composition and architecture of epilithic biofilms in fluvial ecosystems. Water Research 127:211–222.

Risse-Buhl, U., C. Anlanger, C. Noss, A. Lorke, D. von Schiller, and M. Weitere. 2020b. Hydromorphologic sorting of in-stream nitrogen uptake across spatial scales. Ecosystems 24:1184–1202.

Rüegg, J., J. D. Brant, D. M. Larson, M. T. Trentman, and W. K. Dodds. 2015. A portable, modular, self-contained recirculating chamber to measure benthic processes under controlled water velocity. Freshwater Science 34:831–844.

Ruiz-Martínez, G., G. D. Rivillas-Ospina, I. Mariño-Tapia, and G. Posada-Vanegas. 2016. SANDY: A Matlab tool to estimate the sediment size distribution from a sieve analysis. Computers & Geosciences 92:104–116.

Savoy, P., A. P. Appling, J. B. Heffernan, E. G. Stets, J. S. Read, J. W. Harvey, and E. S. Bernhardt. 2019. Metabolic rhythms in flowing waters: An approach for classifying river productivity regimes. Limnology and Oceanography 64:1835–1851.

Schechner, A. E., W. K. Dodds, F. Tromboni, S. Chandra, and A. Maasri. 2021. How do methodological choices influence estimation of river metabolism? Limnology and

Oceanography: Methods 19:659–672.

Scholl, E. A., W. F. Cross, and C. S. Guy. 2022. Geomorphology shapes relationships between animal communities and ecosystem function in large rivers. Oikos e09431.

Strayer, D. L., S. E. G. Findlay, D. Miller, H. M. Malcom, D. T. Fischer, and T. Coote. 2012. Biodiversity in Hudson River shore zones: Influence of shoreline type and physical structure. Aquatic Sciences 74:597–610.

Tank, J. L., E. Martí, T. Riis, D. von Schiller, A. J. Reisinger, W. K. Dodds, M. R. Whiles, L. R. Ashkenas, W. B. Bowden, and S. M. Collins. 2018. Partitioning assimilatory nitrogen uptake in streams: An analysis of stable isotope tracer additions across continents. Ecological Monographs 88:120–138.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29:118–146.

Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: Present state and future trends. Environmental Conservation 29:308–330.

Tromboni, F., W. K. Dodds, V. Neres-Lima, E. Zandonà, and T. P. Moulton. 2017. Heterogeneity and scaling of photosynthesis, respiration, and nitrogen uptake in three Atlantic Rainforest streams. Ecosphere 8:e01959.

Uehlinger, U. 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. Freshwater Biology 51:938–950.

Valett, H. M., M. Peipoch, and G. C. Poole. 2022. Nutrient processing domains: Spatial and temporal patterns of material retention in running waters. Freshwater Science, 41(2), 195-214.

Villamizar, S. R., H. Pai, C. A. Butler, and T. C. Harmon. 2014. Transverse spatiotemporal variability of lowland river properties and effects on metabolic rate estimates. Water Resources Research 50:482–493.

Wagner, K., M. M. Bengtsson, R. H. Findlay, T. J. Battin, and A. J. Ulseth. 2017. High light intensity mediates a shift from allochthonous to autochthonous carbon use in phototrophic stream biofilms. Journal of Geophysical Research: Biogeosciences 122:1806–1820.

Whitledge, G. W., and C. F. Rabeni. 2000. Benthic community metabolism in three habitats in an Ozark stream. Hydrobiologia 437:165–170.

Young, R. G., and A. D. Huryn. 1998. Comment: Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determing whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Sciences 55:1784.

FIGURE CAPTIONS

Fig. 1. Map and setup of the field study (A-C) in the Mulde River, Germany, picturing the locations of the natural meander with the 3 sampled geomorphic units (cut bank, point bar, and thalweg; D) as well as the human-altered meander with the riprap (E).

Fig. 2. Mean grain size (no data for riprap; A), benthic chlorophyll *a* (B) and ash-free dry mass (AFDM; C) of the biofilm at the riprap (white with diagonal lines), cut bank (white), point bar (light gray), and thalweg (dark gray) at a natural meander in the Mulde River, Germany, measured bimonthly from June 2017 to April 2018. Please note that there is no data available for chlorophyll *a* in June 2017 for natural thalweg and in December 2017 for the natural cut bank. The bar charts show mean and SD (error bars) of the replicates from each sampling date. Jun = June, Aug = August, Oct = October, Dec = December, Mar = March, Apr = April.

Fig. 3. Gross primary production (GPP; positive numbers) and respiration (R; negative numbers) at the riprap (white with diagonal lines), cut bank (white), point bar (light gray), and thalweg (dark gray) at the natural meander in the Mulde River, Germany, measured bimonthly from June 2017 to April 2018. The bar charts represent mean and SD (error bars) of the replicates from each sampling date. Jun = June, Aug = August, Oct = October, Dec = December, Mar = March, Apr = April.

Fig. 4. NH_4-N (A), NO_3-N (B), and soluble reactive phosphorus (SRP) (C) uptake (positive numbers) and release (negative numbers) at the riprap (white with diagonal lines), cut bank (white), point bar (light gray), and thalweg (dark gray) at the natural meander in the Mulde River, Germany, measured bimonthly from June 2017 to April 2018. Please note the different scaling of the *y*-axes. The bar charts represent mean and SD (error bars) of the 3 replicates from each sampling date. No NH_4^+ data was available for April 2018 (A)

because the samples were lost. Jun = June, Aug = August, Oct = October, Dec = December, Mar = March, Apr = April.

Table 1. Water column chemical and biological parameters from studied meanders in the Mulde River, Germany. Data represent the mean and SD during the sampling period (June 2017–April 2018; sample size n = 6 for each parameter) at the natural and riprap meander. Chl *a* = chlorophyll *a*, DOC = dissolved organic C, POC = particulate organic C, SRP = soluble reactive P.

	Natural meander		Human-altered meander
Parameter	Cut bank	Point bar	Riprap
Latitude	51°46'12.1"N	51°46'12.2"N	51°44'51.8"N
Longitude	12°17'46.5"E	12°17'48.8"E	12°18'41.5"E
Chl *a* (µg/L)	24.0 ± 27.2	24.7 ± 24.9	18.3 ± 20.7
DOC (mg/L)	4.3 ± 0.8	4.4 ± 0.8	4.7 ± 1.6
NH_4-N (µg/L)	55.7 ±58.3	57.0 ± 60.4	58.8 ± 50.9
NO_3-N (mg/L)	3.2 ± 3.1	3.2 ± 1.4	3.3 ± 1.3
POC (mg/L)	2.4 ± 3.3	2.2 ± 3.2	1.7 ± 2.0
SRP (µg/L)	29.3 ± 21.0	31.8 ± 18.0	33.2 ± 19.5

Table 2. Benthic chemical and biological parameters measured bimonthly during the samplings at each site. Data represent the mean and SD from triplicate measurements. GPP = gross primary production, R = respiration, SRP = soluble reactive P, – = no data available.

			Metabolism		Nutrient uptake rate		
Sampling dates	Site	Geomorphic unit	GPP (mg C m^{-2} h^{-1})	R (mg C m^{-2} h^{-1})	NH_4-N (µmol m^{-2} h^{-1})	NO_3-N (µmol m^{-2} h^{-1})	SRP (µmol m^{-2} h^{-1})
15 June 2017	Natural	Cut bank	98.3 ± 8.6	42.1 ± 8.1	–33.1 ± 24.7	16.9 ± 39.0	7.7 ± 1.4
		Point bar	56.0 ± 26.3	60.7 ± 10.6	–121.7 ± 24.7	67.6 ± 13.4	–0.7 ± 2.3
		Thalweg	0	33.3 ± 3.6	–20.5 ± 12.1	–24.4 ± 46.6	2.1 ± 2.8
14 June 2017	Human-altered	Riprap	27.1 ± 7.2	14.6 ± 5.1	2.6 ± 6.0	127.4 ± 24.8	0.6 ± 1.4
15 August 2017	Natural	Cut bank	0	33.4 ± 13.6	–46.4 ± 42.3	–214.0 ± 58.6	–9.4 ± 2.0
		Point bar	10.8 ± 18.6	60.4 ± 1.1	–42.5 ± 9.5	–118.8 ± 25.1	–5.1 ± 2.2
		Thalweg	0	40.1 ± 6.1	–67.5 ± 36.9	–333.9 ± 44.6	–3.8 ± 5.1
16 August 2017	Human-altered	Riprap	73.7 ± 37.2	18.9 ± 11.6	21.5 ± 5.9	333.8 ± 146.6	3.9 ± 3.2
17 October 2017	Natural	Cut bank	0	7.0 ± 3.8	97.0 ± 53.7	86.4 ± 76.4	34.0 ± 3.4

		Point bar	24.7 ± 8.0	28.4 ± 5.9	214.0 ± 15.4	–54.1 ± 83.8	40.2 ± 6.7
		Thalweg	0	8.0 ± 3.1	264.4 ± 32.5	–293.7 ± 59.8	37.8 ± 3.2
18 October 2017	Human-altered	Riprap	26.0 ± 18.4	6.2 ± 3.9	134.4 ± 41.7	–1.3 ± 70.2	5.1 ± 1.9
5 December 2017	Natural	Cut bank	1.5 ± 1.7	6.2 ± 2.2	–16.4 ± 3.8	–270.6 ± 177.1	23.4 ± 4.1
		Point bar	6.8 ± 1.3	6.2 ± 3.1	38.6 ± 29.8	–263.5 ± 38.5	16.4 ± 4.5
		Thalweg	3.1 ±0.9	5.8 ± 1.6	40.5 ± 24.0	–76.9 ± 20.1	22.8 ± 4.1
6 December 2017	Human-altered	Riprap	5.1 ± 0.8	2.9 ± 0.7	47.1 ± 4.0	8.9 ± 37.1	0.0 ± 0.4
6 March 2018	Natural	Cut bank	1.5 ± 2.6	3.0 ± 2.5	–4.3 ± 15.2	–62.7 ± 138.7	0.1 ± 0.1
		Point bar	32.5 ± 25.7	18.4 ± 12.8	22.5 ± 23.0	288.2 ± 186.3	0 ± 0
		Thalweg	0	2.8 ± 3.2	7.7 ± 3.1	–31.5 ± 62.4	0.1 ± 0.1
7 March 2018	Human-altered	Riprap	18.8 ± 8.7	3.1 ± 2.4	25.6 ± 15.9	47.6 ± 18.9	1.4 ± 0.8
24 April 2018	Natural	Cut bank	4.6 ± 7.9	15.7 ± 3.3	–	–565.9 ± 42.5	–0.1 ± 0
		Point bar	55.0 ± 30.4	55.4 ± 27.2	–	–158.9 ± 424.2	–0.2 ± 0.1
		Thalweg	0	12.5 ± 1.8	–	–442.7 ± 204.9	0 ± 0

25 April 2018	Human-altered	Riprap	15.8 ± 13.9	12.5 ± 11.0	–	–11.4 ± 36.2	1.3 ± 0.9