Hydromorphological restoration stimulates river ecosystem metabolism

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Abstract

Both ecosystem structure and functioning determine ecosystem status and are important for the provision of goods and services to society. However, there is a paucity of research that couples functional measures with assessments of ecosystem structure. In mid-sized and large rivers, effects of restoration on key ecosystem processes, such as ecosystem metabolism, have rarely been addressed and remain poorly understood. We compared three reaches of the third-order, gravel-bed river Ruhr in Germany: two reaches restored with moderate (R1) and substantial effort (R2) and one upstream degraded reach (D). Hydromorphology, habitat composition and hydrodynamics were assessed. We estimated gross primary production (GPP) and ecosystem respiration (ER) using the one-station open-channel diel dissolved oxygen change method over a 50-day period at the end of each reach. Moreover, we estimated metabolic rates of the combined restored reaches (R1+R2) using the two-station open-channel method. Values for hydromorphological variables increased with restoration intensity (D < R1 < R2). Restored reaches had lower current velocity, higher longitudinal dispersion and larger transient storage zones. However, fractions of median travel time due to transient storage were highest in R1 and lowest in R2, with intermediate values in D. The share of macrophyte cover of total wetted area was highest in R2 and lowest in R1, with intermediate values in D. Station R2 had higher average GPP and ER than R1 and D. The combined restored reaches R1+R2 also exhibited higher GPP and ER than the degraded upstream river (station D). Restoration increased river autotrophy, as indicated by elevated GPP:ER, and NEP of restored reaches. Temporal patterns of ER closely mirrored those of GPP, pointing to the importance of autochthonous production for ecosystem functioning. In conclusion, high reach-scale restoration effort had considerable effects on river hydrodynamics and ecosystem functioning, which were mainly related to massive stands of macrophytes. High rates of metabolism and the occurrence of dense macrophyte stands may increase the assimilation of dissolved nutrients and the sedimentation of particulate nutrients, thereby positively affecting water quality.

1. Introduction

River restoration is a pivotal element of catchment management to counteract anthropogenic degradation and depletion of river health and water resources, and to increase overall biodiversity and ecosystem services provisioning (Bernhardt et al., 2005; Strayer and Dudgeon, 2010). Based on legislative frameworks such as the EU Water Framework Directive (WFD) and the Clean Water Act in the United States, large investments have been made to restore rivers. In Europe, degraded river hydromorphology is considered one of the central impacts to the ecological status of rivers (EEA, 2012; Hering et al., 2015). For example, the German national river habitat survey, which evaluates 31 hydromorphological parameters for 100 m river sections, concluded that the majority of German rivers is severely degraded (Gellert et al., 2014; UBA, 2013). As the river biota depend on suited habitats (Beisel et al., 2000; Schröder et al., 2013), about 85% of German rivers failed to reach the 'good ecological status' demanded by the WFD (EEA, 2012). Accordingly, most restoration projects target the hydromorphological improvement of rivers. The majority of restoration measures is implemented at the reach-scale, covering short river stretches typically of one km or less (Bernhardt et al., 2005; Palmer et al., 2014). A variety of reach-scale measures have been implemented (Lorenz et al., 2012): for instance, restoration activities along mountainous rivers in central Europe mainly targeted re-braiding and widening of streams, leading to greater habitat and hydrodynamic heterogeneity (Jähnig et al., 2009; Poppe et al., 2016). In combination with other characteristics of the river ecosystem – e.g., light, organic matter, nutrient availability, temperature, hydrologic and disturbance regimes – such hydromorphological changes likely affect biological community composition and ecosystem functioning, including ecosystem metabolism (Bernot et al., 2010; Tank et al., 2010).

The assessment of restoration effects has mainly focused on responses of aquatic organisms, such as fish (e.g., Roni et al., 2008; Haase et al., 2013; Schmutz et al., 2016), benthic invertebrates (e.g., Jähnig et al., 2010; Friberg et al., 2014; Verdonschot et al., 2016), and macrophytes (e.g., Lorenz et al., 2012; Ecke et al., 2016). Recently, increasing attention has also been given to the response of floodplain organisms (e.g., Hering et al., 2015; Göthe et al., 2016; Januschke and Verdonschot, 2016), while functional characteristics, i.e. the rates and patterns of ecosystem processes, have rarely been addressed. Ecosystem functions are life-supporting processes that are directly linked to ecosystem services, i.e. the benefits people obtain from the environment (Palmer and Filoso, 2009). Thus, an emerging interest in river restoration research is to incorporate the recovery of ecological functioning (Palmer et al., 2014). However, few studies have considered the response of river ecosystem functioning and functional metrics to restoration (e.g., Lepori et al., 2005; Bunn et al., 2010; Kupilas et al., 2016). Consequently, the effects of restoration on key ecosystem processes remain poorly understood.

Ecosystem metabolism, i.e. the combination of gross primary production (GPP) and ecosystem respiration (ER), is a fundamental ecosystem process in rivers. Ecosystem metabolism is a measure of the production and use of organic matter within a river reach by all biota. Therefore, it provides key information about a river's trophic and energetic base (relative contribution of allochthonous and autochthonous carbon) (Young et al., 2008; Tank et al., 2010; Beaulieu et al., 2013). The majority of stream ecosystem metabolism work has investigated natural changes, such as effects of floods and droughts (e.g., Uehlinger, 2000), seasonal or inter-annual changes (e.g., Uehlinger, 2006; Beaulieu et al., 2013), interbiome differences (e.g., Mulholland et al., 2001), or land-use change (e.g., Gücker et al., 2009; Silva-Junior et al., 2014). The majority of these studies have focused on smaller streams, while only few studies measured metabolism of larger streams and rivers (e.g., Uehlinger, 2006; Dodds et al., 2012; Hall et al., 2015; Hall et al., 2016). The response of stream metabolism to hydromorphological changes, e.g. through river widening, is almost unknown, especially for larger rivers (but see Colangelo, 2007).

The widening of the riverbed enhances habitat complexity and diversity of the river channel and the riparian zone (Jähnig et al., 2010; Januschke et al., 2014; Poppe et al., 2016). Moreover, channel widening also favors macrophytes and other autotrophs through the creation of shallow, slow flowing areas and backwaters (Lorenz et al., 2012). Further, it increases light availability and water temperature, which have been identified as major factors controlling river metabolism, especially primary production (Uehlinger, 2006; Bernot et al., 2010; Tank et al., 2010). Accordingly, these changes potentially lead to enhanced in-stream autotrophic processes.

Restoration also increases the retention of allochthonous organic matter (Lepori et al., 2005; Lepori et al., 2006; Flores et al., 2011). Moreover, the reconnection of rivers with their floodplains by creating shallower river profiles and removing bank fixations may enhance inundation frequency, and hence resource transfers from land to water. In combination, these changes can favor heterotrophic activity in the river. Restoration also affects hydrodynamics and surface water-ground water interactions of streams (Becker et al., 2013): for instance, widening of the stream channel reduces flow velocity and the creation of backwaters and pools possibly leads to changes in the size and location of transient storage zones (Becker et al., 2013). Increases in transient storage zones potentially enhance ER (Fellows et al., 2001) and nutrient processing (Valett et al., 1996; Gücker and Boëchat, 2004).

The objective of this study was to quantify reach-scale restoration effects on hydromorphology, habitat composition and hydrodynamics, as factors potentially affecting river ecosystem function, by comparing three contiguous stream reaches (two restored and one upstream non-restored reach) of a mid-sized mountain river in Germany and to determine the corresponding responses of river metabolism. We expected (i) hydromorphological river characteristics, i.e. habitat composition and hydrodynamics, to change following restoration, with the magnitude of change depending on restoration effort (e.g. width and diversity of the river channel, and abundance of primary producers, as well as sizes and locations of transient storage zones in the two restored river reaches compared to the degraded reach). Further, we expected (ii) ecosystem metabolism to respond with increased metabolic rates, i.e. enhanced GPP and ER, mainly as a result of increased abundances of primary producers.

2. Methods

2.1 Study site

This study was conducted in the upper River Ruhr (Federal State of North Rhine-Westphalia, Germany, Fig. 1, Table 1) a tributary to the Rhine. The third-order Ruhr is a mid-sized mountain river with gravel and cobbles as bed sediments. The catchment area upstream of the study site is 1060 km^2, about 64 % of which is forested, 28 % is arable land and pasture, and 8 % is urban area (located mainly in the floodplains). The study site is at an altitude of 153 m a.s.l. and the mean annual discharge was 21.3 $m^3 s^{-1}$ between 2004 and 2009. The Ruhr is draining one of the most densely populated areas of Europe; however, population density of the upstream catchment area is low (135.3 inhabitants/km^2 upstream of the study site). Due to manifold uses, the river's hydromorphology has been largely modified by impoundments, residual flow sections, bank fixation as well as industrial and residential areas in the floodplain. More recently, the hydromorphology of several river sections has been restored.

Restoration aimed to establish near-natural hydromorphology and biota. Restoration measures were implemented between 2007 and 2009 and included the widening of the riverbed and the reconnection of the river with its floodplain by creating a shallower river profile and by removing bank fixations. Moreover, the physical stream quality was enhanced by generating secondary channels and islands, adding instream structures, such as woody debris, and creating shallow habitats providing more space for autotrophs (see Appendix S1 in Supporting Information).

We separated the restored reach into two reaches of approximately similar lengths (1210 and 1120 m) with obvious differences in morphological stream characteristics due to differing restoration effort (R1: moderate restoration effort and R2: high restoration effort). Briefly, in R2 a larger amount of soil was removed and the costs for the implementation of measures were higher than in R1 (see Appendix S1). In R2 the bank fixation was removed at both shorelines and the river was substantially widened and secondary channels and islands were created, while the removal of bank fixation and widening in R1 mainly focused on one side due to constrains posed by a nearby railroad (see Appendix S1). The restored reaches were compared to a degraded "control-section" of 850 m length located upstream of the restored reaches (D). The degraded reach was characteristic for the channelized state of the River Ruhr upstream of the restoration site, and reflected the conditions of the restored sections prior to restoration: The reach was a monotonous, channelized and narrowed river section with fixed banks and no instream structures. A 650 m-long river section separating the degraded from the restored river reach was excluded from the investigations, as its hydromorphology was deviating due to constructions for canoeing and a bridge. As the three sections were neighboring each other, differences in altitude, slope, discharge and catchment land cover between reaches were negligible.

2.2 Hydromorphology and habitat composition

Physical stream quality was quantified from aerial photos. High-resolution photos of the restored reaches were taken in summer 2013 using a Falcon 8 drone (AscTec, Germany). Aerial photos of the degraded reach from the same year at similar discharge conditions were provided by the Ministry for Climate Protection, Environment, Agriculture, Conservation and Consumer Protection of the State of North Rhine-Westphalia. Photos were analyzed in a geographical information system (ArcGIS 10.2, ESRI). For each reach, we measured the width of the wetted channel every 20 m along cross-sectional transects at low flow conditions and calculated mean width and its variation (reach D: n = 42, R1: n = 59, R2: n = 54). For each reach, we recorded thalweg lengths, the area of the wetted stream channel, the floodplain area (defined as bank-full cross-sectional area), and the area covered by islands, woody debris, and aquatic macrophyte stands (Fig. 2). Subsequently, the share of macrophyte stands of the total wetted area was calculated for each reach. Additionally, macrophytes were surveyed according to the German standard method (Schaumburg et al., 2005a; b) in summer 2013. A 100 m reach was investigated by wading through the river in transects every 10 m, and walking along the riverbank (Lorenz et al., 2012). All macrophyte species were recorded and species abundance was estimated following a 5-point scale developed by Kohler (1978), ranging from “1 = very rare” to “5 = abundant, predominant”. The empirical relationship between the values of the 5-point Kohler scale (x) and the actual surface cover of macrophytes (y) is given by the function $y = x^3$ (Kohler and Janauer, 1997; Schaumburg et al., 2004). Using this relationship, we x^3-transformed the values of the Kohler scale into quantitative estimates of macrophyte cover for the studied 100 m reaches.

2.3 Hydrodynamics

Stream hydrodynamics were estimated using a conservative tracer addition experiment with the fluorescent dye Amidorhodamine G. Across the river width, we injected the dissolved dye in a distance sufficiently upstream to the first study reach to guarantee complete lateral mixing at the first sampling station. Breakthrough curves of the tracer were continuously measured in the main current at the upstream and downstream ends of all three reaches (Fig. 1). Concentration of dye was recorded at a resolution of 10 s at the most upstream and downstream sampling stations using field fluorometers (GGUN-FL24 and GGUN-FL30, Albillia, Switzerland). At the other sampling stations (start and end of each investigated river reach) water samples were taken manually at 2 min intervals. The samples were stored dark and cold in the field and subsequently transported to the hydrogeochemical laboratory of the Ruhr University Bochum. Amidorhodamine G concentrations of water samples were measured with a fluorescence spectrometer (Perkin Elmer LS 45; detection limit of 0.1 ppb) and standard calibration curves prepared from the tracer and river water. Field fluorometers were calibrated prior to experiments with the same standard calibration procedure.

Subsequently, we used the one-dimensional solute transport model OTIS-P (Runkel, 1998) to estimate parameters of river hydrodynamics for each reach from the breakthrough curves: advective velocity, longitudinal dispersion, stream channel and storage zone cross-sectional areas, and storage rate. We further calculated fractions of median travel time due to transient storage (F_{med}^{200}) based on the hydrodynamic variables obtained from transport modeling (Runkel, 2002). Additionally, Damköhler numbers were estimated for each reach (Harvey and Wagner, 2000).

2.4 Discharge

Discharge data were provided by the North Rhine-Westphalia State Agency for Nature, Environment and Consumer Production, Germany (Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen) for a gauging station situated at the downstream end of the study site. At this station, discharge was constantly recorded at 5-min intervals.

2.5 Ecosystem metabolism

We estimated river dissolved O_2 (DO) metabolism using the ‘open-channel one-station and two-station diel DO change techniques’ (Odum, 1956; Marzolf et al., 1994; Young and Huryn, 1998; Roberts et al., 2007). We initially chose the one-station method to estimate metabolic rates at the downstream end of each reach (stations D, R1, and R2), as the individual studied reaches were too short for a reliable estimation of ecosystem metabolism with the two-station technique, due to high current velocities and low reaeration rates. According to Demars et al. (2015), the two-station method is applicable to reach lengths 0.4 v/k to 1.0 v/k. For our reaches of the Ruhr, this range corresponds to 3283 - 8280 m for reach D, 2765 - 6912 m for reach R1, 1624 - 4061 m for reach R2, and 2199 - 5497 m for the combined reach R1+R2. Thus, the quantification of metabolism using the two-station method was only possible for the combined reach R1+R2 with a reach length of 2330 m.

Reach lengths influencing the one-station diel dissolved O_2 change technique in our study were typically much longer than the experimental reaches, due to high current velocities and low reaeration (>10 km; estimated according to Chapra and Di Torro, 1991). Following methods in Demars et al. (2015), metabolism estimates at the downstream sampling station R2 were only to 35% influenced by the restored river sections, but to 65% by upstream degraded river sections. Accordingly, differences in metabolic rates among sampling stations at the end of restored and impacted experimental reaches as estimated in our study should be viewed as qualitative indicators of restoration effects, rather than measured metabolic rates of the experimental reaches. To quantitatively support our qualitative findings, we additionally used the two-station method for the combined restored river reach R1+R2, which was long enough for the application of the two-station open-channel method. The selected methods are based on the assumption that changes in DO within a parcel of water traveling downstream can be attributed to metabolism (photosynthesis and respiration) and to gas exchange between water and atmosphere, given that no significant groundwater dilution of river water occurs along the studied river:

$$dDO/dt = GPP - ER - (K_{oxy} * D)$$

where dDO/dt is the change in dissolved oxygen concentration (mg O_2 L^{-1} s^{-1}), GPP is the gross primary production (mg O_2 L^{-1} s^{-1}), ER is the ecosystem respiration (mg O_2 L^{-1} s^{-1}), K_{oxy} is the reaeration coefficient (s^{-1}), and D is the oxygen deficit or surplus in the river (i.e., the difference between the measured oxygen concentration and the value at saturation; mg O_2 L^{-1}). The change in DO was estimated as the difference between consecutive 5-min readings of the same probe for the one station method and as the difference between upstream (top of reach R1) and downstream probes (end of reach R2) for the two station method (Roberts et al., 2007; Beaulieu et al., 2013).

In two consecutive field campaigns in summer 2014, DO and water temperature were continuously measured at the downstream ends of the three reaches and at the top of reach R1 at 5-min intervals for 50 days. The DO probes with data loggers (O_2-Log3050-Int data logger Driesen + Kern GmbH, Germany) were installed in the thalweg of the river in the middle of the water column. The DO probes were calibrated in water-saturated air prior to measurements. Additionally, probes were cross-calibrated for one hour at a single sampling station in the river before and after the measurements. We used the data of this comparison to correct for residual differences among probes (Gücker et al., 2009). This procedure assured that differences between probes were only due to differences in DO and water temperatures and not to analytical errors. In previous laboratory tests, the probes showed no drift and were thus not corrected for drift during the measurement campaigns (Almeida et al., 2014).

In parallel to DO and water temperature, atmospheric pressure was recorded (Hobo U20-001-04; Onset Computer Corporation). We used atmospheric pressure and water temperature data to calculate the oxygen saturation. Reaeration coefficients (K_{oxy}^{20}; standardized for 20°C) were estimated using the nighttime regression approach (Young and Huryn, 1999). For the downstream stations of all three sampling reaches, we calculated reaeration coefficients (K_{oxy}) as the slope of regressions between DO change rates (dDO/dt; mg O_2 L^{-1} s^{-1}) and DO deficits (D; mg O_2 L^{-1}) at night (night hours were defined as the period 1 h after sunset to 1 h before sunrise):

$$dDO/dt = K_{oxy} * D + ER$$

We only considered significant nighttime regressions ($p < 0.05$). Reaeration coefficients for days without significant regressions were estimated as the average value of the coefficients of the days before and after, as we did not observe K_{oxy}^{20} - discharge relationships in our data (see Appendix S2) that could have been used to estimate K_{oxy}^{20} values for days without reliable estimates. Estimated reaeration coefficients were low and ranged from 5 to 15 d^{-1} in our study (see Appendix S2). Subsequently, we calculated ER and GPP as described in detailed elsewhere (Marzolf et al., 1994;

Young and Huryn, 1998; Roberts et al., 2007) from the recorded nighttime river water DO deficit and the daytime DO production, respectively, corrected for atmospheric reaeration (see Appendix S3). Metabolic rates obtained by this method closely matched those obtained with the estimator of Reichert et al. (2009). Ground water dilution was not detected, i.e. discharge differences among the investigated river reaches were within the ranges of method uncertainty of discharge measurements, and was thus not considered into our estimates. Metabolism measurements from days at which floating macrophytes accumulated around probes and affected DO measurements were eliminated from the dataset.

2.6 Data analysis

We used the ARIMA function in [R] to identify an ARIMA model that best represented all time series (metabolic parameters at stations D, R1, R2, and reach R1+R2), estimated average parameter predictions and 95%-confidence limits for each time series based on these models, and used F-tests to test the hypothesis of differences among time series (compare Roley et al., 2014). Data recorded at the time of flooding events were omitted from analyses, because GPP was not detectable, and we cannot be sure whether GPP was indeed zero or very low, or whether high flows prevented the detection of GPP. Overall, data of n = 32 days were used in the analyses. Repeated measures ANOVAs and Tukey’s HSD post-hoc tests were used to test for differences in water temperature among river reaches. Conventional one-way ANOVA was used to test for differences in river width, comparing the transect measurements performed in the three river reaches. All statistical analyses were conducted in [R] (R Development Core Team, 2007).

3. Results

3.1 Hydromorphology and habitat composition

Restored river reaches were morphologically more complex and had significantly wider wetted channels (ANOVA and Tukey post-hoc test, $P < 0.05$) and more variable channel width than the degraded reach (Table 2). Furthermore, the restored reaches had larger wetted channel areas, floodplain areas, island areas and patches of woody debris than the degraded river reach (Table 2). The intensively restored reach R2 showed the highest values for hydromorphological variables (Table 2). The share of macrophyte cover of total wetted area was also highest in R2.

3.2 Hydrodynamics

The reaches differed in hydrodynamic parameters: The restored reaches had lower flow velocity and higher longitudinal dispersion, cross-sectional areas of the advective channel, and storage zone cross-sectional areas than the degraded reach (Table 2). Storage rate and fractions of median travel time due to transient storage (F_{med}^{200}) was highest in R1 and lowest in R2, with intermediate values for D (Table 2). Damköhler numbers between 0.5 and 5.0 indicated reliable transient storage parameter estimates for the reaches (Harvey and Wagner, 2000; Table 2). Tracer breakthrough curves estimated by transport modelling closely corresponded to measured tracer concentrations (Fig. 3).

3.3 Discharge and water temperature

Mean discharge during the first weeks of measurement was 8.4 $m^3 s^{-1}$. The hydrograph was characterized by a large summer flow peak and two minor peaks during the study period (Fig. 4 a). During the flow peaks discharge rapidly increased 3.5- to 7-fold, relative to the mean flow. Trends in water temperature over time were very similar for the three river reaches and are exemplarily shown for R2 (Fig. 4 b). Overall, restored reaches had higher mean daily water temperatures than the degraded reach, with R2 having higher mean daily water temperatures compared to R1 (repeated measures ANOVA, $P < 0.0001$; and Tukey's HSD post-hoc tests, $P < 0.0005$).

3.4 Ecosystem metabolism

We observed significant effects of reach-scale restoration on metabolic rates estimated at the end of the restored river sections (R1 and R2 compared to D; estimated by the one-station method) and between the upstream degraded river (station D) and the combined restored reaches R1+R2 (estimated with the two-station method). According to the ARIMA function estimates, we found higher river GPP, NEP and GPP:ER at the restored river sections (R1 and R2 versus station D; estimated with the one-station method; Fig. 5). Moreover, GPP, ER, NEP, and GPP:ER were also higher (Fig. 5) in the total restored river reach (R1+R2; estimated with the two-station method) than in the upstream degraded river (measured at section D with the one-station method). These findings indicate an increase in the river's metabolism following restoration.

The three sampling stations at the downstream ends of the reaches generally exhibited similar metabolism patterns (Fig. 6). Rates of GPP and ER ranged from 2.59 to 13.06 and -4.96 to -17.52 g O_2 m^{-2} day^{-1} at sampling station D, from 2.33 to 12.36 and -4.04 to -14.02 g O_2 m^{-2} day^{-1} at station R1, and from 3.61 to 17.64 and -5.91 to -24.71 g O_2 m^{-2} day^{-1} at station R2. Daily rates of GPP were highest shortly before the main summer flow peak at all sampling stations (Fig. 6 a). GPP was not detectable during the summer flow peaks. ER generally mirrored the GPP patterns, but showed distinct peaks at the beginning of the summer flow peak. ER exceeded GPP during all but one day at R1 and two days at R2. Consequently, NEP (net ecosystem production) was negative during most of the measured period, i.e. reaches were heterotrophic (Fig. 6 b). NEP ranged from -4.61 to -0.47 g O_2 m^{-2} day^{-1} at station D, from -4.29 to 0.22 g O_2 m^{-2} day^{-1} at station R1, and from -8.24 to 0.14 g O_2 m^{-2} day^{-1} at station R2. The average GPP:ER ratio ranged from 0.66 to 0.97 across all sampling stations, also indicating that the Ruhr was moderately heterotrophic. General patterns in daily rates of both GPP and ER also seemed to be influenced by flow peaks. GPP and ER were both suppressed immediately following the flooding events. The ensuing recovery patterns for GPP and ER were similar for all investigated sampling stations: depending on magnitude of flow, GPP and ER were suppressed for several days, but steadily returned to pre-disturbance conditions. The total restored river reach (R1+R2, two-station method) showed temporal metabolism patterns comparable to those estimated at the three sampling stations with the one-station method (Fig. 6). However, NEP of the total restored river reach (R1+R2) was positive and average GPP:ER ratio higher than 1 during most of the sampling period, indicating a slight change in the river's metabolic balance following restoration.

4. Discussion

Restoration of river hydromorphology usually covers short river stretches of less than one km and is expected to increase the river's habitat and hydrodynamic heterogeneity. Together, these changes may stimulate ecosystem metabolism, i.e. whole-stream rates of GPP and ER, as well as affect the river's metabolic balance. Increases in river metabolism, in turn, may result in increased rates of other ecosystem processes, such as secondary productivity and whole-stream nutrient processing (Fellows et al., 2006; Gücker and Pusch, 2006).

4.1 Hydromorphological characteristics

Recent monitoring and evaluation of restoration projects report positive effects on hydromorphology and habitat composition (Jähnig et al., 2009; Jähnig et al., 2010; Poppe et al., 2016). Similarly, we found greater habitat complexity of restored reaches, as indicated by wider and more diverse river channels. The reach with the highest restoration effort (R2), was characterized by the highest values and heterogeneity of hydromorphological variables; this suggests that restoration effort is indeed crucial for restoration success. According to Lorenz et al. (2012), the success of restoration in mid-sized to larger rivers can also be indicated by increased cover, abundance and diversity of macrophytes as they benefit from more natural and diverse substrate, and the variability in flow. Consequently, the higher share of macrophyte cover of total wetted area in R2 also highlighted the higher morphological quality of this reach.

Moreover, there were no point sources or changes in land use along the studied river section, and therefore, increases in P and N concentrations, and associated eutrophication effects in the studied river section seem unlikely (compare Table 1). Thus, higher macrophyte biomass and metabolic responses are likely to be a result of river restoration, i.e. wider channels increasing light availability, shallower channels providing better habitats for macrophytes, and lower current velocities decreasing hydraulic stress.

Changes in hydromorphology and habitat composition influenced hydrodynamics: we observed lower current velocity, higher longitudinal dispersion and larger transient storage zones in the restored reaches. This corresponds with the larger river width and wetted channel area, and the increased abundance of morphological features such as woody debris, islands and macrophyte patches. However, F_{med}^{200}, i.e. the relative importance of transient storage for whole-stream hydrodynamics, was highest in R1 and lowest in R2, with intermediate values for D. Accordingly, there appeared to be an inverse relationship between F_{med}^{200} and the share of macrophyte cover of total wetted area, which was highest in R2 and lowest in R1, with intermediate values in D. These findings suggest that the dense stands of macrophytes in R2 particularly altered stream hydrodynamics: macrophyte patches built large surface transient storage areas and potentially changed the locations of transient storage zones from the hyporheic zone to the surface water column. Macrophyte fields in R2 may have even been so dense that large parts of them were representing hydrodynamic dead zones. A similar effect was found in streams restored by implementing steering structures to enhance stream quality: the restored reaches were dominated by surface transient storage exchange (Becker et al., 2013). Furthermore, the sedimentation of fine sediment within dense macrophyte stands may further decrease exchange with the hyporheic zone.

4.2 Functional characteristics

Metabolism was measured over a 50-day period to obtain representative data, allowing for comparisons among sampling stations. Furthermore, this time series allowed for the analysis of environmental variability, such as flow peaks. The results were obtained for the summer period, i.e. the time of maximum biomass, which is also relevant for the WFD compliant sampling period (e.g., Haase et al., 2004; Schaumburg et al., 2004; EFI+ CONSORTIUM, 2009). Therefore, results obtained in this study are directly comparable to the river status derived from biological assessment.

In general, the three sampling stations showed similar patterns in metabolism, as our one-station metabolism approach measured a long upstream river section in addition to the experimental reaches. Rates of ER mirrored those of GPP, suggesting that autotrophic respiration largely drove temporal patterns in ER, despite an overall ratio of GPP:ER < 1 and a slightly negative NEP during most of the measurement period. Similar patterns were found in streams in the US (Beaulieu et al., 2013; Hall et al., 2016). The average GPP:ER ratio was significantly higher downstream of the restored reaches in our study (0.86 and 0.97, respectively) and in the combined restored reach (1.16) than in the upstream degraded river (0.66), indicating an increase in autotrophic processes following restoration. The only moderate heterotrophic state of the river together with ER closely tracking GPP indicated the importance of autochthonous production for the metabolism. This is further supported by the comparison of pre- and post-peak flow ER (Fig. 6). McTammany et al. (2003) suggested that higher inputs of allochthonous material may occur after flooding events, subsequently supporting high rates of ER. In line with this, we expected high rates of ER during the last third of the sampling period, especially in restored reaches with a potentially high POM trapping efficiency. However, ER was lower compared to pre-flow peak conditions, with ER still mirroring GPP, thus indicating the coupling of autochthonous production with ER even after floods. This implies that restoration (reconnection of river and floodplain) did not increase resource transfer into the channel to such an extent that it influenced river metabolism.

We observed significantly higher GPP and ER at station R2 compared to the other stations. Metabolism of R1 did not markedly differ from D, corresponding with consistently higher values of hydromorphological variables in R2 only. Given the previously discussed importance of autochthonous production for the metabolism, habitat enhancement supporting the growth of macrophytes is likely the cause for higher GPP and ER in R2. Consequently, only high restoration effort bringing a restored reach close to reference conditions led to pronounced effects on ecosystem metabolism. Restoration effects were mainly related to the growth of aquatic macrophytes, which formed dense stands that augmented ecosystem metabolism. We acknowledge that metabolism was measured during summer, i.e. the time of maximum biomass of aquatic macrophytes. Therefore, high GPP and ER measured in this campaign might be restricted to this season and effects will be lower during winter times when macrophyte abundance will be low.

Ecosystem metabolism of the sampling stations at the restored reaches and of the combined restored river reaches was expected to be at similar levels to those of natural rivers reported in the literature. Therefore, we compared GPP and ER of our sampling stations to those of rivers comparable in size (discharge between 5 - 50 $m^3 s^{-1}$; see Appendix S4, S5). GPP and ER estimated in this study were among the highest values reported for similar sized rivers; especially those of the sampling station R2 and the combined restored reach. Of all the rivers, for which metabolism has been reported, the channelized river Thur (Uehlinger, 2006) is closest to the Ruhr regarding size, sediment, and region. Interestingly, average GPP and ER reported for the Thur were similar to those of the channelized sampling station D. Thus, relatively low GPP and ER in hydromorphologically altered rivers compared to natural ones may be common. However, there is a tremendous variability in ecosystem metabolism among natural river reaches in the literature (see Appendix S4, S5). Considering the limited knowledge about natural geographical gradients in river metabolism, it was not possible to assess if values obtained for restored reaches indicate natural conditions in a broader geographic context. In future analyses of restoration effects on fluvial metabolism, local reference conditions should therefore be assessed whenever possible.

Our experimental reaches reflected typical spatial scales on which restoration measures are implemented. However, individually, these reaches were too short to feasibly use the two-station diel DO change method (see 2.5). Accordingly, we used the one-station approach to assess reach-scale restoration effects on ecosystem metabolism of longer river sections (>10 km). Following methods in Demars et al. (2015), we evaluated to which extent these metabolism estimates reflected the restored river sections. Measurements at sampling station R1 and R2 were only to 16% and 24%, respectively, influenced by the restored experimental reaches directly upstream. However, station R2 was to 35% influenced by the combined reaches R1+R2, and thus to 65% by upstream degraded river sections. Despite this mismatch between lengths of river reaches evaluated and reaches exclusively affected by restoration, we found significant effects of reach-scale restoration on whole-river metabolism. Interestingly, our study therefore also shows that high restoration effort in short river reaches (1 to 2 km) had considerable effects on total whole-river metabolic rates of river stretches exceeding the length of the actually restored reaches (>10 km), and that the one-station method may therefore be an interesting option to qualitatively assess restoration effects in field situation, in which the two-station method is not feasible.

To quantitatively support these qualitative findings, we estimated metabolism of the combined restored reaches R1+R2, which were long enough to permit the application of the two-station method. The obtained metabolic rates should be directly comparable to metabolic rates of the upstream, degraded river (measured at station D with the one-station method) as results obtained with the one-station and the two-station methods often agree remarkably well (e.g., Bernot et al., 2010; Beaulieu et al., 2013). The total restored reach (R1+R2) showed higher GPP, ER, NEP, and GPP:ER than the upstream degraded river. Thus, these results support the findings derived from the one-station method, indicating an increase in the river's metabolism and metabolic balance associated with restoration.

Thus, the restoration of short river reaches may have positive effects on downstream river sections regarding diel DO variability and carbon spiraling. High rates of metabolism and the occurrence of dense macrophyte stands in restored river reaches may also increase the assimilation of dissolved nutrients (Fellows et al., 2006; Gücker et al., 2006) and the sedimentation of particulate nutrients (Schulz and Gücker, 2005), thereby positively affecting water quality.

4.3 Recommendations for restoration monitoring

For most regions and river types, data is missing that could be used to establish limits of good, moderate or poor river conditions. However, based on data from mainly small streams, Young et al. (2008) proposed a useful framework to assess functional stream health using GPP, ER, NEP and GPP:ER. Consequently, metabolic rates for different river types should be surveyed to allow the incorporation of ecosystem metabolism of mid-sized and large rivers as functional indicator in this framework. Our study stresses the benefits of metabolism as a functional indicator complementing the monitoring of restoration projects (compare Young et al., 2008; Bunn et al., 2010): Temporally high-resolution and automated monitoring, that integrates biotic and abiotic variables over time and across habitats may increase our understanding of the effects of river restoration and might help identifying initial changes after restoration. Incorporating functional indicators into monitoring programs may enable a more holistic assessment of river ecosystems and elucidate responses to restoration (and also impairment), which may be related to ecosystem structure and function.

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Table 1: River and study site characteristics

River characteristics	
Catchment size (km^2)	4485
Stream length (km)	219
River type	Gravel-bed
Stream order	3
Ecoregion	Central Highlands
Study site characteristics	
Latitude (N) *	51.44093
Longitude (E) *	7.96223
Catchment size (km^2)	1060
Altitude (m a.s.l.)	153
Mean annual discharge (m^3 s^{-1})	21.3
Catchment geology	siliceous
Restoration length (km)	2.3
Restoration date	2007-2009
Main restoration action	riverbed widening
pH **	8.3
Electric conductance ** (μ S cm^{-1})	340
Total nitrogen ** (mg L^{-1})	2.7
NO_3-N ** (mg L^{-1})	2.53
NH_4-N ** (mg L^{-1})	< 0.1
Total phosphorus ** (mg L^{-1})	0.07
Total organic carbon ** (mg L^{-1})	2.3

* center of reach

** data from ELWAS-WEB (online information system maintained by The Ministry for Climate Protection, Environment, Agriculture, Conservation and Consumer Protection of the State of North Rhine-Westphalia; sampling date: 26.6.2012).

Table 2: Morphological and hydrodynamic characteristics of the investigated river reaches

Variable	**degraded reach (D)**	**1. restored reach (R1)**	**2. restored reach (R2)**
Thalweg length (m)	850	1210	1120
Width (m)	22.5	28.2	36.6
Width variation * (m)	3.3	6.3	10.5
Wetted channel area (m²)	19,114	34,604	41,673
Floodplain area (m²)	27,363	30,630	34,218
Island area (m²)	0	2,666	12,381
Woody debris (m²)	0	467	691
Macrophyte coverage (%)	4.8	1.7	19.8
Flow velocity (m s^{-1})	0.95	0.8	0.47
Longitudinal dispersion, D (m² s^{-1}) **	0.28	0.59	10.21
Channel cross-sectional area, A (m²) **	12.11	14.96	27.05
Storage zone cross-sectional area, A_S (m²) **	2.38	4.48	3.16
Storage rate, α (s^{-1}) **	4.9×10^{-4}	7.4×10^{-4}	2.0×10^{-4}
Transient storage, F_{med}^{200} (%)	1.6	3.9	0.8
Damköhler number	2.8	4.8	4.4

* Width variation calculated as standard deviation; degraded: n = 42, restored 1: n = 59, restored 2: n = 54

** Data on hydrodynamic characteristics represent the final parameters obtained by one-dimensional transport modelling using OTIS-P.

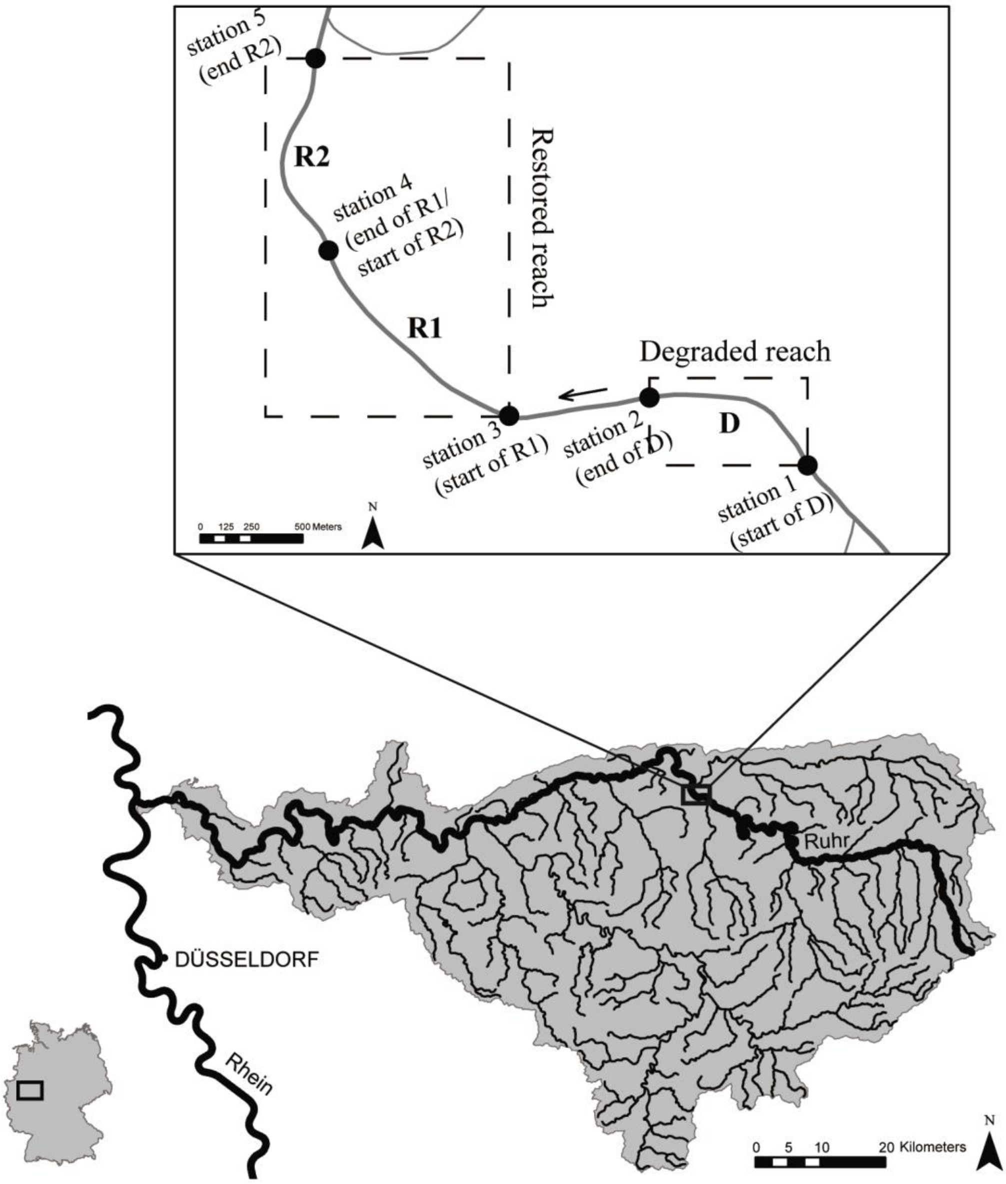


Fig. 1: Location of the study site in the upper catchment of the River Ruhr in Germany. Stations represent start and end of the investigated river reaches (degraded, 1st restored and 2nd restored reach).

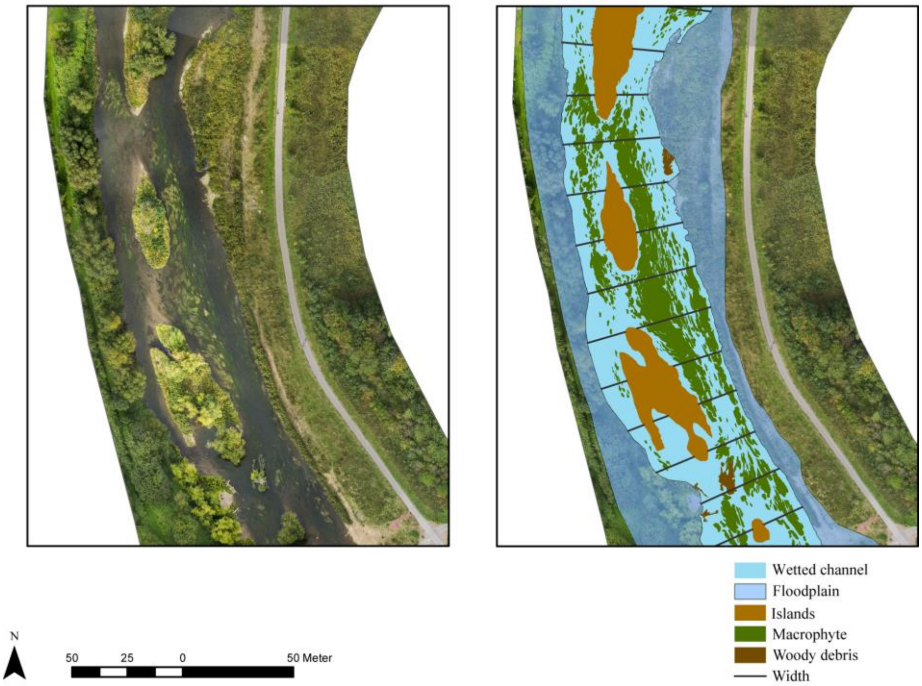


Fig. 2: Analysis of aerial photos. A representative river section of the 2nd restored reach is shown.

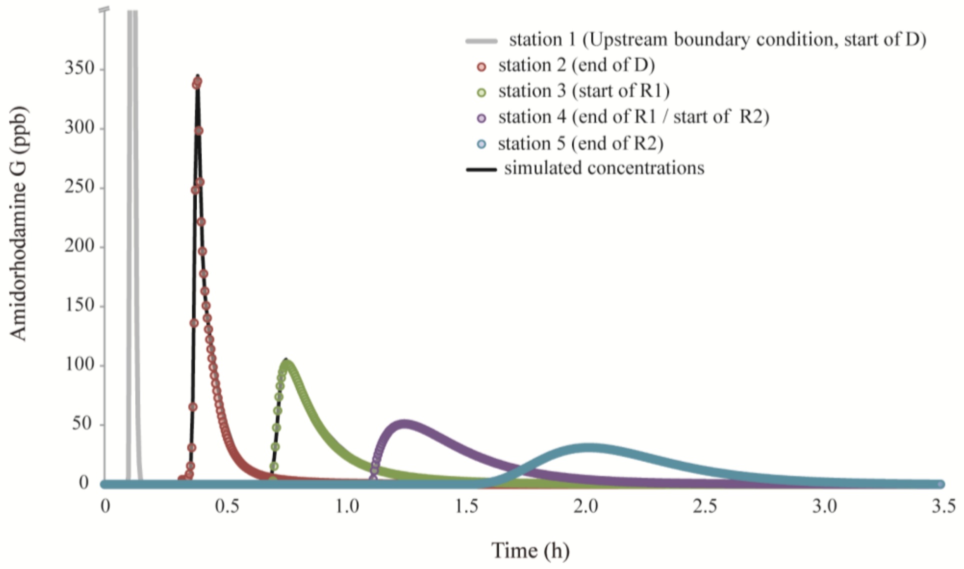


Fig. 3: Tracer breakthrough curves for the conservative tracer addition experiment in the River Ruhr. Upstream boundary condition based on concentrations at sampling station 1 (start of degraded reach, D, grey solid line), observed concentrations at sampling stations 2 (end of degraded reach, empty circles), 3 (start of 1st restored reach, R1, empty squares), 4 (end of 1st restored reach, start of 2nd restored reach, R2, empty triangles), 5 (end of 2nd restored reach, crosses), and simulated concentrations based on final parameter estimates with OTIS-P (solid lines).

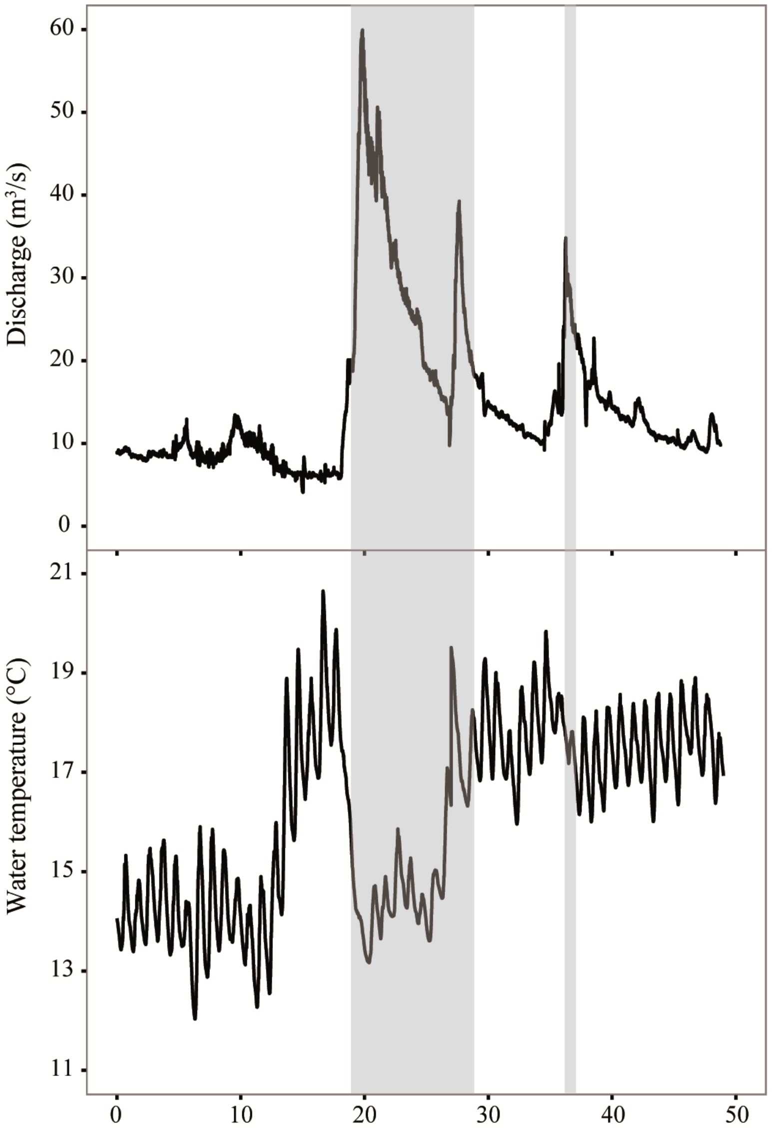


Fig. 4: (a) discharge and (b) water temperature in the River Ruhr during the study period in summer 2014. Trend in water temperature during study period is exemplarily shown for the 2nd restored reach (R2).

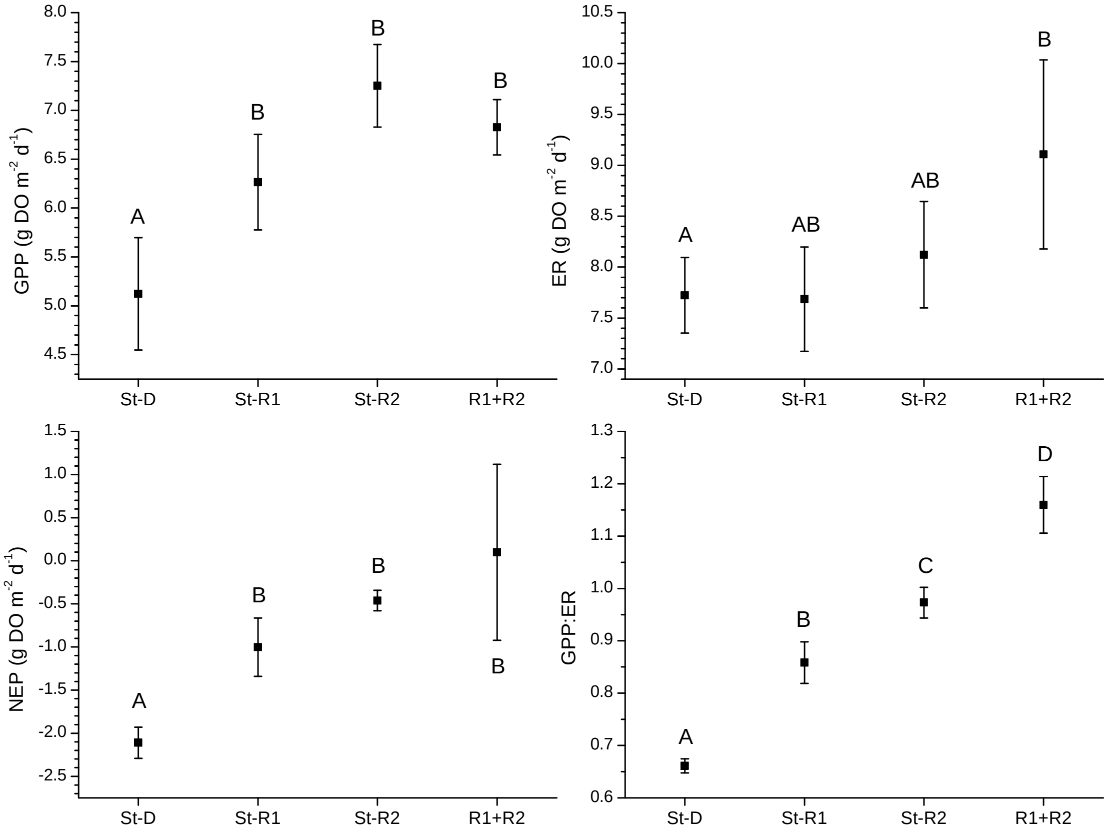


Fig. 5: Average predicted metabolic parameters and 95% confidence intervals of time series estimated by the 1-station open-channel-method at river stations downstream of reaches D, R1, and R2, and by the 2-station open-channel-method for river reach R1+R2. F-tests for all variables were significant (GPP: $p<0.001$; ER: $p<0.05$; NEP: $p<0.005$, GPP:ER: $p<0.0001$). Different letters indicate differences according to Tukey's post-hoc test ($p<0.05$).

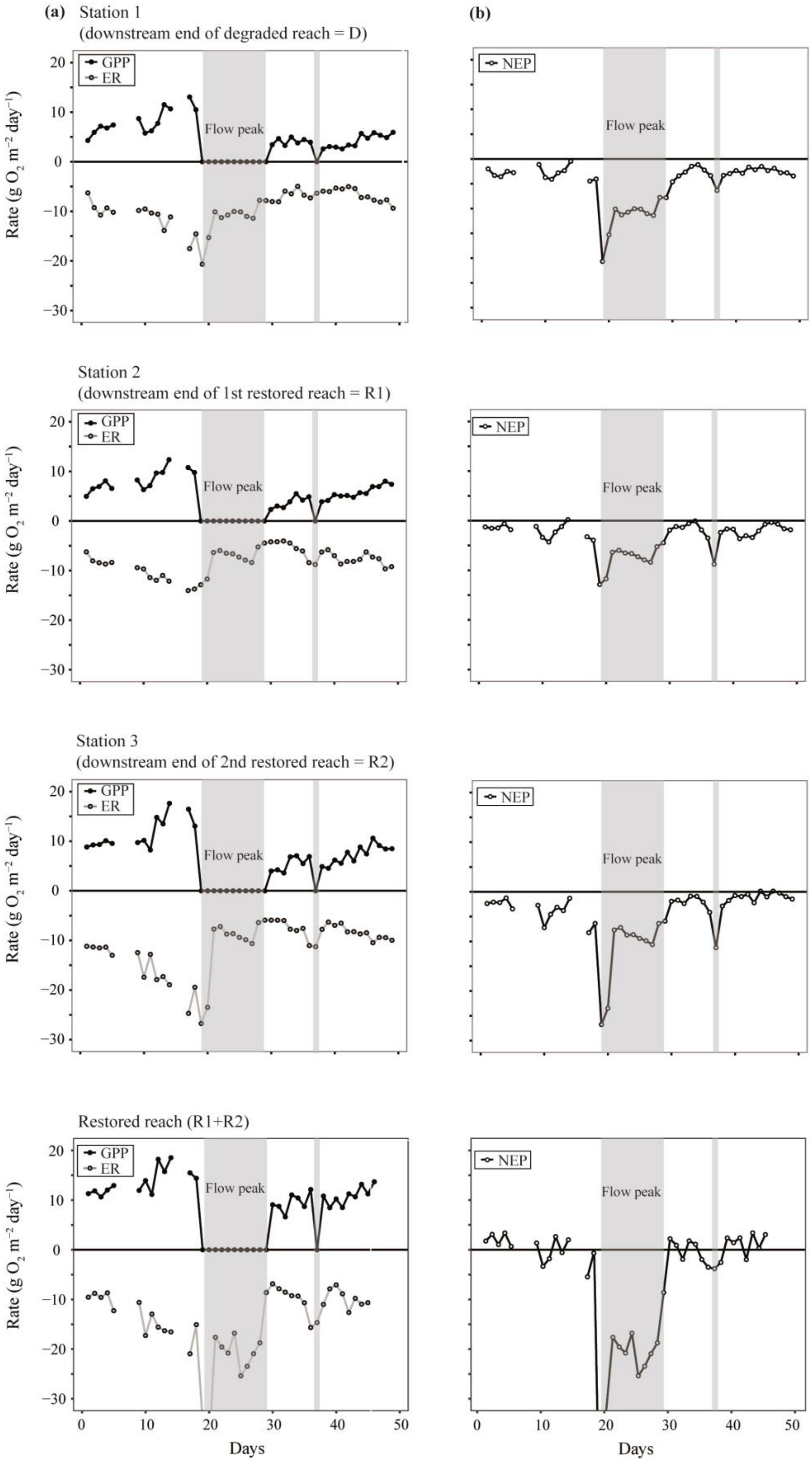


Fig. 6: Daily rates of (a) gross primary production (GPP: positive values, black line) and ecosystem respiration (ER: negative values, grey lines) and (b) net ecosystem production (NEP) measured at the downstream ends of the investigated reaches (degraded = D; 1st restored = R1; 2nd restored = R2) and for the combined reaches R1+R2 of the River Ruhr in summer 2014. Vertical grey bars indicate peak flow events.

Appendix S1: Information about restoration activities and restored reaches

The restored reaches (R1 and R2) were compared to an upstream degraded “control-section”. We selected the degraded reach (D) to be characteristic for the channelized state of the River Ruhr, and to reflect the conditions of the restored reaches prior to restoration (Fig. S1, S2). Accordingly, the hydromorphology of the degraded reach had been largely modified by channelization and bank fixation, resulting in lower physical stream quality (e.g. smaller wetted channel width, no islands and no accumulations of woody debris).

Restoration involved the widening of the riverbed and the reconnection of the river with its floodplain by creating a shallower river profile and by removing bank fixations. Furthermore, secondary channels and island were generated, instream structures - such as woody debris - were added and shallow habitats were created, potentially providing more space for autotrophs (Fig. S3, S4, S5, S6, S7, S8). The restored reaches differed in restoration effort (R1: moderate restoration effort and R2: high restoration effort). Briefly, R2 represented higher effort than R1 due to larger soil moving activities and higher costs for measures implemented (Table S1). Moreover, differences in restoration effort were obvious from measures implemented along the two reaches: In R1, removal of bank fixation and widening of the riverbed mainly focused on one (right) shoreline only, while the other (left) shoreline remained fixed due to railroad constrains (Fig. S7). On the contrary, R2 was substantially widened, bank fixation was removed at both shorelines and islands were created along the reach (Fig. S8). The differences between the restored reaches are further described by measurement results presented in our study (Table 2).

Table S1: Restoration costs and soil moving activities indicating differences in restoration effort between R1 and R2

Reach	**Costs (€)**	**Soil excavation (m^3)**	**Soil shifting (m^3)**
R1	1,400,000	44,000	15,000
R2	1,930,000	61,000	18,000

Fig. S1: Photo of the upstream degraded „control-section“ (D) (photo by A. Lorenz).

Fig. S2: Conditions of restored reaches prior to restoration (photo by A. Lorenz).

Fig. S3: Photo of the 1st restored reach (R1) (photo by B. Kupilas).

Fig. S4: Photo of the 1st restored reach (R1) (photo by B. Kupilas).

Fig. S5: Photo of the 2nd restored reach (R2) (photo by B. Kupilas).

Fig. S6: Photo of the 2nd restored reach (R2) (photo by B. Kupilas).

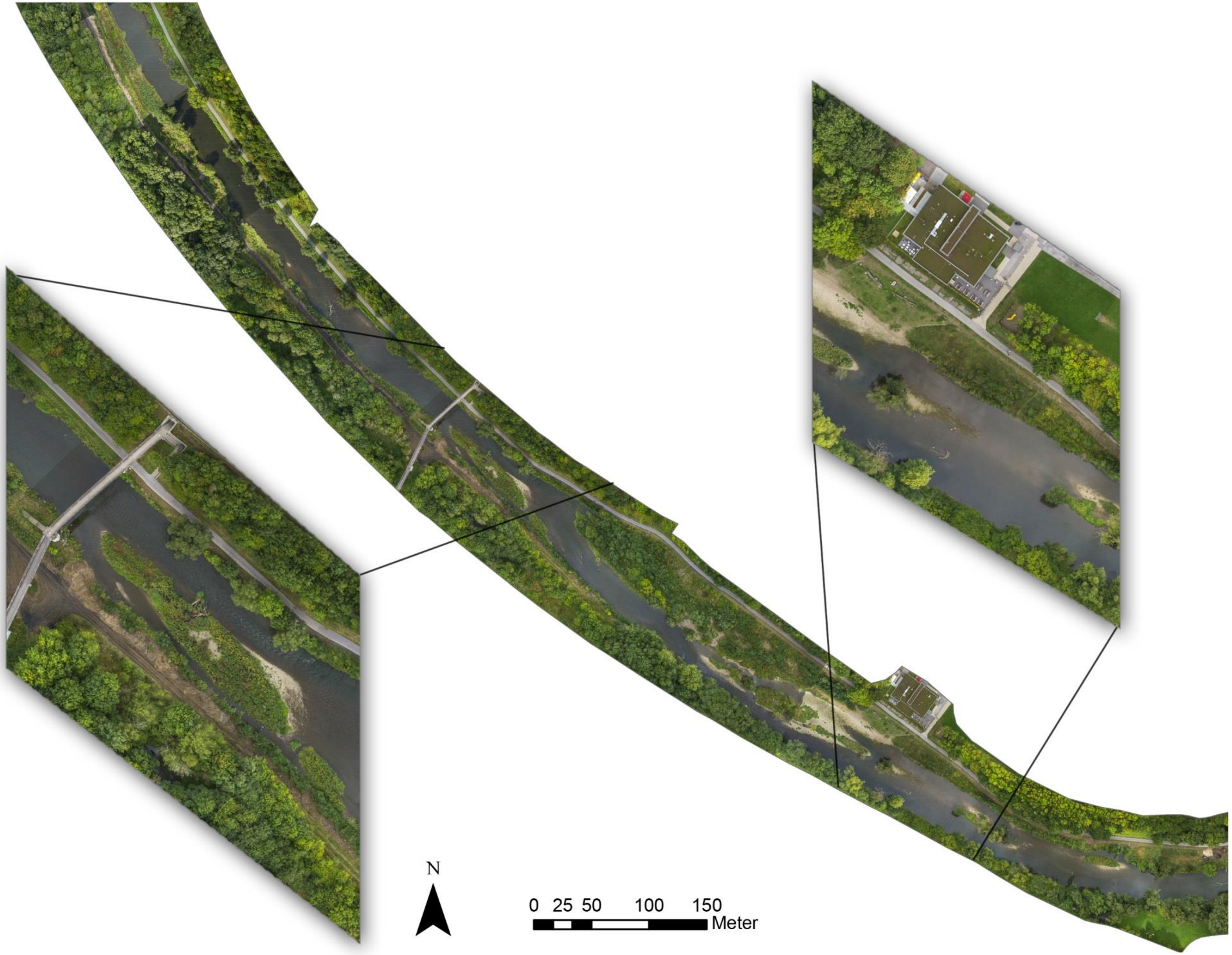


Fig. S7: 1st restored reach (R1) (photo by NZO GmbH, Germany).

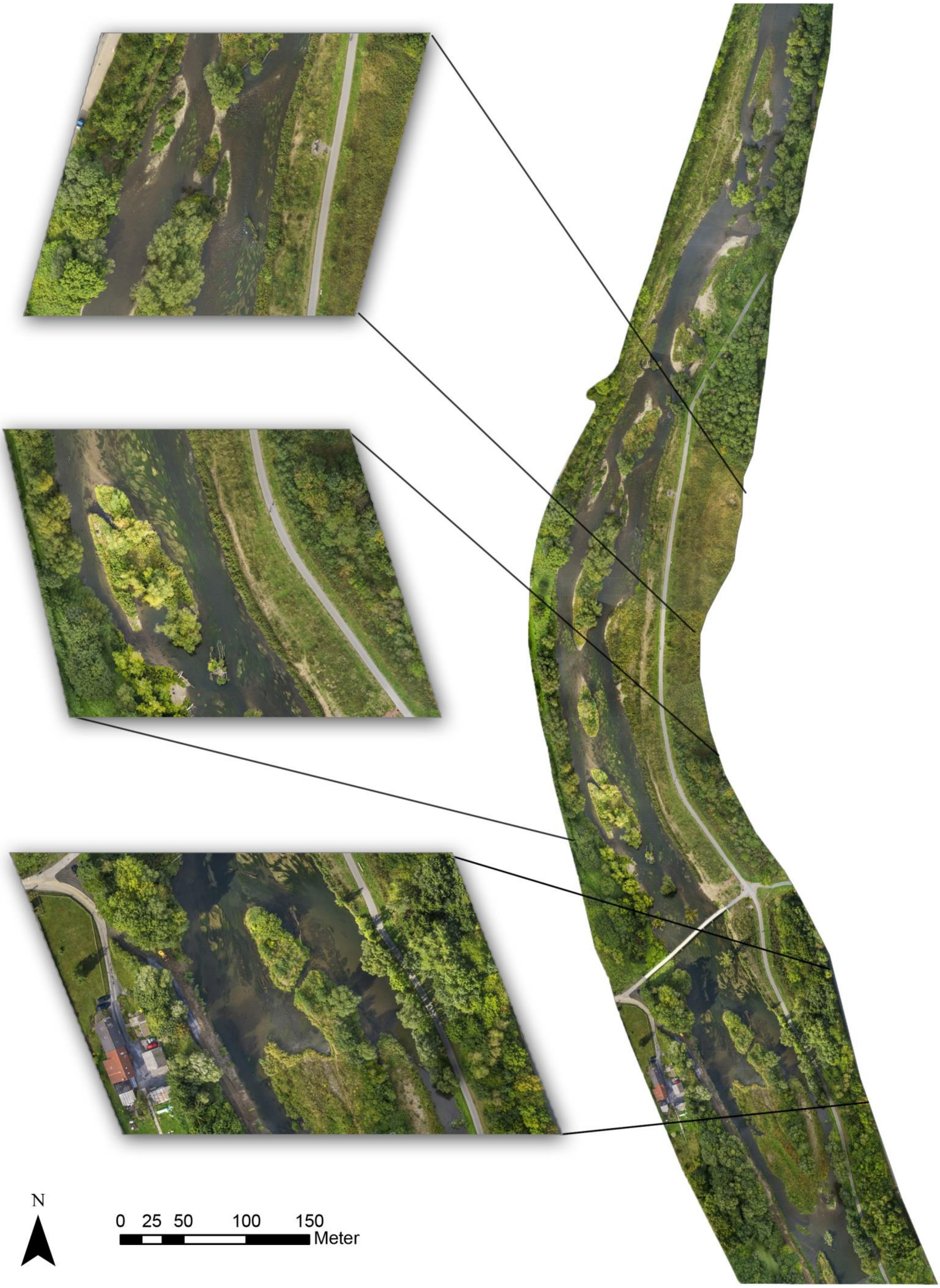
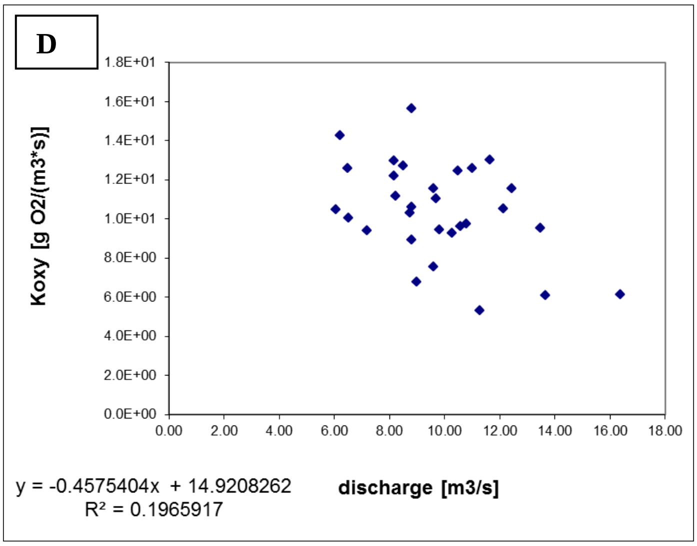


Fig. S8: 2nd restored reach (R2) (photo by NZO GmbH, Germany).

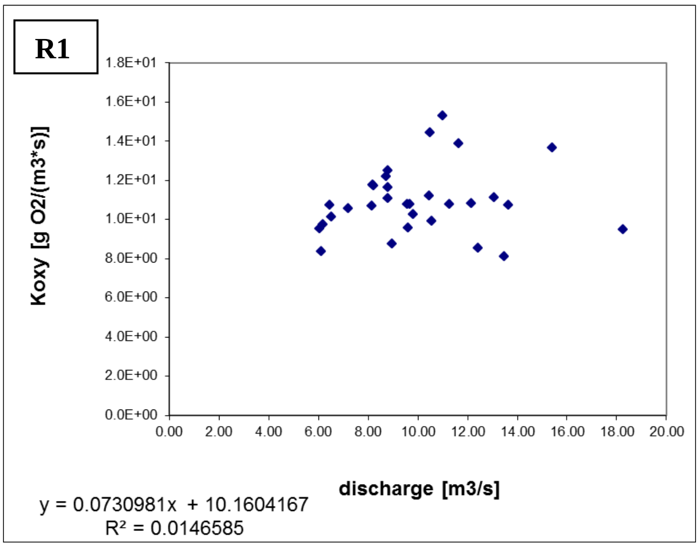
Appendix S2: K_{oxy}^{20} - discharge relationships for stations in D, R1 and R2.

All regressions with P>0.05

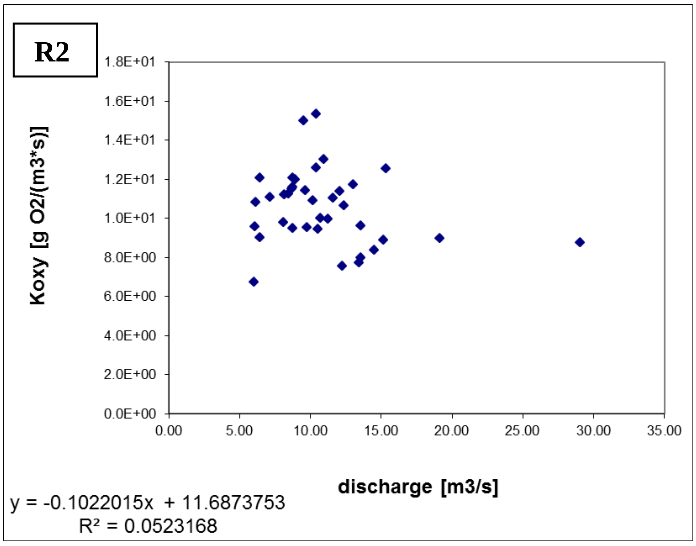
D



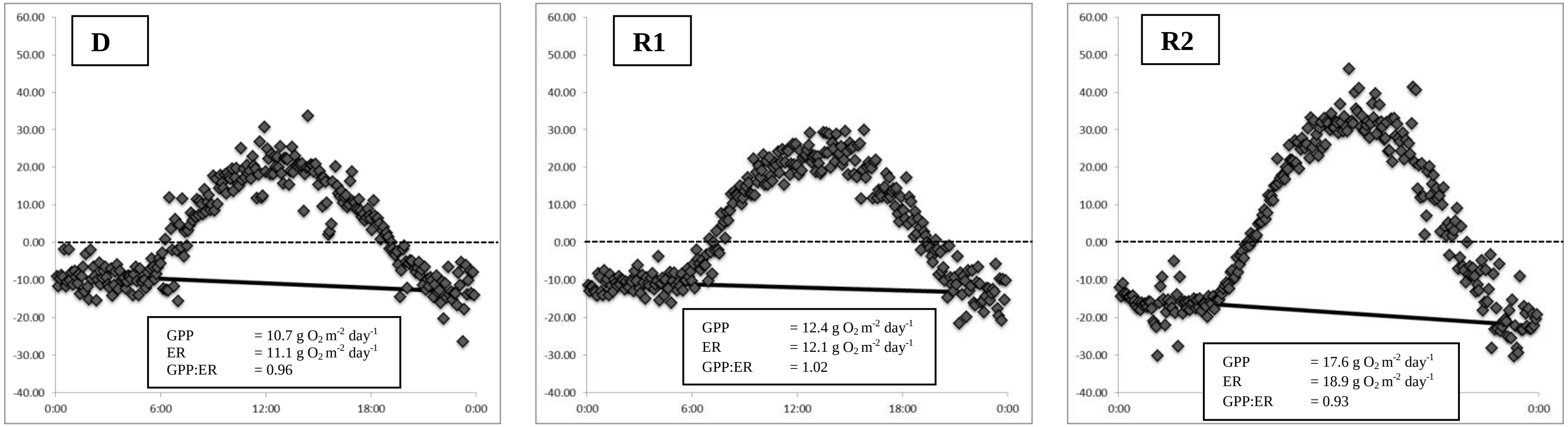
R1



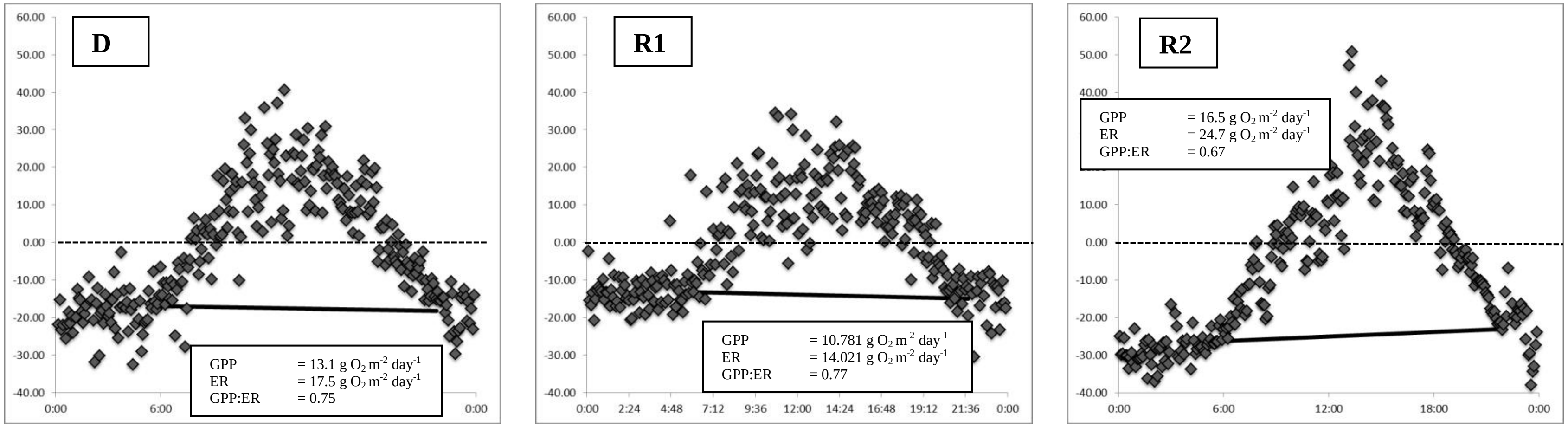
R2



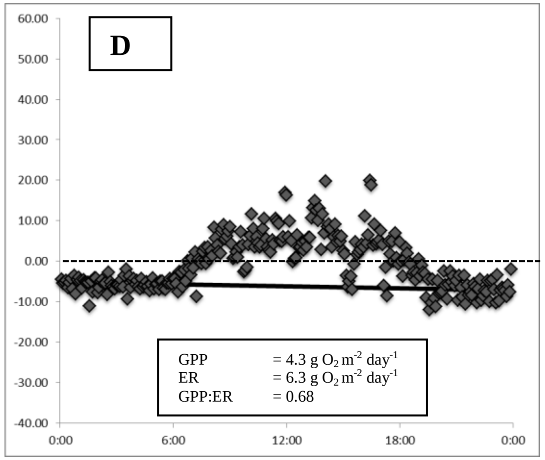
Appendix S3: Diurnal patterns of ecosystem metabolism in the sampling stations at D, R1 and R2 for days on which GPP and ER were among the highest respectively lowest rates measured

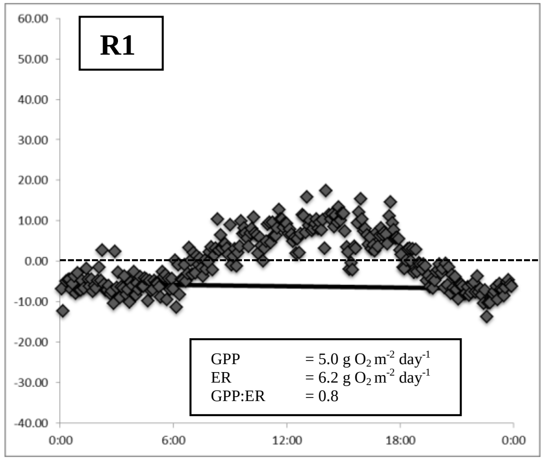


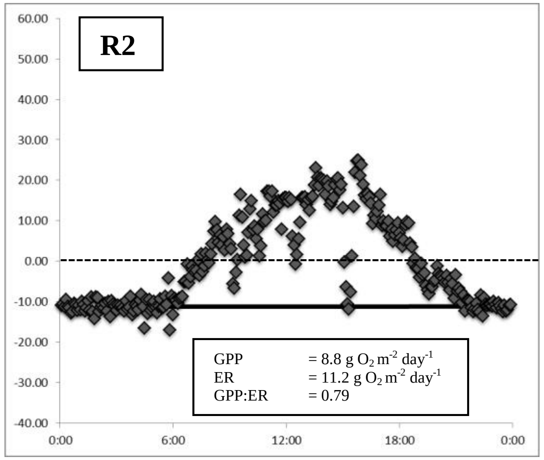
Day 17



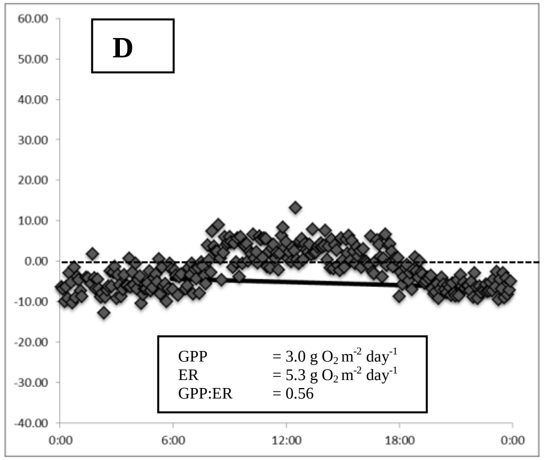
Day 1

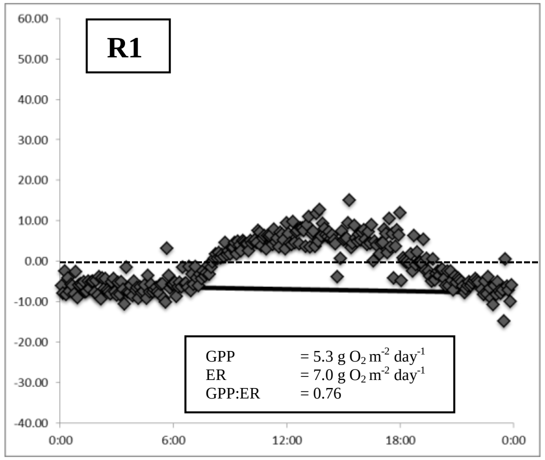

D
60.00
50.00
40.00
30.00
20.00
10.00
0.00
-10.00
-20.00
-30.00
-40.00
0:00
6:00
12:00
18:00
0:00
GPP = 4.3 g O_2 m^{-2} day^{-1}
ER = 6.3 g O_2 m^{-2} day^{-1}
GPP:ER = 0.68

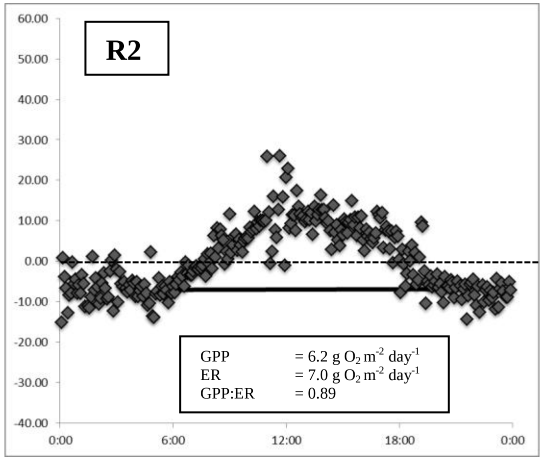

R1
60.00
50.00
40.00
30.00
20.00
10.00
0.00
-10.00
-20.00
-30.00
-40.00
0:00
6:00
12:00
18:00
0:00
GPP = 5.0 g O_2 m^{-2} day^{-1}
ER = 6.2 g O_2 m^{-2} day^{-1}
GPP:ER = 0.8


R2
60.00
50.00
40.00
30.00
20.00
10.00
0.00
-10.00
-20.00
-30.00
-40.00
0:00
6:00
12:00
18:00
0:00
GPP = 8.8 g O_2 m^{-2} day^{-1}
ER = 11.2 g O_2 m^{-2} day^{-1}
GPP:ER = 0.79

Day 40


D
60.00
50.00
40.00
30.00
20.00
10.00
0.00
-10.00
-20.00
-30.00
-40.00
0:00
6:00
12:00
18:00
0:00
GPP = 3.0 g O_2 m^{-2} day^{-1}
ER = 5.3 g O_2 m^{-2} day^{-1}
GPP:ER = 0.56


R1
60.00
50.00
40.00
30.00
20.00
10.00
0.00
-10.00
-20.00
-30.00
-40.00
0:00
6:00
12:00
18:00
0:00
GPP = 5.3 g O_2 m^{-2} day^{-1}
ER = 7.0 g O_2 m^{-2} day^{-1}
GPP:ER = 0.76


R2
60.00
50.00
40.00
30.00
20.00
10.00
0.00
-10.00
-20.00
-30.00
-40.00
0:00
6:00
12:00
18:00
0:00
GPP = 6.2 g O_2 m^{-2} day^{-1}
ER = 7.0 g O_2 m^{-2} day^{-1}
GPP:ER = 0.89

Appendix S4: Comparison of metabolic rates estimated in our study with literature data

GPP and ER estimated in this study were among the highest values reported for similar sized rivers (discharge between 5 - 50 $m^3 s^{-1}$, Appendix S5); especially those of the sampling station R2. In comparison to other streams, higher GPP and ER were reported for formerly polluted streams with a channelized river course and degraded floodplain in the Basque country (Izagirre et al. 2008); accordingly, a direct comparison to the Ruhr seems inappropriate. Besides size, none of the rivers in our literature review was comparable to the Ruhr regarding the river characteristics: sediment structure, hydromorphology/river state, macrophytes, and geographic region (Appendix S5). Consequently, metabolism reference values from rivers similar to the Ruhr are not available. However, higher GPP and ER after restoration of flow patterns have been reported by Colangelo (2007), supporting our findings of higher metabolic rates following restoration. Of all the rivers for which metabolism has been reported, the channelized river Thur (Uehlinger 2006) is closest to the Ruhr regarding size, sediment, and region. Average GPP and ER reported for the Thur were similar to those of the channelized sampling station D. Thus, relatively low GPP and ER in hydromorphologically altered rivers may be common.

References:

Colangelo, D.J. (2007) Response of river metabolism to restoration of flow in the Kissimmee River, Florida, U.S.A. Freshwater Biology, 52, 459–470. doi:10.1111/j.1365-2427.2006.01707.x.

Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi (2008) Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society, 27, 252–268. doi: 10.1899/07–022.1.

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. doi: 10.1111/j.1365-2427.2006.01551.x.

Appendix S5: Comparison with literature data, (a) river charatersitics

Sampled river	**River characteristics**					
Name, geographic region	**Sediment structure**	**Hydromorphology/river state**	**Macrophytes**	**Additional information**	**Width (m)**	**Q (m^3 s^{-1})**
Kissimmee River, Florida, USA	Sand	Channelised, restored habitat structure in river channel with continuous flow	Reduced cover of floating and mat forming vegetation	Sub-tropical, low-gradient, blackwater	15 – 30	36.60
Kansas River, Kansas, USA	Sand	Slightly braided, moderatley degraded (oxbow wetlands gone, bordered by cropland, no heavy industry or large urban area, some reservoirs)	No macrophytes, diatoms main primary producers	Prairie river, shallow	75	14.36
Omo River, Fuji River Basin, Japan	Cobbles, boulders	Relativly good, degraded water quality due to agricultural land use	Less than 5% cover	Open-canopy lowland stream draining urban and agricultural land	N.a.	5.12
Aizarnazabal, Basque Country, Spain	Bedrock, cobble	Narrow and steep valleys with short and steep streams, biotic index: excellent	Occasionally, periphyton main primary producer	Humid-oceanic climate, formerly polluted	22.7	6.27
Alegia, Basque Country, Spain	Bedrock, cobble	Narrow and steep valleys with short and steep streams, biotic index: good	Occasionally, periphyton main primary producer	Humid-oceanic climate, formerly polluted	36.2	6.96
Altzola, Basque Country, Spain	Bedrock, cobble	Narrow and steep valleys with short and steep streams, biotic index: poor	Occasionally, periphyton main primary producer	Humid-oceanic climate, formerly polluted	31.1	9.47
Amorebieta, Basque Country, Spain	Bedrock, cobble	Narrow and steep valleys with short and steep streams, biotic index: very poor	Occasionally, periphyton main primary producer	Humid-oceanic climate, formerly polluted	23.3	5.55
Lasarte, Basque Country, Spain	Bedrock, cobble	Narrow and steep valleys with short and steep streams, biotic index: fair	Occasionally, periphyton main primary producer	Humid-oceanic climate, formerly polluted	46.4	22.74
Little Tennessee River, North Carolina, USA	Sand becoming a mix of bedrock, large boulders, and sand	Broad alluvial valley becoming constrained valley	N.a.	N.a.	N.a.	12.90
Thur River, Switzerland	Gravel	Channelised with stabilised banks, with reach partly being opened (i.e. removal of bank fixation)	N.a.	Alpine river	35	48.70
Murrumbidgee River, Darlington Point, Australia	Clay, silt with sandy bars	Degraded, but not channelized	Very little macrophytes	In an agricultural area	N.a.	22.00
Daly, Australia	Sand, gravel	Natural, about 5% of the land cleared of natural vegetation, no dams, essentially natural flow, intermittent river	Very little macrophytes	5th - 7th order, tropical, shallow, clear water, low nutrient concentration, open canopy	N.a.	24.00
Mitchell River (MCC, upper site), Australia	Sand, bedrock	Continuous run-pool channel morphology	No macrophytes	Dry season sampled, riparian vegetation present	32	27.20
Buffalo Fork, Wyoming, USA	Cobble, gravel/pebble	Natural	No macrophytes	N.a.	35.2	19.10
Green River, Wyoming, USA	Cobble, boulder	Natural	N.a.	Below a dam	62.5	25.50
Salmon River, USA	Cobble, gravel	Natural	No macrophytes	N.a.	50.5	25.90
Tippecanoe River, Indiana, USA	Gravel, pebble with sand and fine sediment	Natural	No macrophytes	N.a.	50.6	19.00
Muskgeon River, Michigan, USA	Sand, silt, clay with gravel and cobbles	Natural	9% cover	N.a.	67	33.00
Manistee River, Michigan, USA	Sand, silt, clay with gravel and pebble	Natural	13% cover	N.a.	52.5	36.50
Bear River, Utah, USA	Sand, silt, clay	Natural morphology but hydrologically altered	No macrophytes	N.a.	37.3	16.00

Green River at Ouray, Utah, USA	Sand, silt, clay	Natural	1% cover	N.a.	111.8	37.90
Green River at Gray Canyon, Utah, USA	Fine sediments with gravel and cobbles	Natural	< 1% cover	N.a.	79.1	41.00
Chena1, Alaska, USA	N.a.	Natural flow regime, undeveloped	N.a.	Sub-arctic, clear-water river, upper catchment ~undeveloped, lower catchment with urban development	N.a.	42.00
Chena2, Alaska, USA	N.a.	Natural flow regime, undeveloped	N.a.	Sub-arctic, clear-water river, upper catchment ~undeveloped, lower catchment with urban development	N.a.	44.50
Chena3, Alaska, USA	N.a.	Natural flow regime, undeveloped	N.a.	Sub-arctic, clear-water river, upper catchment ~undeveloped, lower catchment with urban development	N.a.	47.00
Chena4, Alaska, USA	N.a.	Natural flow regime, undeveloped	N.a.	Sub-arctic, clear-water river, upper catchment ~undeveloped, lower catchment with urban development	N.a.	47.50
Ichetucknee, Florida, USA	N.a.	N.a.	N.a.	N.a.	N.a.	8.90
East Fork, Indiana, USA	N.a.	Natural	N.a.	N.a.	47.9	14.00

N.a. = not available

Appendix S5: comparison with literature data, (b) metabolic rates

Sampled river	**Metabolism**				
Name, geographic region	**GPP (g O_2 m^{-2} d^{-1})**	**ER (g O_2 m^{-2} d^{-1})**	**GPP:ER**	**NEP (g O_2 m^{-2} d^{-1})**	**Reference**
Kissimmee River, Florida, USA	3.95	-9.44	0.42	-5.49	Colangelo, D.J. (2007) Response of river metabolism to restoration of flow in the Kissimmee River, Florida, U.S.A. Freshwater Biology, 52, 459–470.
Kansas River, Kansas, USA	8.40	-12.12	0.69	-3.72	Dodds, W.K., J.J. Beaulieu, J.J. Eichmiller, J.R. Fischer, N.R. Franssen, D.A. Gudder, A.S. Makinster, M.J. McCarthy, J.N. Murdock, J.M. O'Brien, J.L. Tank & R.W. Sheibley (2008) Nitrogen cycling and metabolism in the thalweg of a prairie river. Journal of Geophysical Research, 113, G04029.
Omo River, Fuji River Basin, Japan	3.83	-9.13	0.42	-5.30	Iwata, T., T. Takahashi, F. Kazama et al. (2007) Metabolic balance of streams draining urban and agricultural watersheds in central Japan. Limnology, 8, 243-250.
Aizarnazabal, Basque Country, Spain	11.00	-17.20	0.64	-6.20	Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi (2008) Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society, 27, 252–268.
Alegia, Basque Country, Spain	4.40	-12.50	0.35	-8.10	Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi (2008) Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society, 27, 252–268.
Altzola, Basque Country, Spain	6.40	-42.60	0.15	-36.20	Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi (2008) Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society, 27, 252–268.
Amorebieta, Basque Country, Spain	2.80	-9.80	0.29	-7.00	Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi (2008) Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society, 27, 252–268.
Lasarte, Basque Country, Spain	6.30	-13.50	0.47	-7.20	Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi (2008) Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. Journal of the North American Benthological Society, 27, 252–268.
Little Tennessee River, North Carolina, USA	3.18	-4.07	0.78	-0.89	McTammany, M.E., J.R. Webster, E.F. Benfield & M.A. Neatrour (2003) Longitudinal patterns of metabolism in a southern Appalachian river. Journal of the North American Benthological Society, 22, 359–370.
Thur River, Switzerland	5.00	-6.20	0.81	-1.20	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.
Murrumbidgee River, Darlington Point, Australia	1.71	-1.90	0.90	-0.19	Vink, S., M. Bormans, P.W. Ford & N.J. Grigg (2005) Quantifying ecosystem metabolism in the middle reaches of Murrumbidgee River during irrigation flow releases. Marine and Freshwater Research, 56, 227–241.
Daly, Australia	2.90	-5.34	0.54	-2.44	Townsend, S.A. & A.V. Padovan (2005) The seasonal accrual and loss of benthic algae (Spirogyra) in the Daly River, an oligotrophic river in tropical Australia. Marine and Freshwater Research, 56, 317–327.
Mitchell River (MCC, upper site), Australia	2.12	-4.47	0.47	-2.35	Hunt, R.J., T.D. Jardine, S.K. Hamilton & S.E. Bunn (2012) Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshwater Biology, 57, 435-450.
Buffalo Fork, Wyoming, USA	0.80	-3.40	0.24	-2.60	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Green River, Wyoming, USA	19.90	-17.50	1.14	2.40	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Salmon River, USA	4.00	-5.10	0.78	-1.10	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Tippecanoe River, Indiana, USA	2.60	-5.30	0.49	-2.70	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Muskgeon River, Michigan, USA	3.00	-4.80	0.63	-1.80	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Manistee River, Michigan, USA	3.90	-4.40	0.89	-0.50	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Bear River, Utah, USA	1.10	-1.10	1.00	0.00	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.

Green River at Ouray, Utah, USA	1.10	-1.20	0.92	-0.10	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Green River at Gray Canyon, Utah, USA	0.30	-3.00	0.10	-2.70	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.
Chena1, Alaska, USA	3.25	-8.95	0.36	-5.70	Benson, E.R., M.S. Wipfli, J.E. Clapcott & N.F. Hughes (2013) Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river. Hydrobiologia, 701, 189–207.
Chena2, Alaska, USA	2.25	-5.80	0.39	-3.55	Benson, E.R., M.S. Wipfli, J.E. Clapcott & N.F. Hughes (2013) Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river. Hydrobiologia, 701, 189–207.
Chena3, Alaska, USA	1.85	-6.10	0.30	-4.25	Benson, E.R., M.S. Wipfli, J.E. Clapcott & N.F. Hughes (2013) Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river. Hydrobiologia, 701, 189–207.
Chena4, Alaska, USA	1.95	-5.90	0.33	-3.95	Benson, E.R., M.S. Wipfli, J.E. Clapcott & N.F. Hughes (2013) Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river. Hydrobiologia, 701, 189–207.
Ichetucknee, Florida, USA	10.00	-8.50	1.18	1.50	Heffernan, J.B. & M.J. Cohen (2010) Direct and indirect coupling of primary production and diel nitrate dynamics in a subtropical spring-fed river. Limnol. Oceanogr., 55, 677–688.
East Fork, Indiana, USA	4.70	-5.60	0.84	-0.90	Hall, R.O., J.L. Tank, M.A. Baker, E.J. Rosi-Marshall & E.R. Hotchkiss (2016) Metabolism, Gas Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86.