Hydromorphological restoration stimulates river ecosystem metabolism

Benjamin Kupilas*[1], Daniel Hering[1], Armin W. Lorenz[1], Christoph Knuth[2], Björn Gücker[3]

[1] Department of Aquatic Ecology, University of Duisburg-Essen, Universitätsstr. 5, D-45141 Essen, Germany

[2] Hydrogeology Department, Ruhr-Universität Bochum, Universitätsstr. 150, D-44801 Bochum, Germany

[3] Department of Geosciences, Applied Limnology Laboratory, Campus Tancredo Neves, Federal University of São João del-Rei, 36301-360 São João del-Rei, MG, Brazil

* Author of correspondence

Email: benjamin.kupilas@uni-due.de

Keywords: river restoration, ecosystem function, functional indicators, gross primary production, ecosystem respiration

1   **Abstract**

2   Both ecosystem structure and functioning determine ecosystem status and are important for the

3   provision of goods and services to society. However, there is a paucity of research that couples

4   functional measures with assessments of ecosystem structure. In mid-sized and large rivers, effects of

5   restoration on key ecosystem processes, such as ecosystem metabolism, have rarely been addressed

6   and remain poorly understood. We compared three reaches of the third-order, gravel-bed river Ruhr in

7   Germany: two reaches restored with moderate (R1) and substantial effort (R2) and one upstream

8   degraded reach (D). Hydromorphology, habitat composition and hydrodynamics were assessed. We

9   estimated gross primary production (GPP) and ecosystem respiration (ER) using the one-station open-

10   channel diel dissolved oxygen change method over a 50-day period at the end of each reach.

11   Moreover, we estimated metabolic rates of the combined restored reaches (R1+R2) using the two-

12   station open-channel method. Values for hydromorphological variables increased with restoration

13   intensity (D < R1 < R2). Restored reaches had lower current velocity, higher longitudinal dispersion

14   and larger transient storage zones. However, fractions of median travel time due to transient storage

15   were highest in R1 and lowest in R2, with intermediate values in D. The share of macrophyte cover of

16   total wetted area was highest in R2 and lowest in R1, with intermediate values in D. Station R2 had

17   higher average GPP and ER than R1 and D. The combined restored reaches R1+R2 also exhibited

18   higher GPP and ER than the degraded upstream river (station D). Restoration increased river

19   autotrophy, as indicated by elevated GPP:ER, and NEP of restored reaches. Temporal patterns of ER

20   closely mirrored those of GPP, pointing to the importance of autochthonous production for ecosystem

21   functioning. In conclusion, high reach-scale restoration effort had considerable effects on river

22   hydrodynamics and ecosystem functioning, which were mainly related to massive stands of

23   macrophytes. High rates of metabolism and the occurrence of dense macrophyte stands may increase

24   the assimilation of dissolved nutrients and the sedimentation of particulate nutrients, thereby positively

25   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

3

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.

4

80   Restoration also increases the retention of allochthonous organic matter (Lepori et al., 2005; Lepori et

81   al., 2006; Flores et al., 2011). Moreover, the reconnection of rivers with their floodplains by creating

82   shallower river profiles and removing bank fixations may enhance inundation frequency, and hence

83   resource transfers from land to water. In combination, these changes can favor heterotrophic activity in

84   the river. Restoration also affects hydrodynamics and surface water-ground water interactions of

85   streams (Becker et al., 2013): for instance, widening of the stream channel reduces flow velocity and

86   the creation of backwaters and pools possibly leads to changes in the size and location of transient

87   storage zones (Becker et al., 2013). Increases in transient storage zones potentially enhance ER

88   (Fellows et al., 2001) and nutrient processing (Valett et al., 1996; Gücker and Boëchat, 2004).

89   The objective of this study was to quantify reach-scale restoration effects on hydromorphology, habitat

90   composition and hydrodynamics, as factors potentially affecting river ecosystem function, by

91   comparing three contiguous stream reaches (two restored and one upstream non-restored reach) of a

92   mid-sized mountain river in Germany and to determine the corresponding responses of river

93   metabolism. We expected (i) hydromorphological river characteristics, i.e. habitat composition and

94   hydrodynamics, to change following restoration, with the magnitude of change depending on

95   restoration effort (e.g. width and diversity of the river channel, and abundance of primary producers,

96   as well as sizes and locations of transient storage zones in the two restored river reaches compared to

97   the degraded reach). Further, we expected (ii) ecosystem metabolism to respond with increased

98   metabolic rates, i.e. enhanced GPP and ER, mainly as a result of increased abundances of primary

99   producers.

100   **2. Methods**

101   *2.1 Study site*

102   This study was conducted in the upper River Ruhr (Federal State of North Rhine-Westphalia,

103   Germany, Fig. 1, Table 1) a tributary to the Rhine. The third-order Ruhr is a mid-sized mountain river

104   with gravel and cobbles as bed sediments. The catchment area upstream of the study site is 1060 km²,

105   about 64 % of which is forested, 28 % is arable land and pasture, and 8 % is urban area (located

106   mainly in the floodplains). The study site is at an altitude of 153 m a.s.l. and the mean annual

107   discharge was 21.3 m³ s^{-1} between 2004 and 2009. The Ruhr is draining one of the most densely

108   populated areas of Europe; however, population density of the upstream catchment area is low (135.3

109   inhabitants/km² upstream of the study site). Due to manifold uses, the river's hydromorphology has

110   been largely modified by impoundments, residual flow sections, bank fixation as well as industrial and

111   residential areas in the floodplain. More recently, the hydromorphology of several river sections has

112   been restored.

113   Restoration aimed to establish near-natural hydromorphology and biota. Restoration measures were

114   implemented between 2007 and 2009 and included the widening of the riverbed and the reconnection

115   of the river with its floodplain by creating a shallower river profile and by removing bank fixations.

116   Moreover, the physical stream quality was enhanced by generating secondary channels and islands,

117   adding instream structures, such as woody debris, and creating shallow habitats providing more space

118   for autotrophs (see Appendix S1 in Supporting Information).

119   We separated the restored reach into two reaches of approximately similar lengths (1210 and 1120 m)

120   with obvious differences in morphological stream characteristics due to differing restoration effort

121   (R1: moderate restoration effort and R2: high restoration effort). Briefly, in R2 a larger amount of soil

122   was removed and the costs for the implementation of measures were higher than in R1 (see Appendix

123   S1). In R2 the bank fixation was removed at both shorelines and the river was substantially widened

124   and secondary channels and islands were created, while the removal of bank fixation and widening in

125   R1 mainly focused on one side due to constrains posed by a nearby railroad (see Appendix S1). The

126   restored reaches were compared to a degraded "control-section" of 850 m length located upstream of

127   the restored reaches (D). The degraded reach was characteristic for the channelized state of the River

128   Ruhr upstream of the restoration site, and reflected the conditions of the restored sections prior to

129   restoration: The reach was a monotonous, channelized and narrowed river section with fixed banks

130   and no instream structures. A 650 m-long river section separating the degraded from the restored river

131   reach was excluded from the investigations, as its hydromorphology was deviating due to

6

132   constructions for canoeing and a bridge. As the three sections were neighboring each other, differences

133   in altitude, slope, discharge and catchment land cover between reaches were negligible.

134   *2.2 Hydromorphology and habitat composition*

135   Physical stream quality was quantified from aerial photos. High-resolution photos of the restored

136   reaches were taken in summer 2013 using a Falcon 8 drone (AscTec, Germany). Aerial photos of the

137   degraded reach from the same year at similar discharge conditions were provided by the Ministry for

138   Climate Protection, Environment, Agriculture, Conservation and Consumer Protection of the State of

139   North Rhine-Westphalia. Photos were analyzed in a geographical information system (ArcGIS 10.2,

140   ESRI). For each reach, we measured the width of the wetted channel every 20 m along cross-sectional

141   transects at low flow conditions and calculated mean width and its variation (reach D: n = 42, R1: n =

142   59, R2: n = 54). For each reach, we recorded thalweg lengths, the area of the wetted stream channel,

143   the floodplain area (defined as bank-full cross-sectional area), and the area covered by islands, woody

144   debris, and aquatic macrophyte stands (Fig. 2). Subsequently, the share of macrophyte stands of the

145   total wetted area was calculated for each reach. Additionally, macrophytes were surveyed according to

146   the German standard method (Schaumburg et al., 2005a; b) in summer 2013. A 100 m reach was

147   investigated by wading through the river in transects every 10 m, and walking along the riverbank

148   (Lorenz et al., 2012). All macrophyte species were recorded and species abundance was estimated

149   following a 5-point scale developed by Kohler (1978), ranging from "1 = very rare" to "5 = abundant,

150   predominant". The empirical relationship between the values of the 5-point Kohler scale (x) and the

151   actual surface cover of macrophytes (y) is given by the function $y = x^3$ (Kohler and Janauer, 1997;

152   Schaumburg et al., 2004). Using this relationship, we x^3-transformed the values of the Kohler scale

153   into quantitative estimates of macrophyte cover for the studied 100 m reaches.

154   *2.3 Hydrodynamics*

155   Stream hydrodynamics were estimated using a conservative tracer addition experiment with the

156   fluorescent dye Amidorhodamine G. Across the river width, we injected the dissolved dye in a

157   distance sufficiently upstream to the first study reach to guarantee complete lateral mixing at the first

158   sampling station. Breakthrough curves of the tracer were continuously measured in the main current at

159   the upstream and downstream ends of all three reaches (Fig. 1). Concentration of dye was recorded at

160   a resolution of 10 s at the most upstream and downstream sampling stations using field fluorometers

161   (GGUN-FL24 and GGUN-FL30, Albillia, Switzerland). At the other sampling stations (start and end

162   of each investigated river reach) water samples were taken manually at 2 min intervals. The samples

163   were stored dark and cold in the field and subsequently transported to the hydrogeochemical

164   laboratory of the Ruhr University Bochum. Amidorhodamine G concentrations of water samples were

165   measured with a fluorescence spectrometer (Perkin Elmer LS 45; detection limit of 0.1 ppb) and

166   standard calibration curves prepared from the tracer and river water. Field fluorometers were

167   calibrated prior to experiments with the same standard calibration procedure.

168   Subsequently, we used the one-dimensional solute transport model OTIS-P (Runkel, 1998) to estimate

169   parameters of river hydrodynamics for each reach from the breakthrough curves: advective velocity,

170   longitudinal dispersion, stream channel and storage zone cross-sectional areas, and storage rate. We

171   further calculated fractions of median travel time due to transient storage (F_{med}^{200}) based on the

172   hydrodynamic variables obtained from transport modeling (Runkel, 2002). Additionally, Damköhler

173   numbers were estimated for each reach (Harvey and Wagner, 2000).

174   *2.4 Discharge*

175   Discharge data were provided by the North Rhine-Westphalia State Agency for Nature, Environment

176   and Consumer Production, Germany (Landesamt für Natur, Umwelt und Verbraucherschutz

177   Nordrhein-Westfalen) for a gauging station situated at the downstream end of the study site. At this

178   station, discharge was constantly recorded at 5-min intervals.

179   *2.5 Ecosystem metabolism*

180   We estimated river dissolved O_2 (DO) metabolism using the 'open-channel one-station and two-station

181   diel DO change techniques' (Odum, 1956; Marzolf et al., 1994; Young and Huryn, 1998; Roberts et

182   al., 2007). We initially chose the one-station method to estimate metabolic rates at the downstream end

183   of each reach (stations D, R1, and R2), as the individual studied reaches were too short for a reliable

8

184   estimation of ecosystem metabolism with the two-station technique, due to high current velocities and

185   low reaeration rates. According to Demars et al. (2015), the two-station method is applicable to reach

186   lengths 0.4 v/k to 1.0 v/k. For our reaches of the Ruhr, this range corresponds to 3283 - 8280 m for

187   reach D, 2765 - 6912 m for reach R1, 1624 - 4061 m for reach R2, and 2199 - 5497 m for the

188   combined reach R1+R2. Thus, the quantification of metabolism using the two-station method was

189   only possible for the combined reach R1+R2 with a reach length of 2330 m.

190   Reach lengths influencing the one-station diel dissolved O_2 change technique in our study were

191   typically much longer than the experimental reaches, due to high current velocities and low reaeration

192   (>10 km; estimated according to Chapra and Di Torro, 1991). Following methods in Demars et al.

193   (2015), metabolism estimates at the downstream sampling station R2 were only to 35% influenced by

194   the restored river sections, but to 65% by upstream degraded river sections. Accordingly, differences

195   in metabolic rates among sampling stations at the end of restored and impacted experimental reaches

196   as estimated in our study should be viewed as qualitative indicators of restoration effects, rather than

197   measured metabolic rates of the experimental reaches. To quantitatively support our qualitative

198   findings, we additionally used the two-station method for the combined restored river reach R1+R2,

199   which was long enough for the application of the two-station open-channel method. The selected

200   methods are based on the assumption that changes in DO within a parcel of water traveling

201   downstream can be attributed to metabolism (photosynthesis and respiration) and to gas exchange

202   between water and atmosphere, given that no significant groundwater dilution of river water occurs

203   along the studied river:

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

205   where dDO/dt is the change in dissolved oxygen concentration (mg O_2 L^{-1} s^{-1}), GPP is the gross

206   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

207   reaeration coefficient (s^{-1}), and D is the oxygen deficit or surplus in the river (i.e., the difference

208   between the measured oxygen concentration and the value at saturation; mg O_2 L^{-1}). The change in DO

209   was estimated as the difference between consecutive 5-min readings of the same probe for the one

210   station method and as the difference between upstream (top of reach R1) and downstream probes (end

211   of reach R2) for the two station method (Roberts et al., 2007; Beaulieu et al., 2013).

212   In two consecutive field campaigns in summer 2014, DO and water temperature were continuously

213   measured at the downstream ends of the three reaches and at the top of reach R1 at 5-min intervals for

214   50 days. The DO probes with data loggers (O_2-Log3050-Int data logger Driesen + Kern GmbH,

215   Germany) were installed in the thalweg of the river in the middle of the water column. The DO probes

216   were calibrated in water-saturated air prior to measurements. Additionally, probes were cross-

217   calibrated for one hour at a single sampling station in the river before and after the measurements. We

218   used the data of this comparison to correct for residual differences among probes (Gücker et al., 2009).

219   This procedure assured that differences between probes were only due to differences in DO and water

220   temperatures and not to analytical errors. In previous laboratory tests, the probes showed no drift and

221   were thus not corrected for drift during the measurement campaigns (Almeida et al., 2014).

222   In parallel to DO and water temperature, atmospheric pressure was recorded (Hobo U20-001-04;

223   Onset Computer Corporation). We used atmospheric pressure and water temperature data to calculate

224   the oxygen saturation. Reaeration coefficients (K_{oxy}^{20}; standardized for 20°C) were estimated using the

225   nighttime regression approach (Young and Huryn, 1999). For the downstream stations of all three

226   sampling reaches, we calculated reaeration coefficients (K_{oxy}) as the slope of regressions between DO

227   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

228   as the period 1 h after sunset to 1 h before sunrise):

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

230   We only considered significant nighttime regressions ($p < 0.05$). Reaeration coefficients for days

231   without significant regressions were estimated as the average value of the coefficients of the days

232   before and after, as we did not observe K_{oxy}^{20} - discharge relationships in our data (see Appendix S2)

233   that could have been used to estimate K_{oxy}^{20} values for days without reliable estimates. Estimated

234   reaeration coefficients were low and ranged from 5 to 15 d^{-1} in our study (see Appendix S2).

235   Subsequently, we calculated ER and GPP as described in detailed elsewhere (Marzolf et al., 1994;

10

236 Young and Huryn, 1998; Roberts et al., 2007) from the recorded nighttime river water DO deficit and

237 the daytime DO production, respectively, corrected for atmospheric reaeration (see Appendix S3).

238 Metabolic rates obtained by this method closely matched those obtained with the estimator of Reichert

239 et al. (2009). Ground water dilution was not detected, i.e. discharge differences among the investigated

240 river reaches were within the ranges of method uncertainty of discharge measurements, and was thus

241 not considered into our estimates. Metabolism measurements from days at which floating macrophytes

242 accumulated around probes and affected DO measurements were eliminated from the dataset.

243 *2.6 Data analysis*

244 We used the ARIMA function in [R] to identify an ARIMA model that best represented all time series

245 (metabolic parameters at stations D, R1, R2, and reach R1+R2), estimated average parameter

246 predictions and 95%-confidence limits for each time series based on these models, and used F-tests to

247 test the hypothesis of differences among time series (compare Roley et al., 2014). Data recorded at the

248 time of flooding events were omitted from analyses, because GPP was not detectable, and we cannot

249 be sure whether GPP was indeed zero or very low, or whether high flows prevented the detection of

250 GPP. Overall, data of n = 32 days were used in the analyses. Repeated measures ANOVAs and

251 Tukey's HSD post-hoc tests were used to test for differences in water temperature among river

252 reaches. Conventional one-way ANOVA was used to test for differences in river width, comparing the

253 transect measurements performed in the three river reaches. All statistical analyses were conducted in

254 [R] (R Development Core Team, 2007).

255 **3. Results**

256 *3.1 Hydromorphology and habitat composition*

257 Restored river reaches were morphologically more complex and had significantly wider wetted

258 channels (ANOVA and Tukey post-hoc test, P < 0.05) and more variable channel width than the

259 degraded reach (Table 2). Furthermore, the restored reaches had larger wetted channel areas,

260 floodplain areas, island areas and patches of woody debris than the degraded river reach (Table 2). The

261   intensively restored reach R2 showed the highest values for hydromorphological variables (Table 2).

262   The share of macrophyte cover of total wetted area was also highest in R2.

263   *3.2 Hydrodynamics*

264   The reaches differed in hydrodynamic parameters: The restored reaches had lower flow velocity and

265   higher longitudinal dispersion, cross-sectional areas of the advective channel, and storage zone cross-

266   sectional areas than the degraded reach (Table 2). Storage rate and fractions of median travel time due

267   to transient storage (F_{med}^{200}) was highest in R1 and lowest in R2, with intermediate values for D (Table

268   2). Damköhler numbers between 0.5 and 5.0 indicated reliable transient storage parameter estimates

269   for the reaches (Harvey and Wagner, 2000; Table 2). Tracer breakthrough curves estimated by

270   transport modelling closely corresponded to measured tracer concentrations (Fig. 3).

271   *3.3 Discharge and water temperature*

272   Mean discharge during the first weeks of measurement was 8.4 m^3 s^{-1}. The hydrograph was

273   characterized by a large summer flow peak and two minor peaks during the study period (Fig. 4 a).

274   During the flow peaks discharge rapidly increased 3.5- to 7-fold, relative to the mean flow. Trends in

275   water temperature over time were very similar for the three river reaches and are exemplarily shown

276   for R2 (Fig. 4 b). Overall, restored reaches had higher mean daily water temperatures than the

277   degraded reach, with R2 having higher mean daily water temperatures compared to R1 (repeated

278   measures ANOVA, $P < 0.0001$; and Tukey's HSD post-hoc tests, $P < 0.0005$).

279   *3.4 Ecosystem metabolism*

280   We observed significant effects of reach-scale restoration on metabolic rates estimated at the end of

281   the restored river sections (R1 and R2 compared to D; estimated by the one-station method) and

282   between the upstream degraded river (station D) and the combined restored reaches R1+R2 (estimated

283   with the two-station method). According to the ARIMA function estimates, we found higher river

284   GPP, NEP and GPP:ER at the restored river sections (R1 and R2 versus station D; estimated with the

285   one-station method; Fig. 5). Moreover, GPP, ER, NEP, and GPP:ER were also higher (Fig. 5) in the

286   total restored river reach (R1+R2; estimated with the two-station method) than in the upstream

287   degraded river (measured at section D with the one-station method). These findings indicate an

288   increase in the river's metabolism following restoration.

289   The three sampling stations at the downstream ends of the reaches generally exhibited similar

290   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

291   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

292   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

293   shortly before the main summer flow peak at all sampling stations (Fig. 6 a). GPP was not detectable

294   during the summer flow peaks. ER generally mirrored the GPP patterns, but showed distinct peaks at

295   the beginning of the summer flow peak. ER exceeded GPP during all but one day at R1 and two days

296   at R2. Consequently, NEP (net ecosystem production) was negative during most of the measured

297   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

298   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

299   station R2. The average GPP:ER ratio ranged from 0.66 to 0.97 across all sampling stations, also

300   indicating that the Ruhr was moderately heterotrophic. General patterns in daily rates of both GPP and

301   ER also seemed to be influenced by flow peaks. GPP and ER were both suppressed immediately

302   following the flooding events. The ensuing recovery patterns for GPP and ER were similar for all

303   investigated sampling stations: depending on magnitude of flow, GPP and ER were suppressed for

304   several days, but steadily returned to pre-disturbance conditions. The total restored river reach

305   (R1+R2, two-station method) showed temporal metabolism patterns comparable to those estimated at

306   the three sampling stations with the one-station method (Fig. 6). However, NEP of the total restored

307   river reach (R1+R2) was positive and average GPP:ER ratio higher than 1 during most of the sampling

308   period, indicating a slight change in the river's metabolic balance following restoration.

309   **4. Discussion**

310   Restoration of river hydromorphology usually covers short river stretches of less than one km and is

311   expected to increase the river's habitat and hydrodynamic heterogeneity. Together, these changes may

312   stimulate ecosystem metabolism, i.e. whole-stream rates of GPP and ER, as well as affect the river's

313   metabolic balance. Increases in river metabolism, in turn, may result in increased rates of other

314   ecosystem processes, such as secondary productivity and whole-stream nutrient processing (Fellows et

315   al., 2006; Gücker and Pusch, 2006).

316   *4.1 Hydromorphological characteristics*

317   Recent monitoring and evaluation of restoration projects report positive effects on hydromorphology

318   and habitat composition (Jähnig et al., 2009; Jähnig et al., 2010; Poppe et al., 2016). Similarly, we

319   found greater habitat complexity of restored reaches, as indicated by wider and more diverse river

320   channels. The reach with the highest restoration effort (R2), was characterized by the highest values

321   and heterogeneity of hydromorphological variables; this suggests that restoration effort is indeed

322   crucial for restoration success. According to Lorenz et al. (2012), the success of restoration in mid-

323   sized to larger rivers can also be indicated by increased cover, abundance and diversity of macrophytes

324   as they benefit from more natural and diverse substrate, and the variability in flow. Consequently, the

325   higher share of macrophyte cover of total wetted area in R2 also highlighted the higher morphological

326   quality of this reach.

327   Moreover, there were no point sources or changes in land use along the studied river section, and

328   therefore, increases in P and N concentrations, and associated eutrophication effects in the studied

329   river section seem unlikely (compare Table 1). Thus, higher macrophyte biomass and metabolic

330   responses are likely to be a result of river restoration, i.e. wider channels increasing light availability,

331   shallower channels providing better habitats for macrophytes, and lower current velocities decreasing

332   hydraulic stress.

333   Changes in hydromorphology and habitat composition influenced hydrodynamics: we observed lower

334   current velocity, higher longitudinal dispersion and larger transient storage zones in the restored

335   reaches. This corresponds with the larger river width and wetted channel area, and the increased

336   abundance of morphological features such as woody debris, islands and macrophyte patches.

337   However, F_{med}^{200}, i.e. the relative importance of transient storage for whole-stream hydrodynamics,

338   was highest in R1 and lowest in R2, with intermediate values for D. Accordingly, there appeared to be

339   an inverse relationship between F_{med}^{200} and the share of macrophyte cover of total wetted area, which

340   was highest in R2 and lowest in R1, with intermediate values in D. These findings suggest that the

341   dense stands of macrophytes in R2 particularly altered stream hydrodynamics: macrophyte patches

342   built large surface transient storage areas and potentially changed the locations of transient storage

343   zones from the hyporheic zone to the surface water column. Macrophyte fields in R2 may have even

344   been so dense that large parts of them were representing hydrodynamic dead zones. A similar effect

345   was found in streams restored by implementing steering structures to enhance stream quality: the

346   restored reaches were dominated by surface transient storage exchange (Becker et al., 2013).

347   Furthermore, the sedimentation of fine sediment within dense macrophyte stands may further decrease

348   exchange with the hyporheic zone.

349   *4.2 Functional characteristics*

350   Metabolism was measured over a 50-day period to obtain representative data, allowing for

351   comparisons among sampling stations. Furthermore, this time series allowed for the analysis of

352   environmental variability, such as flow peaks. The results were obtained for the summer period, i.e.

353   the time of maximum biomass, which is also relevant for the WFD compliant sampling period (e.g.,

354   Haase et al., 2004; Schaumburg et al., 2004; EFI+ CONSORTIUM, 2009). Therefore, results obtained

355   in this study are directly comparable to the river status derived from biological assessment.

356   In general, the three sampling stations showed similar patterns in metabolism, as our one-station

357   metabolism approach measured a long upstream river section in addition to the experimental reaches.

358   Rates of ER mirrored those of GPP, suggesting that autotrophic respiration largely drove temporal

359   patterns in ER, despite an overall ratio of GPP:ER < 1 and a slightly negative NEP during most of the

360   measurement period. Similar patterns were found in streams in the US (Beaulieu et al., 2013; Hall et

361   al., 2016). The average GPP:ER ratio was significantly higher downstream of the restored reaches in

362   our study (0.86 and 0.97, respectively) and in the combined restored reach (1.16) than in the upstream

363   degraded river (0.66), indicating an increase in autotrophic processes following restoration. The only

364   moderate heterotrophic state of the river together with ER closely tracking GPP indicated the

365   importance of autochthonous production for the metabolism. This is further supported by the

366   comparison of pre- and post-peak flow ER (Fig. 6). McTammany et al. (2003) suggested that higher

367   inputs of allochthonous material may occur after flooding events, subsequently supporting high rates

368   of ER. In line with this, we expected high rates of ER during the last third of the sampling period,

369   especially in restored reaches with a potentially high POM trapping efficiency. However, ER was

370   lower compared to pre-flow peak conditions, with ER still mirroring GPP, thus indicating the coupling

371   of autochthonous production with ER even after floods. This implies that restoration (reconnection of

372   river and floodplain) did not increase resource transfer into the channel to such an extent that it

373   influenced river metabolism.

374   We observed significantly higher GPP and ER at station R2 compared to the other stations.

375   Metabolism of R1 did not markedly differ from D, corresponding with consistently higher values of

376   hydromorphological variables in R2 only. Given the previously discussed importance of

377   autochthonous production for the metabolism, habitat enhancement supporting the growth of

378   macrophytes is likely the cause for higher GPP and ER in R2. Consequently, only high restoration

379   effort bringing a restored reach close to reference conditions led to pronounced effects on ecosystem

380   metabolism. Restoration effects were mainly related to the growth of aquatic macrophytes, which

381   formed dense stands that augmented ecosystem metabolism. We acknowledge that metabolism was

382   measured during summer, i.e. the time of maximum biomass of aquatic macrophytes. Therefore, high

383   GPP and ER measured in this campaign might be restricted to this season and effects will be lower

384   during winter times when macrophyte abundance will be low.

385   Ecosystem metabolism of the sampling stations at the restored reaches and of the combined restored

386   river reaches was expected to be at similar levels to those of natural rivers reported in the literature.

387   Therefore, we compared GPP and ER of our sampling stations to those of rivers comparable in size

388   (discharge between 5 - 50 $m^3 s^{-1}$; see Appendix S4, S5). GPP and ER estimated in this study were

389   among the highest values reported for similar sized rivers; especially those of the sampling station R2

390   and the combined restored reach. Of all the rivers, for which metabolism has been reported, the

391   channelized river Thur (Uehlinger, 2006) is closest to the Ruhr regarding size, sediment, and region.

392   Interestingly, average GPP and ER reported for the Thur were similar to those of the channelized

393   sampling station D. Thus, relatively low GPP and ER in hydromorphologically altered rivers

394   compared to natural ones may be common. However, there is a tremendous variability in ecosystem

395   metabolism among natural river reaches in the literature (see Appendix S4, S5). Considering the

396   limited knowledge about natural geographical gradients in river metabolism, it was not possible to

397   assess if values obtained for restored reaches indicate natural conditions in a broader geographic

398   context. In future analyses of restoration effects on fluvial metabolism, local reference conditions

399   should therefore be assessed whenever possible.

400   Our experimental reaches reflected typical spatial scales on which restoration measures are

401   implemented. However, individually, these reaches were too short to feasibly use the two-station diel

402   DO change method (see 2.5). Accordingly, we used the one-station approach to assess reach-scale

403   restoration effects on ecosystem metabolism of longer river sections (>10 km). Following methods in

404   Demars et al. (2015), we evaluated to which extent these metabolism estimates reflected the restored

405   river sections. Measurements at sampling station R1 and R2 were only to 16% and 24%, respectively,

406   influenced by the restored experimental reaches directly upstream. However, station R2 was to 35%

407   influenced by the combined reaches R1+R2, and thus to 65% by upstream degraded river sections.

408   Despite this mismatch between lengths of river reaches evaluated and reaches exclusively affected by

409   restoration, we found significant effects of reach-scale restoration on whole-river metabolism.

410   Interestingly, our study therefore also shows that high restoration effort in short river reaches (1 to 2

411   km) had considerable effects on total whole-river metabolic rates of river stretches exceeding the

412   length of the actually restored reaches (>10 km), and that the one-station method may therefore be an

413   interesting option to qualitatively assess restoration effects in field situation, in which the two-station

414   method is not feasible.

415   To quantitatively support these qualitative findings, we estimated metabolism of the combined

416   restored reaches R1+R2, which were long enough to permit the application of the two-station method.

417   The obtained metabolic rates should be directly comparable to metabolic rates of the upstream,

418   degraded river (measured at station D with the one-station method) as results obtained with the one-

419   station and the two-station methods often agree remarkably well (e.g., Bernot et al., 2010; Beaulieu et

420   al., 2013). The total restored reach (R1+R2) showed higher GPP, ER, NEP, and GPP:ER than the

17

421 upstream degraded river. Thus, these results support the findings derived from the one-station method,

422 indicating an increase in the river's metabolism and metabolic balance associated with restoration.

423 Thus, the restoration of short river reaches may have positive effects on downstream river sections

424 regarding diel DO variability and carbon spiraling. High rates of metabolism and the occurrence of

425 dense macrophyte stands in restored river reaches may also increase the assimilation of dissolved

426 nutrients (Fellows et al., 2006; Gücker et al., 2006) and the sedimentation of particulate nutrients

427 (Schulz and Gücker, 2005), thereby positively affecting water quality.

428 *4.3 Recommendations for restoration monitoring*

429 For most regions and river types, data is missing that could be used to establish limits of good,

430 moderate or poor river conditions. However, based on data from mainly small streams, Young et al.

431 (2008) proposed a useful framework to assess functional stream health using GPP, ER, NEP and

432 GPP:ER. Consequently, metabolic rates for different river types should be surveyed to allow the

433 incorporation of ecosystem metabolism of mid-sized and large rivers as functional indicator in this

434 framework. Our study stresses the benefits of metabolism as a functional indicator complementing the

435 monitoring of restoration projects (compare Young et al., 2008; Bunn et al., 2010): Temporally high-

436 resolution and automated monitoring, that integrates biotic and abiotic variables over time and across

437 habitats may increase our understanding of the effects of river restoration and might help identifying

438 initial changes after restoration. Incorporating functional indicators into monitoring programs may

439 enable a more holistic assessment of river ecosystems and elucidate responses to restoration (and also

440 impairment), which may be related to ecosystem structure and function.

441 **Acknowledgements**

453   **References**

454   Almeida, G.H., Boëchat, I.G., and Gücker, B.: Assessment of stream ecosystem health based on

455   oxygen metabolism: Which sensor to use? Ecological Engineering, 69, 134–138, 2014.

456   Beaulieu, J.J., Arango, C.P., Balz, D.A., and Shuster W.D.: Continuous monitoring reveals multiple

457   controls on ecosystem metabolism in a suburban stream. Freshwater Biology, 58, 918–937,

458   2013.

459   Becker, J.F., Endreny, T.A., and Robinson, J.D.: Natural channel design impacts on reach-scale

460   transient storage. Ecological Engineering, 57, 380-392, 2013.

461   Beisel, J.-N., Usseglio-Polatera, P., and Moreteau, J.-C.: The spatial heterogeneity of a river bottom: a

462   key factor determining macroinvertebrate communities. Hydrobiologia, 422/423, 163–171,

463   2000.

464   Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S. et al.: Ecology -

465   synthesizing US river restoration efforts. Science, 308, 636–637, 2005.

466   Bernot, M.J., Sobota, D.J., Hall, R.O., Mulholland, P.J., Dodds, W.K., Webster, J.R. et al.: Inter-

467   regional comparison of land-use effects on stream metabolism. Freshwater Biology, 55, 1874–

468   1890, 2010.

469   Bunn, S.E., Abal, E.G., Smith, M.J., Choy, S.C., Fellows, C.S., Harch, B.D. et al.: Integration of

470   science and monitoring of river ecosystem health to guide investments in catchment protection

471   and rehabilitation. Freshwater Biology, 55, 223-240, 2010.

472   Chapra, S.C. and Di Toro, D.M.: Delta method for estimating primary production, respiration, and

473   reaeration in streams. Journal of Environmental Engineering, 117, 640–655, 1991.

474   Colangelo, D.J.: Response of river metabolism to restoration of flow in the Kissimmee River, Florida,

475   U.S.A. Freshwater Biology, 52, 459–470, 2007.

476   Demars, B. O. L., Thompson, J., and Manson, J. R.: Stream metabolism and the open diel oxygen

477   method: Principles, practice, and perspectives. Limnology and Oceanography-Methods, 13,

478   356-374, 2015.

479   Dodds, W.K., Veach, A.M., Ruffing, C.M., Larson, D.M., Fischer, J.L., and Costigan, K.H.: Abiotic

480   controls and temporal variability of river metabolism: multiyear analyses of Mississippi and

481   Chattahoochee River data. Freshwater Science, 32, 1073-1087, 2013.

482   Ecke, F., Hellsten, S., Köhler, J., Lorenz, A.W., Rääpysjärvi, J., Scheunig, S. et al.: The response of

483   hydrophyte growth forms and plant strategies to river restoration. Hydrobiologia, 769, 41-54,

484   2016.

485   EEA (European Environment Agency): European Waters – Assessment of Status and Pressures. EEA

486   Report No. 8, EEA, Copenhagen. 96 pp., 2012.

487   EFI+ CONSORTIUM: Manual for the application of the new European Fish Index – EFI+. A fish-

488   based method to assess the ecological status of European running waters in support of the

489   Water Framework Directive. http://efi-plus.boku.ac.at/software/doc/EFI%2bManual.pdf, 2009.

490   Fellows, C.S., Valett, H.M., and Dahm, C.N.: Whole-stream metabolism in two montane streams:

491   Contribution of the hyporheic zone. Limnology and Oceanography, 46, 523–531, 2001.

492   Fellows, C.S., Valett, H.M., Dahm, C.N., Mulholland, P.J., and Thomas, S.A.: Coupling nutrient

493   uptake and energy flow in headwater streams. Ecosystems, 9, 788-804, 2006.

494   Flores, L., Larranaga, A., Dìez, J., and Elosegi, A.: Experimental wood addition in streams: effects on

495   organic matter storage and breakdown. Freshwater Biology, 56, 2156–2167, 2011.

496   Friberg, N., Baattrup-Pedersen, A., Kristensen, E.A., Kronvang, B., Larsen, S.E., Pedersen, M.L. et

497   al.: The Gelsa River Restoration Revisited: community persistence of the macroinvertebrate

498   community over an 11-year period. Ecological Engineering, 66, 150–157, 2014.

499   Gellert, G., Pottgiesser, T., and Euler, T.: Assessment of the structural quality of streams in

500   Germany—basic description and current status. Environmental Monitoring and Assessment,

501   186, 3365-3378, 2014.

502   Göthe, E., Timmermann, A., Januschke, K., and Baattrup-Pedersen, A.: Structural and functional

503   responses of floodplain vegetation to stream ecosystem restoration. Hydrobiologia, 769, 79-

504   92, 2016.

505   Gücker, B. and Boëchat, I.G.: Stream morphology controls ammonium retention in tropical

506   headwaters. Ecology, 85, 2818–2827, 2004.

507   Gücker, B., Boëchat, I.G., and Giani, A.: Impacts of agricultural land use on ecosystem structure and

508   whole-stream metabolism of tropical Cerrado streams. Freshwater Biology, 54, 2069–2085,

509   2009.

510   Gücker, B., Brauns, M. and Pusch, M.T.: Effects of wastewater treatment plant discharge on

511   ecosystem structure and function of lowland streams. Journal of the North American

512   Benthological Society, 25, 313-329, 2006.

513   Gücker, B. and Pusch, M.T.: Regulation of nutrient uptake in eutrophic lowland streams. Limnology

514   and Oceanography, 51, 1443-1453, 2006.

515   Haase, P., Lohse, S., Pauls, S., Schindehütte, K., Sundermann, A., Rolauffs, P. et al.: Assessing

516   streams in Germany with benthic invertebrates: development of a practical standardised

517   protocol for macroinvertebrate sampling and sorting. Limnologica, 34, 349–365, 2004.

518   Haase, P., Hering, D., Jähnig, S.C., Lorenz, A.W., and Sundermann, A.: The impact of

519   hydromorphological restoration on river ecological status: A comparison of fish, benthic

520   invertebrates, and macrophytes. Hydrobiologia, 704, 475–488, 2013.

521   Hall, R.O., Yackulic, C.B., Kennedy, T.A., Yard, M.D., Rosi-Marshall, E.J., Voichick, N. et al.:

522   Turbidity, light, temperature, and hydropeaking control daily variation in primary production

523   in the Colorado River, Grand Canyon. Limnology and Oceanography, 60, 512–526, 2015.

524   Hall, R.O., Tank, J.L., Baker, M.A., Rosi-Marshall, E.J., and Hotchkiss, E.R.: Metabolism, Gas

525   Exchange, and Carbon Spiraling in Rivers. Ecosystems, 19, 73-86, 2016.

526   Harvey, J.V. and Wagner, B.J.: Quantifying hydrologic interaction between streams and their

527   subsurface hyporheic zones. In: Streams and Ground Waters (Eds J.B. Jones & P.J.

528   Mulholland), pp. 3–44. Academic Press, San Diego, CA, 2000.

529   Hering, D., Aroviita, J., Baattrup-Pedersen, A., Brabec, K., Buijse, T., Ecke, F. et al.: Contrasting the

530   roles of section length and instream habitat enhancement for river restoration success: a field

531   study on 20 European restoration projects. Journal of Applied Ecology, 50, 97–106, 2015.

532   Jähnig, S.C., Brunzel, S., Gacek, S., Lorenz, A.W., and Hering, D.: Effects of re-braiding measures on

533   hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain

534   rivers. Journal of Applied Ecology, 46, 406 – 416, 2009.

535   Jähnig ,S.C., Brabec, K., Buffagni, A., Erba, S., Lorenz, A.W., Ofenböck, T. et al.: A comparative

536   analysis of restoration measures and their effects on hydromorphology and benthic

537   invertebrates in 26 central and southern European rivers. Journal of Applied Ecology, 47, 671–

538   680, 2010.

539   Januschke, K., Jähnig, S.C., Lorenz, A.W., and Hering, D.: Mountain river restoration measures and

540   their success(ion): effects on river morphology, local species pool, and functional composition

541   of three organism groups. Ecological Indicators, 38, 243–255, 2014.

542   Januschke, K. and Verdonschot, R.C.M.: Effects of river restoration on riparian ground beetles

543   (Coleoptera: Carabidae) in Europe. Hydrobiologia, 769, 93-104, 2016.

544   Kohler, A.: Methoden der Kartierung von Flora und Vegetation von Süßwasserbiotopen. Landschaft

545   und Stadt, 10, 73–85, 1978.

546   Kohler, A. and Janauer, G.: Zur Methodik der Untersuchung von aquatischen Makrophyten in

547   Fließgewässern. In: Handbuch Angewandte Limnologie (Eds C. Steinberg, H. Bernhardt & H.

548   Klapper), pp. 1–22. ecomed Verlagsgesellschaft, Landsberg, 1997.

549   Kupilas, B., Friberg, N., McKie, B.G., Jochmann, M.A., Lorenz, A.W., and Hering, D.: River

550   restoration and the trophic structure of benthic invertebrate communities across 16 European

551   restoration projects. Hydrobiologia, 769, 105-120, 2016.

552   Lepori, F., Palm, D., and Malmqvist, B.: Effects of stream restoration on ecosystem functioning:

553   detritus retentiveness and decomposition. Journal of Applied Ecology, 42, 228–238, 2005.

554   Lepori, F., Gaul, D., Palm, D., and Malmqvist, B.: Food-web responses to restoration of channel

555   heterogeneity in boreal streams. Canadian Journal of Fisheries and Aquatic Sciences, 63,

556   2478–2486, 2006.

557   Lorenz, A.W., Korte, T., Sundermann, A., Januschke, K., and Haase, P.: Macrophytes respond to

558   reach-scale river restorations. Journal of Applied Ecology, 49, 202–212, 2012.

559   Marzolf, E.R., Mulholland, P.J., and Steinman, A.D.: Improvements to the diurnal upstream-

560   downstream dissolved-oxygen change technique for determining whole stream metabolism in

561   small streams. Canadian Journal of Fisheries and Aquatic Sciences, 51, 1591–1599, 1994.

562   McTammany, M.E., Webster, J.R., Benfield, E.F., and Neatrour, M.A.: Longitudinal patterns of

563   metabolism in a southern Appalachian river. Journal of the North American Benthological

564   Society, 22, 359–370, 2003.

565   Mulholland, P.J., Fellows, C.S., Tank, J.L., Grimm, N.B., Webster, J.R., Hamilton, S.K. et al.: Inter-

566   biome comparison of factors controlling stream metabolism. Freshwater Biology, 46, 1503–

567   1517, 2001.

568   Odum, H.T.: Primary production in flowing waters. Limnology and Oceanography, 2,102–117, 1956.

569   Palmer, M.A., and Filoso, S.: Restoration of ecosystem services for environmental markets. Science,

570   325, 575–576, 2009.

571   Palmer, M.A., Hondula, K.L., and Koch, B.J.: Ecological restoration of streams and rivers: shifting

572   strategies and shifting goals. Annual Review of Ecology, Evolution, and Systematics, 45, 247–

573   269, 2014.

574   Poppe, M., Kail, J., Aroviita, J., Stelmaszczyk, M., Giełczewski, M., and Muhar, S.: Assessing

575   restoration effects on hydromorphology in European mid-sized rivers by key

576   hydromorphological parameters. Hydrobiologia, 769, 21-40, 2016.

577   Reichert, P., Uehlinger, U., and Acuña, V.: Estimating stream metabolism from oxygen

578   concentrations: effect of spatial heterogeneity. Journal of Geophysical Research:

579   Biogeosciences, 114(G3), 2009.

580   R Development Core Team: R: A language and environment for statistical computing. R Foundation

581   for Statistical Computing, Vienna, Austria. http://www.R-project.org, 2007.

582   Roberts, B.J., Mulholland, P.J., and Hill, W.R.: Multiple scales of temporal variability in ecosystem

583   metabolism rates: results from 2 years of continuous monitoring in a forested headwater

584   stream. Ecosystems, 10, 588–606, 2007.

585   Roley, S.S., Tank, J.L., Griffiths, N.A., Hall, R.O. and Davis, R.T.: The influence of floodplain

586   restoration on whole-stream metabolism in an agricultural stream: insights from a 5-year

587   continuous data set. Freshwater Science, 33, 1043–1059, 2014.

588   Roni, P., Hanson, K., and Beechie, T.: Global review of the physical and biological effectiveness of

589   stream habitat rehabilitation techniques. North American Journal of Fisheries Management,

590   28, 856–890, 2008.

591   Runkel, R.L.: One-dimensional transport with inflow and storage (OTIS): A solute transport model for

592   streams and rivers. US Geological Survey, Water-Resources Investigation Report 98-4018,

593   Denver, CO. http://co.water.usgs.gov/otis, 1998.

594   Runkel, R.L.: A new metric for determining the importance of transient storage. Journal of the North

595   American Benthological Society, 21, 529–543, 2002.

596   Schaumburg, J., Schranz, C., Foerster, J., Gutowski, A., Hofmann, G., Meilinger, P. et al.: Ecological

597   classification of macrophytes and phytobenthos for rivers in Germany according to the Water

598   Framework Directive. Limnologica, 34, 283–301, 2004.

599   Schaumburg, J., Schranz, C., Meilinger, P., Stelzer, D., Hofmann, G., Foerster, J. et al.: Makrophyten

600   und Phytobenthos in Fließgewässern und Seen – Das deutsche Bewertungsverfahren:

601   Entwicklung, Praxistest und Ausblick. Limnologie aktuell, 11, 63–75, 2005a.

602   Schaumburg, J., Schranz, C., Stelzer, D., Hofmann, G., Gutowski, A., and Foerster, J.: Bundesweiter

603   Test: Bewertungsverfahren „Makrophyten & Phytobenthos“ in Fließgewässern zur Umsetzung

604   der WRRL. Bayerisches Landesamt für Umwelt, München, 2005b.

605   Schmutz, S., Jurajda, P., Kaufmann, S., Lorenz, A.W., Muhar, S., Paillex, A. et al.: Response of fish

606   assemblages to hydromorphological restoration in central and northern European rivers.

607   Hydrobiologia, 769, 67-78, 2016.

608   Schröder, M., Kiesel, J., Schattmann, A., Jähnig, S., Lorenz, A.W., Kramm, S. et al.: Substratum

609   associations of benthic invertebrates in lowland and mountain streams. Ecological Indicators,

610   30, 178-189, 2013.

611   Schulz, M. and Gücker, B.: Macrophytes increase spatial patchiness of fluvial sedimentary records and

612   effect temporal particulate nutrient storage. Aquatic Geochemistry, 11, 89-107, 2005.

613   Silva-Junior, E.F., Moulton, T.P., Boëchat, I.G., and Gücker, B.: Leaf decomposition and ecosystem

614   metabolism as functional indicators of land use impacts on tropical streams. Ecological

615   Indicators, 36, 195– 204, 2014.

616   Strayer, D.L. and Dudgeon, D.: Freshwater biodiversity conservation: recent progress and future

617   challenges. Journal of the North American Benthological Society, 29, 344–358, 2010.

618   Tank, J.L., Rosi-Marshall, E.J., Griffiths, N.A., Entrekin, S.A., and Stephen, M.L.: A review of

619   allochthonous organic matter dynamics and metabolism in streams. Journal of the North

620   American Benthological Society, 29, 118–146, 2010.

621 UBA (Federal Environment Agency): Water Resource Management in Germany Part 1:

622   Fundamentals. Bonn, 2013.

623   https://www.umweltbundesamt.de/sites/default/files/medien/378/publikationen/wawi_teil_01_

624   englisch_barrierefrei.pdf (accessed November, 25th, 2016).

625 Uehlinger, U.: Resistance and resilience of ecosystem metabolism in a flood-prone river system.

626   Freshwater Biology, 45, 319–332, 2000.

627 Uehlinger, U.: Annual cycle and inter-annual variability of gross primary production and ecosystem

628   respiration in a floodprone river during a 15-year period. Freshwater Biology, 51, 938–950,

629   2006.

630 Valett, H.M., Morrice, J.A., Dahm, C.N., and Campana, M.E.: Parent lithology, surface-groundwater

631   exchange, and nitrate retention in headwater streams. Limnology and Oceanography, 41, 333-

632   345, 1996.

633 Verdonschot, R.C.M., Kail, J., McKie, B.G., and Verdonschot, P.F.M.: The role of benthic

634   microhabitats in determining the effects of hydromorphological river restoration on

635   macroinvertebrates. Hydrobiologia, 769, 55-66, 2016.

636 Young, R.G. and Huryn, A.D.: Comment: improvements to the diurnal upstream–downstream

637   dissolved oxygen change technique for determining whole stream metabolism in small

638   streams. Canadian Journal of Fisheries and Aquatic Sciences, 55, 1784–1785, 1998.

639 Young, R.G. and Huryn, A.D.: Effects of land use on stream metabolism and organic matter turnover.

640   Ecological Applications, 9, 1359-1376, 1999.

641 Young, R.G., Matthaei, C.D., and Townsend, C.R.: Organic matter breakdown and ecosystem

642   metabolism: functional indicators for assessing river ecosystem health. Journal of the North

643   American Benthological Society, 27, 605–625, 2008.

644

645 **Table 1:** River and study site characteristics

River characteristics	
Catchment size (km²)	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 (km²)	1060
Altitude (m a.s.l.)	153
Mean annual discharge (m³ 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

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

649   **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

650   * Width variation calculated as standard deviation; degraded: n = 42, restored 1: n = 59, restored 2: n = 54
651   ** Data on hydrodynamic characteristics represent the final parameters obtained by one-dimensional transport modelling using OTIS-P.

652
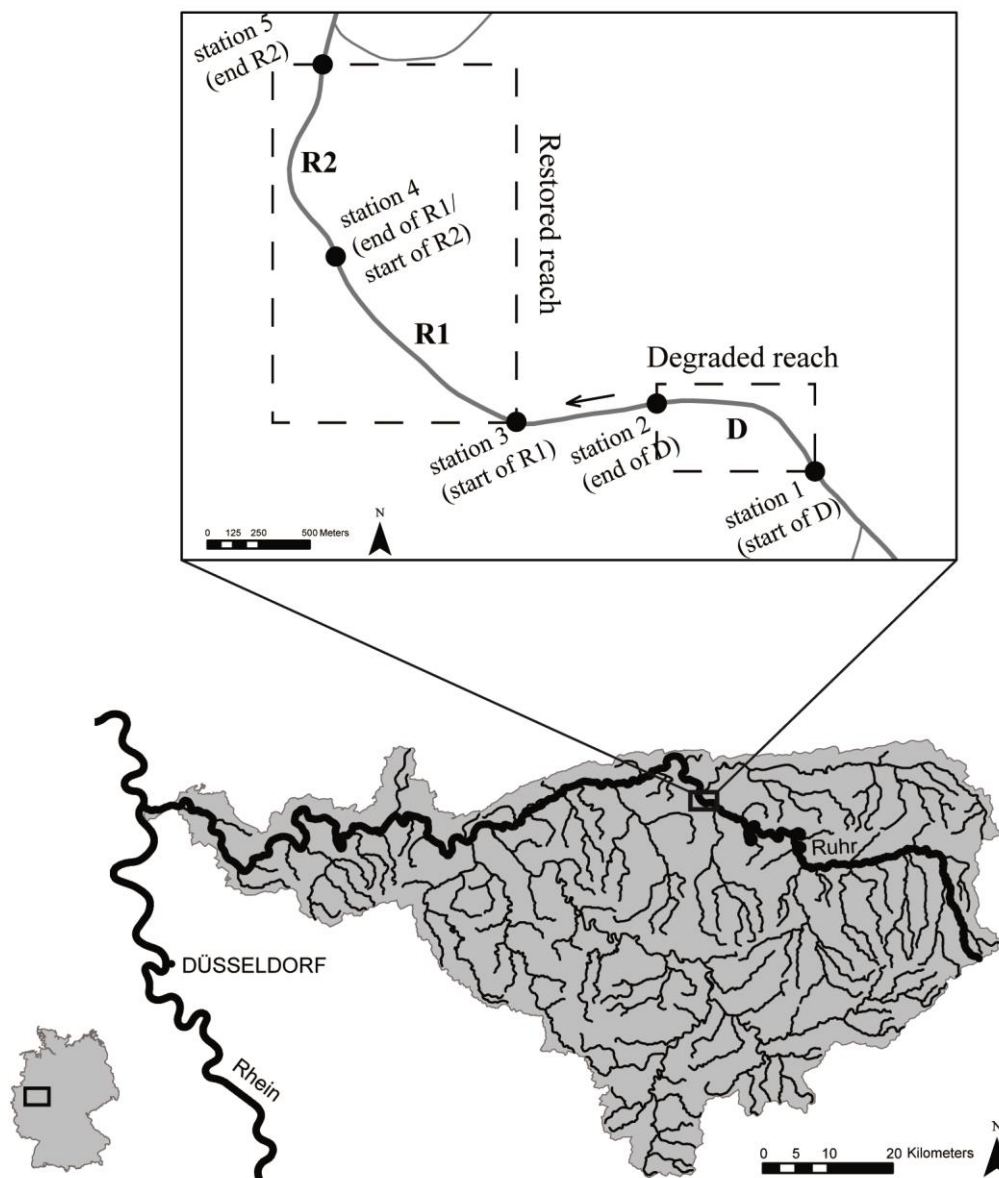
Fig. 1: Location of the study site in the upper catchment of the River Ruhr in Germany. Stations represent start and end of the
investigated river reaches (degraded, 1st restored and 2nd restored reach).
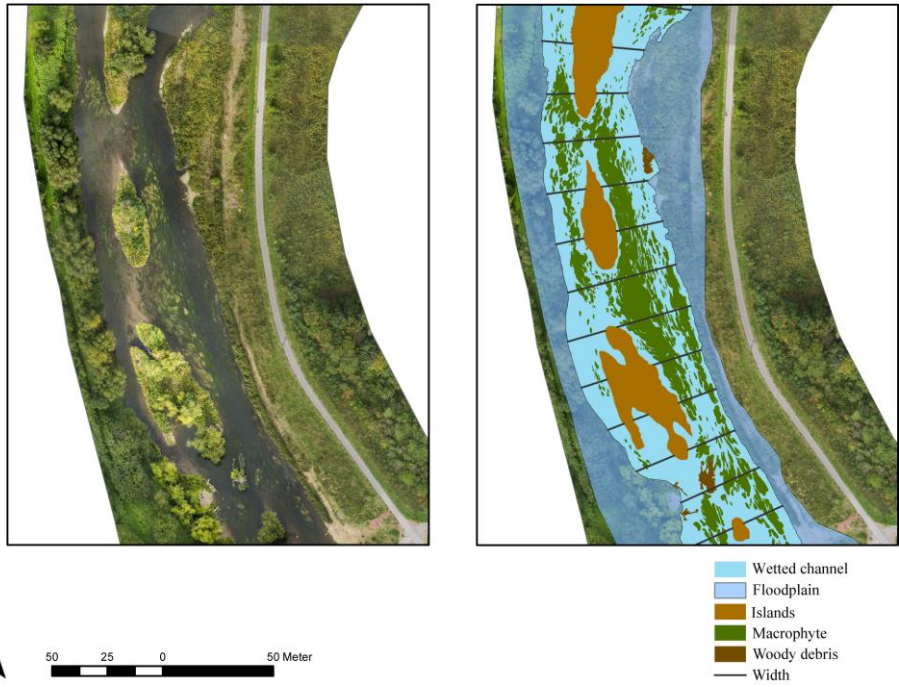
Wetted channel
Floodplain
Islands
Macrophyte
Woody debris
Width

655

656 **Fig. 2:** Analysis of aerial photos. A representative river section of the 2nd restored reach is shown.
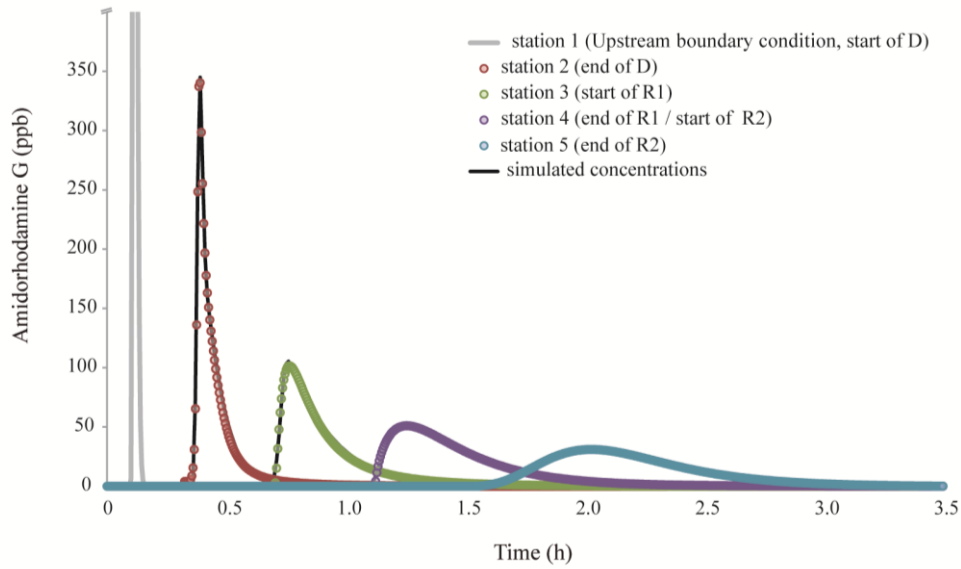
Fig. 3: Tracer breakthrough curves for the conservative tracer addition experiment in the River Ruhr. Upstream boundary condition based on concentrations at sampling station 1 (start of degraded reach, D, grey solid line), observed concentrations at sampling stations 2 (end of degraded reach, empty circles), 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).

663
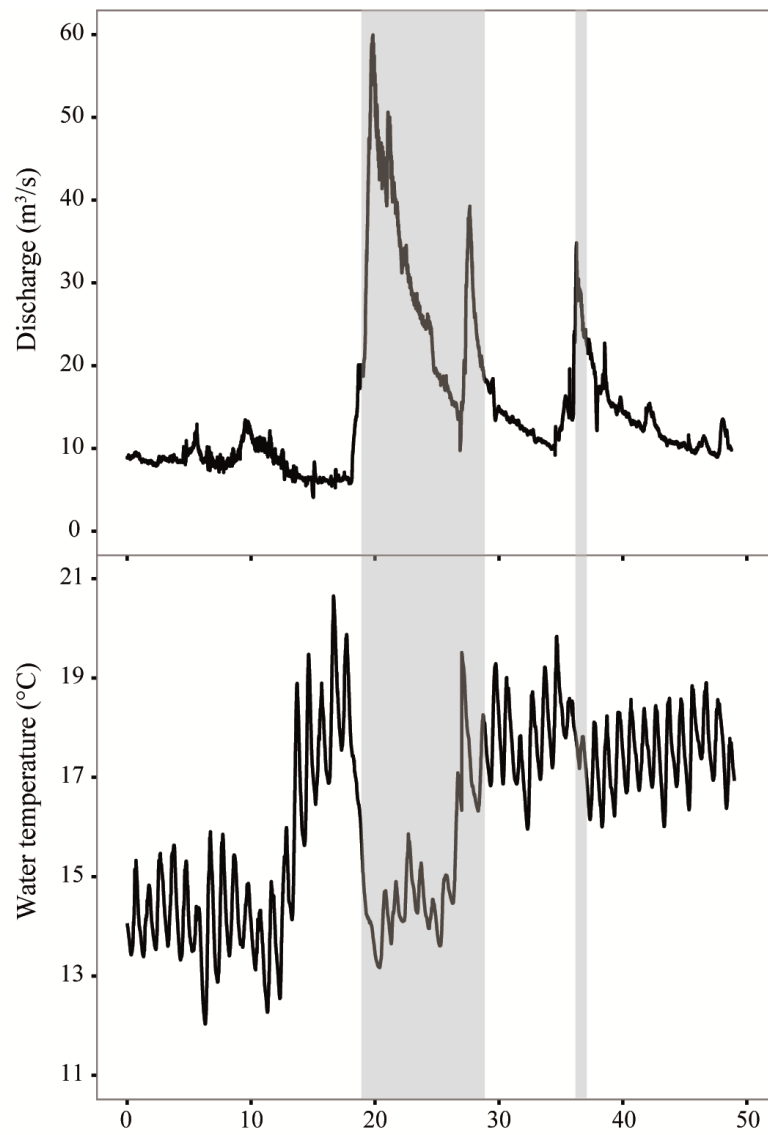
Fig. 4: (a) discharge and (b) water temperature in the River Ruhr during the study period in summer 2014. Trend in water temperature during study period is exemplarily shown for the 2nd restored reach (R2).

666
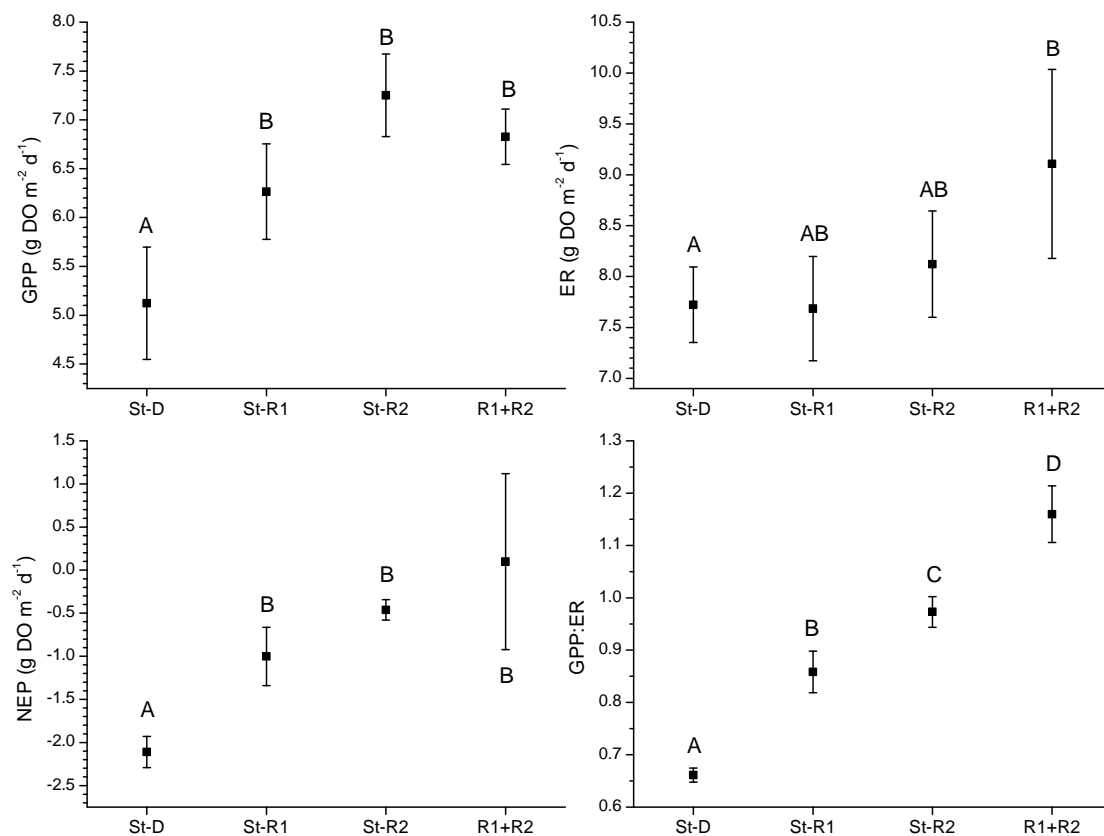
Fig. 5: Average predicted metabolic parameters and 95% confidence intervals of time series estimated by the 1-station open-channel-method at river stations downstream of reaches D, R1, and R2, and by the 2-station open-channel-method for river reach R1+R2. F-tests for all variables were significant (GPP: $p<0.001$; ER: $p<0.05$; NEP: $p<0.005$, GPP:ER: $p<0.0001$). Different letters indicate differences according to Tukey's post-hoc test ($p<0.05$).

671
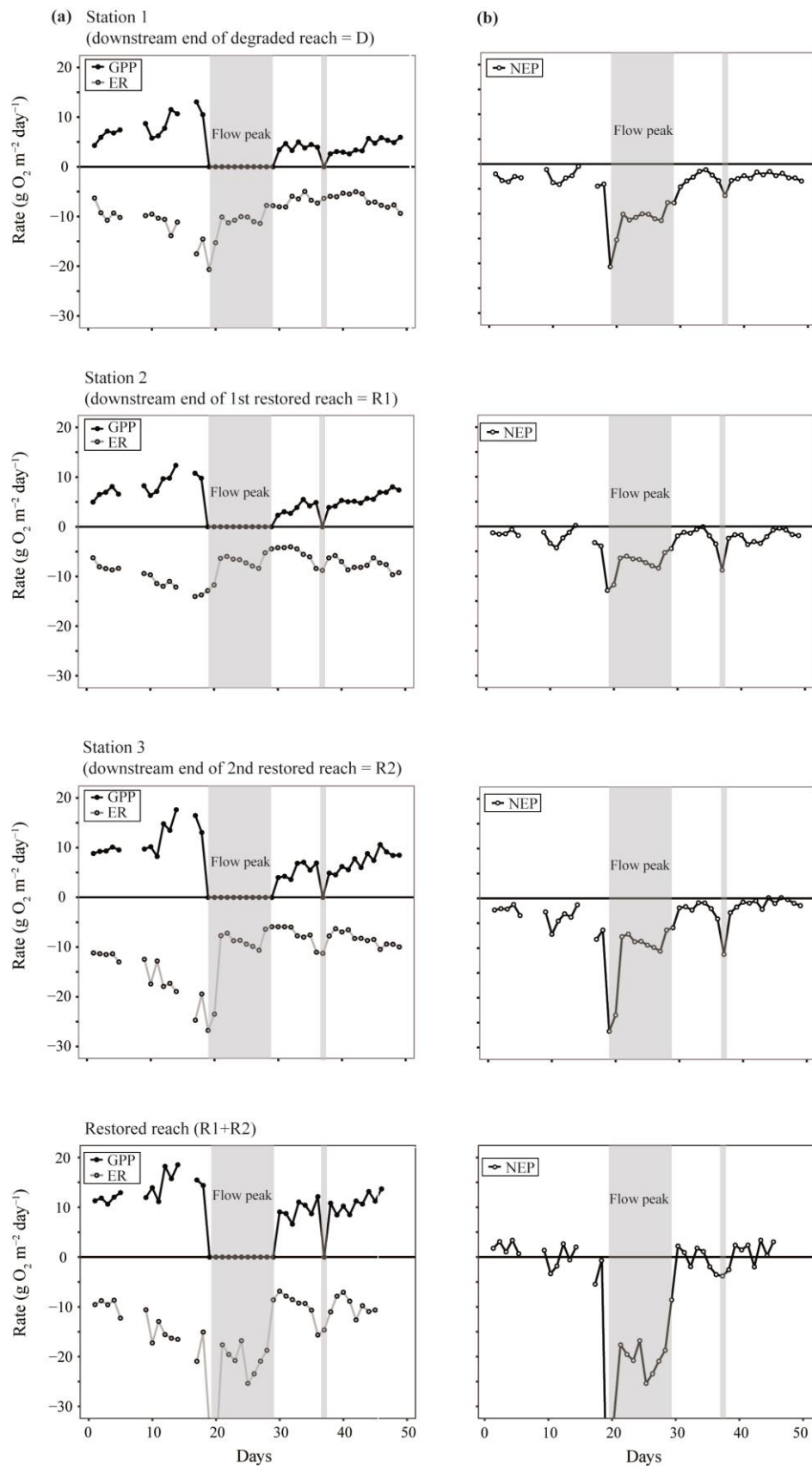
Fig. 6: Daily rates of (a) gross primary production (GPP: positive values, black line) and ecosystem respiration (ER: negative values, grey lines) and (b) net ecosystem production (NEP) measured at the downstream ends of the investigated reaches (degraded = D; 1st restored = R1; 2nd restored = R2) and 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 (m³)	Soil shifting (m³)
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).

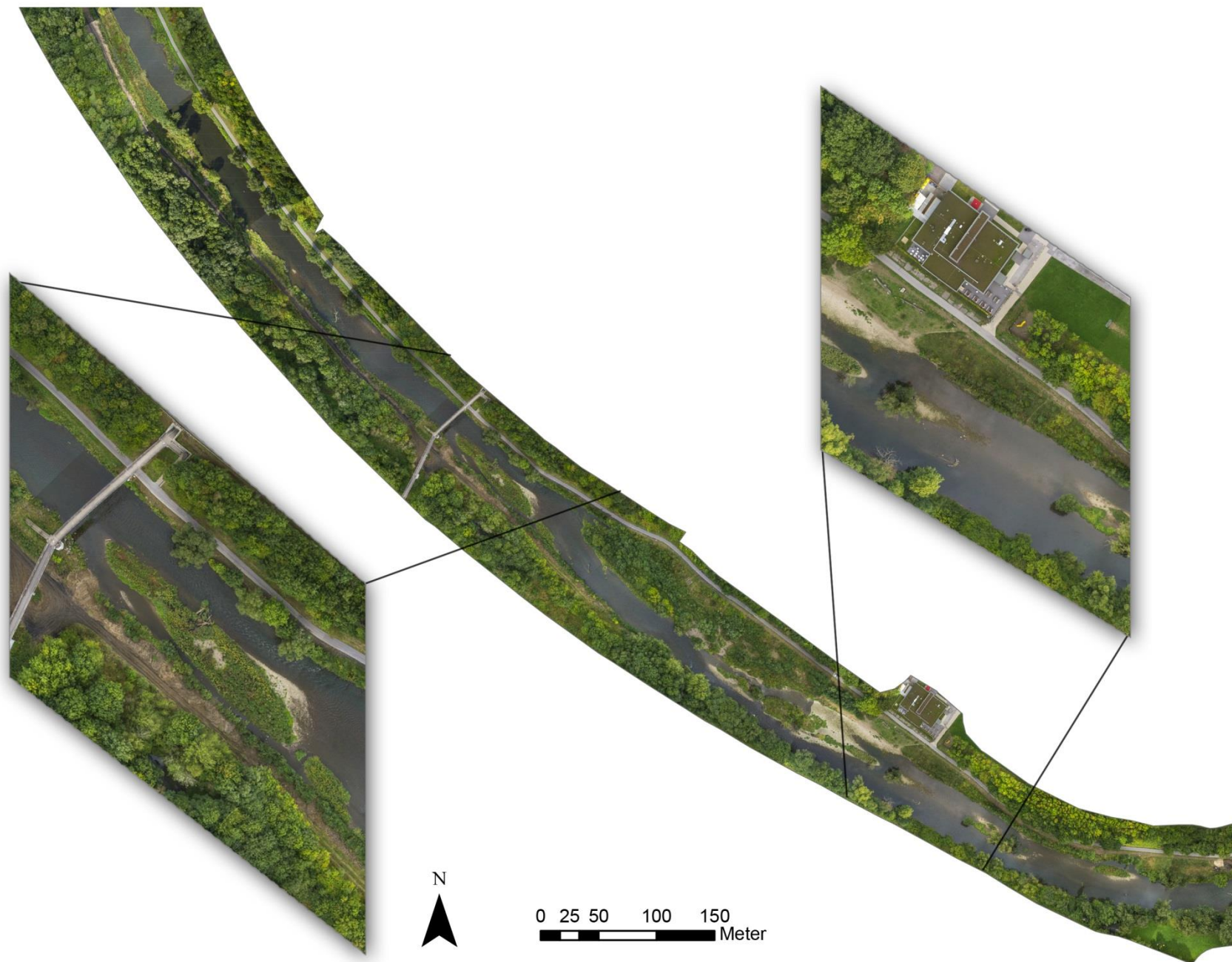**Fig. S5:** Photo of the 2nd restored reach (R2) (photo by B. Kupilas).

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

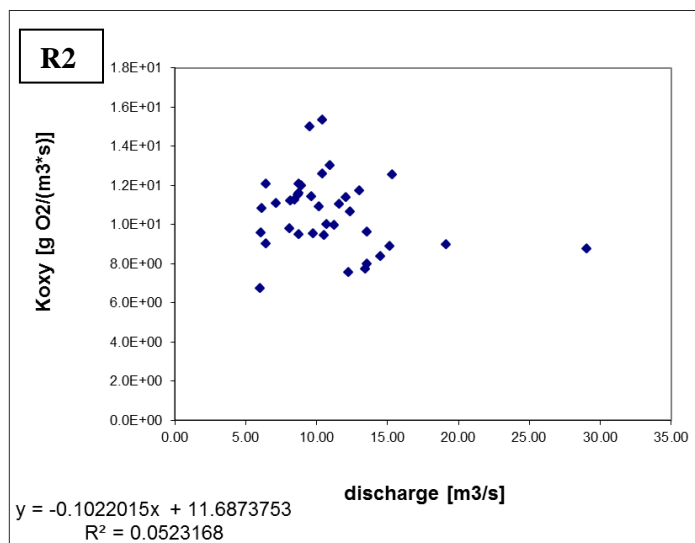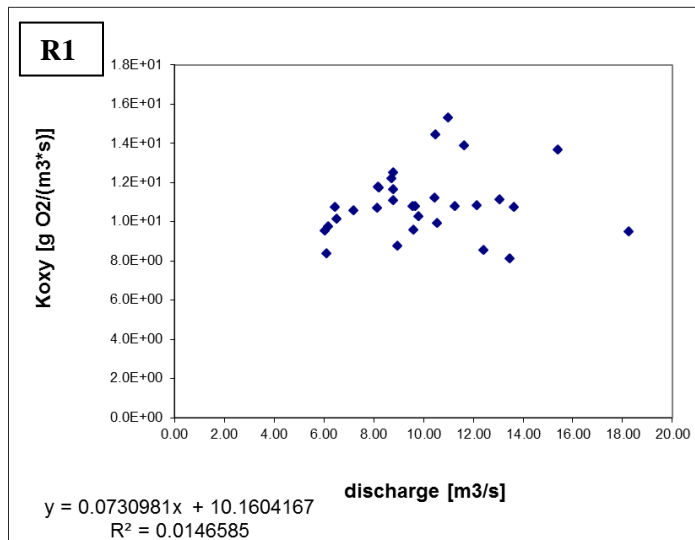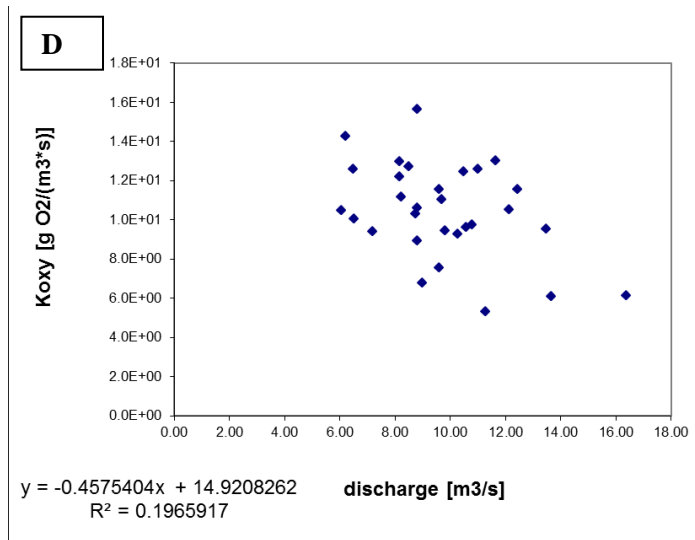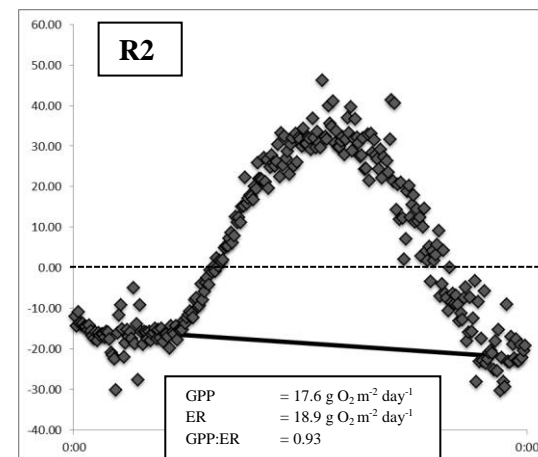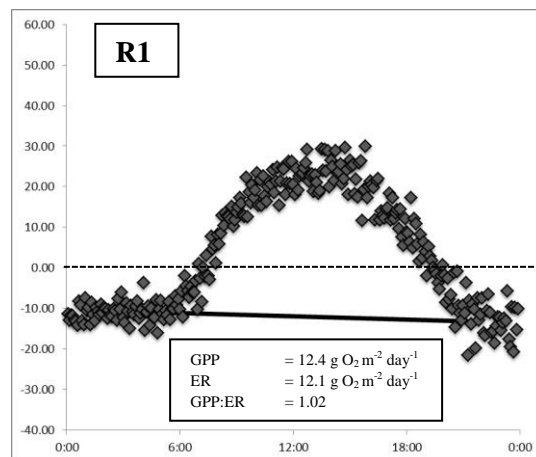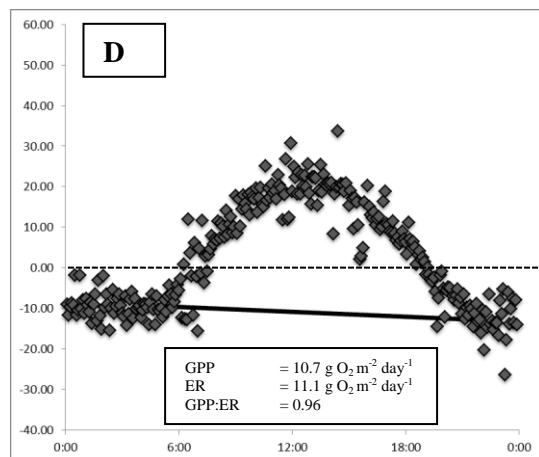**Fig. S7:** 1st restored reach (R1) (photo by NZO GmbH, Germany).

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.
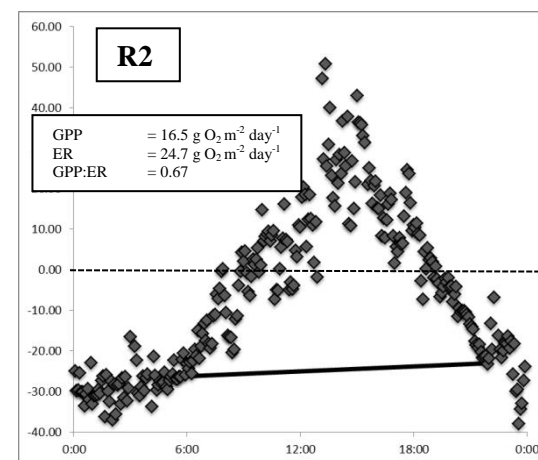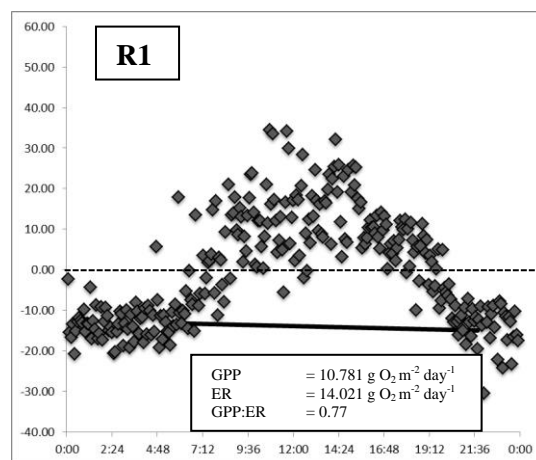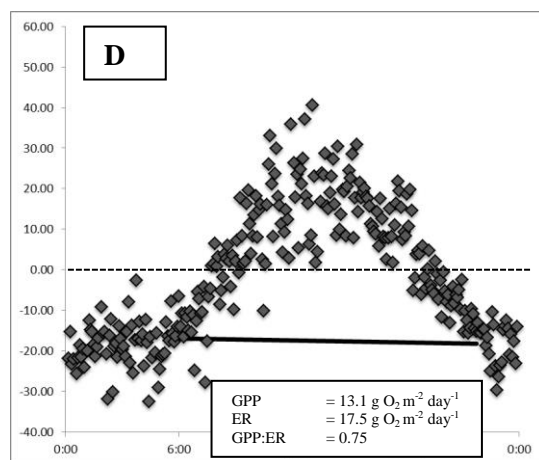
All regressions with P>0.05

D

y = -0.4575404x + 14.9208262
R² = 0.1965917

R1

y = 0.0730981x + 10.1604167
R² = 0.0146585

R2

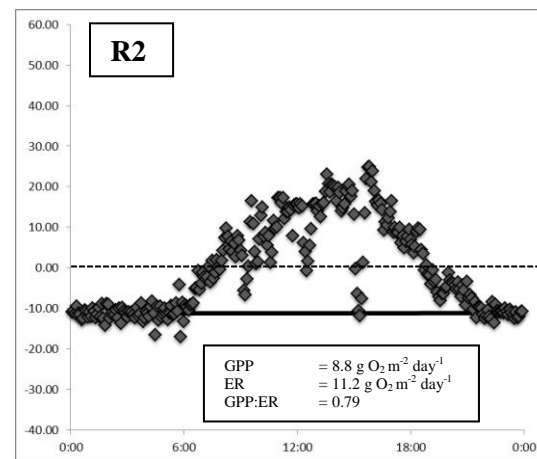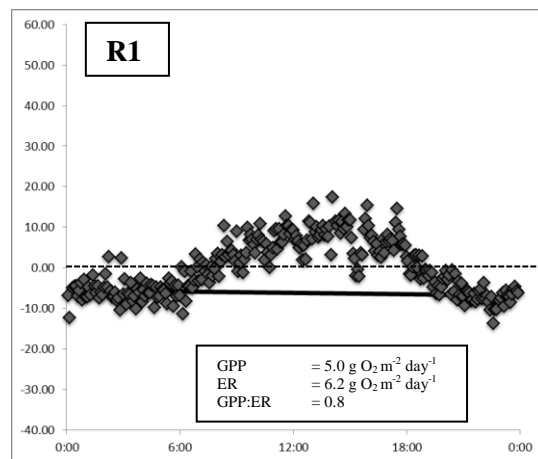y = -0.1022015x + 11.6873753
R² = 0.0523168

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

D		
GPP	= 10.7 g O_2 m^{-2} day^{-1}	
ER	= 11.1 g O_2 m^{-2} day^{-1}	
GPP:ER	= 0.96	

R1		
GPP	= 12.4 g O_2 m^{-2} day^{-1}	
ER	= 12.1 g O_2 m^{-2} day^{-1}	
GPP:ER	= 1.02	

R2		
GPP	= 17.6 g O_2 m^{-2} day^{-1}	
ER	= 18.9 g O_2 m^{-2} day^{-1}	
GPP:ER	= 0.93	

Day 17

D		
GPP	= 13.1 g O_2 m^{-2} day^{-1}	
ER	= 17.5 g O_2 m^{-2} day^{-1}	
GPP:ER	= 0.75	

R1		
GPP	= 10.781 g O_2 m^{-2} day^{-1}	
ER	= 14.021 g O_2 m^{-2} day^{-1}	
GPP:ER	= 0.77	

R2		
GPP	= 16.5 g O_2 m^{-2} day^{-1}	
ER	= 24.7 g O_2 m^{-2} day^{-1}	
GPP:ER	= 0.67	

Day 1

D

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

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

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

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

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

GPP   = 6.2 g O_2 m^{-2} day^{-1}
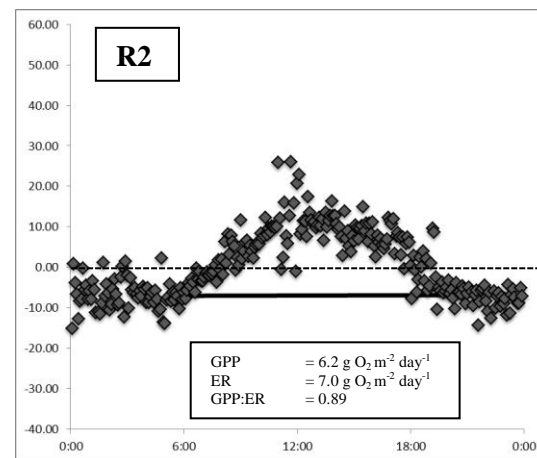ER   = 7.0 g O_2 m^{-2} day^{-1}
GPP:ER = 0.89

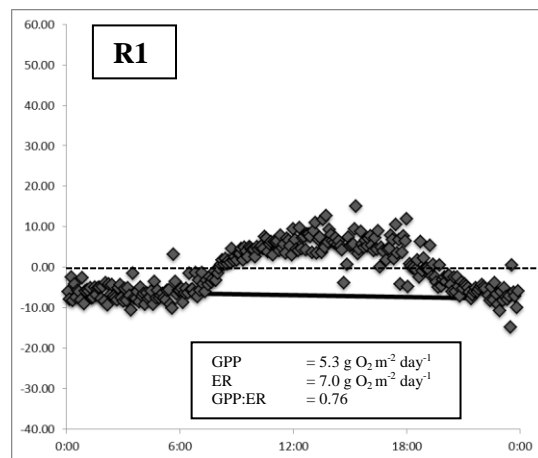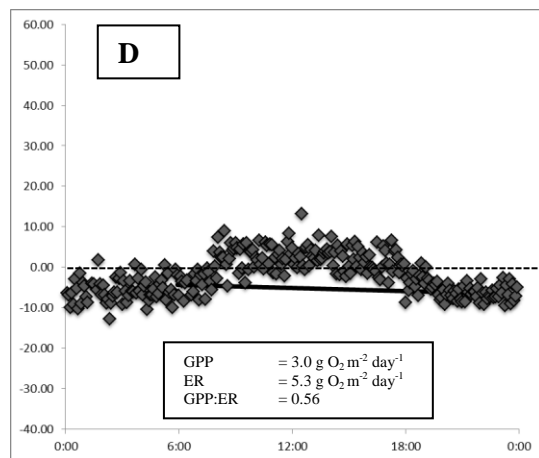**Appendix S4: Comparison of metabolic rates estimated in our study with literature data**

GPP and ER estimated in this study were among the highest values reported for similar sized rivers (discharge between 5 - 50 m³ 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.